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ESTIMATES OF GENETIC PARAMETERS FOR GROWTH AND SURVIVAL IN PACIFIC OYSTER (*Crassostrea gigas*)

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ABSTRACT

The rapid growth associated with high tolerance to adverse environmental conditions has made the Pacific oyster, *Crassostrea gigas*, the species chosen for cultivation in Santa Catarina, Brazil. Variance components and genetic parameters for survival and growth of Pacific oyster families were estimated using data from half-sibs (n = 41) and full-sibs (n = 2) families. In the juvenile stage and at harvest, we measured total weight and shell height of 80 animals per family. In addition, at harvest we measured yield (total weight of animals per floor of lantern) and calculated survival. The covariance components were estimated in the program AIREMLF90 using an animal model. The heritabilities (Standard Deviation) at harvest were: 0.26 (0.05) (individual weight (SD)), 0.34 (0.05) (height), 0.54 (0.09) (yield), 0.58 (0.08) (average individual weight) and 0.16 (0.07) (survival). Genetic correlations were 0.88 (0.03) (between individual weight and height), 0.98 (0.03) (between yield and average individual weight), 0.58 (0.39) (between average individual weight and survival) and 0.47 (0.36) (between yield and survival). The heritability and genetic correlations suggest that gains could be obtained for the studied traits. The yield and mean individual weight should be used as a criterion for selection.

Key words: *Crassostrea gigas*; animal breeding; heritability; genetic correlation; selection.

ESTIMATIVA DE PARÂMETROS GENÉTICOS PARA CRESCIMENTO E SOBREVIVÊNCIA EM OSTRAS DO PACÍFICO (*Crassostrea gigas*)

RESUMO

Componentes de variância e parâmetros genéticos para a sobrevivência e crescimento de ostras do Pacífico *Crassostrea gigas* foram estimadas usando dados de famílias de meio-irmão (n = 41) e de irmãos completos (n = 2). No estágio juvenil e na colheita, medimos o peso total e a altura da concha de 80 animais por família. Além disso, na colheita, medimos o rendimento (peso total de animais por andar de lanterna) e a sobrevivência foi calculada. Os componentes de covariância foram estimados no programa AIREMLF90 usando um modelo animal. As herdabilidades na colheita foram: 0,26 (0,05) (peso individual (DP)), 0,34 (0,05) (altura), 0,54 (0,09) (rendimento), 0,58 (0,08) (peso médio individual) e 0,16 (0,07) (sobrevivência). As correlações genéticas foram de 0,88 (0,03) (entre o peso individual e a altura), 0,98 (0,03) (entre o rendimento e o peso médio individual), 0,58 (0,39) (entre o peso médio individual e a sobrevivência) e 0,47 (0,36) (entre o rendimento e a sobrevivência). As herdabilidades e as correlações genéticas sugerem que podem ser obtidos ganhos para os caracteres estudados. O rendimento e o peso médio individual podem ser utilizados como critério de seleção.

Palavras-chave: *Crassostrea gigas*; melhoramento genético animal; herdabilidade; correlação genética; seleção.

INTRODUCTION

The increasing demand for food from aquaculture has required more efficient production systems and improvements in these systems have been achieved, with advances in nutrition, disease diagnosis, management and breeding for production traits (DUNHAM, 2014). However, it is estimated that less than 10% of world aquaculture production is based on genetically improved stocks (GJEDREM *et al*., 2012; BONDIOLI *et al*., 2017).

Aquaculture production in 2014 was 101,139,072 tons, of which total mollusc production represented 15.6% (FAO, 2016). Of the total mollusc aquaculture (15,777,695

tons), in 2014, oyster production represents 32.6%, and the Pacific oyster, *Crassostrea gigas* (THUNBERG, 1793) contributed 12.1% (625,049 tons) of this total mollusc production worldwide in 2014 (FAO, 2016). In Brazil, the state of Santa Catarina contributes 90% of the total national oyster production and the total mollusc production (included oyster, mussels and scallops) was 15,381.44 tons producing R$ 54,917,813.40 in gross revenue (EPAGRI, 2016).

