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Growth Performance of Larval and Juvenile Manila Clam (*Ruditapes philippinarum*) from Divergently Selected Individuals of a Full-Sib Family

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Abstract In this study, the method of divergent selection was employed to test the larval and juvenile growth performance within a full-sib family of Manila clam *Ruditapes philippinarum*. The 10% largest and 10% smallest clam individuals (on the basis of shell length) of a full-sib family were selected as parents for the fast and slow growing lines, respectively. The difference in shell length was significant among the three lines (fast, control, and slow) tested. The sequence of shell length were fast line>control line>slow line. The responses to selection, realized heritability, and genetic gain were 0.06%–0.81%, 0.04%–0.47% and 0.58%–18.89% in the fast direction, respectively; and were 0.14%–1.27%, 0.08%–0.73%, and 0.31%–49.03% in the slow direction, respectively. The results suggested that there was a large portion of additive genetic variance affecting the growth in the full-sib family. Selection in the fast direction within the full-sib family would greatly improve the growth of *R. philippinarum*.

Key words divergent selection; full-sib family; Manila clam

1 Introduction

The Manila clam *(Ruditapes philippinarum*) is one of the most important aquaculture species in China. Because of its short grow-out time, this species quickly gained acceptance by farmers. By 2015, the annual production of *R. philippinarum* exceeded 3 million tons in China, accounting for an estimated 90% of the world (DOF, 2015). Despite the economic importance of this species, the industry has not yet benefited from genetic improvement. Traditionally, Manila clam farming has been based on wild species whose natural populations are often over exploited and do not fulfill market demand.

Divergent selection is a method commonly used to measure the response to selection in shellfish selective breeding programs (Liang *et al*., 2010). You *et al*. (2010) reported that the large-selected line of small abalone *Haliotis diversicolor* grew 4.58%–12.79% faster than their control lines on shell length. The average realized heritability for shell length was 0.013–0.064. In the tropical oyster *Saccostrea cucullata*, Jarayabhand and Thavornyutikarn (1995) reported that the realized heritability for growth rate is 0.38–0.10 in the upward-selected line and 0.19–0.04 in the downward-selected line. In the European oyster *Ostrea edulis*, statistically significant differences ($P<0.01$) are found between the progeny of the upward and downward selected groups for whole weight and shell height (Toro and Newkirk, 1990).

Assessing response through divergent selection requires two lines that are derived from the same base population, with one line being selected for increased phenotypic value and the other being selected for decreased phenotypic value. The response of the organisms in the two different lines provides additional verification of genetic variation (Falconer, 1981). With the development of efficient hatchery techniques (Yan *et al*., 2006), selective breeding could be used to improve growth traits of the Manila clam. The presence of genetic correlation suggested that the alteration of shell length growth will cause simultaneous changes in other related traits (Falconer, 1981; Toro *et al*., 1990; Huo *et al*., 2010b). A breeding program for the growth in *R. philippinarum* was established in 2007, with the initial establishment of 45

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full-sib families selected for fast growth in shell length (Huo *et al*., 2010a; Yan *et al*., 2014). Consequently, one full-sib family with fast shell length growth was selected for breeding in this study. With our knowledge, this is the first report to test the effect of divergent selection for the growth within the full-sib family of Manila clam. This will help us to determine if the full-sib family retains the additive genetic variance for the growth trait in both directions and if artificial selection in the fast direction within the family is an effective approach for genetic improvement of the Manila clam.

2 Materials and Methods

2.1 Establishment of 45 Families

Forty-five families were established in the hatchery of Hairi Fisheries Food Corporation Limited located in Zhuanghe, Dalian, Liaoning Province, China in 2008. Adult Manila clams (*R. philippinarum*) were sampled from the natural population in Shihe (Dalian, Liaoning Province in the northeastern part of China). This study used a classic nested mating design developed by Comstock *et al*. (1952). Each of the 15 male clams from the natural population was mated with three separate females. This produced a total of 45 full-sib families and 15 sets of half-sib families whose progeny shared a father but had separate mothers. The progenies of the 45 full-sib families were cultured at the same stocking densities (150 clams per bag) in the nursery ponds ($775 \times 200 \times 1.2$ m) for one year (Huo *et al*., 2010a).

