



Short communication

Response to selection for growth in three selected strains of the Pacific oyster *Crassostrea gigas*Jingxiao Zhang^a, Qi Li^{a,b,*}, Chengxun Xu^a, Ziqiang Han^a^aKey Laboratory of Mariculture (Ocean University of China), Ministry of Education, Qingdao 266003, China^bLaboratory of Marine Fisheries Science and Food Production Processes, Qingdao National Laboratory for Marine Science and Technology, China

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ABSTRACT

Applying successive high selection pressures in fecund aquatic animals can easily lead to high increases in inbreeding and, consequently, to reductions in fitness and long-term genetic progress. The Pacific oyster *Crassostrea gigas* is one of the most commercially important aquaculture species worldwide. *C. gigas* from three cultured stocks in China, Japan and Korea were used to establish three mass-selected strains for fast growth, and a positive response to selection for fast growth was observed in the first two generations of these strains. To determine whether continuous progress can be achieved by selection for growth, we evaluated response to selection for the eighth to tenth generations of the three breeding strains. At grow-out stage, a genetic gain of 8.8–15.2%, selection response of 0.506–0.786 and realized heritability of 0.275–0.420 for shell height were observed in the selective breeding strains after seven to nine generations of selection. For body weight of oysters at grow-out stage, an average of 8.12–12.47% in genetic gains and 0.358–0.706 in selection responses were also obtained in the three mass-selected strains. The current response to selection for growth obtained in the eighth-to-tenth-generation selection strains suggests that a large amount of genetic variance still remains in the selected strains and there is a potential for sustained genetic improvement in growth-related traits in these strains through selective breeding. The results obtained in this study provides important information for future breeding programmes for *C. gigas*.

1. Introduction

The Pacific oyster *Crassostrea gigas*, is endemic to China, Japan and Korea and has been introduced worldwide as aquaculture species due to its fast growth and strong adaptability to factors influencing the physiology of marine invertebrates (temperature, salinity, etc.) (Miossec et al., 2009). Nowadays, *C. gigas* has become one of the most important commercial oyster species in global aquaculture, supporting the development of worldwide shellfish industry (Ruesink et al., 2005). China is the top oyster-producing country worldwide with the total oyster production reached to 4835 thousand metric tons in 2016 (BOF, 2017), and *C. gigas* is a major oyster species for shellfish aquaculture in northern China. Undoubtedly, genetic improvement in economically important traits (such as growth-related traits) of *C. gigas* would be of great benefits to oyster culture and farmers.

The potential for genetic improvement through selective breeding are well documented for shellfish species, particularly due to the short generation intervals (just one year for most bivalves) and the possibility of applying high selection pressures as a consequence of their high

reproductive capacity (Gjerde, 1986; Gjedrem and Baranski, 2009). Furthermore, the relatively high heritability for growth-related traits reported in oysters also indicate that artificial selection has high potential to improve the growth performance of this species (Lannan, 1972; Kong et al., 2015). In fact, some of selective breeding programs focused on the improvement of growth-related traits of oysters have been initiated, and have obtained encouraging results (Toro and Newkirk, 1990, 1991; Nell et al., 1996, 2000; Langdon et al., 2003; Nell and Perkins, 2005, 2006; de Melo et al., 2016, 2018; Proestou et al., 2016).

A selective breeding program for improving the growth performance of *C. gigas* was also initiated in China. The first and second generation of mass selection for shell height were performed in the cultured stocks from China, Japan, and Korea in 2007 and 2008, and achieved the genetic gain of 7.2–13.2% and 8.4–10.4% at harvest, respectively (Li et al., 2011; Wang et al., 2012). *C. gigas* is a species with high fecundity and have a high variance in reproductive success, and relatively few individuals can form the contributing parents of the next generation (Boudry et al., 2002). In general, artificial selection of highly fecund aquatic animals is known to carry a high risk of random

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genetic drift and loss of diversity (Falconer and Mackay, 1996). Applying sustained high selection pressures during a long-term successive selection process of *C. gigas*, therefore, might lead to high increases in inbreeding and, consequently, to reductions in fitness (i.e., inbreeding depression) and long-term genetic progress (Saura et al., 2017). Although a positive and remarkable response to selection was obtained in the first two generations of the selected strains of *C. gigas*, there are concerns whether response can be expected in the successive generations of selection.

