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Heritability, genetic correlations and genotype by environment interactions in productive traits of the Caribbean scallop, *Argopecten nucleus* (Mollusca: Bivalvia)

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ABSTRACT

Argopecten nucleus is a hermaphroditic scallop native to the Caribbean Sea, whose aquaculture production currently relies on hatchery-produced seed. Although this species exhibits a relatively fast growth, its survival, fecundity and commercial size are lower than those of other economically important pectinids. To assess the feasibility to improve productive traits in this species through selective breeding, heritabilities (h^2) and genetic correlations (r_G) for survival, fecundity and growth were estimated. The existence of genotype by environment interactions (GEI) associated with the culture depth, i.e. location of culture systems in the water column, ware also examined. Fifty sexually mature individuals were individually spawned, collecting female and male gametes separately. The sperm of one "male" was used to fertilize the eggs of four female individuals randomly chosen from the base population, generating 10 half sibling families and 40 full sibling families, in a nested experimental design. Shell length, height, and width, and total wet weight, were measured in 3.5 (juveniles) and nine (adults) months old progenies. Additionally, at 9 months the adductor muscle and remaining soft tissues wet weight were separately measured, and fecundity and survival recorded. The components of the phenotypic variance and heritabilities were estimated using an animal model. Most of the traits exhibited medium to high heritability ($h^2 \geq 0.26$), with the exception of shell width in juveniles and survival ($h^2 \leq 0.18$). h^2 estimations were generally higher in juveniles than in adults and h^2 for fecundity was not significantly different from zero. The growth related traits exhibit significant positive genetic correlations ($r_G \geq 0.69$), but were not genetically correlated with fecundity or survival. Interestingly, GEI in relation to culture depth were statistically significant. Results suggest a high potential response to direct and indirect selection, indicating that productive traits can be improved through selective breeding. The differential relative performance of different genotypes at different depths will be an important consideration to take into account in designing selective breeding plans for this species.

1. Introduction

The world production of scallops is steadily increasing, with most of it relying on fishing of natural populations and, more recently, on aquaculture production (Stotz, 2000). Due to the extreme deterioration of natural beds because of overfishing or their naturally extreme low density, the only sustainable production strategy is aquaculture (DiSalvo et al., 1984; Stotz, 2000). *Argopecten nucleus* is a pectinid species native from the Caribbean Sea, whose natural populations have very low density (Díaz and Puyana, 1994; Castellanos and Campos, 2007) and there are no known records for their extractive fisheries. The development of aquaculture technologies based on hatchery-derived seeds has allowed developing their production, commercialization and consumption, especially in local tourism oriented markets, conferring to *A. nucleus* a promising place in the Caribbean aquaculture (Velasco et al., 2013; Velasco and Barros, 2015; Valderrama et al., 2016).

Abbreviations: 3.5_m, 3.5 month; 9_m, 9 month; σ_P, standard phenotypic deviation; CV_A, additive genetic coefficient of variation; F, fecundity; FS, full siblings; G, potential selection gain; GEI, genotype by environment interactions; H, shell height; h^2, heritability; HS, half siblings; *i*, selection intensity; L, shell length; r_G, genotic correlations; r_P, phenotypic correlations; S, survival; T, shell width; V_A, additive genetic variance; V_R, residual variance; W_m, adductor muscle wet weight; W_t, total wet weight; W_{st}, soft tissue wet weight

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A. nucleus is a small scallop species with a continuous reproductive activity along the year. It is a functional simultaneous hermaphrodite with external fertilization, which normally involves the release the male gametes first and the female gametes afterwards (Velasco, 2008a). Adults of 9 months old can reach, on average, 40 mm in shell length (L) and 21 g total weight (W_t). Soft total tissues represent approximately 8 g of the total weight, with adductor muscle (W_m) representing approximately half of that. Survivals from D-larvae to post-larvae stage is about 25%, and mean fecundity of 1.9×10^6 eggs individual^{-1} (Velasco, 2008b, 2008c; Velasco et al., 2009, 2013; Velasco and Barros, 2015). Because of its small size, this species is sold commercially whole, in-shell, as a low-value clam. At the present, one of the key challenges to support *A. nucleus* aquaculture, making it more economically attractive, is to improve the size and net weight at harvest of farmed scallops. This can be achieved applying selective breeding programs.

Several studies have demonstrated that is possible to improve the growth rate in scallops through selective breeding (Stiles et al., 1996, 1998; Stiles and Choromanski, 1997; Ibarra et al., 1999; Pérez and Alfonsi, 1999; Zheng et al., 2006; Zhang et al., 2008; Liang et al., 2010; Liu and Liu, 2012). To respond to selection, a trait must be variable and, at least part of that variation must be heritable (Gjedrem and Baranski, 2009).