In oyster farming, the potential for rapid growth associated with high tolerance to adverse environmental conditions has made the Pacific oyster, *Crassostrea gigas* (THUNBERG, 1793), the species chosen for cultivation in several regions of the world, included in Brazil (FAO, 2015). Genetic breeding program for *C. gigas* have been developed in the United States (LANNAN, 1972; LANGDON *et al*., 2003; MELO *et al*., 2016), Australia (KUBE *et al*., 2011), France (BOUDRY *et al*., 2004; TARIS *et al*., 2006; DÉGREMONT *et al*., 2015) and China (LI *et al*., 2011; GE *et al*., 2015; KONG *et al*., 2015) with the aim of increasing production. For this species, studies evaluating characteristics such as height (LI *et al*., 2011), yield and survival (LANGDON *et al*., 2003; MELO *et al*., 2016), mortality (DÉGREMONT *et al*., 2007; DÉGREMONT *et al*., 2010), shell color (FENG *et al*., 2015; GE *et al*., 2015) and resistance to pathogens (DÉGREMONT, *et al*., 2015) indicate the potential for genetic gain through selection.

According to HERSHBERGER *et al*. (1984), studies developed by LOOSANOFF (1945) on spawning techniques of *C. gigas* and by LOOSANOFF and DAVIS (1963) on Pacific oyster larviculture, have boosted the use of genetic approaches in the United States.

In Australia, KUBE *et al*. (2011) identified that the yield in *C. gigas* cultivation is influenced by economically important traits (growth, mortality and uniformity), which were incorporated into the genetic breeding program of this country.

Researchers reported moderate to high heritability of *C. gigas* in China for growth trait (LI *et al*., 2011) and shell color (GE *et al*., 2015) and in France for survival (BOUDRY *et al*., 2004; TARIS *et al*., 2006; DÉGREMONT *et al*., 2015), growth, time to reach the pediveliger stage and successful settlement (TARIS *et al*., 2006).

In Brazil, there are not heritabilities values published for desirable traits in *C. gigas* which could demonstrate the possibility of genetic gain through selection in the *C. gigas* population grown. Thus, the goal of this study was to estimate variance components, to calculate genetic parameters for desirable traits (survival, height, individual fresh weight, mean fresh weight and yield) and to evaluate the implications of breeding program of *C. gigas* oysters.

METHODS

C. gigas oysters used for the production of families came from the broodstock of the Laboratory of Marine Molluscs (LMM) kept in the field in the experimental cultivation area located in the Northern Bay, Sambaqui Beach, Florianópolis (27°29'18"S and 48°32'12"W). The families used in this study were produced in the LMM, located in Barra da Lagoa, Florianópolis (27º35'S and 48º26'W).

Families of half-sibs (n = 41) and full-sibs (n = 2) were produced through hierarchical mating (a male mating with two females) in three larvicultures, L1, L2 and L3, in the months of December 2014, January and April 2015, respectively. The families produced in the L1, L2 and L3 larviculture remained in the laboratory, respectively, for 42, 41 and 59 days, and for 180, 175 and 158 days in field cultivation.

Spawning was performed by strip of the gonadal tissue. Fertilization of female gametes (sieved at 18 µm) was carried out in 20 L seawater containers (filtered at 1 µm and UV-treated) by adding three doses (at 20-minute intervals) of 20 ml of a solution of seawater and sperm. The fertilized gametes (150 eggs mL^{-1}) were packed in individual containers with seawater at a salinity of 35 and constant aeration.

After 24 hours, each tank unit was stocked with a density of 100 D-larvae mL^{-1} of each family. In this system, each family was farmed in duplicate. Each tank consisted of acrylic conical cylinders (3.5 L, with a working volume of 2.4 L) with constant aeration (at the bottom) and constant flow of seawater plus food at 100 mL $minute^{-1}$. To avoid escape of larvae, filters (35 to 100 µm mesh, according to larval development) were coupled to the water outlet and aeration inflow of each tank. The culture was maintained in a recirculation system using two 500 L reservoirs, one Skimmer (Altamar 300R) and one UV sterilizer (Sibrape) of 75W. At every 72 h, partial water change of the whole system was carried out in addition to larval sieving (35 to 500 µm mesh) and cleaning of the units with freshwater and lemon solution (CARVALHO *et al*., 2013; TURINI *et al*., 2014). The water temperature was kept at 28°C and the salinity at 27.

