



Short communication

Estimation of genetic parameters for female reproduction traits in the Pacific oyster, *Crassostrea gigas*

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ABSTRACT

The Pacific oyster (*Crassostrea gigas*) is one of the most important aquaculture species worldwide. Female reproduction traits are considered as the major factor for production efficiency. Estimating genetic parameters for female reproduction is a common method for formulating breeding program, which has not been evaluated in the Pacific oysters. Therefore, this study aimed to estimate the genetic parameters for female reproduction traits in Pacific oysters. Genetic parameters were performed on 44 full-sib Pacific oyster families, including 646 individuals from three cultured populations ("Haida No. 1" strain, South Korean population, and Japanese population) and a wild population. The heritability of female reproduction traits including relative brood amount and egg diameter ranged from 0.32 to 0.38, while the heritability of growth traits were in the range of 0.13–0.37, suggesting that both traits may benefit from successive selection breeding. The genetic and phenotypic correlations between female reproduction and growth traits were low at -0.44 to 0.33 , indicating that these traits were relatively independent traits that could be improved respectively. The four populations showed significant growth differences, whereas no significant difference was observed in female reproduction traits. This study represents the first report of genetic parameters for female reproduction in Pacific oysters, which suggests that these traits may be improved through selection breeding.

1. Introduction

Pacific oysters (*Crassostrea gigas*) are naturally distributed along the coast of northwest Asia (Troost, 2010). Owing to their rapid growth and high adaptability to various environmental conditions, the Pacific oyster has been introduced to >60 countries for aquaculture (Maria et al., 2002) and has become one of the most widely cultivated and commercially important shellfish worldwide (Mottier et al., 2013). To meet the increased demand for oysters, breeding programs have been conducted for genetic improvement over the last century (Melo et al., 2016). The main breeding methods, including selection, hybridization, and ploidy breeding, have been used to improve yield, growth rate, and disease resistance in the Pacific oyster (Dégremont et al., 2007; Wang et al., 2012; Azéma et al., 2017; Xu et al., 2017; Chi et al., 2021; Fang et al., 2021).

The larval stages of bivalves are often reported as most sensitive to environmental stress (His et al., 1999; Geffard et al., 2002; Mai et al., 2012). Female reproduction traits are crucial for larval production

(D'Ambrosio et al., 2020; Bestin et al., 2021; Song et al., 2022). Female reproduction traits include relative brood amount (RBA), egg diameter (ED), and egg weight, among others (D'Ambrosio et al., 2020; Bestin et al., 2021). RBA is an important index of all farmed aquatic animals, which is closely related to larvae survival rate (Caballero-Zamora et al., 2015). A large egg diameter can provide more nutrition, conferring low mortality during fertilization, hatching, and first feeding (Jones et al., 1992; Yong et al., 2004). The selection of high-performance spawners using traits associated with RBA and ED could be an important strategy to improve larval survival rate (Macbeth et al., 2007; Deekae and Abo-wei, 2010).

In breeding programs, genetic parameters are important indices (Liu et al., 2014; Fu et al., 2015). They are the basis for assessing genetic gains and are critical to create and optimize breeding programs. Heritability estimation can provide a better understanding of the impact of genetic factors on specific population traits (Fu et al., 2015). To date, selective breeding has been successfully conducted in many aquatic species to improve commercial traits (Lind et al., 2012), such as growth

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and survival in rohu carp (*Labeo rohita*) (Gjerde et al., 2019), growth and egg-related traits in Russian sturgeon (*Acipenser gueldenstaedtii*) (Song et al., 2022), growth and fillet traits in Asian seabass (*Lates calcarifer*, Bloch 1790) (Pattarapanyawong et al., 2021), growth traits and intermuscular bones in grass carp (*Ctenopharyngodon idella*) (Xiong et al., 2023). In the Mollusca, the heritability of some traits had been evaluated, such as productive traits in the Caribbean scallop, *Argopecten nucleus* (Mollusca: Bivalvia) (Barros et al., 2018), gonadal development traits in the Fujian oyster (*C. angulata*) (Han et al., 2022), ammonia resistance and growth-related traits in the razor clam (*Sinonovacula constricta*) (Xu et al., 2022), low salinity survival traits in the Eastern oyster (*C. virginica*) (Carty et al., 2020). The genetic parameters for growth traits and disease resistance traits have been studied vastly in the *C. gigas* (Appleyard et al., 2007; Kong et al., 2015; Gomes et al., 2018; Gutierrez et al., 2018; Vu et al., 2020; Chi et al., 2021; Fang et al., 2021; Zhai et al., 2021), while genetic parameter estimation for female reproduction traits remains unexplored.

The purpose of this study was to estimate the genetic parameters of growth and female reproduction traits involving 646 individuals from 44 full-sib families which were constructed using three populations with different genetic background after multigenetation of selection breeding and a wild population.

