Heritability estimates for growth-related traits in the Pacific oyster (

Hershberger (1991) estimated the narrow-sense heritability of meat weight in harvest body size to be approximately 0.20. Using a nested half-sib mating design, Ernande, Clobert, McCombie and Boudry (2003) estimated the narrow-sense heritability of larval growth rate to be 0.24, and Ernande, Boudry, Clobert and Haure (2004) found heritability of growth in 1-year-old Pacific oyster to differ under different grow-out conditions. 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, by analysing full-sib families. Dégremont, Ernande, Bédier and Boudry (2007) reported the heritability estimates for growth varied from 0.07 ± 0.07 to 0.15 ± 0.08 in 6- to 8-month-old *C.* . Li, Wang, Liu and Kong (2011) reported realized heritability of shell height to be 0.149 to 0.402, which resulted from one-generation mass selection in three stocks of the Pacific oyster.

Most of the researches showed moderate-to-high heritability of growth-related traits, which indicated high potential for selective breeding programme in *C.* . However, in these studies, heritability was calculated by comparing offspring grown in different tanks. The traditional approach not only was space and labour intensive but also introduced additional environmental variation which could lead to imprecise estimation of heritability and slow genetic improvement (Wang, Lo, Zhu, Lin, Feng, Li, Yang, Tan, Chou & Lim 2008).

An alternative is communal rearing of families with a reconstruction of pedigrees using highly polymorphic DNA markers (Dupont-Nivet, Vandeputte, Vergnet, Merdy, Haffray, Chavanne & Chatain 2008). The main advantages of this method are the absence of between-families environmental effects, and the possibility to use full-factorial design which allows greater separation of additive, maternal and dominance components of variation (Vandeputte, Dupont-Nivet, Chatain & Chevassus 2001).

In this work, we firstly estimated genetic parameters (heritability and correlations) for *C.* at 12 months of age by applying mixed-family approach combined with a full-factorial design.

Materials and methods

Broodstock and spawning

The broodstock of 2-year-old *C.* was collected from Shuangdao Bay and maintained at Beihai Hatchery, Shandong Province, China. A full-factorial design, where five dams were crossed with nine sires, was employed to produce progeny. Eggs and sperm were obtained by stripping from each broodstock. A suspension of eggs from each dam was divided into nine equal portions and fertilized separately by sperm from each of the nine sires, before being rinsed and pooled together for larval culturing. We appropriately increased the sperm concentration to ensure all viable eggs fertilized and kept the volume of egg suspension even between fertilizations. One male broodstock (sire 9) fertilized a substantially lower number of eggs than the other sires. From each of the parents used in the cross, adductor muscle was collected and stored in 70% ethanol for DNA analysis.

Rearing of experimental oyster

Eggs from the five dams were hatched in separate containers until 24 h post fertilization. Approximately equal numbers of competent D-shaped larvae from sires 1–8 were added to all of the available larvae from sire 9, and these were mixed in a 500 L plastic bucket. The rearing of the larvae, spat and adults was carried out using standard practices. Stocking densities were initially set to about 15 larvae mL^{-1}, and decreased with larval growth. Water temperature was maintained at 23–24°C, with salinity at 30 psu. Water change was made at 50% twice every day and 100% every 10 days. Veligers were supplied with daily rations of *I* , , at early stage (shell length <120 μm), and *P* , and *C* , , , were supplemented at later stage. When eye spots developed, strings of scallop shells were placed in the bucket as settlement substrate. After 5 days, all eyed larvae metamorphosed to spat and then transferred to an outdoor nursery tank. After 30 days, spat were inserted into nylon ropes randomly and deployed to grow-out areas in Shuangdao Bay, Shandong Province. The density was about 15–20 spat per shell.

Sampling and growth measurement

At 12 months of age, 300 cultured offsprings were chosen from the same water depth in a random manner. Shell height, shell length and shell width of each oyster were measured using an electronic vernier calliper (0.01 mm accuracy), and wet weight was measured using an electronic balance

(0.1 g accuracy). Adductor muscle of each individual was taken and stored in 70% ethanol for DNA analysis.

