Selective breeding for summer survival in Pacific oyster (*Crassostrea gigas*): Genetic parameters and response to selection

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ABSTRACT

Pacific oyster (*crassostrea gigas*) is an economically important farmed oyster species which is now severely threatened by summer mortality all over the world. Selective breeding for natural disease resistance is an effective and sustainable method to reduce mortality outbreak. We established a basic breeding population by using two fast-growing lines and then two successive generations of selection for summer survival was conducted. The aim of this study was to estimate the genetic parameters and detect the selection response over two generations of family selection. Summer survival was defined as binary trait and analyzed by two animal models (linear animal model (LAM) and threshold (logit) animal model (TAM)). Across generations, low to moderate heritability values (0.12–0.28) were estimated for summer survival by using two different models, suggesting that this population will continue show response to future selection. The genetic correlations between summer survival and growth traits were low but positive in different generations (0.056–0.229), which implies that selection for summer survival would not result in adverse responses in growth traits. The realized genetic gain of summer survival from the G1 to G3 generation ranged from 10.71% to 13.55%. The accumulated realized genetic gain (24.26%) expressed as a percentage was 41.97%. Moreover, there were also positively correlated changes in growth traits which selected population had a higher growth than did the control population in each generation. The results indicate that there are good prospects for the genetic improvement of summer survival in *C. gigas*.

1. Introduction

Pacific oyster (*Crassostrea gigas*), which is native to the northwest Pacific Ocean, has been introduced to many countries due to its environment adaptability and fast growth (Troost, 2010). Nowadays, *C. gigas* has become the most important commercial oyster species with great economic value. In the past five decades, however, this oyster species has been experiencing significantly summer mortality outbreak in different parts of world. Massive mortality episodes were first reported on Japanese coasts in 1945 (Koganezawa, 1975), again in the late 1950s in North America (Glude, 1975), since 1980s in France (Maurer et al., 1986; Segarra et al., 2010) and more recently in the North of Ireland (Ashton et al., 2020), Mexico (Cáceres-Martínez et al., 2018) and China (Yang et al., 2021). It has been estimated that the average loss of annual crop by summer mortality is more than 50% (Cheney et al., 2000), which often occurs in cultural farms and natural oyster beds during summer periods. Such large-scale mortalities can cause the loss of production stocks, with significantly decreased production and serious economic losses.

These mortalities affects both juveniles and adults and both diploids and triploids of oysters (Cheney et al., 2000; Calvo et al., 1999). Considered together, summer mortalities cannot be explained by a single factor but rather by the consequence of complex interactions between the environment factors (temperature, salinity, and nutrient levels), host factors (life stage, genetic variation, and physiological status) and biotic factors (Oyster Herpes virus and opportunistic bacteria) (Alfaro et al., 2019). Firstly, summer mortality outbreak in *C. gigas* associated with *Ostreid herpesvirus* 1 (OsHV-1) and its microvariant (μVar) have been reported in many countries and are interpreted as the main causes (Mortensen et al., 2016; Hwang et al., 2013; Roque et al., 2012; Renault et al., 1994; Segarra et al., 2010). Secondly, environment factors such as temperature is also an important risk factor for mortality events, particularly when the sea temperature abnormally elevated (Chávez-Villalba et al., 2007). Thirdly, reproduction is energetically costly and oyster summer mortality has been interpreted as a physiological disorder and metabolic disturbance associated with their

reproductive effort (Huvet et al., 2010; Wendling and Wegner, 2013). Finally, a significant genetic component for summer survival exist in *C. gigas* (Dégremont et al., 2007), indicating that summer survival can be improved by selective breeding.

Selective breeding is an effective method for genetic improvement of cultured species and has been broadly applied in aquaculture (Gjedrem and Rye, 2018). It can offer the genetic gain and the gain is permanent, sustainable, and cumulative over generations (Gjedrem and Baranski, 2009). Oysters are well suited to a selective breeding method due to its high fecundity, relatively short generation cycle and adequate genetic variation (Newkirk and Haley, 1982). In fact, selective breeding programs have been widely reported in China (Li et al., 2011; Zhang et al., 2019), France (Dégremont et al., 2010; Dégremont et al., 2015; Dégremont et al., 2020), USA (Langdon et al., 2003; De Melo et al., 2016; Divilov et al., 2021), Australia (Ward et al., 2000; Kube et al., 2018) and New Zealand (Camara and Symonds, 2014; Camara et al., 2017) for *C. gigas* and have obtained encouraging results.