2. Methods

2.1. Generation of families

The initial generation of broodstock were from three cultured populations ("Haida No. 1" strain, South Korean population, and Japanese population) and a wild population. The cultured populations used in this experiment originated from selective populations underwent multigenerational selection and a wild population that was collected from Rushan, Shandong province, China (Zhang et al., 2019). The parental generation used in the experiment were 12 months old in ripe stage. The experiment was performed in a hatchery in Laizhou, Shandong Province, China. In the 2020 spawning season, mature eggs and sperm were harvested from the oysters. Mating experiments were performed following the process described by Li et al. (2011), and a total of 44 full-sib families were successfully established. Detailed information on the families is provided in Supplementary Table 1. During the larval stages, larvae were given *Isochrysis galbana*, the water temperature was 23–25 °C, the salinity was 30 psu. When the shell height (SH) of the spat reached 2–3 mm, all families were transferred to Rongcheng, Shandong province, China, for natural culture.

2.2. Sampling measurement

The 13 months old oysters in ripe stage were collected and cleaned before data measurement; we obtained three-twenty oysters from each family. The standard SH and shell length (SL) were measured at the maximum horizontal and vertical distance, respectively, using a Vernier caliper with a precision of 0.01 mm. The total weight (TW) and shell weight (SW) were measured using an analytical balance with a precision of 0.01 g. Body weight (BW) was calculated as the SW subtracted from the TW.

The sex of each oyster was determined by observing the gonad tissue with Olympus light microscope. Mature eggs were removed from the mature female oyster in ripe stage and collected separately in seawater in beakers. The tissue fragments and tissue fluid were removed by screening. Eggs were collected with a 25- μ m nylon screen and diluted in a beaker to achieve the same density. For each female oyster, ten eggs were measured, and average diameter for ten eggs was used. ED was evaluated for every egg by observed with a microscope. Egg number (EN) was evaluated by measuring the average number of three fields of view under microscope. The RBA was calculated as the EN divided by BW. All the measurements were performed in the same environment.

2.3. Statistical analyses

SL, SH, TW, BW, RBA and ED were analyzed using SPSS 20.0 software with family as a fixed factor. Data were assessed for normality and homogeneity of variances. The statistical significance was set as $P < 0.05$. The growth and female reproduction traits were analyzed by multiple comparisons Duncan's test using one-way ANOVA.

The heritability (h^2) and phenotypic (r_p) and genetic (r_g) correlations for female reproduction and growth traits were evaluated from linear mixed models using the ASReml software (3.0) (Gilmour and Gogel, 2009). The REML model was applied to each trait as follows:

$$y_i = \mu + a_i + d_j + e_i$$

In this model, observation y_i is the phenotypic trait of individual i ; μ , a_i , d_j and e_i represents the mean value of the trait, the additive effect for the animal, the common random effect (a combination of maternal and environmental effects from dam j), and the residual error, respectively. d_j was removed from the model because the logarithmic likelihood ratio test d_j was not significant for any of the traits. The reduced model was applied as follows:

$$y_i = \mu + a_i + e_i$$

In this model, all parameters were set as described above.

The heritability estimations of growth and female reproduction traits were calculated as:

$$h^2 = \sigma_a^2 / (\sigma_a^2 + \sigma_e^2)$$

where σ_a^2 is the additive genetic variance and σ_e^2 is the residual variance. The genetic correlation (r_g) between growth and female reproduction traits was calculated:

$r_g = \sigma_{a12} / \sqrt{\sigma_{a1}^2 \sigma_{a2}^2}$ where σ_{a12} was estimated as the additive genetic or phenotypic variance between the two traits; σ_{a1}^2 and σ_{a2}^2 are the additive genetic or phenotypic variances of two traits, respectively (Xing et al., 2018).

The phenotypic correlation formula is:

$r_p = (\sigma_{a12} + \sigma_{e12}) / \sqrt{(\sigma_{a1}^2 + \sigma_{e1}^2)(\sigma_{a2}^2 + \sigma_{e2}^2)}$ where σ_{e12} is the residual covariance between two traits, and σ_{e1}^2 and σ_{e2}^2 are the residual variances of two traits, respectively. The t -test was used to test the significance level.

3. Results

3.1. Descriptive statistics

A total of 646 female individuals were measured. The ED ranged from 43.16 to 62.93 μ m, and the average ED of the 646 oysters was 48.83 μ m (Table 1). The lowest mean ED was presented in family 0523–19, and the highest was in family 0523–07 (Fig. 1). The RBA ranged from 0.03 to 2.04 million/g with an average number of 0.60 million/g. The family with the highest mean RBA was family 0512–10,

Table 1
Descriptive statistics in 44 oyster families.

Trait	Number	Mean	SD	Min	Max	CV (%)
Egg diameter (ED, μ m)	646	48.83	2.48	43.16	62.93	5.08
Relative brood amount (RBA, million/g)	646	0.60	0.30	0.03	2.04	50.00
Body weight (BW, g)	646	13.01	3.26	2.99	30.49	25.06
Total weight (TW, g)	646	39.42	10.10	12.96	76.41	25.62
Shell height (SH, mm)	646	77.54	12.62	12.60	122.00	16.28
Shell length (SL, mm)	646	46.96	7.64	12.21	69.71	16.27

