SHORT COMMUNICATION

Estimates of Heritability for Growth and Shell Color Traits and Their Genetic Correlations in the Black Shell Strain of Pacific Oyster *Crassostrea gigas*

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Abstract The Pacific oyster *Crassostrea gigas* has been introduced widely and massively and became an economically important aquaculture species on a global scale. We estimated heritabilities of growth and shell color traits and their genetic correlations in black shell strain of *C. gigas*. Analyses were performed on 22 full-sib families in a nested mating design including 410 individuals at harvest (24 months of age). The parentage assignment was inferred based on four panels of multiplex PCR markers including 10 microsatellite loci and 94.9% of the offspring were unambiguously assigned to single parent pairs. The Spearman correlation test ($r = -0.992$, $P < 0.001$) demonstrated the high consistency of the shell pigmentation (SP) and L^* and their same efficacy in shell color measurements. The narrow-sense heritability estimated under the animal model analysis was 0.18 ± 0.12 for shell height, 0.25 ± 0.16 for shell length, 0.10 ± 0.09 for shell width, 0.42 ± 0.20 for total weight, 0.32 ± 0.18 for shell weight, and 0.68 ± 0.16 for L^*, 0.69 ± 0.16 for shell pigmentation, respectively. The considerable additive genetic variation in growth and shell color traits will make it feasible to produce genetic improvements forrr-188eb(ge)27(ai)18(ts)-261(an-18()-342(a)-14(ees)11(g)21(co)19(nv-188ege)27(bv)16(ee)19(ti)17(7(10)21(ov)16(eg)

Evans et al. (2009) used digital image analysis calculating optical density to determine the shell pigmentation and recently, Wan et al. (2017) applied computer vision system (CVS) employing $L^*a^*b^*$ color system to evaluate shell color-related traits. These truly continuous measurements outweigh hazily defining it as "lighter" or "darker" through unaided eyes and individual perceptions. The CIE $L^*a^*b^*$ color space is suggested as the suitable color space for quantification in foods with curved surfaces, less affecting by the degree of curvature, shadows and glossiness (Mendoza et al. 2006). In view of these strengths, it has great potential to be applied in color measurement of rugged surface, like oyster shell, however, limited researches have been carried out. Gu et al. (2014) applied $L^*a^*b^*$ color space to evaluate the nacre coloration of pearls and shells of donor and host oysters of *Pinctada martensii*. Both of the digital image analysis and CVS mentioned above quantify shell color by analyzing photo of samples, but apply different color measure indexes. Currently, there was no research performed to compare these different indexes for color quantification.

In selective breeding, the target traits possess heritable genetic variation is essential to favorably respond to selection. Reliable estimates of genetic parameters (heritability and correlation) can provide guidance to make reasonable decisions regarding design and implementation of breeding plans (Wang et al. 2006). Traditionally, heritability is calculated by comparing families grown in separate tanks, in which the number of families is restricted by space- and labor-intensive, hence, limited the conclusions that can be drawn from it (Lucas et al. 2006). An alternative is to raise families communally, which is becoming widely used for aquatic species (Fu et al. 2016; Kong et al. 2015; Nguyen et al. 2014). This greatly reduces cost of rearing and avoids confounding effects of environment which allows better separation of non-addictive variation from the overall variation components (Dupont-Nivet et al. 2002; Vandeputte et al. 2001; Vandeputte et al. 2004).

In our selective breeding practice of Pacific oyster, we established black shell color strain through four-generation of successive selective breeding. The work presented here estimated heritability for growth and shell color traits and their correlations in the black shell strain of *C. gigas* at harvest (24 months of age). These scientific data can be used to design and optimize a selective breeding scheme for not only fast growth but true-breeding dark-shelled strain of this species.