The heritability (h^2) estimates the proportion of the phenotypic variation attributable to the additive effect of genes, and it allows inferring the potential selection response for a specific trait in a population (Falconer and Mackay, 2006). There are several studies that report estimation of h^2 for traits such as length, height, and width of shell, total weight, growth and survival in different mollusk species (Toro and Newkirk, 1990; Ibarra et al., 1999; Ernande et al., 2003; Toro et al., 2004; Dégremont et al., 2007; Dégremont et al., 2010; Kvingedal et al., 2010; Wang et al., 2011; Liu and Liu, 2012; Brokordt et al., 2015a; Farías et al., 2017). For different populations of the same species, these estimations can show a large variation with age (Jónasson et al., 1999; Brokordt et al., 2015a), environmental conditions, and the estimation method being applied (Gjedrem and Baranski, 2009). In aquatic species, these estimations for productive traits are generally medium to high ($\geq$0.30 to $\geq$0.50) (Newkirk et al., 1977; Gjedrem, 1983; Wada, 1989; Gjedrem and Baranski, 2009), suggesting a high potential response to selection (Gjedrem and Baranski, 2009). In scallop, as in other mollusks, heritability for productive traits are medium to high, ranging from 0.24 to 0.93 for growth traits (Rawson and Hilbish, 1990; Toro and Newkirk, 1990; Hilbish et al., 1993; Alcapán et al., 2007; Guiñez et al., 2017); 0.03 to 0.60 for body weight (Toro and Newkirk, 1990; Ernande et al., 2004; Evans and Langdon, 2006; Alcapán et al., 2007), and 0.19 to 0.83 for survival (Evans and Langdon, 2006; Dégremont et al., 2007).

The selection in favor of a specific traits can generate a response that positively or negatively correlates to other important traits (Falconer and Mackay, 2006; Gjedrem and Baranski, 2009). The magnitude and direction of this response can be estimated if the genetic correlations between those traits are known (Falconer and Mackay, 2006; Lynch and Walsh, 1998), providing the opportunity to correct possible undesirable effects when applying a selective breeding program. Furthermore, selection can be applied on a trait genetically correlated to that of interest when this latter cannot be directly measured in the potential broodstocks, when the error in its measurement is too large, or when its heritability is low (Falconer and Mackay, 2006). In scallops, the most important productive trait is the adductor muscle and gonad weight. In some markets, like USA and Canada, only the adductor muscle is sold and consumed, while in Europe both adductor muscle and gonad are consumed (Pacheco-Aguilar et al., 2001). Due to its small size, *A. nucleus* is sold and consumed in its own shell, therefore the main productive traits are total weight and shell length. Since this species becomes sexually mature at 3 months old (Velasco, 2008a), it is important to know the genetic correlation between productive traits at this age, in addition to the correlation at harvest age, information that would allow a better design of selective breeding programs.

In order to assess the feasibility to improve productive traits in *A. nucleus* through selective breeding, the purpose of this study was to estimate the variability of the growth traits in families of full siblings (FS) and half siblings (HS) of this species, and the components of the phenotypic variance for different productive traits were estimated. Heritabilities, genetic correlations and expected selection gains for these characters were estimated in juveniles and adults scallops.

2. Materials and methods

2.1. Broodstock sourcing and conditioning

One hundred and fifty adult individuals of *A. nucleus* (> 40 mm shell length) were randomly chosen from a population derived from wild spat collected in Neguanje bay, Santa Marta, Colombia (11°20′03″ N, 74°09′24″ W), which were provided by the Instituto de Investigaciones Marinas y Costeras (INVEMAR, Santa Marta). They were transported under wet and cold conditions (18 °C) to the Laboratorio de Moluscos y Microalgas of the Universidad del Magdalena in Taganga, Santa Marta. Animals were conditioned following the Velasco and Barros (2007) protocols, with filtered (1 μm) and UV-treated seawater at 25 ± 1 °C, salinity of 37 ± 2 ppt, and continuous aeration. They were drip-fed daily with a 1:1 mixture of *Isochrysis galbana* and *Chaetoceros calcitrans*, at a rate that allowed to keep a density of 40 cells μL^{-1} in the culture tank, based on an average clearance rate of 5.8 L h^{-1} previously reported for scallops of the same size (Velasco, 2006, 2007). The animals were kept under these conditions until they reached the highest maturity state (State IV: bright and completely ripe gonad).

2.2. Obtaining of gametes and fertilization

Mature scallops (n = 56; state IV) were individually tagged adhering a paper label to the shell using epoxic glue. Shell length (L), height (H), width (T) and total wet weight (Wt) of each animal was recorded. Six spawning events were performed between September 2014 and September 2015, following the protocol described by Velasco et al. (2007). The shell surface of each brooder was cleaned with a brush to remove epibionts and then exposed to the air for 30 min. After that, they were put back in a tank with seawater and a high concentration of microalgae (560 ± 20 cells μL^{-1}) at 22 °C for 30 min, followed by filtered clean water renewal at 30 °C for another 30 min. After scallops release the first gametes pulse, they were washed with filtered seawater and transferred to individual 8 L containers to collect gametes. Prior to fertilization, a 10 mL aliquot was taken from each container with oocytes to estimate selfing rate (Winkler and Estévez, 2003).

The mating was performed following a nested design, in which each individual chosen as male was crossed with four females haphazardly chosen from the population, generating 40 full sib families (FS) and 10 half sib families (HS). Among 4 to 8 FS families were formed in each spawning event. Fertilization was carried out by adding aliquots of seawater having sperms from each "male" (10 mL) to the containers containing oocytes of each "female".

2.3. Embryos, larvae and post-larvae rearing

Embryos from each FS family were placed in cylindrical tanks (500 L) at a density of approximately 3 embryos mL^{-1}. The culture of embryos and larvae was performed following the Velasco and Barros (2008) protocols, without aeration during the first day. After the first day, aeration was added and larvae were maintained with full water renewals every 2 days, and daily fed with a 1:1 mixture of *I. galbana* and *C. calcitrans* (40 cells μL^{-1} day^{-1}), keeping a density of 2 larvae mL^{-1} from days 1 to 9, and a density of 0.7 larvae mL^{-1} afterwards.