In the present study, in order to evaluate the potential for current growth improvement in the selective breeding program, the response to mass selection for fast growth in the eighth to tenth generation of the three breeding strains of *C. gigas* were examined, and temporal changes of genetic parameters were also compared.

2. Materials and methods

2.1. Establishment of the selected parents, broodstock and conditioning

In 2007, two-year-old Pacific oysters from three cultured stocks in Rushan in Shandong province, China (stock C, 36.4°N, 121.3°E), Onagawa Bay in Miyagi Prefecture, Japan (stock J, 38.3°N, 141.3°E), and Pusan, South Korea (stock K, 35.1°N, 129.1°E) were used to establish three first-generation mass-selected strains of *C. gigas* (CS1, JS1 and KS1) for fast growth (Li et al., 2011). The second to seventh generations of the three breeding strains were constructed in 2008–2014, respectively.

In June 2015, a total of 100, 90 and 100 oysters in the seventh-generation selection strain (CS7), the eighth-generation selection strains (JS8, KS8) were selected from the top end of size distribution of each strain at a top of 10% selection pressures and served as the parents for the next generation of selection. Additionally, 80 oysters were randomly taken from each strain prior to removal of the selected parents and used to produce three control populations (CC8, JC9 and KC9) for the CS8, JS9 and KS9 strains. In June 2016, the ninth-generation selection strain (CS9), the tenth-generation selection strains (JS10, KS10) were produced in the same way as the selection of the previous generation (top 10% of the largest individuals selected), with parents derived from CS8, JS9 and KS9 strains, respectively. Prior to the selection experiment, 80 oysters were randomly taken from CS8, JS9 and KS9 to produce three control populations (CC9, JC10 and KC10). Information of selected parents, cutoff point and selection intensity of each selected strains are presented in Table 1. Fertilization, larval rearing, spat nursery and grow-out culture of oysters in each strain followed the method described by Li et al. (2011).

Table 1

Shell height (mean ± SD) of selected parents, cutoff point, and selection intensity in different selective breeding strains of *Crassostrea gigas*.

Year	Selected strains	Selected parents			Cut point (mm)	Selection intensity
		Sire	Dam	Shell height (mm)		
2015	CS8	50	50	88.52 ± 10.07	73.84	1.86
	JS9	40	50	93.06 ± 12.36	76.39	1.88
	KS9	50	50	82.35 ± 10.35	66.41	1.84
2016	CS9	50	50	77.36 ± 9.14	65.45	1.79
	JS10	40	50	77.91 ± 7.94	62.99	1.87
	KS10	50	50	68.76 ± 6.45	56.22	1.90

CS8, the eighth generation of mass selection strain from stock C; JS9, the ninth generation of mass selection strain from stock J; KS9, the ninth generation of mass selection strain from stock K; CS9, the ninth generation of mass selection strain from stock C; JS10, the tenth generation of mass selection strain from stock J; KS10, the tenth generation of mass selection strain from stock K. Stocks C, J and K represent Chinese, Japanese and Korean stocks of *C. gigas* respectively.

2.2. Sampling and growth measurement

At days 5, 10, 15 and 20 post-fertilization, 30 larvae per strains were randomly sampled for measurement of shell height using a light microscopy equipped with an ocular micrometer. During spat and grow-out, the shell height of 50 oysters per strains was measured using an electronic vernier caliper (0.01 mm accuracy) on days 90, 180, 270, 360 and 450. For oysters at grow-out stage, the live body weight of 50 oysters per strains was individually measured using electronic balance (0.01 g accuracy) on days 360 and 450.

2.3. Estimation of genetic parameters

According to Falconer and Mackay (1996), the intensity of selection (*i*) was calculated as the difference in mean shell height between the selected parents and the base line divided by the standard deviation of the line. The realized heritability (h_R^2) was calculated following Hadley et al. (1991) as:

$$h_R^2 = \frac{X_S - X_C}{i\sigma_C}$$

Where X_S and X_C are the mean phenotypic value of progeny in selected and control populations, respectively; σ_C is the standard deviation of control progeny; *i* is the intensity of selection.