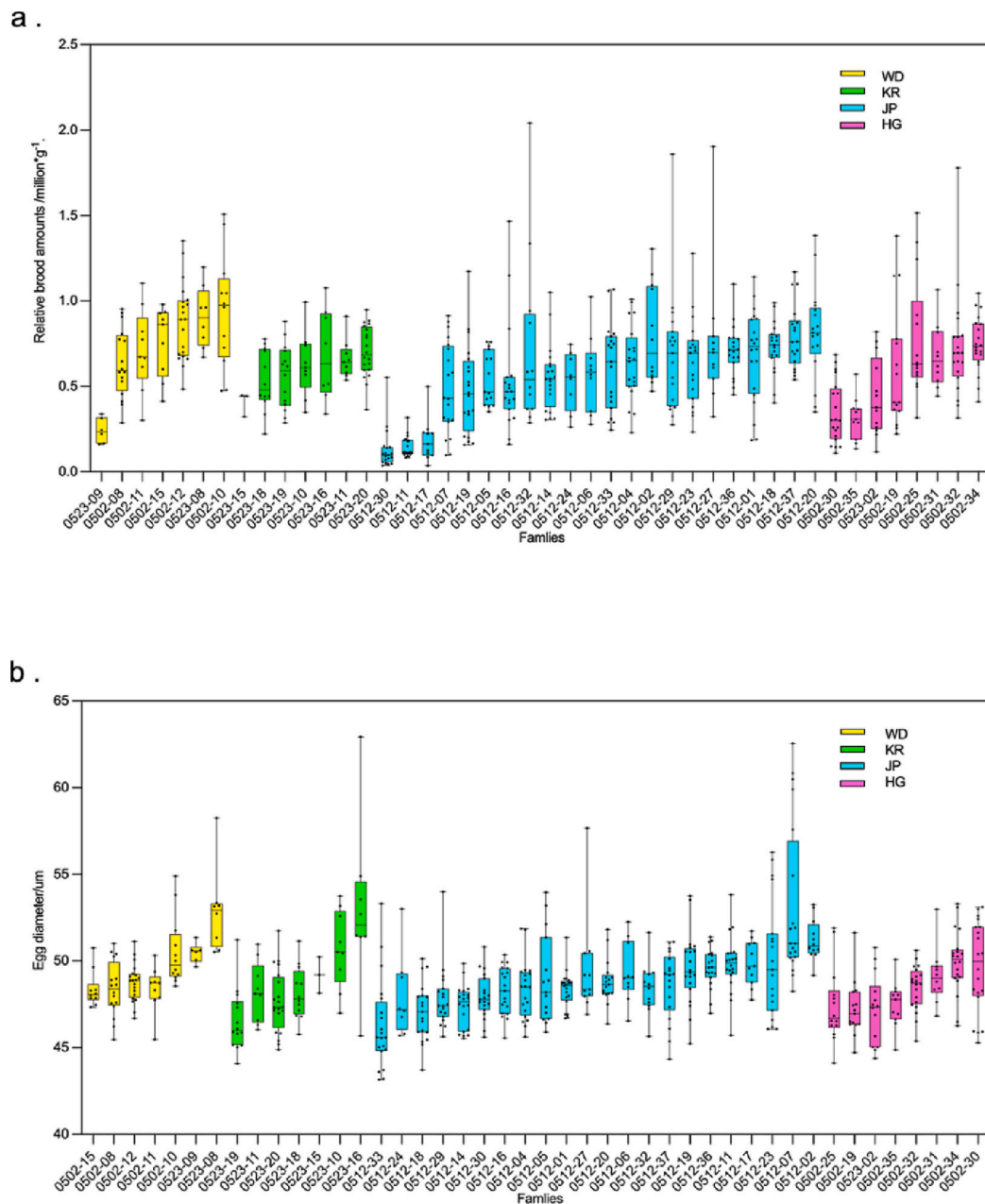


Fig. 1. The female reproduction traits of each family. a: the relative brood amount of each family; b: the egg diameter of each family. Abbreviations: KR, South Korea population; JP, Japan population; HG, “Haida No. 1” strain; WD, wild population.

which had 0.93 milliom/g, while the family with the lowest mean RBA was family 0512–30, which had 0.13 milliom/g. The BW ranged from 2.99 to 30.49 g, and the average BW of the 646 oysters was 13.01 g. The TW ranged from 12.96 to 76.41 g with an average weight of 39.42 g. The SH ranged from 12.60 to 122.00 mm, and the average SH of the 646 oysters was 77.54 mm. The SL ranged from 12.21 to 69.71 g with an average length of 46.96 mm. The coefficient of variation indicated that there was significant phenotypic variation in these traits.

Among the four populations, the female percentage in “Haida No. 1” strain was 46.40%, in South Korea population was 41.67%, in Japan population was 53.42%, and in wild population was 45.00%. The SH was significantly different ($P < 0.05$), the SH was 83.33 ± 13.04 mm in “Haida No. 1” strain, 75.97 ± 9.72 mm in South Korea population, 76.98 ± 11.82 mm in Japan population, and 73.27 ± 14.91 mm in wild population. The BW of “Haida No. 1” strain (15.64 ± 3.55 g) was significantly higher than other populations ($P < 0.05$). However, no significant

difference in female reproduction traits were observed among four populations ($P > 0.05$).