Table 1
Mean values for productive traits in *A. nucleus*, additive genetic variance (V_A), residual variance (V_R), heritability (h^2 ± se), additive genetic coeficient of variance (CV_A) and hoped genetic gain (G) at 3.5 and 9 month age. Length (L), height (H) and width of shell (T); total wet weight (Wt), soft tissues weight (Wst), adductor muscle weight (Wm), survival (S) and fecundity (F). m: month age.

Trait	n	Mean ± SD	V_A	V_R	h^2 ± se	CV_A	G	G (%)
$L_{3.5m}$ (mm)	1988	20.5 ± 4.9	10.21	3.12	0.76 ± 0.14*	0.16	7.8	37.9
$H_{3.5m}$ (mm)	1988	20.2 ± 4.5	7.68	4.17	0.65 ± 0.13*	0.14	6.1	30.1
$T_{3.5m}$ (mm)	1988	9.0 ± 2.6	2.19	9.83	0.18 ± 0.06*	0.16	1.0	11.0
$Wt_{3.5m}$ (g)	1988	2.5 ± 1.0	0.74	0.72	0.51 ± 0.13*	0.34	1.1	42.0
L_{9m} (mm)	839	40.9 ± 3.5	2.82	7.89	0.26 ± 0.09*	0.04	1.9	4.6
H_{9m} (mm)	839	38.6 ± 3.0	2.68	5.25	0.34 ± 0.10*	0.04	2.1	5.4
T_{9m} (mm)	839	22.8 ± 2.1	1.42	2.76	0.34 ± 0.10*	0.05	1.5	6.5
Wt_{9m} (g)	839	18.6 ± 4.3	6.47	9.32	0.41 ± 0.11*	0.14	3.6	19.4
Wst_{9m} (g)	530	7.5 ± 2.2	1.29	1.59	0.45 ± 0.17*	0.15	2.0	27.2
Wm_{9m} (g)	530	2.4 ± 0.9	0.44	0.15	0.74 ± 0.19*	0.28	1.4	56.2
S_{9m} (%)	40	30.0 ± 15.6	0.040	0.16	0.20 ± 0.05*	0.01	6.4	21.5
F_{9m} (ooc × 10^6 animal^{-1})	839	1.5 ± 0.1	0.022	0.57	0.04 ± 0.03	–	–	–

* $P < .05$.

When 50% of larvae developed the eye spot, 24 polypropylene onion bags (70 × 90 cm and ∅ = 1 cm) conditioned for 5 days in microalgal suspensions of *I. galbana* and *C. calcitrans* were introduced in each cylindrical tank (500 L) for settlement. Larvae were maintained at a density of 0.7 larvae mL^{-1}, daily fed with *I. galbana* and *C. calcitrans* (1:1) at a single dose equivalent to 40 cells µL^{-1} day^{-1} (Velasco and Barros, 2009). During the first 48 h, temperature was kept at 20 ± 1 °C to stimulate the larvae settling, and set to 25 ± 1 °C afterward.

2.4. Post-larvae and juveniles grow-out

Collectors containing post-larvae were placed individually inside polypropylene mesh bags (30 × 80 cm and ∅ = 1 mm). A total of 8 bags with spats from each FS family were randomly tied up in pairs at the end of 4 labeled rope lines of three different lengths (1; 3 and 5 m), and transported to the aquaculture station of the Universidad del Magdalena in Taganga bay (11°16′04″ N, 74°11′36″ W). The ropes were randomly distributed in 4 different sections along a 100 m long-line, and replicates of every FS family were suspended at each of the 3 different depth-levels (6, 8 and 10 m), with 8 collector bags per depth-level in each section of the long-line. After 45 days, when the scallops were 2.5 months old, bags were extracted from the sea, juveniles were manually removed from collecting bags and transferred to pearl nets (30 × 30 cm and mesh ∅ = 6 mm), with a 30% of bottom coverage, and then re-suspended in the long-line at the same depth-levels from which collectors were extracted.

After 1 month in these conditions, i.e. approximately at 3.5 months old, 33 juveniles from each FS family maintained at each depth-level (99 in total) were individually tagged with a label with the family code adhered to the shell with synthetic glue epoxy resin. For each individual, length (L), height (H) and width (T) of shell were measured using a caliper (± 0.1 mm) and total weight (Wt) was measured with a digital balance (± 0.01 g). Individuals from different FS families coming from the same depth-level were mixed and transferred to 10 tier lantern nets (50 cm diameter, 2 m height and mesh ∅ = 6 mm), with a 30% coverage of the net bottom. Then, they were suspended in the long-line at the same position and depth-level as before, keeping the animals in the same conditions for another 6 months, following Velasco et al. (2009) procedures. Once a month, water temperature and salinity were measured with a mercury thermometer and a refractometer (± 1 ppt), respectively, and the seston and its organic content were analyzed according to Strickland and Parsons (1972). Measurements were taken again at the end of the farming period (9 months old), plus the number of live animals per family. Survivorship (S) was estimated as the rate of individual recovery per family from the base of 99 juveniles. Twenty individuals were randomly chosen from each deep group of each FS family (60 scallops per family), and transferred to the laboratory. Those animals were conditioned and induced to spawn as previously described, and two samples of the produced oocytes (1 mL) were counted under the microscope. Individual fecundity (F) was estimated as the number of oocytes produced per individual. After that, individuals were sacrificed and dissected, and wet weight of adductor muscle (Wm) and the remaining soft tissues (Wst) were separately measured.