Materials and Methods

Spawning and Rearing

In 2010, 2-year-old Pacific oysters with relatively dark shell color from wild population in Rushan, Shandong Province, China (36.5° N, 121.4° E), were collected to establish the first family selection line (F_1). Targeting at fixing the black shell trait, four generations of successive family selection were implemented. In May 2014, oysters from six families with darker shell individuals in F_4 generation were taken as the broodstock in this study. A nested mating design including 30 dams and 10 sires was employed to reproduce 30 full-sib families of black shell color strain of *C. gigas*, in which each sire mated with three corresponding dams elaborately. Fertilized eggs were hatched and reared in separate containers, with even volume and concentration among each family, until 24 h post fertilization. Approximately equal numbers of competent D-shaped larvae from each family were mixed and added to a 500-L bucket. For all sires and dams, the adductor muscle was collected and kept in 95% ethanol for subsequent DNA extraction.

The rearing of larvae, spat and adults was carried out with standard practices as per Li et al. (2011). Veligers were fed with daily rations of *Isochrysis galbana* at early stage (shell length < 120 μm) and *Platymonas* sp., and *Chlorella vulgaris* were supplemented at later stage. When eyed larvae were observed, spat collectors made of cleaned scallop shells were placed in the bucket. After metamorphosed, the cultch with about 15–20 spats per scallop shell were kept in the concrete tanks until they reached 500–600 μm. Then, the settlement substrates with spats were not deployed to sea area immediately but transferred to an outdoor sedimentation tank temporarily in order to circumvent the settlement of wild larvae. The spats reached 2–3 mm in shell height after about 40 days, then were transported to Rushan Bay in Yellow Sea, Shandong province. The settlement substrates were placed on nylon ropes and suspended from rafts along the coastal regions. Spats were separated to lantern net after grew up to 3–4 cm in shell height, and reloaded regularly being adjusted to appropriate rearing density with growing up.

Sampling and Trait Measuring

After 24 months, 432 cultured offspring were harvested in May 2016 from the same water depth randomly and shipped to laboratory. After brushed with caution to remove mud and attachments, their shell height, shell length and shell width were measured using an electronic vernier caliper at 0.01 mm accuracy, while total weight and shell weight weighed using an electronic balance at 0.01 g accuracy. Adductor muscle of all offspring was taken and stored in 95% ethanol for subsequent DNA extraction. Immediately following shucking, the left shells were processed with procedures below to quantify color more accurately. Referring to Sturm et al. (2006) and Evans et al. (2009), shells were immersed in 5% sodium hypochlorite solution for 2 h to remove biotic and abiotic fouling like encrustations and adhered algae. After rinsed thoroughly, the whole surface of left shells were given a thin coating of mineral oil against dulling and fading.

The simplified CVS consisting of digital camera, computer, and graphics software were applied (Yam and Papadakis 2004). Two daylight lamps with a color temperature of 6500 K were situated with a distance of 50 cm between them and 20 cm above samples to provide uniform and consistent illumination in a dark room. Nikon D80 digital camera (Nikon Corporation) with 10 M-pixels of resolution was placed vertically 30 cm above samples. The angle between the camera lens axis and the lighting source axis was around 45°. As standard capture conditions, camera settings were as follows: manual mode with the lens aperture at f5.6 and speed 1/20 s, automatic zoom, no flash, ISO = 200, storage in non-compressed file (NEF format). In addition, all images included a standard neutral gray card to ensure uniform exposure among photographs. The white balance of the camera was set using the gray card picture photographed in the same illumination. The camera was connected to the USB port of a computer provided with Camera Control Pro 2 (Nikon Corporation) to visualize and acquire the digitalized images directly from the computer screen. Photoshop CS6 (Adobe System Incorporated) was used to cutout the injured part and toughly attached fouling, and then obtained the raw lightness, a and b values from the Histogram Window. Cutout images were also analyzed using Image-Pro Plus v. 6.0.0.260 (Media Cybernetics Inc.) to determine the optical density so as to measure shell pigmentation (SP). Total shell pigmentation is defined as the overall lightness or darkness of the entire shell, due to variation in both pigmentation intensity and coverage, on a scale ranging from 0 (completely white) to 255 (completely black) (Evans et al. 2009).