Parentage assignment

DNA was extracted from each broodstock and progeny following Li . (2006). Six microsatellite markers: *C 129*, *C 134*, *C 148*, *C 149*, *C 160* and *C 196* (Li, Hubert, Bucklin, Ribes & Hedgecock 2003) were selected for genotyping based on their heterozygosity and genotyping reliability. Amplification products were resolved via 6% denaturing polyacrylamide gel and visualized by silver staining. A 10-bp DNA ladder (Invitrogen, Carlsbad, CA, USA) was used as a reference marker for allele size determination. To avoid inaccuracy in scoring because of the differences in gels, two control DNA samples were included in each set of samples for each gel. Parentage assignment was determined using the likelihood-based approach with CERVUS 3.0 (Kalinowski, Taper & Marshall 2007). Any individual whose full parentage was unclear was excluded from subsequent analyses. A total of 270 of 300 sampled progeny were available for parentage assignment.

Data analyses

The polymorphic information content (PIC) and two exclusion power (Excl 1, Excl 2) for every locus were calculated with CERVUS 3.0. Parentage analysis was conducted using the likelihood-based approach in CERVUS. The critical Δscore (defined as the difference in log likelihood ratios between the two most-likely parents) calculated by the simulation module was used to assign the offspring to the most-likely candidate parent. The parameters for this simulation run were as follows: 10 000 replication cycles, 5 candidate mothers and 9 candidate fathers, 100% of the candidate parents sampled and genotyped and a default typing error rate of 1% was used. Cumulative assignment success was evaluated based on broodstock and offspring genotypes by adding loci from the most informative to the least one according to their PIC values. Levels of genetic variation for broodstock and offspring populations were assessed, as the number of alleles per locus, expected heterozygosity (H) and observed heterozygosity (H) using CERVUS 3.0. Significance was tested using the Wilcoxon matched pairs test implemented with SPSS 16.0 software (SPSS, Chicago, IL, USA).

The effective population size was first calculated for unequal sex ratio after Crow and Kimura (1970) as: $N = 4\ N\ N/(N\ + N)$, where N and N are actual number of sires and dams. Then the N was recalculated based on the differences in reproductive success of individuals, where N and N are the effective number of sires and dams respectively. N and N were estimated following Lande and Barrowclough (1987): $N = (N - 1)/[+ (\sigma^2 /) - 1]$, where N is the actual number of sires, is the average number of offspring produced by an individual sire and σ^2 is the variance of . The same formula was used to compute the effective number of dams.

A chi-squared test was performed to evaluate the equity of survival of progeny from sires and dams assuming contributions from each broodstock to be equal (sire 9 was excluded from this analysis due to its substantially lower fertilization rate). All data of growth-related traits were tested for normality and homogeneity of variances, and then analysed using univariate animal model implemented in ASREML (Gilmour, Gogel, Cullis, Welham & Thomson 2002) to estimate heritability for shell height, shell length, shell width and wet weight. To evaluate variance components, the following animal model was applied:

$$= \mu + A + C + I +$$

Observation from sire , dam and animal within sire and dam was predicted from the random genetic effect of the th animal (A), the random common environment effect C of the th dam (C), the interaction of the th sire and the th dam (I) and the residual error ( ). As the C was not different from zero, the model was simplified as:

$$= \mu + A + I +$$

Genetic and phenotypic correlations were calculated between shell height, shell length, shell width and wet weight using bivariate model in ASREML.

Results

Polymorphism information of microsatellite markers

Summary statistics for the six markers used in the sampled population are given in Table 1. The allele number of these loci ranged from 11 to 14

Table 1 Numbers of alleles (k), polymorphic information content (PIC) and probabilities of exclusion based either on genotype of no parent known (Excl 1) or one parent known (Excl 2) for the six microsatellite loci analysed in this work

Locus	k	PIC	Excl 1	Excl 2
ucdCg148	14	0.859	0.591	0.744
ucdCg160	12	0.884	0.644	0.785
ucdCg129	11	0.856	0.584	0.739
ucdCg196	14	0.897	0.678	0.809
ucdCg149	14	0.861	0.597	0.749
ucdCg134	11	0.861	0.594	0.747
Average	12.7	0.870	0.615	0.762

with an average of 12.7 and the mean PIC of 0.870. Probabilities of exclusion per locus ranged from 0.584 to 0.678 when only information of offspring was available (Excl 1) and from 0.739 to 0.809 when one parent was known (Excl 2).