2.5. Genetic and statistical analysis

The components of the phenotypic variance (V_P) and heritabilities (h^2), as well as genetic correlations (r_G) between traits at 3.5 and 9 month, were estimated using an animal model, which includes HS and FS families data (Lynch and Walsh, 1998) based on the Restricted Maximum Likelihood (REML) model (Johnson and Thompsom, 1995). Survival was treated as a threshold trait using a probit model (Falconer and Mackay, 2006).

The general statistical model was:

$$\boldsymbol{y} = X\boldsymbol{\beta} + Z\boldsymbol{a} + Z\boldsymbol{d} + \boldsymbol{e} \quad (1)$$

where $\boldsymbol{y}$ is the vector for observations in all individuals, $\boldsymbol{\beta}$ is the vector for fixed and covariate effects, $\boldsymbol{a}$ is the vector for additive genetic effects (random), $\boldsymbol{d}$ is the effect of the random non-genetic quantitative variables and $\boldsymbol{e}$ is the vector for residual errors. Both X and Z are known incidence design matrices (Lynch and Walsh, 1998). The components of the phenotypic variance were estimated using the software ASReml version 4.0 (Gilmour et al., 2009). Prior to the estimation of genetic parameters, the significance of fixed (culture depth and date of birth), random (position of the culture systems in the long-line and maternal effects) and covariate (self-fertilization rate, temperature and seston) effects were verified. The statistical significance of fixed and covariate effects were estimated using Wald F statistic. Maternal/common environment effects were estimated comparing the results of the model including dams in the pedigree with those considering dams as a random effect. The significance of random non-additive genetic effects were verified using a log-likelihood ratio test (log-LR test) (Lynch and Walsh, 1998). Statistically significant effects were included in the model for the estimation of the components of the phenotypic variance and heritability. When the inclusion of more than one factor does not change the estimation of the phenotypic variance components, only one of those variables was included in the model. Consequently, the models for juveniles include the fix effects of position in the long line for shell length; age and depth for shell width and high; birth date for weight. For adult scallops the model included mean water temperature along the grow up period as a covariate effect and the culture depth as a fixed

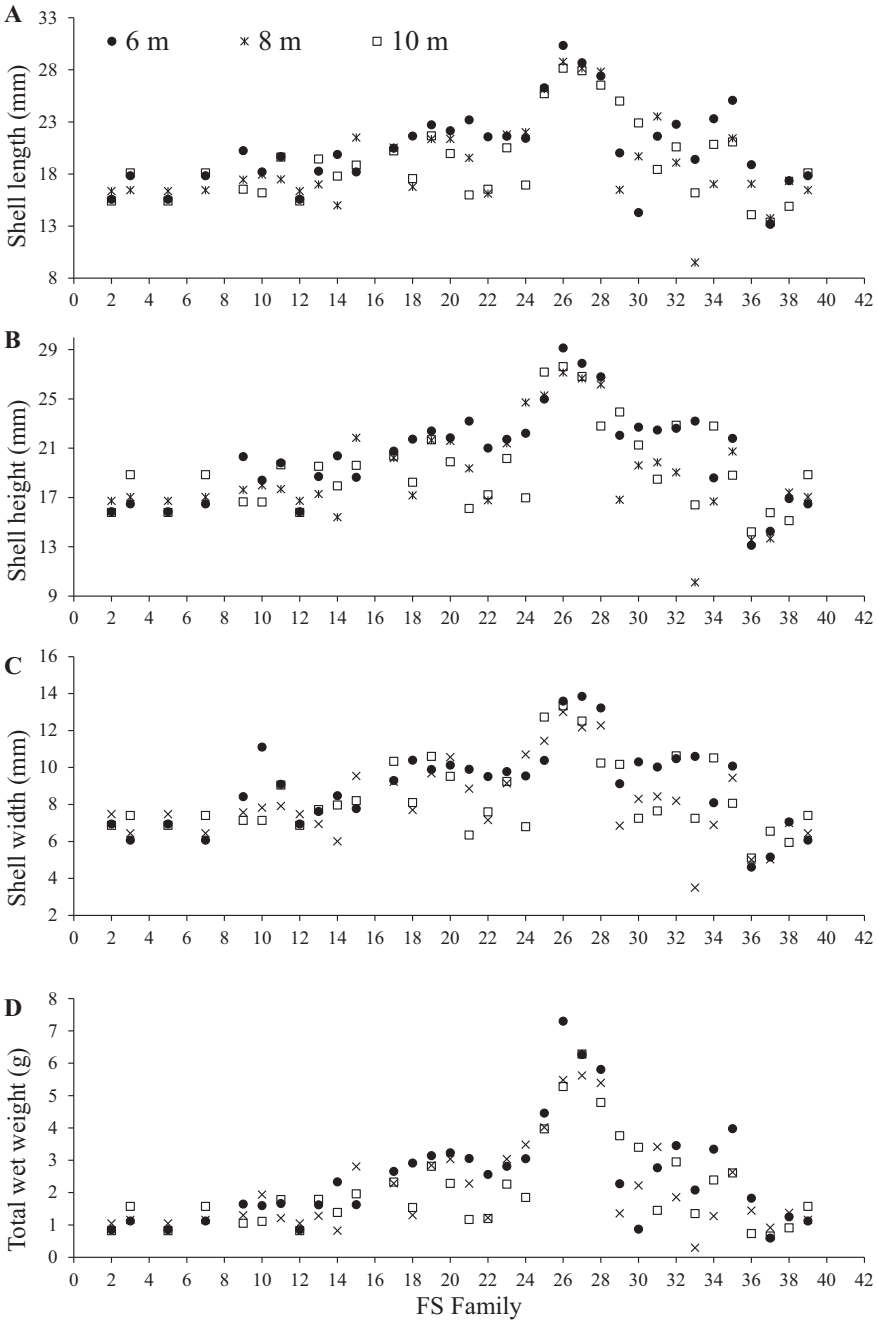

Fig. 1. Family mean values of juvenile (3.5 month old) growth traits of *A. nucleus* grown at different depths in Taganga Bay. (A) Shell length, (B) height (C), width and (D) total wet weight.

effect, except for adductor muscle weight, that only included the mean temperature.