Genotyping and Pedigree Reconstruction

Genomic DNA of each parent and offspring was extracted from adductor muscle by standard protocol of proteinase K digestion, phenol-chloroform extraction and DNA precipitation (Li et al. 2006). DNA was diluted to 100 ng/ml in 1× TE buffer and stored at − 20 °C until further analysis. Four panels of microsatellite multiplex PCR markers (Panel 1: ucdCg-120, ucdCg-198, and ucdCg-117; Panel 2: Crgi3, ucdCg-146, and uscCgi-210; Panel 4: otgfa0_0129_E11, Crgi4 and otgfa0_0007_B07; Panel 6: otgfa0_408293, otgfa0_0139_G12 and ucdCg-200) of *C. gigas* developed by Liu et al. (2017) were employed for pedigrees reconstruction, Two loci, otgfa0_0139_G12 in Panel 6 and Crgi4 in Panel 4, were eliminated because only two alleles were detected in all parents. PCRs were amplified in 10-μL volume as described, however, for each panel, forward and reverse primer concentration and annealing temperature were adjusted to equalize the peaks of fluorescence signal, so as to balance the amplification for each locus within each panel. Subsequent allele sizes were determined on capillary sequencer, ABI 3130 genetic analyzer (Applied Biosystems), with GeneScan LIZ 500 (Applied Biosystems) as internal size standard, and genotyping was assessed automatically with GeneMapper software v. 4.0 (Applied Biosystems). We recovered pedigrees by Vitassign (Vandeputte et al. 2006), an exclusion-based parentage assignment software, allowing up to 2 alleles mismatches as Vitassign is very sensitive to genotyping errors. Any individual failed in parentage assignment was excluded from subsequent analyses. A chi-squared test was performed to evaluate the equity of survival of progeny from sires and dams assuming contributions from each dam and sire to be equal respectively.

Data and Genetic Parameter Analysis

The *L*a*b** model is an international standard for color measurement developed by the Commission Internationale d'Eclairage (CIE) in 1976. The *L** corresponds to the degree of luminance or lightness ranging from 0 (black) to 100 (white), *a** and *b** are the two chromatic components range from − 120 to 120, in which *a** represents green (negative values) and red (positive values); *b** represents blue (negative values) and yellow (positive values). The lightness, a, and b values obtained in Photoshop were not standard color values and should be converted to *L*, a** and *b** values using the following formulas (Yam and Papadakis 2004):

$$L^* = \frac{\text{Lightness}}{255} \times 100$$

$$a^* = \frac{240\text{a}}{255} - 120$$

$$b^* = \frac{240\text{b}}{255} - 120$$

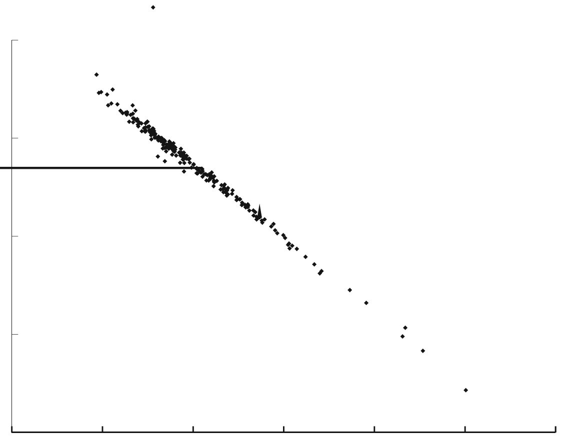
As the shell color of black strain of *C. gigas* is mainly reflected in *L** value in *L*a*b** color system, the Spearman correlation test was implemented in SPSS Statistics 19 (IBM Corporation) to evaluate the consistency and comparability of *L** and SP (shell pigmentation). Preliminary statistical analyses of data for all traits were completed using SPSS. All data were tested for normality (Kolmogorov-Smirnov test) and homogeneity of variances, and abnormal data were nature log transformed (e.g., *L**) or square root transformed (e.g., shell width) before being used to calculate the variance components.