China is the largest countries for oyster aquaculture, contributing to over 85% of the global aquaculture production (FAO, 2020). To improve the growth traits of *C. gigas*, a selective breeding program focused on the establishment of selected lines by mass selection for shell height was initiated in 2007 (Li et al., 2011). Significant positive selective responses were observed in selected populations (Zhang et al., 2019). In recent years, China oyster industry has been affected by summer mortality and these mortalities can cause serious economic implications. Mortality events were usually observed in spat stage and often cause high mortality. A pathogenic strain of *Vibrio alginolyticus* was isolated from moribund oyster collected in Sanggou bay (37.1°N, 122.5°E), but its role in mortality outbreaks in China cultured oyster is unclear (Yang et al., 2021). Interestingly, no mass mortalities related to OsHV-1 infection have been reported in China, although an OsHV-1 variant has been found in *C. gigas* (Bai et al., 2015). To meet future requirements, sustainable development of oyster farming requires genetically improved breeds with good growth performances and high summer survival. Hence, we initiated an oyster selective breeding program to address the problem of summer mortality, which affect the economic viability of the oyster industry.

In this study, we estimated the heritability and selection response using date involving 26,160 individuals from 147 full sib families in the three generations. In addition, the growth traits (shell height, shell length, shell width and individual weight) were also recorded to estimate the impact of survival selection had on these important commercial traits.

2. Materials and method

2.1. Family construction and breeding

The selective breeding program of *C. gigas* was established in Laizhou breeding base, Shandong Province, China in 2019 (Fig. 1). The base population (G1) was derived from two fast-growing stocks which mass selection for shell height was performed over ten and eight generations, respectively. Two fast-growing stocks were crossed following a nested design by randomly mating selected males and females, which resulted in 49 full-sib families (Chi et al., 2021). During subsequent generations, all oyster families were ranked according to their family summer survival. Then, selected families were used as parents to produce subsequent generations. Parents of G2 were mainly selected from 14 full-sib families (G1 families) with top summer survival rate. Parents of G3 were mainly selected from 12 full-sib families (G2 families) with top summer survival rate. Families with average survival rate were used to produce control populations. Note that the control population were produced from the selected population of each new generation, rather than established as a separate control line. To accurately estimate the genetic correlation between growth and survival, growth traits were not selected when parents are selected. The actual number of female and male breeders used in each generation was shown in Table 1.