The heritabilities (h^2) was estimated as the ratio of the additive genetic variance with respect to the phenotypic variance (Kruuk, 2004; Falconer and Mackay, 2006) and its statistical significance was verified using the log-LR test (Lynch and Walsh, 1998). The r_G were estimated with a bivariate animal model using the ASReml 3.0 software (Gilmour et al., 2009). The statistical significance of the genotypic correlations between traits were estimated using the log-LR test (Lynch and Walsh, 1998). All phenotypic correlations (r_P) between traits were estimated based on the Pearson correlation between traits using the software Statgraphics Centurion XVII X64.

The potential selection response for each character was estimated as:

$$G = ih^2\sigma_P \quad (2)$$

where i is the selection intensity and σ_P the standard phenotypic deviation of the trait. All estimations were performed assuming the selection of the superior 5% of the population as broodstock ($i = 2.06$) (Falconer and Mackay, 2006). The correlated response was:

$$CG = ih_x h_y r_G \sigma_{Py} \quad (3)$$

where h_x and h_y are the square roots of the heritabilities for the selected (x) and the correlated traits (y), respectively; r_G the genetic correlation between traits x and y, and σ_{Py} is the standard deviation of the trait y (Falconer and Mackay, 2006).

The existence of genotype by environment interactions (GEI) for each trait, measured in juveniles and adults, were confirmed using a factorial ANOVA (Truberg and Hühn, 2000), with FS families and culture depth level as factors. Data normality and homoscedasticity for each variable was verified in advance. All the analyses were performed using the statistical software Statgraphics Centurion XVII X64, with an

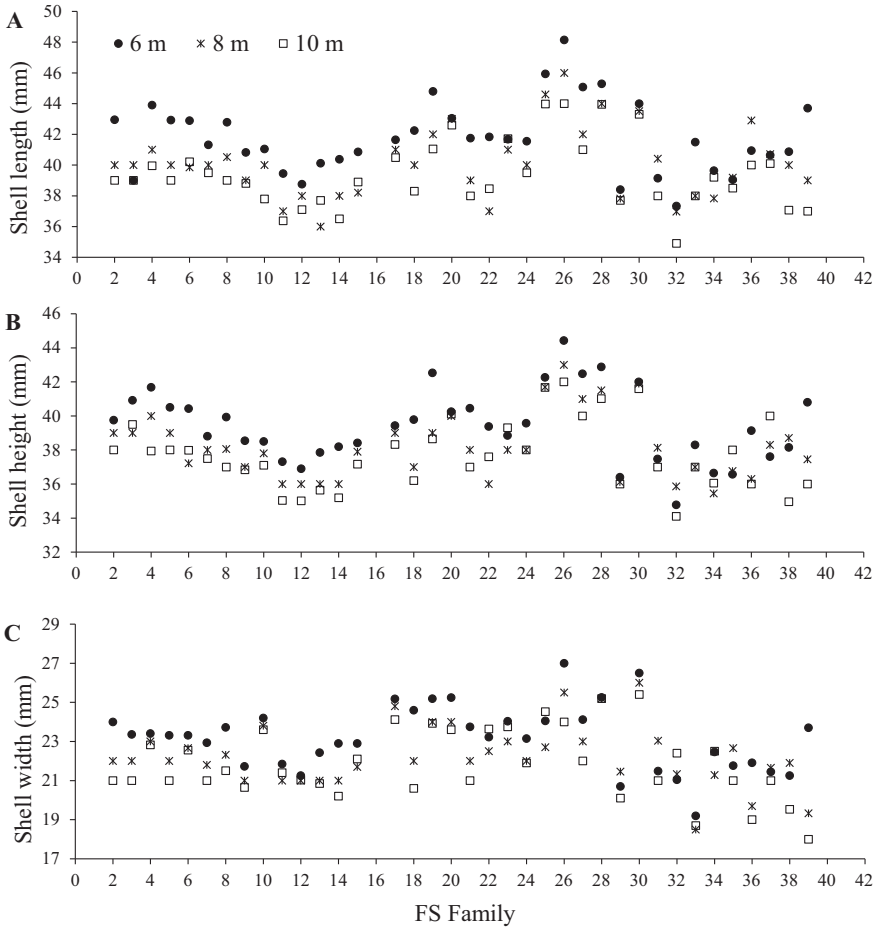

Fig. 2. Family mean values of adult (9 month old) growth traits of *A. nucleus* grown at different depths in Taganga Bay. (A) Length, (B) height (C) and width of shell.

alpha of 0.05 for significance decisions.