3.2. Heritability

The heritability for SH, TW, ED and RBA was moderate, with values ranging from 0.32 to 0.38 (Table 2). The heritability for BW and SL was low, with values of 0.17 ± 0.03 and 0.13 ± 0.03 , respectively.

3.3. Genetic correlation

The phenotypic correlations between ED and RBA, BW and SH were -0.05 ± 0.01 , -0.19 ± 0.06 , -0.22 ± 0.06 , and genetic correlations were -0.41 ± 0.17 , -0.29 ± 0.06 , -0.44 ± 0.14 , respectively (Table 3). The genetic correlations between RBA and growth traits were low and positive, with values ranging from 0.22 to 0.33. The

Table 2

Variance components and heritability (\pm standard error) of growth and female reproduction traits.

Trait	σ_a^2	σ_e^2	$h^2 \pm$ SE
ED	10.61 \pm 0.26	17.31 \pm 0.60	0.38 \pm 0.05
RBA	5.89 \pm 1.30	12.51 \pm 0.92	0.32 \pm 0.08
BW	30.28 \pm 5.02	143.14 \pm 9.01	0.17 \pm 0.03
TW	96.32 \pm 28.94	161.60 \pm 19.58	0.37 \pm 0.09
SH	8.41 \pm 4.84	14.86 \pm 1.68	0.36 \pm 0.06
SL	38.85 \pm 21.21	259.99 \pm 24.59	0.13 \pm 0.03

SL: shell length; SH: shell height; BW: body weight; TW: total weight; ED: egg diameter; RBA: relative brood amount.

Table 3

Phenotypic (above diagonal) and genetic correlations (below diagonal) between growth and female reproduction traits.

Trait	ED	RBA	BW	SH
ED	–	–0.05 \pm 0.01*	–0.19 \pm 0.06***	–0.22 \pm 0.06***
RBA	–0.41 \pm 0.17**	–	0.30 \pm 0.05***	0.20 \pm 0.07***
BW	–0.29 \pm 0.06***	0.33 \pm 0.21***	–	0.47 \pm 0.03***
SH	–0.44 \pm 0.14***	0.22 \pm 0.15*	0.70 \pm 0.37*	–

SH: shell height; BW: body weight; ED: egg diameter; RBA: relative brood amount.

*** Significance at 0.001 level.

** Significance at 0.01 level.

* Significance at 0.05 level.

corresponding phenotypic correlations were low, with a range of 0.20 to 0.30. The genetic and phenotypic correlations between SH and BW were moderate to high, 0.70 \pm 0.37 and 0.47 \pm 0.03, respectively.

4. Discussion

In economically important aquaculture species, female reproduction traits are crucial for reproductive efficiency (Gall and Neira, 2004; D'Ambrosio et al., 2020; Song et al., 2022). Commercial production and farming with high reproductive capacity may reduce the cost of breeding (Caballero-Zamora et al., 2015). In Pacific oysters, improving reproductive efficiency has been the main goal of breeding (Li et al., 2011; Gomes et al., 2018). The goal of this study was to compare the differences in growth and reproduction between the three cultured populations ("Haida No. 1" strain, South Korean population, and Japanese population) and a wild population. The logarithmic likelihood ratio tests were not significant for any of the traits, thus were omitted from further analysis. Genetic selection in livestock production has focused mainly on economically important traits (Buitenhuis et al., 2013; Ghaderi-Zefrehei et al., 2017). High intensity breeding for growth traits will cause the decline of reproductive performance (Veerkamp and Beerda, 2007; Carthy et al., 2016). These issues have not been considered for aquaculture species, possibly because of their high prolificacy. In this study, the growth rate of the cultured population was significantly higher than the other traits, which may have resulted from the cultured population exhibiting a significantly higher response to selection and realized heritability (Li et al., 2011; Wang et al., 2012; Kong et al., 2015). However, no significant difference in female reproductive traits was observed among the four populations.

Genetic parameter estimates of specific traits require large sample sizes, reliable statistical methods, and accurate models (Wang et al., 2011). In this study, genetic analysis was conducted using a linear mixed animal model. Four levels of heritability were defined by previous studies: low (0.00–0.20), moderate (0.20–0.40), high (0.40–0.60), and very high (> 0.60) (Navarro et al., 2009; Xu et al., 2015; Li et al., 2018). Female reproduction traits varied widely in 44 families, indicating