Combined assignment success of the six loci was calculated by adding loci from the most to the least PIC one (Fig. 1). Figure 1 showed that the assignment success of 10 000 simulated offspring to their 14 hypothetical parents would be over 90% if the loci were up to 5. In a strict level of 95% confidence interval, the 270 progeny would all be unambiguously assigned if the loci were up to 6.

Parentage assignment and genetic variability

The 270 progeny available for parentage assignment were all successfully assigned to 42 of the 45 possible families (Table 2). The recovered individuals were not evenly distributed to each family. Chi-squared tests indicated that survival of progeny was significantly affected by sire (chi-square = 93.42, d.f. = 7, $P < 0.001$) and by dam (chi-square = 60.33, d.f. = 4, $P < 0.001$).

Number of alleles per locus, alleles range and expected and observed heterozygosity of each locus at six microsatellite loci in broodstock and offspring is shown in Table 3. The number of alleles for all loci in offspring was in accordance with that in broodstock, which indicated that there was no allele missing in offspring. The observed heterozygosity exhibited a little increase in the offspring population, but no significant differences were presented ($P = 0.057$). However, the expected heterozygosity of the offspring was significantly lower than that of the parental oysters ($P = 0.004$).

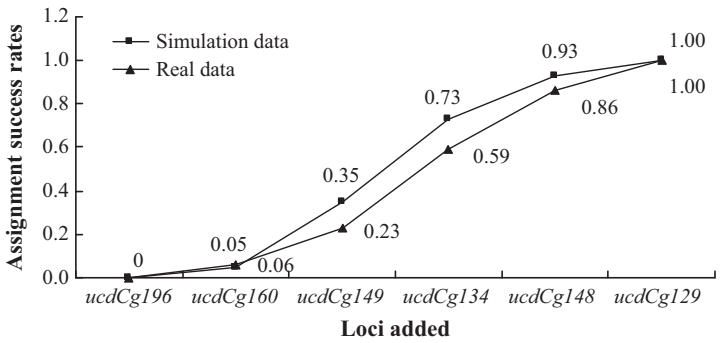


Figure 1 Cumulative assignment success rates by CERVUS 3.0 of 10 000 simulated offsprings to their 14 hypothetical candidate parents and real genotype data sampled in a strict level of 95% confidence interval, adding loci from the most to the least polymorphic information content one.

Table 2 Number of progeny assigned to each of the 45 crosses based on microsatellite genotyping

	Sire 1	Sire 2	Sire 3	Sire 4	Sire 5	Sire 6	Sire 7	Sire 8	Sire 9	Total
Dam 1	3	3	5	2	36	7	6	2	1	65
Dam 2	4	3	5	3	1	2	4	1	2	25
Dam 3	4	9	3	10	14	6	6	3	0	55
Dam 4	2	2	1	2	13	3	3	4	0	30
Dam 5	8	31	9	5	15	12	12	3	0	95
Total	21	48	23	22	79	30	31	13	3	270

Table 3 Genetic variability in the broodstock and offspring of Pacific oyster *C*

Population	Locus						Mean
	ucdCg148	*ucdCg160*	*ucdCg129*	*ucdCg196*	*ucdCg149*	*ucdCg134*	
Broodstock							
Sample size	14	14	14	14	14	14	
Alleles range (bp)	198–284	220–290	215–285	200–300	200–300	205–250	
No. of alleles	14	12	11	14	14	11	12.67
Expected heterozygosity	0.939	0.913	0.899	0.939	0.913	0.902	0.918
Observed heterozygosity	0.857	0.357	0.571	0.929	0.786	0.786	0.714
Offspring							
Sample size	249	244	260	264	251	268	
Alleles range (bp)	198–284	220–290	215–285	200–300	200–300	205–250	
No. of alleles	14	12	11	14	14	11	12.67
Expected heterozygosity	0.870	0.894	0.869	0.906	0.873	0.875	0.881
Observed heterozygosity	0.932	0.893	0.919	0.939	0.904	0.907	0.916

Growth performances and effective population size

Based on the pedigree information, we evaluated the growth performance of each family and calculated the effective population size. Growth performances in terms of shell height, shell length, shell width and wet weight of the 42 full-sib families at 12 months of age are shown in Fig. 2. The full-sib family produced by sire 2 and dam 5 has the largest average shell height of 8.80 mm, whereas the family produced by sire 4 and dam 2 has the heaviest average wet weight of 92.1 g.