Family production and rearing were followed the standard procedure described by Li et al. (2011), and the rearing conditions were maintained the same for each family. Families were produced via stripping and artificial fertilization. 24 h after fertilization, D-larvae of each family was separately reared in a 100-L plastic bucket at 23-25 °C using filtered seawater. Seawater was filtered through sand filters and non-wovens polypropylene fabric. Larvae were fed algae diet of
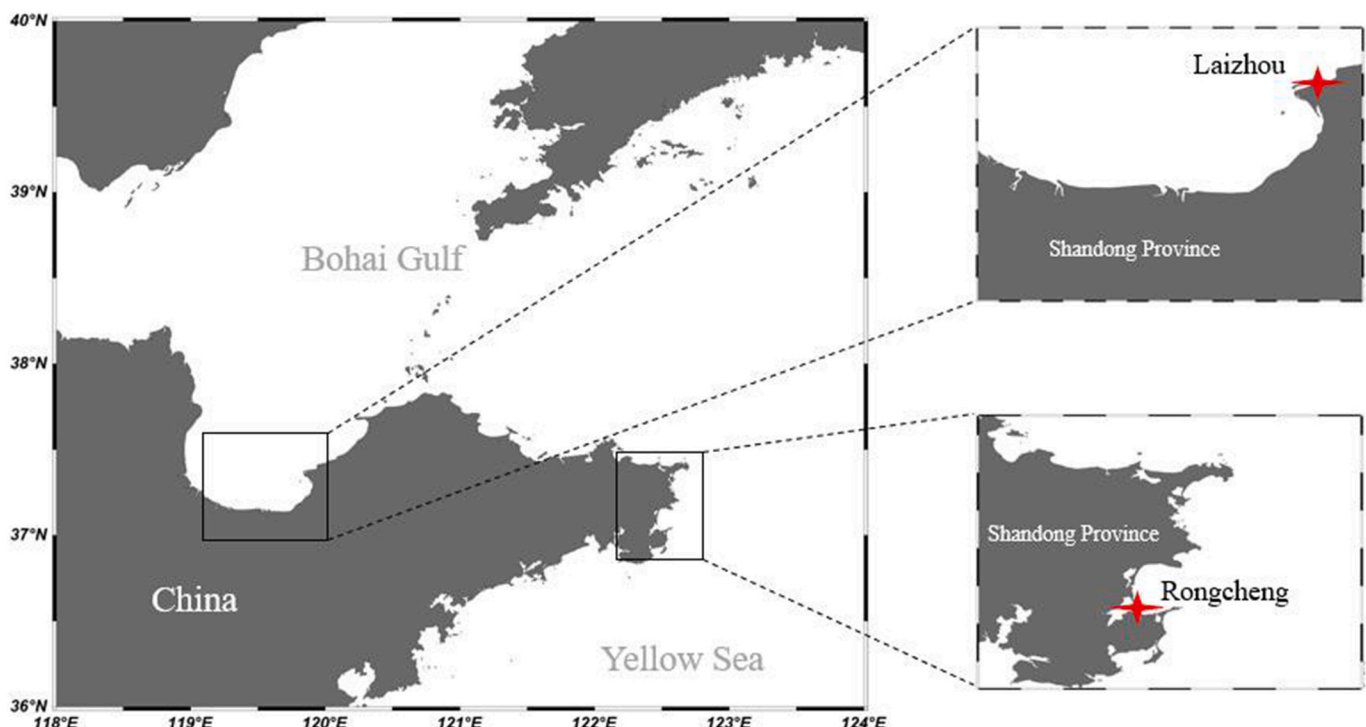

Fig. 1. Location of the broodstocks origin and experimental grow-out sites in China.

Table 1
Population structure of breeders used to produce full-sib families in different generations of *C. gigas* (G1-G3).

Generation	Population	Sires	Dams	Full-sib families	Half-sib families	Selected family no. / Total family no.
G1	base	29	49	49	15	–
G2	Selection	31	36	36	5	14/49
	Control	11	11	11	0	–
G3	Selection	34	38	41	10	12/36
	Control	10	10	10	0	–

Isochrysis galbana three times a day until they reached 120 μm and then *Nitzschia closterium* supplemented. Filtered seawater was changed once a day. When 30% of the larvae appear eyespots, scallop shells were placed into the plastic bucket to collect the spat metamorphosed from eyed larvae. After all eyed larvae metamorphosed to spat, each family were marked and transferred to an outdoor nursery pond for temporary rearing.

2.2. Field testing

In August 2019, the first generation (G1) was deployed in Rongcheng, Shandong province, China, which is a major site dedicated to oyster culture (Fig. 1). Oyster were placed in lantern nets and cultured on suspended long lines according to local practices. Each family was replicated three times to alleviate common full-sib effects. Each replicate lantern nets held 100 oysters from a single family. Survival was determined by counting live and dead oysters for each lantern in October 2019 (Table 2). In addition, 30 oysters per family were individually measured for shell height and shell length using an electronic Vernier caliper.

For the second generation (G2), spat were planted in the same vicinity as G1 in July 2020. Each family were represented by three replicates of 20 to 50 oysters. Replicates were planted and checked for mortality as in the previous generations. For the second generation, survival was recorded until October 2020 (Table 2). In addition, 30 oysters were individually measured for shell height, shell length, shell width and individual weight for each family at the endpoint.

For third generation (G3), three replicates of 40 spat per family were deployed in field in June 2021. Survival was recorded in September 2021(Table 2), as well as the growth traits (shell height, shell length and shell width) at the endpoint.