To compare the response to selection at different life-history stages of oysters, the standard response to selection (SR) was estimated following the equation (Zheng et al., 2006):

$$SR = \frac{X_S - X_C}{\sigma_C}$$

Genetic gain (GG) was defined as the proportional increment in the phenotypic values achieved by selection. GG was calculated following Zheng et al. (2006) as:

$$GG = \frac{X_S - X_C}{X_C} \times 100$$

2.4. Statistical analysis

Differences in shell height and body weight among different strains at different ages were analyzed by multiple comparisons of means using a one-way ANOVA followed by post hoc Duncan's test. Differences in genetic parameters (GG, SR and h_R^2) among different selected strains were analyzed using two-way ANOVA followed by Duncan's test. Statistical analyses were performed using the SPSS 23.0 statistical package (IBM Inc., Armonk, NY, USA). Significance level for all analyses was set to $P < .05$.

3. Results

3.1. Comparison of growth in shell height

At harvest on day 450, oysters from CS8 and CC8 reached 102.48 (± 17.39) and 94.05 (± 15.45) mm, respectively; oysters from JS9 and JC9 reached 115.48 (± 15.46) and 101.08 (± 18.90) mm, respectively; oysters from KS9 and KC9 reached 90.35 (± 15.02) and 82.52 (± 12.30) mm, respectively (Table 2). Oysters from selective breeding strains in 8th or 9th generations consistently grew faster than those from its controls at all sampling date throughout this study. Significant differences ($P < .05$) between selected strains and controls in 8th or 9th generations were detected at larval stage on day 20 and harvest on day 450 (Table 2).

At harvest on day 450, oysters from CS9 and CC9 reached 95.26 (± 16.96) and 85.27 (± 12.64) mm, respectively; oysters from JS10 and JC10 reached 102.34 (± 14.85) and 90.02 (± 15.93) mm, respectively; oysters from KS10 and KC10 reached 86.65 (± 14.68) and

Table 2

Mean \pm SD shell height of *C. gigas* from the eighth and ninth generations of selected strains and their control populations at different ages.

Oyster ages (days)	Strains					
	CS8	CC8	JS9	JC9	KS9	KC9
Larvae (μ m)						
5	94.7 \pm 2.0 ^a	92.9 \pm 2.6 ^b	92.8 \pm 1.8 ^b	91.4 \pm 3.8 ^{bc}	90.4 \pm 2.04 ^{cd}	89.3 \pm 2.6 ^d
10	146.8 \pm 8.5 ^a	142.1 \pm 8.8 ^{abc}	143.4 \pm 6.0 ^{ab}	140.0 \pm 5.7 ^{bc}	140.4 \pm 7.4 ^{abc}	138.3 \pm 6.2 ^c
15	220.1 \pm 15.0 ^{ab}	212.6 \pm 12.0 ^{cd}	225.9 \pm 15.4 ^a	216.1 \pm 13.0 ^{bc}	211.0 \pm 13.5 ^{cd}	205.7 \pm 12.0 ^d
20	287.9 \pm 17.1 ^b	275.8 \pm 18.2 ^c	297.7 \pm 16.0 ^a	280.9 \pm 23.6 ^{bc}	276.1 \pm 19.9 ^c	265.9 \pm 14.8 ^d
Spat (mm)						
90	22.81 \pm 5.56 ^a	21.20 \pm 3.05 ^a	20.39 \pm 3.56 ^{ab}	19.19 \pm 3.05 ^{bc}	19.19 \pm 3.31 ^{bc}	18.03 \pm 2.97 ^c
180	35.65 \pm 4.11 ^{ab}	32.85 \pm 5.29 ^c	37.25 \pm 4.87 ^a	33.96 \pm 5.83 ^{bc}	32.77 \pm 4.81 ^c	30.35 \pm 5.51 ^d
270	53.22 \pm 11.07 ^b	48.01 \pm 9.33 ^{bc}	58.25 \pm 12.66 ^a	51.27 \pm 12.16 ^b	48.11 \pm 9.11 ^{bc}	44.34 \pm 8.67 ^c
Grow-out (mm)						
360	72.48 \pm 10.01 ^b	65.08 \pm 12.05 ^c	80.37 \pm 15.48 ^a	69.19 \pm 17.2 ^{bc}	68.38 \pm 15.36 ^{bc}	63.22 \pm 13.81 ^c
450	102.48 \pm 17.39 ^b	94.05 \pm 15.45 ^{cd}	115.48 \pm 15.46 ^a	101.08 \pm 18.9 ^{bc}	90.35 \pm 15.02 ^d	82.52 \pm 12.3 ^c

Different letters within the same row indicate significant differences ($P < .05$) among means. The definitions of abbreviations in selective breeding strains are given in the Table 1. CC8, JC9 and KC9 represent control populations of CS8, JS9 and KS9 strains respectively.