Food consisted of the combination of the microalgae *Isochrysis* aff. *galbana* and/or *Pavlova lutheri*, *Nannochloropsis oculata* and *Chaetoceros muelleri* and/or *Chaetoceros calcitrans*, at a final concentration varying from $4x10^4$ a $6x10^4$ cells mL^{-1}, according to the larval development stage. Food was added steadily into the water inlet pipe of the tank units with the help of a peristaltic pump (SEKO®, Pr4).

With 12 days of larviculture, the larvae retained in the 230 µm mesh sieve, at eyed-larval stage (larvae suitable for settlement), were taken, immersed in seawater and placed in a screened container, immersed in seawater, at low temperature (4 to 8°C) for 3 days. The others remained in the larval system for up to three more days, totaling 15 days of hatchery. After this period, the larvae not retained in the 230 µm mesh were discarded.

Settlement was performed in a downweller system in the first 7 days, using shell powder for single oysters production and upweller system from the 8^{th} to the 30^{th} day, for spats growth. The system operated with water recirculation and consisted of a 1,500 L-distribution and receiving tank, four 500 L-tanks (with adjustable depth) containing 15 containers each, coupled to the sides of the tank. The settlement units consisted of cylindrical PVC containers 20 cm diameter and 30 cm high, screened at the bottom (200 µm) and with an upper side outlet of 32 mm diameter to be attached to the side of the tank. Water was kept at room temperature (23 to 25°C) and salinity at 35.

The cleaning of the tanks was carried out daily and consisted in their total emptying and cleaning of the screens with seawater. After, the system was refilled with seawater (filtered at 10 µm and UV) and the food was added to the distribution tank. The daily

food consisted of 2 microalgae (*I.* aff. *galbana* and *C. muelleri*) at a final concentration varying from $6x10^4$ to $16x10^4$ cells mL^{-1}, according to the development of the spats.

After 27, 26 and 44 days (L1, L2 and L3 respectively) of settlement, animals (~4 mm height) of each family were placed in nursery lanterns and transferred to the field (experimental growing area at sea; Table 1).

Field cultivation

The oysters were farmed in longline using nursery lantern-net (NL) with 2 mm mesh size and 400 mm dish diameter and intermediate lantern-net (IL) with 5 mm mesh size and 400 mm dish diameter. During the experimental period, the management was performed according to SÜHNEL *et al*. (2017), which consisted basically of taking lanterns-nets from the sea, pressurized freshwater cleaning (weekly in NL and monthly in IL), removal of fouling organisms and sieving every 30 days. Random and proportional discards per size class were performed in each family, to avoid the effect of density on oyster growth. When transferred to IL 840 oysters per family were randomly taken and planted in three lantern-nets at a density of 70 oysters by lantern-net floor, totaling 12 floors.

Data collection

During field cultivation, water temperature was monitored (hourly) using a temperature logger (V2 Temp Logger, Tidbit®). Once a week, the salinity was checked (using a refractometer) and water was collected for seston quantification.

In the seston, total particulate matter (TPM), particulate organic matter (POM) and particulate inorganic matter (PIM) were evaluated according to the gravimetric method proposed by STRICKLAND and PARSONS (1972).

To estimate the genetic parameters, two data collections (juvenile and at harvest) were performed. The initial collection (juvenile phase) was performed after 47, 73 and 63 days of field cultivation and the final collection (at harvest) after 180, 175 and 158 days respectively for L1, L2 and L3 (Table 1).

For juvenile and at harvest, height data (n = 80 oysters per family) and individual fresh weight (n = 80 oysters per family) were collected. At harvesting, in addition to height and individual fresh weight, yield (total fresh weight of animals per lantern-net floor, n = 3 lantern-nets), average individual fresh weight (total fresh weight of live oysters per lantern-net floor/number of live animals on the floor, n = 3 lantern-nets) and survival (number of live animals per lantern-net floor, n = 3 lantern-nets).