2.3. Statistical analysis

2.3.1. Genetic parameters

Preliminary statistical analyses of data for growth traits and survival were performed using SPSS22.0 software. The datasets for each generation and complete dataset were analyzed using two animal models with complete pedigree information. Models were defined as follows:

(1) linear animal model (LAM)

$$Y_{ijk} = \mu + a_i + c_j + e_{ijk}$$

Where Y_{ijk} is the observed phenotype (0 = dead, 1 = alive) of oyster i; μ is the overall mean; a_i is the random additive genetic effect of oyster i; c_j is the random common environment effect to the jth full-sib family; e_{ijk} is the random residual effect.

(2) Threshold (logit) animal model (TAM)

$$Pr(Y_{ijk} = 1) = \frac{exp(\mu + a_i + c_j)}{1 + exp(u + a_i + c_j)}$$

Where Y_{ijk} is the observed phenotype (0 = dead, 1 = alive) for oyster i. The other parameters were as described above.

The significance of fixed effect (Year) was estimated using Wald-F statistics, which was omitted from models because it was not significant ($P > 0.05$). For G1 and G2, the common environment effect was not significant (z. ration < 1.5, the constraint is boundary), so it was omitted from models. Heritability was estimated as $h^2 = \sigma_a^2/(\sigma_a^2 + \sigma_e^2)$. Where σ_a^2 is the additive genetic variance and σ_e^2 is the residual variance ($\pi^2/3$ for TAM). In G3 and across generations, heritability was estimated as $h^2 = \sigma_a^2/(\sigma_a^2 + \sigma_c^2 + \sigma_e^2)$. Where σ_c^2 is the common full-sib environmental variance. The other parameters were as described above.

In all genetic analyses, the additive genetic effect was assumed to be $\sim$N (0, Aσ_a^2), common environment effects were assumed to be $\sim$ N (0, Iσ_c^2), and residuals were assumed to be $\sim$N (0, Iσ_e^2). Where I is the identity matrix, A is the additive genetic relationship matrix.

Genetic correlations between summer survival and growth traits were expressed as Pearson correlation between breeding values predicted in three separate univariate model for these traits. The variance components and heritability were obtained by the Restricted Maximum Likelihood method using ASReml-R package.

2.3.2. Comparison of growth

All growth traits are analyzed using the SPSS 22.0 software. Means of these traits between selected population and control population were analyzed by independent sample *t*-tests.

2.3.3. Response to selection

The following model was fitted to estimate the marginal means of the selection and control populations in each generation (Gilmour et al., 2009).

$$Y_{jkl} = \mu + pop_j + a_k + e_{jkl}$$

Where Y_{jkl} is the observed phenotype (0 = dead, 1 = alive) of oyster l; μ is the overall mean; pop_j is the fixed effect of the jth population (selection and control population);a_k is the random additive genetic effect of oyster k; e_{jkl} is the random residual effect.

The realized genetic gain for summer survival in each generation was evaluated as the difference marginal means between the selected group and the control group. In addition, the realized genetic gain was also expressed as a percentage of the marginal means of the control population in each generation.

Table 2
Summary of the key dates for field testing of the oyster produced in each generation.

Generation	Spawn date	Start date	End date	time of duration (d)	Number of replicates per family	Density per replicate
G1	19/05/20	19/08/08	19/10/15	69	3	100
G2	20/05/07	20/07/20	20/10/18	91	3	20–50
G3	21/03/07	21/06/06	21/09/18	104	3	40

3. Results

3.1. Descriptive statistics of summer survival

The survival rate among families in G1 ranged from 25.00% to 90.00%, with a population average of 62.27%. For the G2, the means survival rate of selected population and control population were 67.69% and 53.79%, respectively, with coefficient variation ranging from 18.11% to 18.23%. For the following generation G3, the means survival rate of selected population and control population were 74.47% and 63.83%, respectively, with coefficient variation ranging from 16.68% to 17.55%. In selected population, the coefficient of variation of summer survival in *C. gigas* decreased from 27.30% to 16.68%. Within generation, the mean summer survival of the selected population was higher than those of the control population ($P < 0.05$). In addition, mean family survival of selected population had a wide range in each generation: from 25.00% to 90.00% (G1), from 38.33% to 90.00% (G2), and from 39.17% to 93.33% (G3) (Table 3).