significant phenotypic variation. Heritability estimation for ED in our study was moderate of 0.38. The heritability of ED has been estimated in coho salmon (0.44 \pm 0.07), rainbow trout (0.28 \pm 0.16) and Siberian sturgeon (0.36 \pm 0.06) (Gall and Huang, 1988; D'Ambrosio et al., 2020; Bestin et al., 2021). Various mechanisms of female reproduction may contribute to the different heritability of ED among different species (Bestin et al., 2021). Heritability for RBA showed that it is possible to manipulate the number of eggs spawned through genetic selection in the *C. gigas*. RBA as an index of reproductive performance could more accurately evaluate reproductive potential than EN (Trong et al., 2013; Bestin et al., 2021). Low to moderate heritability for fecundity have been reported in the Caribbean scallop (Barros et al., 2018), Pacific oyster (Ernande et al., 2004), pearl oyster (Kvingedal et al., 2010), Catarina scallop (Ibarra et al., 1999), which are consistent with observation in our study. The heritability value of BW, TW, SH and SL were low to moderate in various studies. For instance, Kong et al. (2015) reported that heritability value of BW was 0.35 \pm 0.17. Gomes et al. (2018) found that at 2- and 6-months the heritability of TW were 0.29 \pm 0.06 and 0.26 \pm 0.05. Xu et al. (2017) estimated the heritability value of SH and SL to be 0.18 \pm 0.12 and 0.25 \pm 0.16, respectively. Zhang et al. (2019) estimated heritability of SH to range from 0.27 to 0.42. It's also observed that the heritability varied among different populations. In our study, the selective populations used have undergone multigenerational selection for growth traits, which may be the reason why their heritability for growth is lower than other populations. Previous studies have reported that traits with low heritability are suitable for family selection (Rye and Lillevik, 1990; Slater et al., 2014; Wang et al., 2018). Therefore, female reproduction traits could be improved rapidly through selection.

Genetic correlation estimates are commonly used for the design of breeding programs for different traits (Zhang et al., 2014). The correlation values were divided to three levels: low (0–0.45), medium (0.45–0.55), and high (0.55–1) (Zhai et al., 2021). The genetic and phenotypic correlations between RBA and ED were negative. A trade-off exists between egg size and RBA in aquaculture (Closs et al., 2013; Jónsdóttir, 2018). The genetic correlations and phenotypic correlation between female reproduction and growth traits were low to moderate, suggesting that the genes controlling these traits may be unrelated. In Fujian oyster, the genetic correlations between gonadal development traits and growth traits (–0.02–0.30) were low and not significant (Han et al., 2022). In Caribbean scallop, the genetic correlations between fecundity and growth traits were low and not significant (Barros et al., 2018). In Nile tilapia, the genetic correlations between ED and growth traits were negative, the genetic correlations between relative fecundity and growth traits were low and positive (Trong et al., 2013), which are consistent with our observations. Genetic and phenotypic correlation estimates between BW and SH were positive. Xu et al. (2017) reported a high genetic correlation (>0.6) between weight-related traits and shell related traits. High genetic correlation between weight-related traits and shell related traits were reported in the European oyster (Toro and Newkirk, 1990), Catarina scallop (Barros et al., 2018), Pearl oyster (Kvingedal et al., 2010), Hard clam (Wang et al., 2011), which are consistent with our results.

5. Conclusion

The study is the first to report the genetic parameters for female reproduction in Pacific oysters. The heritability of female reproduction traits was estimated to be moderate, suggesting that these traits could be improved by family selection. The correlations between female reproduction and growth traits were low, demonstrating that these traits were relatively independent and potential for genetic improvement. Selection of growth related traits will not result in significantly correlated response in reproduction traits.

CRedit authorship contribution statement

Dongshu Wu: Investigation, Formal analysis, Writing – original draft. **Ben Yang:** Investigation. **Qi Li:** Supervision, Resources. **Shikai Liu:** Supervision, Conceptualization, Resources, Writing – review & editing, Funding acquisition.

Declaration of Competing Interest

The authors declare no conflict of interest.

Data availability

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.aquaculture.2023.739387>.