The effective population size calculated for unequal sex ratio of this mass-spawning event was 12.86, which diminished 8.14% of the absolute parents. When combined with variance in reproductive success of broodstock, the calculated *N* was 9.87, which accounted for another reduction of 21.36% of the absolute parents. The effective number of sires and dams are 6.55 and 3.96, respectively.

Genetic parameters

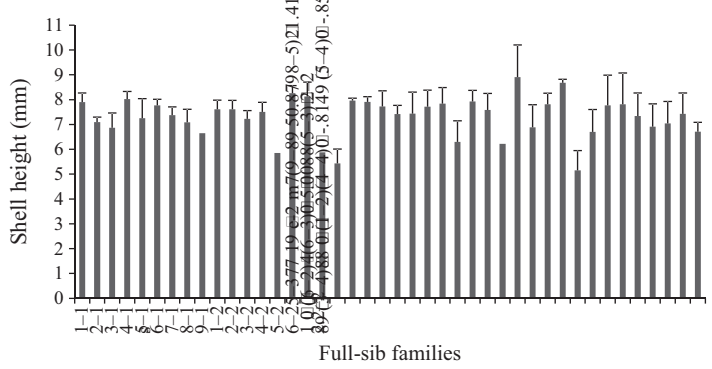
Genetic parameters for target traits are shown in Table 4. Heritability estimates were significantly different from zero for the four traits, and fell in the 0.3–0.5 range. Shell height gave the highest heritability, although shell length, shell width and wet weight were also highly heritable. Phenotypic and genetic correlations between the four traits were all positive, with low-medium values (0.31–0.50) for phenotypic correlations and medium–high values (0.55–0.86) for genetic correlations. The genetic correlation between shell height and shell length was the highest, whereas their phenotypic correlation was lower than the others.

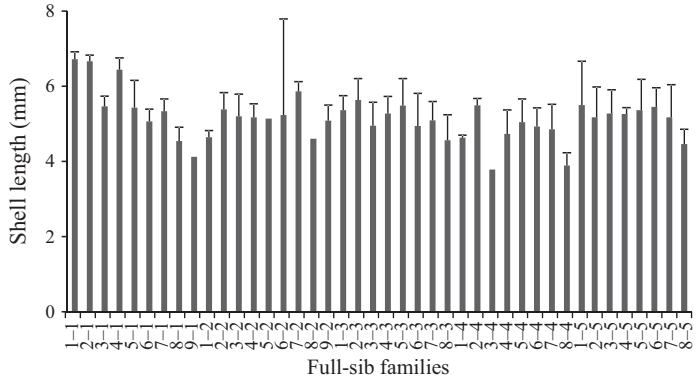
Discussion

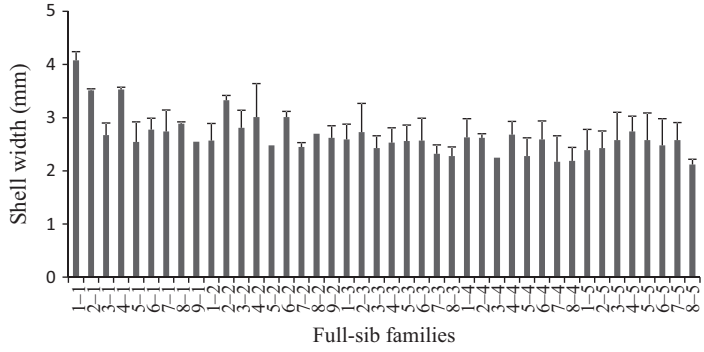
Microsatellite-based parentage assignment

Microsatellite-based traceability methods, which eliminated the need for separate rearing of full- or half-sib families that can introduce environmental effects, have been proved very effective in accurately acquiring pedigree information in many aquatic species (Estoup, Gharbi, SanCristobal, Chevalet, Haffray & Guyomard 1998; Waldbieser & Wolters 1999; Liu & Cordes 2004; Dong, Kong, Zhang, Meng & Wang 2006; Hatanaka, Yamada, Sakamoto & Mitsuboshi 2006). The six polymorphic microsatellites used in this experiment yielded unambiguous parentage assignment for 100% of the 270 progeny assayed. The same assignment efficiency was also obtained by Li, Li and Yu (2009) when dealing with D-larvae of the Pacific oyster.