3.2. Genetic parameters

Variance components, heritabilities (h^2) and the common environmental effect (c^2) for two different models were showed in Table 4. In LAM model, the heritability of the different generations ranged from 0.14 to 0.28, with an across value (across all generations with complete dataset) of 0.20. In LTM model, the heritability of the different generations ranged from 0.12 to 0.15, with an across value of 0.14. The common environmental effect estimates obtained from both models in G3 and across generation were low, but still significantly different from zero ($P < 0.05$). In G1 and G2, the common environmental effects obtained from both models were fixed at boundary.

The genetic correlations between growth traits and summer survival were not statistically significant in different generations ($P > 0.05$) (Table 5). In G2, the estimated genetic correlation between summer survival and three growth traits (Shell length, Shell width and individual weight) was low and positive, 0.022, 0.106 and 0.165, respectively. In G3, the estimated genetic correlation between summer survival and three growth traits (Shell heigh, Shell length and Shell width) was also low and positive, 0.229, 0.186 and 0.056, respectively.

3.3. Comparison of growth

For the G1, the mean shell height, shell length, shell width and individual weight were respectively 34.37 mm, 21.09 mm, 14.45 mm and 11.82 g for the selected population, and 33.71 mm, 20.75 mm, 14.10 mm and 11.37 g for the control population (Fig. 2). For the G2, the mean shell height, shell length and shell width of the selected population was 40.97 mm, 25.35 mm and 14.24 mm respectively, while it was 40.25 mm, 23.78 mm and 14.15 mm for the control population (Fig. 3). Oysters from all generations consistently grew faster than those from its controls throughout this study.

3.4. Selection response

The marginal means for summer survival per generation was given in

Table 4

Generation Estimates of additive genetic variance (σ_a^2), common to full-sib environmental variance (σ_c^2) residual variance (σ_e^2) and heritability ($h^2 \pm$ SE) for *C. gigas* survival for two models in each generation.

Model	Generation	σ_a^2	σ_c^2	σ_e^2	$h^2 \pm$ SE	$c^2 \pm$ SE
ALM	G1	0.0670	–	0.1738	0.28 ± 0.05	–
	G2	0.0285	–	0.1936	0.13 ± 0.03	–
	G3	0.0267	0.000	0.1629	0.14 ± 0.03	0.00 ± 0.00
	Across	4.3e-02	2.2e-06	1.79e-01	0.20 ± 0.02	0.00 ± 0.00
ATM	G1	0.5880	–	3.2898	0.15 ± 0.03	–
	G2	0.4438	–	3.2898	0.12 ± 0.02	–
	G3	0.5211	0.004	3.2898	0.14 ± 0.02	0.00 ± 0.00
	Across	5.5e-01	5.4e-05	3.2898	0.14 ± 0.01	0.00 ± 0.00

Table 5

Genetic correlations between summer survival and growth traits (Shell height, Shell length, Shell width and Individual weight) recorded in different generations of *C. gigas*.

Generation	Survival			
	Shell height	Shell length	Shell width	Individual weight
G2	–	0.022	0.106	0.165
G3	0.229	0.186	0.056	–

Table 6. The realized genetic gains for the two generations varied from 10.71% to 13.55%. The accumulated realized genetic gain (24.26%) expressed as a percentage was 41.97% after performing two generations of family selection or 20.99% per generation.

4. Discussion

It is of great importance to improve the summer survival of cultured oyster for sustainable development of the oyster industry. One approach to solve this problem is a selective breeding program to enhance survival when oyster are facing natural mortality outbreaks. In many aquaculture species, challenge experiment under controlled environment has been proven to be an effective method to improve the disease resistance (Ødegård et al., 2011). However, the cause of summer mortality in *C. gigas* are more complex, selecting resistant populations by challenge-based methods is more problematic. Natural survival is a desirable breeding trait and selective breeding for this trait will benefit farmers directly.