References

- Appleyard, S.A., Kube, P.D., Ward, R.D., 2007. Estimation of genetic parameters in cultured Pacific oysters (*Crassostrea gigas*) grown in Tasmania, based on animal models. *Aquaculture* 272, S240.
- Azéma, P., Lamy, J.B., Boudry, P., Renault, T., Travers, M.A., Dégremont, L., 2017. Genetic parameters of resistance to *Vibrio aestuarianus*, and OshV-1 infections in the Pacific oyster, *Crassostrea gigas*, at three different life stages. *Genet. Sel. Evol.* 49 (1), 23.
- Barros, J., Velasco, L.A., Winkler, F.M., 2018. Heritability, genetic correlations and genotype by environment interactions in productive traits of the Caribbean scallop, *Argopecten nucleus* (Mollusca: Bivalvia). *Aquaculture* 488, 39–48.
- Bestin, A., Brunel, O., Malledant, A., Debeuf, B., Benoit, P., Mahla, R., Chapuis, H., Guéméné, D., Vandeputte, M., Haffray, P., 2021. Genetic parameters of caviar yield, color, size and firmness using parentage assignment in an octoploid fish species, the Siberian sturgeon *Acipenser baerii*. *Aquaculture* 540, 736725.
- Buitenhuis, A.J., Sundekilde, U.K., Poulsen, N.A., Bertram, H.C., Larsen, L.B., Sørensen, P., 2013. Estimation of genetic parameters and detection of quantitative trait loci for metabolites in Danish Holstein milk. *J. Dairy Sci.* 96 (5), 3285–3295.
- Caballero-Zamora, A., Cienfuegos-Rivas, E.G., Montaldo, H.H., Campos-Montes, G.R., Martínez-Ortega, A., Castillo-Juárez, H., 2015. Genetic parameters for spawning and growth traits in the Pacific white shrimp (*Penaeus (Litopenaeus) vannamei*). *Aquac. Res.* 46 (4), 833–839.
- Carthy, T., Ryan, D., Fitzgerald, A., Evans, R., Berry, D., 2016. Genetic relationships between detailed reproductive traits and performance traits in Holstein-Friesian dairy cattle. *J. Dairy Sci.* 99, 1286–1297.
- Carty, A.J., McFarland, K., Small, J., Allen, S.K., Plough, L.V., 2020. Heritability of acute low salinity survival in the eastern oyster (*Crassostrea virginica*). *Aquaculture* 529, 735649.
- Chi, Y., Li, Q., Liu, S., Kong, L., 2021. Genetic parameters of growth and survival in the Pacific oyster *Crassostrea gigas*. *Aquac. Res.* 52 (1), 282–290.
- Closs, G.P., Hicks, A.S., Jellyman, P.G., 2013. Life histories of closely related amphidromous and non-migratory fish species: a trade-off between egg size and fecundity. *Freshw. Biol.* 58 (6), 1162–1177.
- D'Ambrosio, J., Morvezen, R., Brard-Fudulea, S., Bestin, A., Acin Perez, A., Guéméné, D., Poncet, C., Haffray, P., Dupont-Nivet, M., Phocas, F., 2020. Genetic architecture and genomic selection of female reproduction traits in rainbow trout. *BMC Genomics* 21 (1), 558.
- Deekae, S.N., Abowei, J.F.N., 2010. The fecundity of *Macrobrachium macrobrachion* (Herklots, 1851) from Luubara Creek Ogoni land, Niger Delta, Nigeria. *Int. J. Anim. Vet. Adv.* 2, 148–154.
- Dégremont, L., Ernande, B., Bédier, E., Boudry, P., 2007. Summer mortality of hatchery-produced Pacific oyster spat (*Crassostrea gigas*). I. Estimation of genetic parameters for survival and growth. *Aquaculture* 262 (1), 41–53.
- Ernande, B., Boudry, P., Clobert, J., Haure, J., 2004. Plasticity in resource allocation based life history traits in the Pacific oyster, *Crassostrea gigas*. I. Spatial variation in food abundance. *J. Evol. Biol.* 17 (2), 342–356.
- Fang, J., Han, Z., Li, Q., 2021. Effect of inbreeding on performance and genetic parameters of growth and survival traits in the Pacific oyster *Crassostrea gigas* at larval stage. *Aquac. Rep.* 19, 100590.
- Fu, J., Shen, Y., Xu, X., Li, J., 2015. Genetic parameter estimates for growth of grass carp, *Ctenopharyngodon idella*, at 10 and 18 months of age. *Aquaculture* 450, 342–348.
- Gall, G.A.E., Huang, N., 1988. Heritability and selection schemes for rainbow trout: female reproductive performance. *Aquaculture* 73 (1), 57–66.
- Gall, G.A.E., Neira, R., 2004. Genetic analysis of female reproduction traits of farmed coho salmon (*Oncorhynchus kisutch*). *Aquaculture* 234 (1–4), 143–154.
- Geffard, O., He, A., le Ne Budzinski, A., His, E., 2002. The effects of elutriates from PAH and heavy metal polluted sediments on *Crassostrea gigas* (Thunberg) embryogenesis, larval growth and bio-accumulation by the larvae of pollutants from sedimentary origin. *Ecotoxicology* 11, 403–416.
- Ghaderi-Zefrehei, M., Rabbanikhah, E., Baneh, H., Peters, S.O., Imumorin, I.G., 2017. Analysis of culling records and estimation of genetic parameters for longevity and some production traits in Holstein dairy cattle. *Taylor Francis* 45 (1), 524–528.
- Gilmour, A.R., Gogel, B.J., 2009. *ASReml User Guide*.
- Gjerde, B., Mahapatra, K.D., Reddy, P.V.G.K., Saha, J.N., Jana, R.K., Meher, P.K., Sahoo, M., Khaw, H.L., Gjedrem, T., Rye, M., 2019. Genetic parameters for growth and survival in rohu carp (*Labeo rohita*). *Aquaculture* 503, 381–388.
- Gomes, R.B., Dybas, P.R., Silva, F.C., Sühnel, S., Albuquerque, M.C.P., Melo, C.M.R., 2018. Estimates of genetic parameters for growth and survival in Pacific oyster (*Crassostrea gigas*). *Bol. Inst. Pesca* 44 (2), 1678–2305.