The correct inference of genealogy is essential for genetic parameter estimates (Dodds, Tate & Sise 2005), especially in mass-spawning species where the contribution of breeders is unknown. Factors affecting the resolution power of microsatellite sets include: number and polymorphisms of markers, null allele frequency, number of breeders contributing to spawning, the increase in homozygosity and genotyping errors (Navarro, Zamorano, Hildebrandt, Ginés, Aguilera & Afonso 2009). Although the panel of six markers used in our work provided high assignment rate, the assignment success


Shell height (mm)
Full-sib families


Shell length (mm)
Full-sib families


Shell width (mm)
Full-sib families

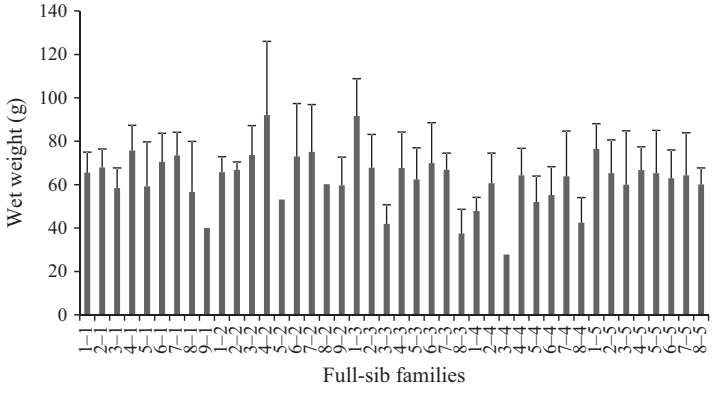

Wet weight (g)
Full-sib families

Table 4 Phenotypic (above diagonal) and genetic correlations (below diagonal) with heritabilities in the diagonal

	Shell height	Shell length	Shell width	Wet weight
Shell height	0.49 ± 0.25	0.31 ± 0.10	0.33 ± 0.10	0.35 ± 0.08
Shell length	0.86 ± 0.18	0.36 ± 0.19	0.41 ± 0.08	0.50 ± 0.06
Shell width	0.55 ± 0.33	0.82 ± 0.17	0.45 ± 0.23	0.37 ± 0.08
Wet weight	0.79 ± 0.25	0.82 ± 0.17	0.61 ± 0.29	0.35 ± 0.17

might be reduced if the number of potential families or parents increased considerably. Therefore, more polymorphic and informative markers would be required for a greater number of parents (Gheyas, Woolliams, Taggart, Sattar, Das, McAndrew & Penman 2009).

Survival, effective population size and genetic variability

The overall survival rate of mixed families from D-shaped larvae to sampling stage was about 3%. Despite the standardization of larvae numbers across sires 1–8 (sire 9 had low numbers from the beginning), the number of individuals retrieved after 12 months was not evenly distributed among families (Table 2). Differential survival observed here was consistent with that seen in other studies (Boudry, Collet, Cornette, Hervouet & Bonhomme 2002; Vandeputte, Kocour, Mauger, Dupont-Nivet, De Guerry, Rodina, Gela, Vallod, Chevassus & Linhart 2004; Lucas, Macbeth, Degnan, Knibb & Degnan 2006). Chi-squared tests indicated that both sire and dam affected survival of progeny. Therefore, besides sampling errors, parent-related factors such as quality of gametes, larval competitiveness and viability can be proposed to explain differential survival.

High variance in offspring survival is very prevalent in marine organisms, which would result in a decline in effective population size (Hedgecock 1994; Frankham 1995; Boudry . 2002; Vandeputte . 2004; Lucas . 2006). As for the Pacific oyster, Boudry . (2002) showed a high variance in reproductive success even though the gametic contributions had been balanced, and Li . (2009) reported a reduction of 16.39% in effective population size caused by parental contributions variance. In this study, the high variance in offspring survival accounted to a decline of 21.36% in effective population size. Chi-squared tests indicated that both sire and dam affected the survival of progeny. Therefore, besides sampling errors and few progeny produced by sire 9, parent-related factors such as quality of gametes, larval competitiveness and viability can be proposed to explain the differential survival and a decline in effective population size.