4.1. Heritability and common environment effects

Estimation of heritability for selected traits is crucial for the study of the genetic variation and the selective breeding of aquatic animals. Previous studies have reported that a strong genetic basis exists for
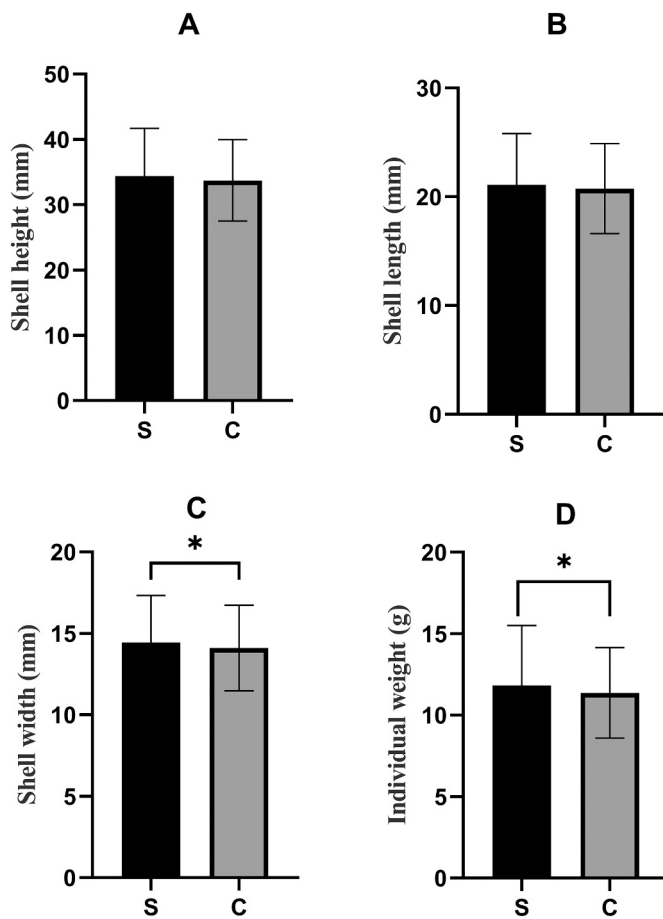
Table 3

Number of oyster (N), mean, minimum, maximum, standard deviation, and coefficient variation for summer survival by generation and population.

Generation	population	N	Mean (%)	Maximum (%)	Minimum (%)	Standard deviation	Coefficient Variation (%)
G0	Base	14,700	62.27	90.00	25.00	17.00	27.30
G1	Selection	4020	67.69	90.00	38.33	12.26	18.11
	Control	1320	53.79	73.33	40.83	9.81	18.23
G2	Selection	4920	74.47	93.33	39.17	12.52	16.68
	Control	1200	63.83	82.50	47.50	11.20	17.55

Fig. 2. Mean Shell height (mm) (Fig. A), Shell length (mm) (Fig. B), Shell width (mm) (Fig. C) and individual weight (g) (Fig. D) of the control (C in grey) and selected (S in black) populations for both lines of G2 at Rongcheng in October 2020. The errors bars represent the SE.

summer survival and that selective breeding could improve this trait (Beattie et al., 1980; Hershberger et al., 1984; Dégremont et al., 2005). In this study, estimates of heritability of summer survival within-generation (0.12–0.28) and across-generation (0.14–0.20) for *C. gigas* were low to moderate using two different models. Our estimates of heritability were similar to those reported by Ernande et al. (2004) who estimated a low to moderate (0.16–0.43) heritability in either controlled or field environmental conditions of adult *C. gigas*. However, our estimates were lower than those observed in France (0.47–1.08)

(Dégremont et al., 2007), in Japan (0.77) (Usuki, 2002), on the west coast of USA (0.49–071) (Evans and Langdon, 2006) as well as in Australia (0.68) (Ward et al., 2005). The estimated heritabilities are not only affected by environmental conditions but also strongly affected by source populations for broodstock. In the present study, the base population was established from two fast-growing lines. The genetic variation from different sources that formed the base population may not fully captured, which could explain the deflated heritability estimates (Sui et al., 2016). Furthermore, the low heritabilities for summer survival may be due to the low genetic variation in these two fast-growing strains of *C. gigas*. The two fast-growing line was performed over ten and eight generations of mass selection, respectively, which may result in inbreeding and loss of potentially valuable alleles and net additive genetic variation (In et al., 2016).