3. Results

Thirty-eight of 40 mating produce juveniles and two FS families were lost during the grow-out period. The average length of scallops at 3.5 and 9 months old are shown in Table 1. A large between FS families variation was observed in productive traits, with ranged from 13 to 29 mm in shell length (Fig. 1A), 13 to 28 mm in shell height (Fig. 1B), 5 to 13 mm for shell width (Fig. 1C), and 0.72 to 6.02 g in total weight (Fig. 1D) in 3.5 months old scallops. Similar variation was also observed in 9 months old scallops, with 37 to 46 mm for shell length (Fig. 2A), 35 to 43 mm for shell height (Fig. 2B) and 19 to 25 mm shell width (Fig. 2C). Averages for total weight (Fig. 3A), weight of soft tissue (Fig. 3B) and adductor muscle weight (Fig. 3C) also exhibited a large between families variation. The weight of soft tissues and adductor muscle at 9 months represent, on average, 40% and 13% of the total weight, respectively. The survival range, from 10% to 68%, exhibit a different pattern between FS families at different depths (Fig. 4A). In turn, scallops produce from 0.19 to 1.9 $\times$ 10^6 eggs animal^{-1} after being induced to spawn, with no obvious different patterns associated with the depth where individuals were grow-out (Fig. 4B).

During the timespan from juveniles to adults (November 2015 to May 2016), the water temperature was between 25 and 29 °C, and the salinity remained relatively constant, between 35 and 37 ppt. The concentration of seston in the water was between 2 and 8 mg L^{-1}, with 21 to 61% of organic content. Self-fertilization levels range from 0 to 25% among different crosses.

The culture depth had significant effects ($P < .001$) in 3.5 months old scallops on shell width (T) and height (H), and at 9 months on shell length (L), height and width, as well as on total weight (Wt), soft tissues weight (Wst) and survival (S). Similarly, the birth date had a significant effect on total weight (Wt) at 3.5 months ($P < .001$). The self-fertilization percentage exhibited a covariate effect on the shell width and height only at 3.5 months old ($P < .05$), but not on other traits at this age nor in 9 months old scallops ($P > .05$). Mean water temperature over the grow-out period also had covariate effects on shell length, height and width, as well as on total weight, weight of soft tissues and adductor muscle weight, at 9 months ($P < .05$), but not seston amount ($P > .05$). The simultaneous inclusion of birth date and temperature did not produce changes on the estimation of the phenotypic variance components at this age. Finally, the position of the culture systems in the long-line had significant effects only on shell length at 3.5 months old. No significant maternal/common environment effects were detected for any trait ($P > .05$).

The juvenile growth traits showed higher proportion of additive genetic variability ($CV_A \geq 0.14$; Table 1), than adults ($CV_A \leq 0.05$), with the exception of total weight, and weight of soft tissues and adductor muscle ($CV_A \geq 0.14$). The heritabilities for all the traits measured in juveniles and adults, excluding fecundity, were significantly different from zero ($P < .05$; Table 1). Most of the h^2 estimations were moderate to high ($h^2 = 0.18$–0.76), excepting for adult fecundity which was no different from zero ($h^2 = 0.04$; $P < .05$), being h^2 usually lower in adults than in juveniles (Table 1).

The expected responses to direct selection were moderate to very high (4.6 to 56.1% per generation), depending on the trait and age of the animals being selected. Adductor muscle weight exhibit highest potential of response to selection and adult shell length the lowest one (Table 1). In accordance with the observed heritabilities and CV_A, the expected selection responses for the most traits were higher in juveniles

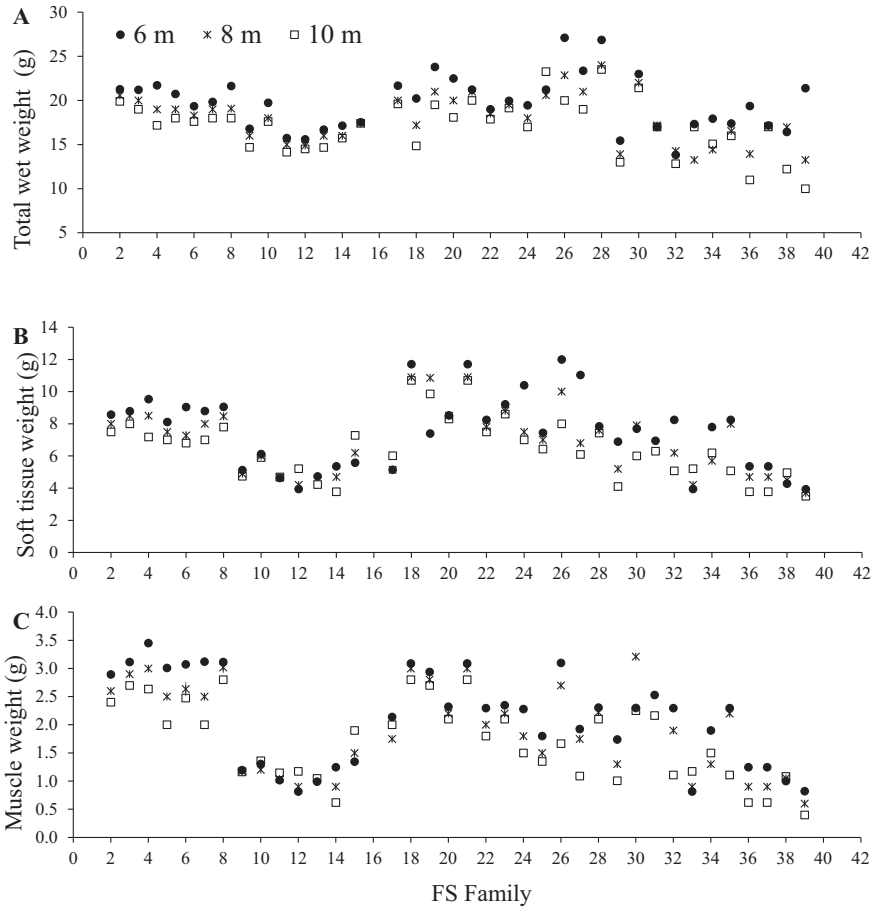

Fig. 3. Family mean values of adult (9 month old) growth traits of *A. nucleus* grown at different depths in Taganga Bay. (A) Total wet weight, (B) soft tissues weight and (C) adductor muscle weight.