Table 3

Mean \pm SD shelref6Tme6T9re8(heightC9)-33.2(CS1Tf3.92810TTd(9itions)-2CCC8,.49J-4gas1Tf0-1.33573.6119tions)-2fromS8,saminkS9of2(CS8,.43e)-264.4edhelre8-339.4(r

80.06 (\pm 11.88) mm, respectively (Table 3). Similarly, mean shell height of the selective breeding strains in 9th or 10th generations is significantly larger than their control populations on days 20 and 450 post-fertilization ($P < .05$) (Table 3).

3.2. Comparison of growth in body weight

At harvest on day 450, oysters from CS8, JS9 and KS9 strains reached 66.69 (\pm 11.01), 62.71 (\pm 12.31) and 56.07 (\pm 11.16) g, respectively; oysters from CS9, JS10 and KS10 strains reached 59.40 (\pm 11.57), 64.70 (\pm 14.14) and 50.84 (\pm 7.22) g, respectively

(Table 4). The increase in body weight of the selected strains over the controls was 11.0% in CS8, 12.5% in JS9, 9.1% in KS9, 12.2% in CS9, 13.1% in JS10 and 9.0% in KS10, respectively.

3.3. Genetic parameters

The mean GG of shell height at grow-out stage were 10.2 (\pm 1.7), 15.2 (\pm 1.4), 8.8 (\pm 0.9), 11.3 (\pm 0.6), 14.1 (\pm 0.6) and 9.4 (\pm 1.7) % for CS8, JS9, KS9, CS9, JS10 and KS10, respectively (Fig. 1). Relatively high levels of mean SR and h_R^2 were also observed in selected strains at different stages. At grow-out stage, the mean SR ranged from