The heritability, genetic and phenotypic correlations for shell color and growth traits were estimated using linear mixed models in ASReml 3.0 software (Gilmour et al. 2009). For each trait, two animal models (Wilson et al. 2010) were implemented using Restricted Maximum Likelihood (REML) algorithm as follows:

$$y_{ij} = \mu + \alpha_{ij} + c_j + e_{ij} \quad \text{(model 1)}$$

$$y_{ij} = \mu + \alpha_i + e_{ij} \quad \text{(model 2)}$$

In model 1, observation y from sire i, dam j was predicted from the additive genetic effects for the ijth animal (α_{ij}), the random effect common to full-sibs (a combination of maternal, environmental and partially dominant effects) (c_j) and the residual error (e_{ij}). The μ is the overall mean for the specific trait. All families in this study were pooled together as soon as hatching and then raised communally for 24 months, total of 22 full-sib families including 10 paternal half-sib families were represented in the 410 offspring samples with a mean of 18.6 descendents per family (ranging between 1 and 143) (Table 1). Sire 1 × dam 5 had a very remarkable offspring contribution (more than seven times the average); however, there was still representation distortion when they were removed. Chi-squared tests indicated that survival was significantly affected by dam (chi-square = 583.34, df = 28, $P < 0.001$) and by sire (chi-square = 243.5, df = 8, $P < 0.001$) after dam 5 and sire 1 were removed, respectively.



Descriptive Statistics of Traits

The unadjusted means, standard deviations, skewness, kurtosis and coefficients of variation (CV) for growth and shell color traits are listed in Table 2. For growth-related traits, the average shell height at harvest (24 months) was about 95.01 mm, corresponding to a total weight of 86.74 g. For shell color-related traits, the L^* had an average of 19.87 while SP had a mean value of 201.95. Figure 1 demonstrated three typical individuals of black shell strain whose "degree of black" is under, close to, and above the average degree, respectively. L^* and SP were compared by the Spearman correlation test and result showed that these two values were highly and negatively correlated ($r = -0.992$, $P < 0.001$) (Fig. 2). L^* ranged from 0 (black) to 100 (white), while SP (shell pigmentation) ranged from 0 (white) to 255 (black). The high and negative correlation between L^* and SP suggests the consistency of these two measurement indexes for quantifying shell color.

Heritabilities and Correlations

The heritability estimates from animal model (model 2) for all traits and their genetic and phenotypic correlations are presented in Table 3. Heritability estimates were significantly different from zero for all shell color traits and TW, and heritability of all traits fell in the 0.10–0.69 range. For growth traits, weight-related traits (TW and SWe) gave higher heritability than that of shell size-related traits (SH, SL and SWi), in which total weight was the highest (0.42 ± 0.20), whereas shell width was the lowest (0.10 ± 0.09). All shell color traits were highly heritable ranging from 0.52 to 0.69.

Genetic and phenotypic correlations among growth-related traits were all positive, with medium-high values (0.55–0.99) for genetic correlations. Both genetic and phenotypic correlations between total weight and shell weight were the highest. For color-related traits, correlations among L^*, a^* and b^* were all positive, while correlation between SP and a^* or b^* was negative. Since the L^* and SP both measure the shell darkness trait, the correlations between these two indexes were not calculated. Genetic correlations between SP and growth-related traits were all medium-high but negative (from − 0.78 to − 0.38), which were in consistent with the medium-high and positive genetic correlations between L^* and growth-related traits (from 0.32 to 0.73). The phenotypic correlations among