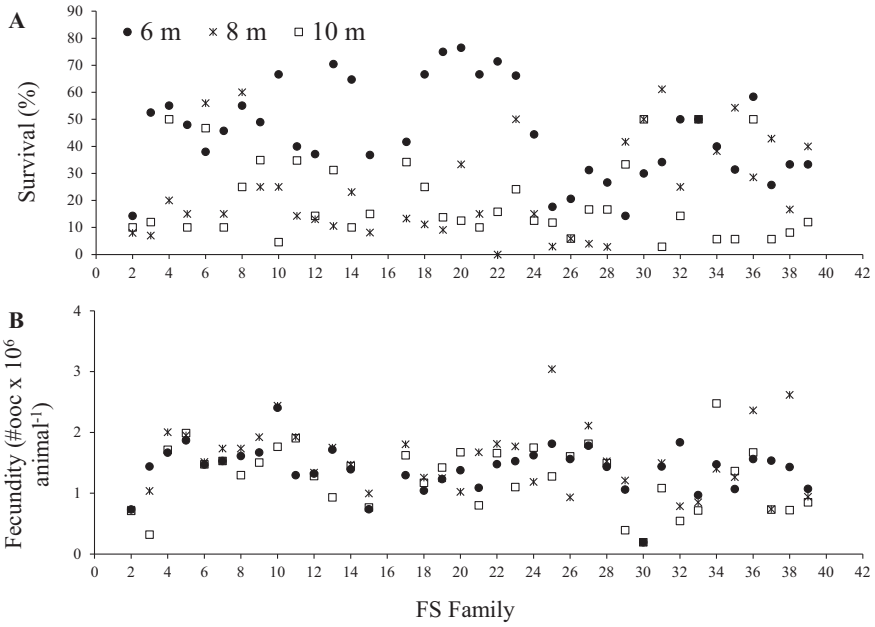

Fig. 4. Family mean values of survival (A) and fecundity (B) of *A. nucleus* adults (9 month old) grown at different depths in Taganga Bay.

(11.0 to 42.0%) than in adults (4.6 to 19.4%) (Table 1).

The phenotypic and genotypic correlations between growth traits measured in 3.5 and 9 month old scallops were positive and significant ($P < .05$; Tables 2 and 3). The r_P between survival and other traits in adults were low and negative ($P < .05$), but the r_G were even lower and not significant ($P > .05$; Tables 3 and 4). Phenotypic correlations between fecundity and other traits were no significantly different from zero ($P > .05$), and genetic correlations could not be estimated. Genetic correlations between age groups, i.e. juveniles and adults, were positive and significant ($P < .05$) for all traits (Table 4) although moderate ($r_G \leq 0.73$), with the exception of survival ($P > .05$). In general, juvenile total weight shows the highest genetic correlation with all the adult traits ($r_G \geq 0.44$), with the exception of the shell width and adductor muscle weight, that look best genetically correlated

Table 2
Genetic (above the diagonal) and phenotypic (under the diagonal) correlations between the production traits of *A. nucleus* juveniles of 3.5 month old. Length (L), height (H), and width of shell (T); total wet weight (Wt). n = 1765. m: month age.

Traits	$L_{3.5m}$	$H_{3.5m}$	$T_{3.5m}$	$Wt_{3.5m}$
$L_{3.5m}$	–	0.876*	0.835*	0.939*
$H_{3.5m}$	0.282*	–	0.316*	0.882*
$T_{3.5m}$	0.277*	0.937*	–	0.792*
$Wt_{3.5m}$	0.465*	0.424*	0.386*	–

* $P < .05$.

with shell high (Table 4).

The expected correlated responses to selection range from 2.7 to 48.3% per generation, depending on the traits and age that selection is exerted (Table 5). These estimations show that the use of juvenile shell length as selection criteria would produce the highest correlated response to selection on juvenile total weight (48.3%), adult total weight (19%) and adductor muscle weight at harvest (27%) (Table 5). In adults, in turn, higher gain in total weight at harvest per generation would be obtained by directly selecting for total wet weight, criteria that can also produce the highest correlated gain on adductor muscle weight (33.8%; Table 5).

Growth traits exhibit significant differences between families and culture depth, as well as genotype-environment interactions (Table 6; $P < .001$), with the only exception of the weight of soft tissues in adults that did not showed significant GEI (Table 6; $P > .05$). No significant effects of family, culture depth and genotype-environment interaction were found for fecundity or survival ($P > .05$).