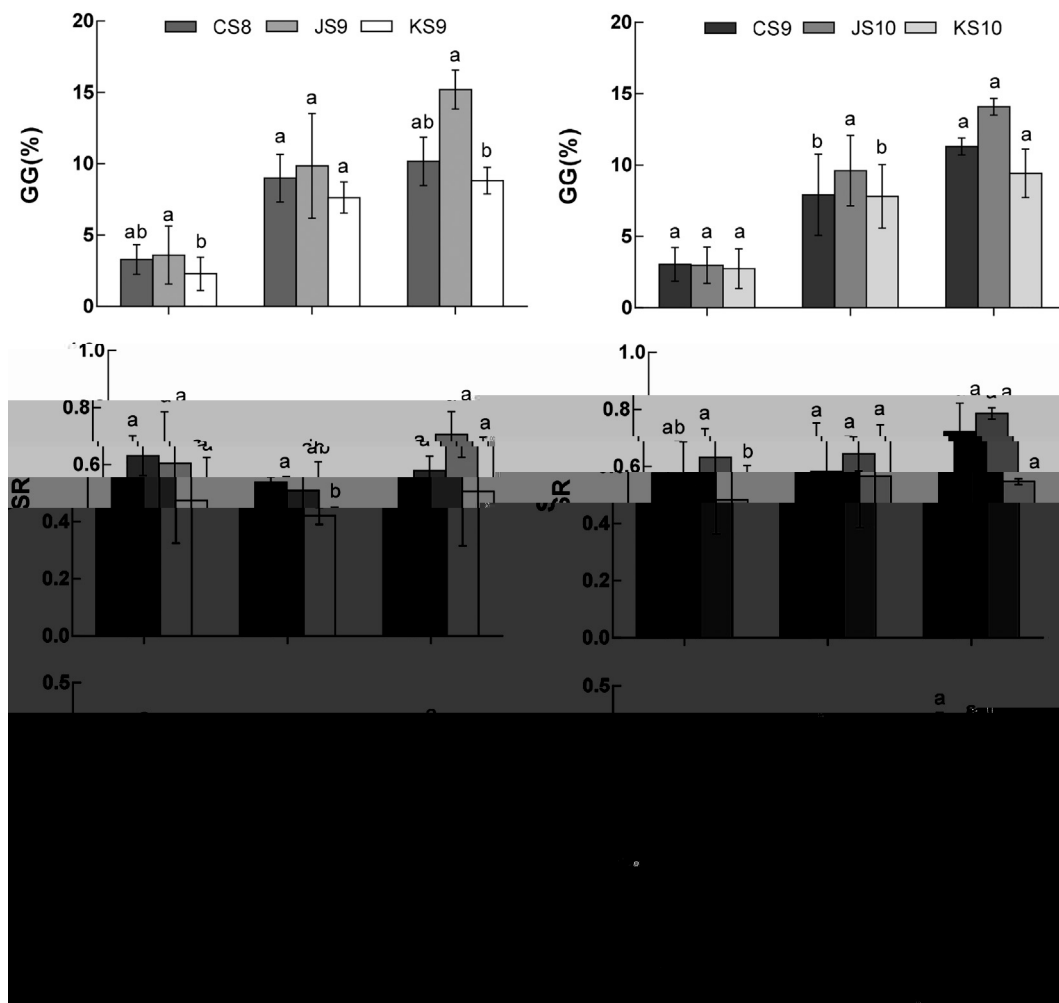


Fig. 1. Genetic gains (GG), standardized response to selection (SR) and realized heritability (h_R^2) of shell height in the selected strains of *C. a. o. e. giga* at different ages. Means not sharing the same superscript within the same stage are significantly different ($P < .05$); Error bars represent standard deviation. See Table 1 for definitions of strain abbreviations.

0.506 to 0.706 for CS8, JS9 and KS9, and ranged from 0.547 to 0.786 for CS9, JS10 and KS10. The mean h_R^2 ranged from 0.275 to 0.376 for CS8, JS9 and KS9, and ranged from 0.288 to 0.420 for CS9, JS10 and KS10, respectively. No significant differences in GG or SR or h_R^2 were observed among the selective breeding strains at grow-out stage, with the ranking of JS9 > CS8 > KS9 and JS10 > CS9 > KS10. The exception was the genetic gain obtained in KS9 which was significantly lower than that obtained in JS9 and CS8 ($P < .05$).

The mean genetic gain of body weight at harvest stage (days 360 and 450) were 10.7 (± 0.4), 10.8 (± 2.4), 8.9 (± 0.4), 11.5 (± 0.9), 12.5 (± 0.9) and 8.1 (± 1.2) % for CS8, JS9, KS9, CS9, JS10 and KS10, respectively (Fig. 2). The mean estimates of SR were 0.602 (± 0.162), 0.706 (± 0.214), 0.358 (± 0.015), 0.567 (± 0.064), 0.444 (± 0.063) and 0.438 (± 0.064) for CS8, JS9, KS9, CS9, JS10 and KS10, respectively.

4. Discussion

In the present study, oysters from the selected strains were significantly larger than those from the control populations at larval stage on day 20 and grow-out stage on day 450, indicating that the selection for shell height of *C. giga* is still effective after seven to nine generations of selection for fast growth. Since oysters from the three selective breeding strains were grown under the identical environmental conditions at any stage, it can be concluded that the differences among the

three selected strains are genetic and reflect different responses to selection (Liang et al., 2010).

At grow-out stage, genetic gains of 8.8–15.2% in shell height were obtained in the selective breeding strains after seven to nine generations of selection. This level of improvement is comparable to those obtained in our previous study. Genetic gains of shell height were ranged from 7.2% to 13.2% for the first generation of selective breeding strains, and ranged from 8.4% to 10.4% for the second generation of selective breeding strains (Li et al., 2011; Wang et al., 2012). Genetic gains obtained in this study were also comparable to those reported in other aquaculture species. Gjedrem (2005) listed 21 estimates of genetic gain for growth rate in 10 aquatic species, averaging 14% per generation. For oysters, Nell et al. (1996, 1999) reported a genetic gain of 4% and 18% in increased growth rate in Sydney rock oyster *Saccostrea commeciali* after one and two generations of selection, respectively. Toro et al. (1996) reported a genetic gain of 9–12% in growth rate in Chilean native oyster *O. edulis* with the first generation of selection. In the mass selected European oyster (*O. edulis*), the range in sizes of the selected lines was from 8% to 38% larger than the control lines with an average of 23% after one generation of selection (Newkirk and Haley, 1982). Similarly, Langdon et al. (2003) found a positive response to selection in *C. giga*, with the family-selected lines showing a general yield 10–20% higher than that of control lines per generation. The remarkable gains were achieved in the eighth- to tenth-generation selection strains indicate that a high genetic variation still