Table 2 Descriptive statistics of growth and shell color traits of black shell strain of *C. gigas*

Trait	*N*	Mean value	Standard deviation	Skewness	Kurtosis	CV (%)
SH/mm	410	95.01	12.57	0.17	−0.20	13.23
SL/mm	410	57.77	7.47	0.20	2.44	12.93
SWi/mm	410	31.23	5.65	0.51	1.28	18.08
TW/g	410	86.74	22.77	0.41	−0.18	26.25
SWe/g	410	59.40	17.63	0.59	0.53	29.69
L^*	402	19.87	6.47	1.38	2.71	32.55
a^*	402	−0.69	0.95	0.67	−0.04	136.95
b^*	402	−4.97	1.90	1.18	3.72	38.28
SP	402	201.95	14.43	−1.39	2.88	7.14

N number of samples, *SH* shell height, *SL* shell length, *SWi* shell width, *TW* total weight, *SWe* shell weight, *SP* shell pigmentation, *CV* coefficient of variation

Table 3 Genetic (in italics above the diagonal) and phenotypic (below the diagonal) correlations with heritabilities (in bold at the diagonal) for growth and shell color traits

	SH	SL	SWi	TW	SWe	*L**	*a**	*b**	SP
SH	**0.18 (0.12)**	*0.91 (0.27)*	*0.91 (0.12)*	*0.92 (0.09)*	*0.66 (0.12)*	*0.73 (0.11)*	*0.73 (0.28)*	*0.84 (0.25)*	*−0.78 (0.12)*
SL	0.24 (0.07)	**0.25 (0.16)**	*0.55 (0.37)*	*0.92 (0.09)*	*0.84 (0.16)*	*0.59 (0.34)*	*0.80 (0.18)*	*0.84 (0.19)*	*−0.68 (0.39)*
SWi	0.14 (0.05)	0.39 (0.05)	**0.10 (0.09)**	*0.94 (0.16)*	*0.90 (0.18)*	*0.52 (0.23)*	*0.85 (0.22)*	*0.86 (0.22)*	*−0.56 (0.21)*
TW	0.66 (0.04)	0.54 (0.06)	0.55 (0.04)	**0.42 (0.20)**	*0.99 (0.01)*	*0.32 (0.23)*	*0.90 (0.10)*	*0.91 (0.11)*	*−0.38 (0.19)*
SWe	0.58 (0.04)	0.53 (0.05)	0.54 (0.04)	0.92 (0.01)	**0.32 (0.18)**	*0.39 (0.25)*	*0.88 (0.12)*	*0.88 (0.12)*	*−0.44 (0.21)*
*L**	0.15 (0.07)	0.06 (0.08)	0.10 (0.07)	0.15 (0.09)	0.16 (0.08)	**0.68 (0.16)**	*0.56 (0.23)*	*0.58 (0.21)*	-
*a**	0.19 (0.09)	0.08 (0.06)	0.14 (0.07)	0.27 (0.10)	0.25 (0.10)	0.32 (0.10)	**0.65 (0.22)**	*0.98 (0.03)*	*−0.58 (0.24)*
*b**	0.08 (0.09)	0.04 (0.06)	0.14 (0.09)	0.20 (0.11)	0.16 (0.11)	0.30 (0.09)	0.76 (0.04)	**0.52 (0.20)**	*−0.57 (0.25)*
SP	−0.15 (0.07)	−0.09 (0.08)	−0.10 (0.07)	−0.17 (0.09)	−0.18 (0.08)	-	−0.33 (0.10)	−0.35 (0.09)	**0.69 (0.16)**

Trait abbreviations given in Table 2

Standard errors in parentheses

all traits were generally consistent in sign with corresponding genetic correlations but had a lower magnitude.