Estimation of genetic parameters

Variance components were estimated using the AIREMLF90 software (MISZTAL *et al*., 2002; MISZTAL, 2008) and a multivariate animal model.

For the analysis of height (initial and final) and individual fresh weight data, the following statistical model (Equation 1) was used:

$$y_{ijk} = L_i + f_j + u_k + e_{ijk} \quad [1]$$

where:

y_{ijk} is the height and individual fresh weight of animal *k* belonging to larviculture *i* and family *j*;

L_i is the fixed effect of larviculture;

f_j is the random genetic effect of family;

u_k is the additive genetic effect of animal;

e_{ijk} is the random error.

The following statistical model (Equation 2) was used for the data of yield (kg), average individual fresh weight (g) and survival (%):

Table 1. Larviculture, spawning month, transfer to the field and data collection, age of the animals (days after spawning) and initial (N_i) and final (N_f) numbers of families in the phases (juvenile and harvesting) of cultivation in laboratory and field.

Larviculture	Spawning month/ year	Ni	Transfer to the field month/ year (age in days)	Data collection month/year (age in days)		Nf
				Juvenile	Harvesting	
L1	12/2014	10	01/2015 (42)	03/2015 (47)	07/2015 (180)	8
L2	01/2015	20	03/2015 (41)	05/2015 (73)	08/2015 (175)	18
L3	04/2015	20	06/2015 (59)	08/2015 (63)	11/2015 (158)	17

Table 2. Total sampled animals (N), mean (standard deviation), minimum and maximum height and individual fresh weight for juvenile and at harvest.

Phase	Trait	N	Mean (SD)	Minimum	Maximum
Juvenile	**Height (mm)**	3385	33.31 (13.84)	4.70	96.66
	Individual fresh weight (g)	3385	3.35 (3.80)	0.05	30.16
Harvesting	**Height (mm)**	3390	87.04 (15.26)	10.19	166.99
	Individual fresh weight (g)	3390	47.50 (16.11)	6.00	113.97

$$y_{ijkl} = L_i + D_j + c_k + f_l + e_{ijkl} \quad [2]$$

where:

y_{ijkl} is the yield, average individual fresh weight and survival of family *l*, belonging to larviculture *i*, cultivated in floor (depth) *j*, in lantern *k*;

L_i is the fixed effect of larviculture;

D_j is the fixed effect of floor of cultivation (depth);

c_k is the random effect of common environment (represented by interaction between family x lantern);

f_l is the random genetic family effect;

e_{ijkl} is the random error.

Heritabilities were calculated as $h^2_a = var_a/var_p$ (model 1) and $h^2_f = var_f/var_p$ (family heritability (HOLLAND *et al*., 2003); model 1 e 2) and the common environment effect was calculated as $c^2 = var_c/var_p$. Where: var_a, var_f, var_c and var_p are additive genetic, family, common environment and phonotypic variance, respectively.

RESULTS

In this study, 50 families were produced, of which 43 families were used for analysis (Table 1). Seven families were lost during field cultivation.

Environmental parameters

The mean (SD) monthly temperature of seawater during the growing period ranged from 19.12°C (0.45) to 28.19°C (1.30) (Figure 1). The overall mean throughout the experiment was 22.49°C (2.98). The lowest temperature was registered in June (16.15ºC) and the highest in February (34.37ºC).

The mean (SD) monthly salinity of seawater during the growing period ranged from 30 (1.87) to 35.33 (0.58) (Figure 1). The overall mean over the entire experimental period was 34.31 (1.74). The lowest salinity was observed in March (27) and the highest in August (36).

During the experimental period, the mean total particulate matter (TPM) was 63.85 (13.40) mg L^{-1}, with the highest value recorded in November (79.75 (0.35) mg L^{-1}) and the lowest in February (31.80 (12.73) mg L^{-1}) (Figure 2). For particulate organic matter (POM), the mean value was 19.77 (4.31) mg L^{-1}, with the highest value observed in November (26.50 (9.19) mg L^{-1}) and the lowest, in January (13.56 (0.34) mg L^{-1}). In the case of particulate inorganic matter (PIM), the mean value was 44.09 (10.95) mg L^{-1}, with the highest value verified in November (53.67 (6.47) mg L^{-1}) and lower, in January (18.00 (9.26) mg L^{-1}). The mean PIM/POM ratio was 2.17 (0.40) for the whole experimental period, the lowest value observed in February (1.30) and the highest, in May (2.92).