Genetic variability was measured by allelic diversity and heterozygosity in this study. Except for a decrease in the expected heterozygosity, there were no significant changes in allelic diversity or observed heterozygosity in the offspring population. Our highly controlled breeding practice, which ensured that all parental oysters contribute to the next generation, made the genetic diversity of the original broodstock has the best chance of being represented in the offspring.

Genetic parameters and genotype × environment interactions

First of all, we would like to emphasize that due to the single cohort rearing of offspring from hatching, genetic parameters were not likely to be strongly biased by environmental effects (Kocour, Mauger, Rodina, Gela, Linhart & Vandeputte 2007). Using the same method, Vandeputte . (2004) obtained heritability estimates for common carp (*C* L.) of 0.33 for weight, 0.33 for length and 0.37 for Fulton's condition factor at 8 weeks of age. Gheyas . (2009) reported the heritability estimates for harvest weight and harvest length to be 0.67 and 0.51 respectively. Applying communal rearing of 84 families, Lucas . (2006) estimated heritability for growth in the tropical abalone *H* at 12 months of age ranging from 0.36 to 0.48.

In *C.* , our estimate is firstly obtained by applying mixed-family approach combined with a full-factorial design. In our study, heritability was the highest for shell height (0.49 ± 0.25). Recently, Li . (2011) reported realized heritability estimates for shell height resulting from mass selection ranged from 0.149 to 0.402 in *C.* at 12 months of age. In other oyster species,

heritability for shell height was 0.34 in the Chilean oyster *O* (Toro & Newkirk 1991); and was 0.11 at 6 months and 0.19 at 18 months in the European oyster *O* (Toro & Newkirk 1990). The heritability of wet weight (0.35 ± 0.17) fell in the usual range for the Pacific oyster (Lannan 1972; Hedgecock . 1991; Langdon . 2003; Ernande . 2004; Evans & Langdon 2006a,b) and was consistent with published heritability estimates for body weight in other oyster species (see review by Sheridan 1997). The moderate-to-high heritability (0.35–0.49) estimated in our study indicates that the growth-related traits are under a high degree of genetic control and a substantial fraction of selection differential would be expected to be gained through selective breeding programme (Wang, Ross, Saillant, Gatiln and Gold 2006).

Genetic correlations between the four traits were all positive, with values ranging from 0.55 to 0.86. The magnitude of genetic correlations is thought to generally reflect the extent to which the same genes are involved in expression of the traits (Falconer & Mackay 1996). A selective breeding programme would mainly be interested in weight improvement (Lucas . 2006), which is more closely related to market value than shell height. Because of the high genetic correlation between the two traits (0.79 ± 0.25), coupled with highest heritability for shell height, selection for increased wet weight can be performed on shell height, which is much easier to measure in the field on a large number of oysters.

Genotype × environment interactions are pervasive in cultured shellfish. Rawson and Hilbish (1991) found significant genotype × environment interactions on growth performance in hard clams (*M*). Langdon . (2003) indicated that yields of Pacific oyster families were significantly affected by G × E interactions ($P < 0.001$). A French study of Pacific oyster (Dégremont, Bedier, Soletchnick, Ropert, Huvet, Moal, Samain & Boudry 2005) reported significant G × E interactions on yield, accounting for 5.1% of the total phenotypic variation. Evans and Langdon (2006b) detected significant G × E interactions, which were not large enough to prevent selection in a limited number of environments from resulting in favourable gains in other environments. This study was limited to a single environment, where G × E interactions cannot be evaluated. The growth performances of studied families may differ if they were raised in different environment, which would result in different heritability estimates. Therefore, the applicability of our results should be reassessed when they are applied to other environments.

The strength of our work lies in estimating heritability excluding environmental effects. However, a fly in the ointment is the relatively large standard errors associated with heritability estimates, which may be caused by the low number of families and sampled progeny. Moreover, different experimental populations and growing environments will generate different heritability estimates (Falconer & Mackay 1996). Therefore, a selection experiment is recommended to validate the data obtained in our work.

In conclusion, this study further confirmed the potential of *C.* in aquaculture as a candidate for a selective breeding programme. In addition, heritability estimation by applying communal rearing of families with a reconstruction of pedigrees using microsatellite is proved to be feasible in the Pacific oyster.

Acknowledgments

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