Discussion

Communal rearing allows precise genetic parameter estimation in breeding programs but relies on accurate inference of pedigree information. Microsatellite marker has made the reconstruction of pedigrees possible and has been extensively employed to clarify relations among offspring (Liu and Cordes 2004; Yue and Xia 2014). The use of multiplex PCRs can minimize errors and counterbalances genotyping costs (Navarro et al. 2009). In addition to 3-microsatellite multiplex assay used here, the introducing of dye-labeled primer M13(−21) circumvents labeling every primer with fluorescent dyes further decreases the cost of genotyping (Schuelke 2000). The four panels of multiplex PCRs containing 10 microsatellites used in this experiment yielded unambiguous parentage assignment for 94.9% of the 432 progeny assayed. As occurred in other aquatic species, missing genotyping, genotype and human errors are quite common in parentage assignment practice (Fu et al. 2016; Lucas et al. 2006; Vandeputte et al. 2011), which caused ambiguous or unsuccessful assignment in this study.

In aquaculture breeding schemes, distortion family representations is pervasively observed in many mass-spawning species (Li et al. 2013; Lucas et al. 2006), which may result in higher rates of inbreeding in long-term selection due to a gradual decline of effective population size (Kong et al. 2015). In this study, approximately equal numbers of D-shaped larvae from each family were controlled when initiated communal cultivation, however, high variance in offspring survival was also occurred. Thus, the monitoring of genealogy and genetic information using molecular markers would be essential in artificial breeding (Fu et al. 2016).

The principal objectives of the present study were to learn if growth-related and shell color-related traits of black shell stain of Pacific oyster can be improved by genetic selection, and further, synchronously improved. Under the animal model analysis, moderate-high additive genetic variance for growth and shell color traits (except shell width) at harvest were obtained in our study, indicating the genetic improvements are prone to be achievable.

A number of studies have been performed to estimate heritability of growth rate in *C. gigas*. Our results revealed that heritability was the highest for total weight (0.42 ± 0.20). Evans and Langdon (2006a, b) estimated the heritability of body weight at harvest in two studies to be 0.003 to 0.313 and 0.471 to 0.569, respectively. The heritability of shell height (0.18 ± 0.12) obtained here was in keeping with the estimates from Li et al. (2011) but lower than that obtained by Kong et al. (2015). In addition, we found the shell width at a rather low heritability level (0.10 ± 0.09) and were in consistent with the results from Park et al. (2009). It is noticeable that both the broodstock population and the growing environments will generate different heritability estimates (Falconer and Mackay 1996). In general, most researches demonstrated moderate-to-high heritability for growth traits of *C. gigas*, which also found in this study, indicating high potential for selective breeding in black shell stain. However, a fly in the ointment is the relatively large standard errors associated with heritability estimates for growth traits, which may be caused by the low number of families and progenies left. Furthermore, the majority of genetic correlations among growth traits were near unity, suggesting that growth traits were closely genetically correlated hence can be improved simultaneously by only any one of them used in a selection scheme without requirement for taking different measurements.

As with previous researchers, we treated oyster shell color as a quantitative trait and evaluate it using two digitized indexes. The shell pigmentation (SP) measures variation in pigmentation intensity and coverage of the entire shell, while $L^*a^*b^*$ color system describes color in lightness, hue and saturation. The high and negative Spearman correlation coefficient ($r = -0.992$, $P < 0.001$) demonstrated the high consistency of the SP and L^* and their same efficacy in shell color measurements, at least in black shell color (Fig. 2). The $L^*a^*b^*$ is a perceptually uniform and device-independent color space providing consistent color regardless of the input or output device and very close to human perception of color (Mendoza et al. 2006). Besides, it has greater potential in chromatic body color measurement in aquatic animals due to its ability of depicting color with three values, especially those with rugged and uneven surface. Further evaluating other colors except black using these two indexes would help to better understand the relationship between SP and $L^*a^*b^*$ indexes. In this study, we have found shell color traits are highly heritable (0.52–0.69). Similarly, Evans et al. (2009) estimated broad-sense and narrow-sense heritability of total left-shell pigmentation in *C. gigas* as 0.91 ± 0.38 and 0.59 ± 0.19, respectively. Moreover, Ge et al. (2015a) identified three single-locus PCR-based markers linking to the gene controlling the shell background color for the Pacific oyster. All these results associated with our high shell color heritabilities here confirmed that shell color is under a high degree of genetic control and amenable to improve through selective breeding program.