Means and genetic parameters

The mean values of oyster height at the juvenile and harvesting phases were 33.31 (13.84) mm and 87.04 (15.26) mm, respectively, and the individual fresh weight observed was 3.35 (3.80) g and 47.50 (16.11) g, respectively, in the juvenile and at harvest (Table 2).

Height and individual fresh weight

The additive genetic variance (SD) ranged from 31.23 (6.32) to 77.83 (13.87) (for height in the juvenile phase and at harvesting, respectively) and from 2.67 (0.55) to 64.16 (12.11) (for individual fresh weight in the juvenile phase and at harvesting, respectively) (Table 3).

The narrow-sense heritability (h^2_a) for the height trait was lower for the juvenile (0.24 (0.05)) than at harvest animals (0.34 (0.05)). However, narrow-sense heritability for individual fresh weight was similar at the juvenile phase (0.29 (0.06)) and at harvesting (0.26 (0.05)) (Table 3).

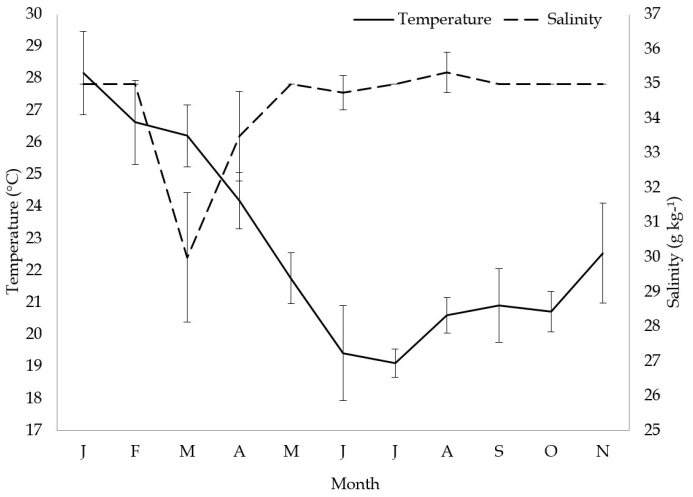

Figure 1. Temperature (°C) and mean salinity (g kg^{-1}) (standard deviation) of seawater during field cultivation period, experimental area at LMM, Sambaqui Beach, Florianópolis, State of Santa Catarina.

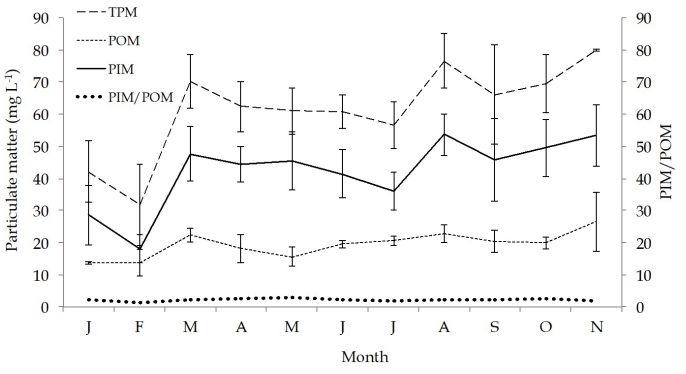

Figure 2. Mean concentration (mg L^{-1}) (standard deviation) of total particulate matter (TPM), particulate organic matter (POM), particulate inorganic matter (PIM) and the PIM/POM ratio in the experimental area of the LMM during the cultivation period.

The genetic correlations between the traits were all positive and ranged from 0.48 (0.12) (between height at the juvenile phase and individual fresh weight at harvesting) to 0.88 (0.03) (between individual fresh weight and height at harvesting) and the correlations of family effect ranged from -0.42 (0.94) (between height at harvesting and individual fresh weight at the juvenile phase) to 0.88 (0.12) (between individual fresh weight at the juvenile phase and height at harvesting) (Table 4).