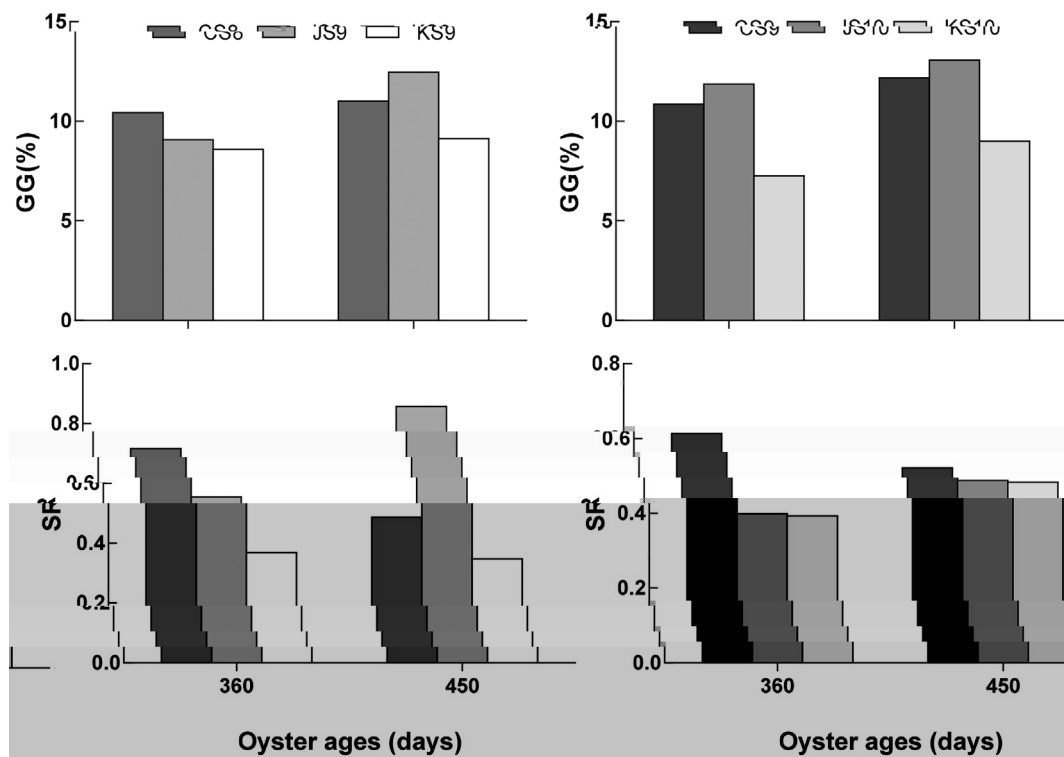


Fig. 2. Genetic gains (GG) and standardized response to selection (SR) of body weight in the selected strains of *C. gigas* at harvest on days 360 and 450. The definitions of the strain abbreviations are given in the Table 1.

existed in the three selective breeding stains. The results of our study was in line with that of Wang et al. (2016), who analyzed the genetic variation with microsatellites in mass selected strains of *C. gigas* in China and found that the genetic variation was not greatly affected by mass selection progress.