It's necessary to monitor the genetic variation in the successive generations. In this study, the estimates of heritability showed variation within generations which should be attributed to the different degrees of phenotypic variance in each generation (Gjedrem and Baranski, 2009). In addition, the estimated heritability showed a downward trend may be due to the 'Bulmer effect", which interpret that genetic variance decreased significantly in the first generation of selection, but the effects will be smaller in the subsequent generations (Bulmer, 1971). In short term, increasing the number of broodstock per generation may be an effect way to recover the genetic variation, which sufficient selection intensity can be obtained. In addition, the introduction of a wild population is an alternative method to obtain a long-term genetic gain, which should concern that population performance may be compromised. In our study, the common environmental effects (c^2) were extremely low for summer survival, which indicated that the separate rearing during the larvae period had minimal effect on phenotypic variance. The common environmental effects are known to mainly occurred in the early life stage and dissipate rapidly (Fu et al., 2016). The low and not significant c^2 have been reported in many aquaculture species. For example, in *Crassostrea virginica*, McCarty et al. (2020) found that the c^2 effects were not significant for acute low salinity

Table 6
Estimates of selection response for summer survival in each generation.

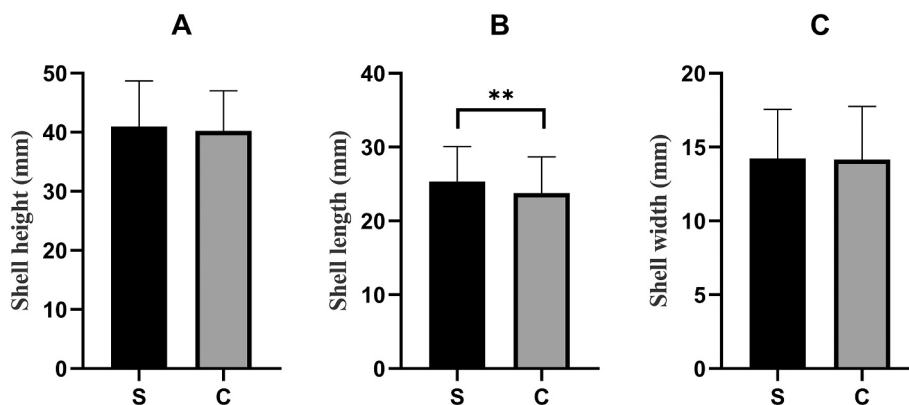| Generation	Population	Survival (%)	Selection response	
			Genetic gain (%)	Percentage
G1	Selection	67.34	13.55	25.19
	Control	53.79	–	–
G2	Selection	74.54	10.71	16.78
	Control	63.83	–	–
Average	–	–	12.13	20.99
Cumulative	–	–	24.26	41.97

Fig. 3. Mean Shell height (mm) (Fig. A), Shell length (mm) (Fig. B) and Shell width (mm) (Fig. C) of the control (C in grey) and selected (S in black) populations for both lines of G3 at Rongcheng in September 2021. The errors bars represent the SE.

survival. In *Litopenaeus vannamei*, Trinh et al. (2019) obtained close to zero c^2 for some harvest body traits.

4.2. Genetic correlations and correlated response

Growth and survival are the most important economic traits of oysters, which should be comprehensively considered in the selective breeding program. In our study, the genetic correlations between growth traits and summer survival were all low but positive in each generation (0.106–0.229), which implies that selection for summer survival would not result in adverse responses in growth traits. Encouragingly, the positively correlated responses in growth traits were also observed, and it would be of great interests to farmers. For each generation, the oysters of the selected population had a higher growth than did the control population, which suggested that selection to improve summer survival did not reduce but rather increased growth traits. This was in line with our observations of positive genetic correlations between growth traits and summer survival. These changes are desired, as our selective breeding program was originally focused on mass selection of the shell height before incorporating selection for summer survival. Similar findings were observed in selection to increase OsHV-1 resistance in *C. gigas* (Dégremont et al., 2015) and resistance to the spring mortality outbreaks in *Mytilus edulis* (Dégremont et al., 2019). Conversely, Beattie (1985) found negative correlations between growth and summer survival of *C. gigas*. It should be noted that these traits should be recorded until market size to confirm that there is no negative correlations between survival and growth, but the results reported during the spat stage were already encouraging. The current results are potentially important for the profitability and sustainability of oyster industry, because two economically relevant aspects such as growth and summer survival could be improved through a selective program for *C. gigas*.