Yield, average individual fresh weight and survival

Estimates of family heritabilities (SD) ranged from 0.16 (0.07) (survival) to 0.58 (0.08) (average individual fresh weight) and the family variance ranged from 0.31 (0.09) (yield) to 63.81 (17.46) (average individual fresh weight) (Table 5).

Genetic family correlations (SD) between yield, average individual fresh weight and survival were all positive and ranged from 0.47 (0.36) (between mean individual fresh weight and survival) to 0.98 (0.03) (between yield and mean individual fresh weight). Correlations of common environment effect ranged from -0.14 (0.83) (between yield and survival) to 0.81 (0.08) (between yield and mean individual fresh weight) (Table 6).

DISCUSSION

Although there have been no large variations in environmental parameters, environmental effects may influence the productive characteristics of the animals (JERRY *et al*., 2012; WANG *et al*., 2013). MANZONI and SCHMITT (2006) reported that temperatures

Table 3. Estimation (standard deviation) of genetic additive (var_a), residual (var_e), family (var_f) and phenotypic (var_p) variance, narrow-sense heritability (h^2_a) and family heritability (h^2_f) for height and individual fresh weight of oysters at the juvenile and at harvest.

Variance/ Parameter	Juvenile		Harvesting	
	Height (mm)	Individual fresh weight (g)	Height (mm)	Individual fresh weight (g)
var_a	31.23 (6.32)	2.67 (0.55)	77.83 (13.87)	64.16 (12.11)
var_e	78.26 (3.86)	4.54 (0.30)	142.34 (8.12)	172.26 (7.75)
var_f	21.75 (6.93)	2.13 (0.74)	5.46 (5.43)	11.05 (7.96)
var_p	131.24 (7.53)	9.34 (0.74)	225.63 (8.75)	247.47 (9.51)
h^2_a	0.24 (0.05)	0.29 (0.06)	0.34 (0.05)	0.26 (0.05)
h^2_f	0.16 (0.05)	0.22 (0.07)	0.02 (0.02)	0.04 (0.03)

Table 4. Genetic additive correlations (standard deviation) (above diagonal) and correlations of family effect (below diagonal) between individual fresh weight and height of oyster at the juvenile phase and at harvesting.

Phase	Trait	Juvenile		Harvesting	
		Height (mm)	Individual fresh weight (g)	Height (mm)	Individual fresh weight (g)
Juvenile	Height (mm)	-	0.88 (0.12)	0.51 (0.11)	0.48 (0.12)
	Individual fresh weight (g)	0.71 (0.07)	-	0.60 (0.10)	0.85 (0.05)
Harvesting	Height (mm)	-0.16 (0.71)	-0.42 (0.94)	-	0.24 (2.06)
	Individual fresh weight (g)	0.70 (0.69)	0.37 (1.98)	0.88 (0.03)	-

Table 5. Estimation (standard deviation) of family variance (var_f), residual variance (var_e), variance of common environment effect (var_c), phenotypic variance (var_p), family heritability (h^2_f) and common environment effect (c^2) for yield, average individual fresh weight and survival.

Variance/ Parameter	Yield (kg)	Average individual fresh weight (g)	Survival (%)
var_f	0.31 (0.09)	63.81 (17.46)	1.81 (0.84)
var_e	0.13 (0.01)	27.15 (2.45)	8.34 (0.74)
var_c	0.12 (0.03)	17.21 (4.85)	0.84 (0.66)
var_p	0.56 (0.09)	108.17 (14.49)	10.96 (1.00)
h^2_a	0.54 (0.09)	0.58 (0.08)	0.16 (0.07)
c^2	0.22 (0.07)	0.16 (0.05)	0.08 (0.06)

Table 6. Genetic correlations (standard deviation) (above diagonal) and correlations of common environment effect (below diagonal) between yield, average individual fresh weight and survival at harvesting.