During grow-out stage, the mean SR ranged from 0.506 to 0.706 for CS8, JS9 and KS9, and ranged from 0.547 to 0.786 for CS9, JS10 and KS10, respectively. The estimates of SR were also similar to those obtained in the first generation (ranging from 0.269 to 0.684) and second generation (ranging from 0.573 to 0.834) of the strains of *C. gigas* (Li et al., 2011; Wang et al., 2012). The fact that SR is sustained with little change over several generations also suggests a high level of genetic variation still remains in the selected strains. Moreover, artificial fertilization was applied in our mass selective breeding program so that all males and females can be guaranteed to contribute gametes to the next generation, and the sex ratio of broodstocks is approximately maintained at 1:1, resulting in the estimates of effective population size (N_e) in the three selective breeding strains were still at a relatively high level ($N_e > 50$ per generation) (Wang et al., 2016; Zhang et al., 2018). Bijma et al. (2000) and Ponzoni et al. (2010) reported that a minimum population size of 50–100 could constrain inbreeding 1% per generation in selection programs. Therefore, effects of inbreeding on growth traits in the selected strains are not significant in this study, and it is not surprising to see continued selection response in the three selective breeding strains.

Realized heritability of shell height in adult oyster ranged from 0.275 to 0.376 for CS8, JS9 and KS9, and ranged from 0.288 to 0.420 for CS9, JS10 and KS10 in this study, respectively. Heritability values of 0.20 or larger indicate that there is still a potential for sustained genetic improvement in shell height in the three selected strains of *C. gigas* (Lannan, 1972; Falconer and Mackay, 1996). The estimate of heritability was also comparable to that observed in the first generation ($h_R^2 = 0.149–0.402$) and second generation ($h_R^2 = 0.312–0.457$) of the three selected strains. The additive genetic effect of objective traits depends on the gene heterozygosity and genetic structure of strains

(Falconer and Mackay, 1996). Wang et al. (2016) reported that a high genetic variation still remained in the four generations of mass selection strains from stock C. Zhang et al. (2018) also found no significant reduction in heterozygosity in the six successive generations of selected strains from stock J and stock K. Therefore, the high gene heterozygosity per generation of the three breeding strains could be responsible for the high-level heritability of shell height observed in the eighth- to tenth-generation selection strains.

In the present study, estimates of genetic parameters (GG, SR and h_R^2) for shell height were different among the strains, with the ranking of JS9 > CS8 > KS9 and JS10 > CS9 > KS10 at grow-out stage. Li et al. (2006) found that geographically separated cultured populations of *C. gigas* could be genetically differentiated unless seeds are transplanted among them. The asymmetrical response to selection obtained in the three selective breeding strains could be attributed to the asymmetrical genetic structure of base stocks and the possible occurrence of random genetic drift during successive mass selection (Falconer and Mackay, 1996). Besides, the potential impact of genotype by environmental interactions on oyster growth also should be considered (Dégremont et al., 2005; Evans and Langdon, 2006; de Melo et al., 2018).

The mean body weight of progeny from the selected strains were also higher than those from control populations at grow-out stage on days 360 and 450. An average of 8.1–12.5% in genetic gains and 0.358–0.706 in selection response of body weight were also achieved in the three selective breeding strains after seven to nine generations of selection. The results indicated that a positive correlated response for body weight at grow-out stage were obtained when selection for shell height was performed. A positive genetic correlations between shell shape-related traits and body weight have been observed in other bivalves. In the European oyster, Toro and Newkirk (1990) found a high positive genetic correlation between live weight and shell height. In the catarina scallop *A go ec en en ico*, Ibarra et al. (1999) also found a significantly higher correlated response of shell width when selection was on total weight. The presence of positive correlation among

growth-related traits in selective breeding strains of *C. giga* implies that selection for shell height of these strains would result in favorable correlated responses in body weight, which would be of great interests to farmers.

In conclusion, estimates of GG, SR and h_R^2 are still at a relatively high level in the selective breeding strains after seven to nine generations of selection, which are comparable to the selection response obtained in the first- and second-generation selection strains, suggesting that a considerable genetic variance still remains in the selected strains and there is a potential for genetic improvement in growth-related traits in these strains through selective breeding. This finding also suggests that the appropriate mating strategy, for example, artificial fertilization, equal sex ratio of parents (50 females \times 50 males), applied in the breeding program might play an important role in the achievement of constrain inbreeding and remarkable selection response in selected strains. Moreover, a positive correlated response for body weight at grow-out stage were also obtained when selection for shell height was performed in the three selective breeding strains after several generations of selection. The results obtained in this study provides important information for future breeding programmes for *C. giga*.

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