2.2 Base Stock and Experimental Design

Of the 45 1-year-old full-sib families, the family with the largest size (on the basis of mean shell length) was selected as the brood stock for this study. The mean shell lengths of the 45 families and the selected family were (15.82 ± 1.22) mm and (18.37 ± 1.09) mm, respectively. The production of the selected family was 3000 individuals. Fifty clams were randomly sampled from the selected family to produce the family control line (*CL*). Five hundred clams were randomly taken from the selected family for measurement, and the size-frequency distribution of shell lengths was determined. For the selection experiments, the 10% largest (50 largest clams) and 10% smallest clams (50 smallest clams) were selected as parents for the fast and slow growing lines, respectively. Therefore, the following three lines of parents were selected: fast line (hereafter *FL*), slow line (hereafter *SL*) and Control line (*CL*).

2.3 Establishment of Selection and Control Lines

The clams in the replicate experiments were induced to spawn by drying for 4 h in the shade. The water temperature and salinity at spawning were 25℃ and 28, respectively. Each line of clams was placed in a separate 100 L tank for spawning. Every experimental line was taken out from the beakers when the spawning was observed using torch. After that, all the experimental lines were put back again to the beakers to make sure the fertilization simultaneous. After spawning, the gonad of each clam was checked with microscopy to ensure that all the clams had contributed to fertilization. The fertilized eggs each line hatched at an initial density of 40–50 eggs mL^{-1}. After about 24 h, the fertilized eggs developed into D-larvae. Each D-larva line was separated into three portions as replicates. Larvae and juveniles for all experimental lines were reared under the same conditions. Initially, the D-larvae density in each replicate bucket was 5–6 larvae mL^{-1}. During larval rearing, 100% of the water was exchanged with sand-filtered seawater every day, and the temperature was maintained at 25–28℃. Salinity was kept at 28–29. The larvae were fed with *Isochrysis galbana* during days 1–3 and a mixture of *I. Galbana* and *Chlorella* spp. (2:1) from day 4 to the juvenile stage. The feeding ration was increased with larval development. Larvae were fed a ration of 2000–10000 cells $mL^{-1}\,d^{-1}$. The juveniles were fed with a mixture of *I. Galbana* and *Chlorella* spp. (2:1) at a ration of 30000–60000 cells $mL^{-1}\,d^{-1}$.

After 60 d, the juveniles were transferred to the same nursery ponds ($775\,m \times 200\,m \times 1.2\,m$) and placed in bags with a mesh size of 700 μm. The stocking densities were 150 clams per bag, 20 bags per batch. The bags were cleaned every 3 d. During this period, the water temperature was 19–22℃ and the salinity was 26–28. The progenies of each line were cultured for one month.

2.4 Sampling and Measurement

Totally 10 mL samples were taken from each replicate. The larvae were killed using 4% formaldehyde, and then the shell lengths of the larvae were measured using a microscope (100×) on days 3, 6, and 9. The larval survival rate was calculated based on the total numbers of live larvae on days 3, 6, and 9 after fertilization. Juveniles were measured using a vernier caliper (0.02 mm accuracy), and the numbers of live and dead clams per replicate bag for each line were counted to calculate the juvenile survival rate on days 30, 60, and 90.

2.5 Data Analysis

When studying divergent selection, the most common method to calculate realized heritability is comparing the selection between offspring and parent at the same age. However, this method is not applicable to the estimation of realized heritability of shellfish because any change in environmental condition may impact the yearly growth of shellfish. By establishing a comparison line within the full-sib family, however, we eliminated this environmental impact. The formulas are as follows (Ibarra *et al*., 1999; Zheng *et al*., 2004, 2006):

$$SR = \frac{x_s - x_c}{S_c},$$

$$h^2_R = \frac{x_s - x_c}{is_c},$$

$$GG = \frac{x_s - x_c}{x_s} \times 100\% .$$

In the formulas, SR, h^2_R, GG mean response to selection, realized heritability, and genetic gain, respectively. x_s and x_c are the mean shell lengths of the selected line and the control, respectively; Sc is the standard deviation of the CL; and i is selection intensity, $I = 1.76$.