- Gutierrez, A.P., Matika, O., Bean, T.P., Houston, R.D., 2018. Genomic selection for growth traits in Pacific oyster (*Crassostrea gigas*): potential of low density marker panels for breeding value prediction. *Front. Genet.* 9, 391.
- Han, Z., Guo, X., Lu, Z., Song, Y., Chen, R., Han, X., Yu, S., Tu, K., Liu, L., Que, H., 2022. Heritability estimates for gonadal development traits and their genetic correlations with growth and heat tolerance traits in the Fujian oyster *Crassostrea angulata*. *Front. Mar. Sci.* 9, 986441.
- His, E., Beiras, R., Seaman, M.N.L., 1999. The assessment of marine pollution - bioassays with bivalve embryos and larvae. *Adv. Mar. Biol.* 37, 1–178.
- Ibarra, A.M., Ramirez, J.L., Ruiz, C.A., Cruz, P., Avila, S., 1999. Realized heritabilities and genetic correlation after dual selection for total weight and shell width in catarina scallop (*Argopecten ventricosus*). *Aquaculture* 175 (3), 227–241.
- Jones, J., Randall, C., Thrush, M., Davies, B., Springate, J., Duston, J., Barker, G., 1992. Broodstock management, fecundity, egg quality and the timing of egg production in the rainbow trout (*Oncorhynchus mykiss*). *Aquaculture* 100 (1–3), 1.
- Jónsdóttir, I.G., 2018. Effects of changes in female size on relative egg production of northern shrimp stocks (*Pandalus borealis*). *Reg. Stud. Mar. Sci.* 24, 270–277.
- Kong, N., Li, Q., Yu, H., Kong, L.F., 2015. Heritability estimates for growth-related traits in the Pacific oyster (*Crassostrea gigas*) using a molecular pedigree. *Aquac. Res.* 46 (2), 499–508.
- Kvingedal, R., Evans, B.S., Lind, C.E., Taylor, J.J.U., Dupont-Nivet, M., Jerry, D.R., 2010. Population and family growth response to different rearing location, heritability estimates and genotype×environment interaction in the silver-lip pearl oyster (*Pinctada maxima*). *Aquaculture* 304 (1), 1–6.
- Li, Q., Wang, Q., Liu, S., Kong, L., 2011. Selection response and realized heritability for growth in three stocks of the Pacific oyster *Crassostrea gigas*. *Fish. Sci.* 77 (4), 643–648.
- Li, Y., Zhang, B., Lu, S., Tian, Y., Yang, Y., Chen, S., 2018. Genetic parameters estimate for growth performance traits at harvest in Japanese flounder (*Paralichthys olivaceus*). *Aquaculture* 489, 56–61.
- Lind, C.E., Ponzoni, R.W., Nguyen, N.H., Khaw, H.L., 2012. Selective breeding in fish and conservation of genetic resources for aquaculture. *Reprod. Domest. Anim.* 47 (SUPPL.4), 255–263.
- Liu, J., Lai, Z., Fu, X., Wu, Y., Bao, X., Hu, Z., Lai, M., 2014. Genetic parameters and selection responses for growth and survival of the small abalone *Haliotis diversicolor* after four generations of successive selection. *Aquaculture* 436, 58–64.
- Macbeth, M., Matthew, K., Matthew, S., Benzie, J., Knibbd, W., Wilson, K., 2007. Heritability of reproductive traits and genetic correlations with growth in the black tiger prawn *Penaeus monodon* reared in tanks. *Aquaculture* 270, 51–56.
- Mai, H., Cachot, J., Brune, J., Geffard, O., Belles, A., Budzinski, H., Morin, B., 2012. Embryotoxic and genotoxic effects of heavy metals and pesticides on early life stages of Pacific oyster (*Crassostrea gigas*). *Mar. Pollut. Bull.* 64 (12), 2663–2670.
- Maria, J., Schwindt, E., Pastorino, G., Bortolus, A., Casas, G., Darrigran, G., Elías, R., López Gappa, J.J., Obenat, S., Pascual, M., Penchaszadeh, P., Piriz, M.L., Scarabino, F., Spivak, E.D., Vallarino, E.A., 2002. No longer the pristine confines of the world ocean: a survey of exotic marine species in the southwestern Atlantic. *Biol. Invasions* 4 (1), 115–143.
- Melo, C.M.R., Durland, E., Langdon, C., 2016. Improvements in desirable traits of the Pacific oyster, *Crassostrea gigas*, as a result of five generations of selection on the west coast, USA. *Aquaculture* 460, 105–115.
- Mottier, A., Kientz-Bouchart, V., Serpentine, A., Lebel, J.M., Jha, A.N., Costil, K., 2013. Effects of glyphosate-based herbicides on embryo-larval development and metamorphosis in the Pacific oyster, *Crassostrea gigas*. *Aquat. Toxicol.* 128, 67–78.
- Navarro, A., Zamorano, M.J., Hildebrandt, S., Ginés, R., Aguilera, C., Afonso, J.M., 2009. Estimates of heritabilities and genetic correlations for body composition traits and G × E interactions, in gilthead seabream (*Sparus auratus* L.). *Aquaculture* 295 (3–4), 183–187.
- Pattarapanyawong, N., Sukhavachana, S., Senanan, W., Srithong, C., Joerakate, W., Tunkijjanukij, S., Poopuang, S., 2021. Genetic parameters for growth and fillet traits in Asian seabass (*Lates calcarifer*, *Bloch 1790*) population from Thailand. *Aquaculture* 539, 736629.
- Rye, M., Lillevik, K.M., 1990. Survival in the early fresh-water period in Atlantic salmon (*Salmo salar*) and rainbow trout (*Salmo gairdneri*): heritabilities for survival and genetic correlation between survival and growth. *Aquaculture* 85 (1), 328–329.