Concerning shell color selection, knowledge about their genetic correlations with growth traits is essential to make suitable strategies to achieve optimal improvement in both growth and shell color. The genetic correlations of shell color were high but negative with growth in current study (Table 3). There are three chief reasons leading to correlation between characters, genetic causes of correlation, changes brought about by selection and natural selection (Falconer and Mackay 1996). The genetic cause of correlation is chiefly pleiotropy, which is simply the property of the genes that affects two or more characters, and sometimes linkage, which is a cause of transient correlation particularly in populations derived from crosses between divergent strains (Falconer and Mackay 1996). Moreover, the estimates of genetic and phenotypic correlations may differ with various rearing environments and different ages (Falconer and Mackay 1996). This study was limited to a single environment and single stage, where G × E interactions and variation between different stages cannot be evaluated; therefore, our results should be reassessed when animals are at different ages and applied to other environments.

Total weight was treated as a key economic parameter for production yield. And in this study, total weight was genetically correlated to all growth traits (0.90–0.94) with the highest heritability (0.42 ± 0.20). Notable is the fact that the genetic correlation of total weight was the lowest than that of other performance traits with shell color (0.32 with L^* and − 0.38 with SP), it thus implied that selection for increased harvest weight could result in favorable changes in other growth traits and impose least negative changes on shell color. In consideration of the these high but negative correlations, it would be feasible to take both total weight and shell color as target traits in black shell strain breeding programs to improve both types of traits jointly.

On the contrary, Wan et al. (2017) found genetic correlation between shell color-related and growth-related traits in the golden shell strain were generally inconspicuous ranging from − 0.02 to 0.11. It is likely to be explained by their different genetic basis of golden and black shell strain as indicated by Ge et al. (2015b), who found that in *C. gigas*, dark pigmentation (defined as foreground color) have different pattern with golden coloration (defined as background color). There were other authors reported positive genetic correlation between body traits and both cooked and uncooked body color in shrimp (Nguyen et al. 2014) and between flesh color and body traits in fish (Vieira et al. 2007). It may be derived by similar biological and metabolic pathways involved in the process of controlling color expressions in fish and shrimp, which however, are entirely different from the biological mechanism and processes of pigmentation in oysters. Further studies focusing on characterization of color-related genes by QTL or other molecular tools may help to better unravel the underlying inheritance patterns of shell color in this species (Ge et al. 2015a) and facilitate developing preferable breeding strategies of genetic improvement for shell color. Another option to efficiently improve shell color and growth simultaneously, from a practical perspective, is to use molecular information to assist genetic evaluations for combined selection for these negatively correlated traits. The incorporation of molecular information can be particularly advantageous for increasing selection response for economically important traits for which responses are low, due to unfavorable correlations with other characters which have higher heritability (Dekkers 2007).

Conclusion

This study is the first report to date on the quantitative genetic analysis of growth and shell color traits in black shell strain of *C. gigas*. The presence of additive genetic variation for these traits indicated the feasibility of improving them genetically through selective breeding and bringing about potential economic benefits to the oyster sector worldwide. There were different levels of negative genetic correlations between growth-related traits and shell color. This undesirable genetic relation must be taken into account when incorporating them into the breeding objectives simultaneously. For the purpose of developing not only fast growth but true-breeding black shell strain, we propose to take both total weight and shell color as joint objective traits in black shell strain genetic improvement plans. Another possible solution was to perform molecular marker-assisted selection.

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