Differences in shell length of the parents in FL, SL, and CL were analyzed using ANOVA. Differences in shell length of the offspring among FL, SL, and CL were analyzed using ANCOVA with time as the covariate. The shell length was transformed (log), and survival was transformed (asin) when it's necessary to meet the assumptions of statistical methods used. All analyses were performed using the Statistical Package for the *R* statistical software. Significance level for all analyses was set to $P < 0.05$.

3 Results

3.1 Base Stock and Selection Intensity

The shell length of the parental family was 18.38 mm, and the one-sample Kolmogorov–Smirnov test indicated a normal distribution (Fig.1). The mean shell lengths ranged from 13.2 ± 1.00 to (22.7 ± 1.01) mm and were significantly different among the three lines (Table 1). The cut-off points were 21.5 and 14.5 mm for *FL* and *SL*, respectively (Table 1).

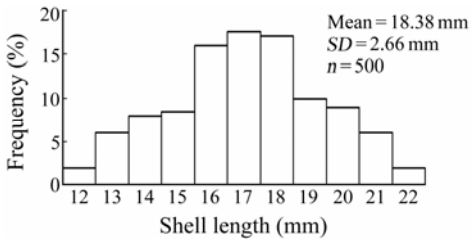

Fig.1 Size-frequency distribution of the full-sib family of *R. philippinarum*.

Table 1 Mean shell lengths of the parents of the fast line (*FL*), control line (*CL*), slow line (*SL*), and cut-off points in the *R. philippinarum* at the age of 1-year-old

Shell length of parents (mm)			Cut-off point (mm)	
FL	CL	SL	Fast line	Slow line
22.74 ± 1.01[a]	18.62 ± 1.49[b]	13.2 ± 1.00[c]	21.48[a]	14.54[b]

Notes: Different superscript letters indicate significant differences ($P < 0.05$) among means. ± represents standard deviations.

3.2 Growth

Significant differences in the mean shell lengths of the three lines were detected with ANCOVA at all times of measurement (Figs.2 and 3; Table 2). Mean shell lengths were in the following order: $FL > CL > SL$ (Figs.2, 3; Table 3). On day 90, the shell length of the juveniles from *FL* was 18.91% larger than that of juveniles from *CL*; In comparison, the shell length of juveniles from *SL* was 49.04% smaller than that of the juveniles from *CL*. The

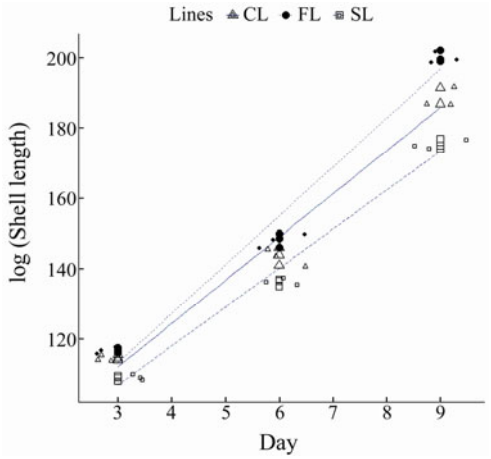

Fig.2 Shell length relative to age for fast line (*FL*), control line (*CL*) and slow line (*SL*) at larval stage. The line is the least-squares regression from ANCOVA.

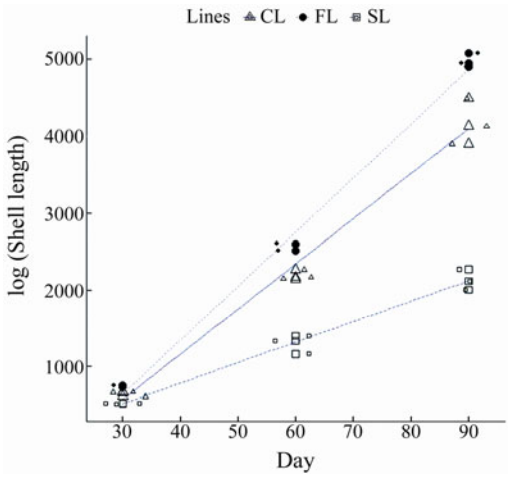

Fig.3 Shell length relative to age for fast line (*FL*), control line (*CL*) and slow line (*SL*) at juvenile stage. The line is the least-squares regression from ANCOVA.