Traits	Yield (kg)	Average individual fresh weight (g)	Survival (%)
Yield (kg)	-	0.98 (0.03)	0.58 (0.39)
Average individual fresh weight (g)	0.81 (0.08)	-	0.47 (0.36)
Survival (%)	-0.14 (0.83)	0.21 (2.81)	-

higher than 28°C can cause mortality and slow the growth of *C. gigas* seeds. The best development of *C. gigas* in the waters of the State of Santa Catarina occurs in winter (POLI, 2004), with the lowest water temperatures. SÜHNEL *et al*. (2017) observes high mortality for seeds planted in end summer and lower mortality for seeds planted in the early and end autumn. Thus, for better performance it is preferable that to start the cultivation in periods with lower water temperature to ensure greater growth and survival of the animals.

The salinity during the experimental period presented a sharp decline between February and March (35 in February to 30 in March), but remained stable in the other months. The low salinity in these months may be related to a period with high rainfall, which may have increased the inflow of freshwater into the bay, causing the reduction of salinity. Data from the Meteorological Database for Teaching and Research (BDMEP, 2016) reinforce this hypothesis. During the cultivation period, a total accumulated rainfall of 2,060.5 mm was recorded in the region, above the accumulated average for the same period (1,666.74 mm) in the last five years.

The mean (SD) values of total particulate matter were similar (66.41 (8.45) mg L^{-1} from May to July 2008) to those reported by TURECK *et al*. (2014) and higher than those recorded by LAGREZE-SQUELLA (2008) (38.06 (14.87) mg L^{-1} from March to December 2007) for the same study area. Increasing values of total particulate matter were observed by CURTIUS *et al*. (2003) at Sambaqui beach in different sampling periods (10.7 (0.7) mg L^{-1} in April and 16.3 (2.1) mg L^{-1} in October 1999 and 12.5 (2.2) mg L^{-1} in April and 16.8 (1.5) mg L^{-1} in October 2000, respectively). The values observed for the PIM/POM ratio are below the stipulated value (3.5) by WALLACE and REINSNES (1985) with a critical value for *Chlamys islandica* growth. In fact, the seston may vary according to the collection season and be influenced by environmental and anthropogenic factors. The high amount of total particulate matter observed in this study can be related to the characteristics of the farming area that presents low depth (approximately 3-4 m) and proximity to the coast (1,500-2,000 m). Sea currents and winds can also act by influencing the movement of water bodies, carrying the particulate material from the bottom to the water column. The availability of food from the environment directly affects the growth of molluscs in the farms (PROENÇA, 2002) and although the bivalves select the filtered particles for ingestion or rejection (BAYNE *et al*., 1988), probably in environments with a higher concentration of suspended matter, there will be higher energy expenditure for selection of the edible fraction, which may interfere with growth.

Estimation of genetic parameters

Heritability

In the present study, the heritability estimates for the analyzed traits presented, in general, intermediate to high values, ranging from 0.16 (0.07) (for survival) to 0.58 (0.08) (for mean individual fresh weight). The heritability values registered for height (0.34 (0.05)) and individual fresh weight (0.26 (0.05)) at harvesting are lower than those reported by KONG *et al*. (2015), who reported values of narrow-sense heritability of 0.49 (0.25) for height and 0.35 (0.17) for fresh weight for *C. gigas* at 12 months of age.

Similar narrow-sense heritability values were estimated for individual fresh weight at the juvenile phase (0.29 (0.06)) and at harvesting (0.26 (0.05)). Nevertheless, the heritability for juvenile shell height (0.24 (0.05)) was lower than that observed at harvesting (0.34 (0.05)).

At harvesting, a medium-high narrow-sense heritability for individual fresh weight (0.26 (0.05)) and for height (0.34 (0.05)) was found, however for both traits family heritability (h_f^2) was low (0.02 (0.02) for individual fresh weight and 0.04 (0.03) for height), different from values for the juvenile phase (0.16 (0.05) for individual fresh weight and 0.22 (0.07) for height). The greatest family heritability for juveniles is probably due to that in larval stages and settlement family was represented by only one the farming unit (tank and container, respectively) and family variance is biased by common environmental effect.