- Slater, A.T., Wilson, G.M., Cogan, N.O., Forster, J.W., Hayes, B.J., 2014. Improving the analysis of low heritability complex traits for enhanced genetic gain in potato. *Theor. Appl. Genet.* 127 (4), 809–820.
- Song, H., Xu, S., Luo, K., Hu, M., Luan, S., Shao, H., Kong, J., Hu, H., 2022. Estimation of genetic parameters for growth and egg related traits in Russian sturgeon (*Acipenser gueldenstaedtii*). *Aquaculture* 546, 737299.
- Toro, J., Newkirk, G.F., 1990. Divergent selection for growth rate in the European oyster *Ostrea edulis*: response to selection and estimation of genetic parameters. *Mar. Ecol. Prog. Ser.* 62, 219–227.
- Trong, T.Q., Arendonk, J.A.M., Komen, H., 2013. Genetic parameters for reproductive traits in female Nile tilapia (*Oreochromis niloticus*): II. Fecundity and fertility. *Aquaculture* 416–417, 72–77.
- Trong, T.Q., Mulder, H.A., Arendonk, J.A.M., Komen, H., 2013. Heritability and genotype by environment interaction estimates for harvest weight, growth rate, and shape of Nile tilapia (*Oreochromis niloticus*) grown in river cage and VAC in Vietnam. *Aquaculture* 384–387, 119–127.
- Troost, K., 2010. Causes and effects of a highly successful marine invasion: case-study of the introduced Pacific oyster *Crassostrea gigas* in continental NW European estuaries. *J. Sea Res.* 64 (3), 145–165.
- Veerkamp, R.F., Beerda, B., 2007. Genetics and genomics to improve fertility in high producing dairy cows. *Theriogenology* 68, S266–S273.
- Vu, S.V., Knibb, W., O'Connor, W., Nguyen, N.T.H., In, V., Dove, M., Nguyen, N.H., 2020. Genetic parameters for traits affecting consumer preferences for the Portuguese oyster, *Crassostrea angulata*. *Aquaculture* 526, 735391.
- Wang, H., Chai, X., Liu, B., 2011. Estimation of genetic parameters for growth traits in cultured clam *Meretrix meretrix* (Bivalvia: Veneridae) using the Bayesian method based on Gibbs sampling. *Aquac. Res.* 42 (2), 240–247.
- Wang, Q., Li, Q., Kong, L., Yu, R., 2012. Response to selection for fast growth in the second generation of Pacific oyster (*Crassostrea gigas*). *J. Ocean Univ. China* 11 (3), 413–418.
- Wang, Y., Sun, G., Zeng, Q., Chen, Z., Hu, X., Li, H., Shi, W., Bao, Z., 2018. Predicting growth traits with genomic selection methods in Zhikong scallop (*Chlamys farreri*). *Mar. Biotechnol.* 20, 769–779.
- Xing, D., Li, Q., Kong, L., Yu, H., 2018. Heritability estimates for mantle edge pigmentation and correlation with shell pigmentation in the white-shell strain of Pacific oyster, *Crassostrea gigas*. *Aquaculture* 482, 73–77.
- Xiong, X.M., Huang, W.J., Dong, Q., Zhang, D.Y., Wan, S.M., Gao, Z.X., 2023. Genetic parameter estimates for intermuscular bone trait in grass carp (*Ctenopharyngodon idella*). *Aquaculture* 563, 739011.
- Xu, L., Wang, W., Kong, J., Luan, S., Hu, Y., Ma, Y., 2015. Estimates of heritability and correlation for growth traits of turbot (*Scophthalmus maximus L.*) under low temperature conditions. *Acta Oceanol. Sin.* 34 (2), 63–67.
- Xu, L., Li, Q., Yu, H., Kong, L., 2017. Estimates of heritability for growth and shell color traits and their genetic correlations in the black shell strain of Pacific oyster *Crassostrea gigas*. *Mar. Biotechnol.* 19 (5), 421–429.
- Xu, H., Mo, T., Liu, S., Sun, C., Lv, L., Lin, Z., Dong, Y., 2022. Heritability estimates for ammonia resistance and growth-related traits in the razor clam *Sinonovacula constricta*. *Aquaculture* 549, 737750.
- Yong, A., Kian, S., Mustafa, S., Rahman, R.A., 2004. Broodstock condition and egg quality in tiger prawn, *Penaeus monodon*, resulting from feeding bioencapsulated live prey. *Aquac. Int.* 12, 423–433.
- Zhai, S., Yang, B., Zhang, F., Li, Q., Liu, S., 2021. Estimation of genetic parameters for resistance to *vibrio alginolyticus* infection in the Pacific oyster (*Crassostrea gigas*). *Aquaculture* 538, 736545.
- Zhang, T., Kong, J., Liu, B., Wang, Q., Cao, B., Sheng, L., Wang, W., 2014. Genetic parameter estimation for juvenile growth and upper thermal tolerance in turbot (*Scophthalmus maximus Linnaeus*). *Acta Oceanol. Sin.* 33 (8), 106–110.
- Zhang, J., Li, Q., Xu, C., Han, Z., 2019. Response to selection for growth in three selected strains of the Pacific oyster *Crassostrea gigas*. *Aquaculture* 503, 34–39.