Table 2 Analysis of ANCOVA in shell length and survival of the offspring among the fast line (*FL*), control line (*CL*) and slow line (*SL*)

Sources		*df*	*MS*	*F*	*P*
Larval growth	Lines	3	0.32	11.52	< 0.01
	Days	1	2.74	999.82	< 0.01
Juvenile growth	Lines	3	1.33	49.61	< 0.01
	Days	1	29.06	1.08	< 0.01
Survival	Lines	3	10.98	0.001	0.748
	Days	1	21269	2.13	< 0.01

Table 3 Mean shell length of the fast line (*FL*), control line (*CL*), slow line (*SL*) at different growth ages in day

Age (days)	*FL*	*CL*	*SL*
Larval (μm)			
3	115.33 ± 10.25	114.67 ± 10.50	113.17 ± 7.13
6	145.83 ± 13.65	143.67 ± 12.17	142.00 ± 19.32
9	204.00 ± 15.45	188.50 ± 27.39	170.67 ± 32.37
Juvenile (mm)			
30	7.47 ± 1.33	6.49 ± 1.21	5.25 ± 0.89
60	25.44 ± 5.33	21.93 ± 7.01	12.98 ± 4.52
90	49.68 ± 14.58	41.78 ± 19.13	21.29 ± 1.12

mean *FL* shell length was 1.3 times larger than the mean *SL* shell length (Table 3).

3.3 Survival

The survival rates of the three lines in the larval and juvenile stages are presented in Fig.4. No significant difference in survival among three lines was detected with ANCOVA at any of the ages examined (Fig.4; Table 2). The range of the responses to selection (*SR*), realized heritability (h^2_R), and genetic gain (*GG*) were 0.06–0.81, 0.04–0.47, and 0.58%–18.89% for the fast line; and were 0.14–1.27, 0.08–0.73, and 1.60%–49.03% for the slow line (Table 4). Asymmetric differences were observed between the fast and slow lines.

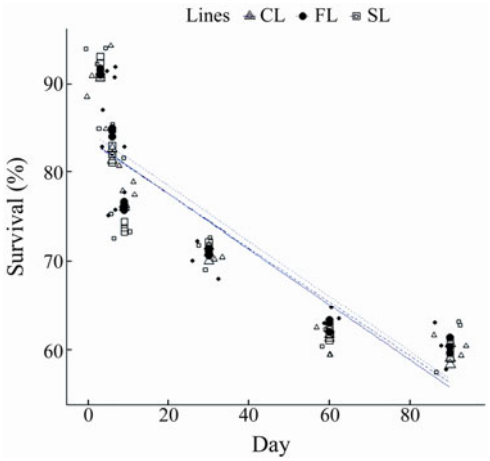

Fig.4 Survival relative to age for fast line (*FL*), control line (*CL*) and slow line (*SL*) at larval and juvenile stages. The line is the least-squares regression from ANCOVA.

Table 4 Response to selection (*SR*), realized heritability (h^2_R), and genetic gain (*GG*) in the fast line (*FL*) and slow line (*SL*)

Age (days)	*SR*		h^2_R		*GG*	
	FL	*SL*	*FL*	*SL*	*FL*	*SL*
3	0.06	0.14	0.04	0.08	0.58	1.31
6	0.18	0.14	0.1	0.08	1.51	1.16
9	0.57	0.65	0.32	0.37	8.22	9.46
30	0.81	1.02	0.47	0.59	15.11	19.01
60	0.5	1.27	0.29	0.73	16	40.78
90	0.41	1.07	0.24	0.61	18.89	49.03