4.3. Selection response

Summer mortality are easily influenced by environments and field placement timing (Dégremont et al., 2005), which varied considerably among different generations. Therefore, it's very necessary to use enough parents representing the average genetic performance of each generation to produce the controls in order to get the accurate estimate of selection response. The use of parental offspring with average summer survival of each generation as controls is expected to be more powerful against unintended selection and accumulated genetic drift than using a separate control line (Rye and Gjedrem, 2005). The coefficient of variation of summer survival in *C. gigas* decreased from 18.68% to 10.10%, which indicating that the summer survival trait of *C. gigas* gradually stabilized after selective breeding. The greater mean summer survival in the selected population compared with the control is indicative of a positive selection response for summer survival. It should be noted that sibs within families was unable to be distinguished the survival performance, which limits the genetic gain that can be obtained while maintaining genetic diversity. Recent advances in Genomic Selection (GS) and marker-assisted selection (MAS) offers new possibilities for selective breeding for summer survival. Using these methods, it possible to evaluate sibs within families, rather than phenotypes of families only (Houston et al., 2020).

Our study shows high progress in the improvement of summer survival of the *C. gigas*. The accumulated realized genetic gain (24.26%) expressed as a percentage was 41.97% after performing two generations of selection or 20.99% per generation, which is higher than the range (10% to 20% per generation) reported for most aquaculture species (Gjedrem, 2000). Other researchers have also obtained promising results for survival or disease resistance in oyster species. For instance, Barber et al. (1998) reported that in *C. virginica*, survival of the selected population to Roseovarius Oyster Disease (ROD) was 85% after two generations of mass selection, equivalent to an improvement of about 20%

per generation. In another study based on selection for summer survival in *C. gigas*, an increase in summer survival about 21% in selected group was showed compared with control group after three years family-based selection (Dégremont et al., 2010). Dove et al. (2013) reported a response of 17% for survival per generation in Sydney rock oyster (*Saccostrea glomerata*) selected for resistance to winter mortality (WM). Ford and Haskin (1987) reported that the selection response for resistance to *Haplosporidium nelsoni* (MSX) was almost 60% after five generation of selection in *C. virginica*. Naciri-Graven et al. (1998) obtained survival rates of 45% in *Ostrea edulis* selected for one generation to increase resistance to *Bonamia ostreae*. Recently, Dégremont et al. (2020) reported that dual selection for OsHV-1 and the *Vibrio aestuarianus* increased the field survival of *C. gigas* from 11% to 68%. These results clearly show the power of selection to improve survival or disease resistance traits, and that it may play a key role in breeding improvements for oyster.

We have demonstrated the superiority of the selection population over the control population in our major culture site, but oyster families were tested in a single site, where G × E interactions cannot be estimated. Dégremont et al. (2010) reported that a selective breeding program based at a single site should significantly improve the summer survival along French Atlantic coasts. Future studies are required to determine if this superiority was also expressed in the different culture environment. As the performance of an animal depends on both their genotype and culture environment, different genotypes may vary in their response to different environment changes. For example, Langdon et al. (2003) reported that G × E interactions significantly affected the yield of Pacific oyster families ($P < 0.001$). Evans and Langdon (2006) found significant G × E interactions, which were insufficient to offset favourable gains in different culture environments. De Melo et al. (2018) reported moderate-to-highly positive G × E correlations (> 0.45) for survival, yield, and average individual harvest weight of oyster families planted in two different sites.

5. Conclusion

In conclusion, our study clearly showed that family selection to increase summer survival in *C. gigas* was successful after only two generation of selection. The low to moderate heritability suggest that this trait is heritable and this breeding population still contains the potential for genetic improvement by selection. Meanwhile, the positive genetic correlations between summer survival and growth traits, suggesting that survival and growth traits can be simultaneously improved through selection. In addition, there were also correlated positively correlated changes in growth traits (shell height, shell length, shell width and individual weight). Our successful selective breeding program for summer survival in *C. gigas* would be beneficial for oyster industry.

Credit author statement

Yong Chi: Completion of the experiment, data analysis, and manuscript drafting. **Gaowei Jiang**: Data analysis. **Yuanxin Liang**: Data analysis. **Chengxun Xu**: Data analysis. **Qi Li**: Experimental design and coordination and manuscript revision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgments

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