The estimated family heritabilities for yield (0.54 (0.09)) and average individual fresh weight (0.58 (0.08)) were higher than those obtained for survival (0.16 (0.07)), indicating that the survival is more sensitive to environmental factors than growth. Moreover, the heritability values estimated in the present study were higher than the heritability values (0.00 (0.07); 0.313 (0.08)) reported by EVANS and LANGDON (2006). Other studies (TORO *et al*., 1995; DAVIS, 2000; ERNANDE *et al*., 2003; DÉGREMONT *et al*., 2007; DENG *et al*., 2009) have also reported estimates of heritabilities for oyster seed or juvenile growth ranging from 0.15 (0.08) (for Pacific oysters from 6 to 8 months of age) at 0.69 (0.11) (for 8 month old *Ostrea chilensis*). Meantime, in the present study, the genetic effect in the model was the family for yield, average individual fresh weight and for survival, so the estimates of heritabilities for those effects may contain,

in addition to the additive genetic effect, non-genetic additive effects, such as the dominance effect. NYQUIST and BAKER (1991) concluded that the estimator based on family variance is biased upward by small fractions of additive-by-additive types of epistatic variance in the numerator, compared to the formal definition of heritability (see NYQUIST and BAKER (1991); page 279) using ANOVA for data analysis; however, there are no reports on potential biases using mixed model combined with a relationship matrix. Furthermore, MELO *et al*. (2016) reported that the effects of common environment and dominance may be confused with the additive genetic effect making impossible an estimate of accurate heritability. Nevertheless, this is a difficult situation to consider in oyster breeding, given the difficulty of individual marking of the animals.

Moderate-high estimates of realized heritability (ranging from 0.34 (0.05) to 0.63 (0.04) were registered by DÉGREMONT *et al*. (2015) for *C. gigas*. In other studies (DÉGREMONT *et al*. 2007; DÉGREMONT *et al*. 2010), narrow-sense heritability (between 0.47 to 1.08) and realized heritability (between 0.55 (0.18) and 0.98 (0.15)) were reported for survival of *C. gigas*. The aforementioned values are higher than obtained in our study (0.16 (0.07)), however we considered only the final phase (approximately 60 to 170 days of age) to calculate heritability for survival. At this stage of cultivation, survival among families is generally more homogeneous than in the early stages, which may explain in part the lower estimate of heritability obtained in our study.

DÉGREMONT *et al*. (2010) found that, in oysters selected for survival, there was no influence of survival on growth at different farming sites, but an impact on yield was detected. In fact, yield is dependent on survival and average individual size (DÉGREMONT *et al*., 2007; MELO *et al*., 2016, and data from this study, see item 4.1.2), these traits directly affect the yield, so the mortality of oysters is a worrying factor in the production and selection for survival is crucial.

Correlations

In the present study, the lowest genetic correlation was found between average individual fresh weight and survival (0.47 (0.36)) and the highest, between average individual fresh weight and yield (0.98 (0.03)). MELO *et al*. (2016) also detected positive correlations between yield and survival of *C. gigas* oysters with genetic correlations ranging from 0.21 (0.07) to 0.96 (0.007) for third and second generation of selection, respectively. The positive correlation between yield and survival found in this study agrees with that reported by DÉGREMONT *et al*. (2015). However, in another study, DÉGREMONT *et al*. (2007) reported a negative genetic correlation (-0.17 (0.14)) between growth and survival for *Crassostrea gigas* at three cultivation sites in France. Negative genetic correlations between growth and survival traits may be related to competition for food or even stress sensitivity in fast-growing families (MELO *et al*., 2016) or simply by the increase in density within the farming units, reducing the space for growth.

In summary, the moderate to high heritability estimates obtained in this study indicate that productive traits of oysters can be increased by selection. The moderate to high positive correlations between the traits examined suggest that indirect gains can be achieved for all the traits studied. In this context, is recommended the use of yield, which is composed of survival and individual weight, and survival with selection criteria for *C. gigas* oysters in Brazil.

CONCLUSIONS

Moderate to high heritability estimates obtained in this study indicate that productive traits of oysters can be increased by selection. The moderate to high positive correlations between the traits examined suggest that indirect gains can be achieved for all the traits studied.

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