4 Discussion

Measurements of response to selection and realized heritability are useful approaches to the study of additive gene effects (Liang *et al*., 2010). Positive and encouraging responses to selection have been reported in numerous studies of bivalve growth (Newkirk *et al*., 1982; Ibarra *et al*., 1999; Nell *et al*., 1999; Zheng *et al*., 2004, 2006; He *et al*., 2008; Li *et al*., 2011) and survival (Dégremont *et al*., 2010). In the present study, the positive response to selection for the fast line was 0.06–0.81, and the positive realized heritability was 0.04–0.47, these results are consistent with the previous reported in bivalves (Newkirk, 1982; Nell *et al*., 1999; Zheng *et al*., 2006), which indicated that a large portion of the growth trait is associated with additive gene action (Becker, 1984). Therefore, further mass selection could be carried out in this full-sib family to improve growth of the Manila clam.

In the present study, the response to selection and the realized heritability of shell length were asymmetric between the fast (*SR*, 0.06–0.81; h^2_R, 0.04–0.47) and slow lines (*SR*, 0.14–1.27; h^2_R, 0.08–0.73). In marine bivalves, divergent selection has been applied to estimate genetic parameters for oysters (Toro *et al*., 1990; Toro *et al*., 1991; Jarayabhand *et al*., 1995) and scallops (Liang *et al*., 2010). The results of these studies revealed significant difference in the growth trait among the fast, control, and slow lines. Asymmetric responses have been found in most two-way selection experiments in bivalves (Toro *et al*., 1991; You *et al*., 2010; Liang *et al*., 2010). The possible causes of these asymmetry responses are: 1) differences in the selection differential; 2) scaling effects; 3) inbreeding depression; 4) directional dominance; and 5) unequal gene frequencies (Falconer, 1981). In this study, the brood stock was the family with the largest size (based on the mean shell length) selected from 45 full-sib families. This might have improved the gene frequencies of the brood stock in the fast growth direction, and the asymmetric responses and realized heritability could have been caused by unequal gene frequencies.

In the present study, the genetic gain was improved by 10.05% and 20.13% (Mean value from day 3 to day 90) for *FL* and *SL*, respectively. This result agrees with the expectations for shellfish species, as Newkirk (1982) predicted genetic gains between 10% and 20% per generation in the European oyster *Ostrea edulis*. Nell *et al*. (1999) found an 18% increase in body weight after selection for two generations in the Sydney rock oyster *Saccostrea commercialis*. Zheng *et al*. (2006) observed a genetic gain in shell length of 17.56% after two generations of selection for fast growth in the bay scallop *A. irradinas*. Langdon *et al*. (2003) reported a 9.5% increase in live weight after selection in Pacific oyster, *Crassostrea gigas*, for one generation. He *et al*. (2008) reported a genetic gain in shell height of 16.03% ± 4.79% in the second generation of the pearl oyster *P. fucata*. Our results indicated that selection within the full-sib family could change the growth of *R. philippinarum*. The growth difference in mean shell length was significant among the three lines, following an order of fast line>control line> slow line. This result suggested that selection for shell length in the fast direction within the full-sib family is an effective approach to larger genetic change in growth.

Understanding the importance of inbreeding in shellfish is essential for developing efficient long-term breeding strategies (Evans *et al*., 2004). Harmful effects of inbreeding depression (ID) on progenies resulting from within-family-crosses have been observed in shellfish. ID arises both from the expression of partially recessive deleterious alleles and from the loss of heterozygosity. ID is more likely to occur for traits related to growth and survival, which was indicated by previous studies of

Crassostrea virginica (Longwell *et al*., 1973), *Pecten maximus* (Beaumont *et al*., 1983), *Ostrea edulis* (Bierne *et al*., 1998), *H. discus hannai* (Deng *et al*., 2005), and *C. gigas* (Hedgecock *et al*., 1995; Launey *et al*., 2001; Evans *et al*., 2004). The success of divergent selection within a family in this study confirmed that a large portion of additive genetic variance for growth exists in the full-sib family. The difference on the survival was not observed within this full-sib family. For the further studies in the future, attention should be paid to a possible problem arising from inbreeding effects to selective breeding within full-sib family of *R. philippinarum*.

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