4. Discussion

In general, the results provide evidence of relatively high levels of additive genetic variance in juveniles of *A. nucleus*, and lower levels in adults. Similarly, heritabilities for productive traits were medium to high in juveniles, but they were low to medium in adults. However, the potential selection response is high to very high (> 5% per generation) for most traits, in spite of the large variation between traits and among ages. The genetic correlations between traits, with the exception of those related to fecundity and survival, were positive and significant, which would allow to obtain correlated selection responses to improve productive traits. The culture depth had significant effects on most of the traits variation, with significant genotype by environment interactions for most of them.

The average values of shell length, survival and fecundity of *A. nucleus* at 3.5 and 9 months old were similar to those previously reported for the same species (Lodeiros et al., 1993; Velasco et al., 2007; Velasco et al., 2009; Gómez-León et al., 2010; Valderrama et al., 2016). They were also similar to those observed in other small pectinid species such as *Argopecten irradians concentricus* (Crenshaw Jr. et al., 1991) and *Argopecten gibbus* (Sarkis and Lovatelli, 2007). This suggests that our results reasonably represent the performance of this species in farming conditions, and thus it would be extrapolated to similar studies.

Table 4
Genetic correlations between productive traits of juveniles (3.5 month old) and adults (9 month old) *A. nucleus*. Length (L), height (H), and width of shell (T); total wet weight (Wt), soft tissue wet weight (Wst), adductor muscle weight (Wm) and survival (S). n = 325. m: month age.

Traits	L_{9m}	H_{9m}	T_{9m}	Wt_{9m}	Wst_{9m}	Wm_{9m}	S_{9m}
$L_{3.5m}$	0.727*	0.674*	0.580*	0.686*	0.501*	0.430*	0.126
$H_{3.5m}$	0.581*	0.581*	0.632*	0.599*	0.553*	0.572*	0.018
$T_{3.5m}$	0.667*	0.656*	0.580*	0.603*	0.520*	0.499*	0.110
$Wt_{3.5m}$	0.728*	0.692*	0.605*	0.689*	0.590*	0.437*	0.059

* $P < .05$.

The heritabilities for most of the growth related traits in juveniles and adults of *A. nucleus* are at the upper limit of the range of realized heritabilities reported in other scallop species. For example, h_r^2 for shell length in *Argopecten irradians irradians* at 3 and 8 month range from 0.07 to 0.34 (Zheng et al., 2004; Zheng et al., 2006); total weight and shell width h_r^2 in 7 month old *Argopecten ventricosus* were of 0.33 to 0.59 and 0.10 to 0.18, respectively (Ibarra et al., 1999). The occurrence of self-fertilization is a factor that could spuriously increase the h^2 estimations (Falconer and Mackay, 2006; Gjedrem and Baranski, 2009; Toro et al., 2009). In the present study, self-fertilization only showed a covariate effect on shell height and width at 3.5 months old, but not on other traits at juvenile or adult stages and is unlikely to significantly affect the estimated h^2 values.

Lower heritabilities estimations for survival and fecundity ($h^2 < 0.2$) have being reported for other bivalves, such as *A. ventricosus* (Ibarra et al., 1999), *C. gigas* (Ernande et al., 2003) and *P. maxima* (Kvingedal et al., 2010), than those found in this study. According to Fisher's (1930) theorem, low heritability values are expected in traits that have a high impact on fitness. Fecundity and survival are in direct relation to biological fitness (Falconer and Mackay, 2006), therefore low h^2 values are expected for them. In *A. nucleus*, the CV_A for both traits were low (≤ 0.04), which agrees with this hypothesis, suggesting that most of the observed variation is related to non-genetic additive factors. However, although virtually all the individuals are reproductive in 9 month old adults, and conditioning synchronized their sexual maturation, this species is a partial spawner (Velasco et al., 2007). This means that the observed phenotypic variation in fecundity could be associated to this spawning offset. This phenomenon would also explain the low heritability for the weight of soft tissues in scallops, which also include the post-spawn gonad, in contrast to the high values estimated for total weight and adductor muscle weight.

The decrease of h^2 estimations with age in *A. nucleus*, observed for most of the measured traits, is similar to previous reports for shell length, width and weight in *Chlamys nobilis* (Liu and Liu, 2012), *Mytilus chilensis* (Alcapán et al., 2007), *Mytilus edulis* (Strömgren and Nielsen, 1989) and *P. maxima* (Kvingedal et al., 2010). On the contrary, in many bivalve species like *A. irradians irradians* (Zheng et al., 2004), *Euvola*

Table 3
Genetic (above the diagonal) and phenotypic (under the diagonal) correlations between productive traits in 9 month old *A. nucleus* adults. Length (L), height (H), and width of shell (T); total wet weight (Wt), soft tissue wet weight (Wst), adductor muscle weight (Wm) and survival (S). n = 325. m: months of age.

Traits	L_{9m}	H_{9m}	T_{9m}	Wt_{9m}	Wst_{9m}	Wm_{9m}	S_{9m}
L_{9m}	–	NE	0.914*	0.981*	0.834*	0.730*	−0.032
H_{9m}	0.868*	–	0.902*	0.976*	0.809*	0.692*	−0.068
T_{9m}	0.686*	0.896*	–	0.955*	0.850*	NE	−0.064
Wt_{9m}	0.858*	0.809*	0.791*	–	0.833*	0.704*	−0.073
Wst_{9m}	0.658*	0.629*	0.547*	0.697*	–	0.910*	−0.180
Wm_{9m}	0.498*	0.409*	0.464*	0.572*	0.905*	–	−0.121
S_{9m}	−0.342*	−0.334*	−0.252*	−0.407*	−0.448*	−0.476*	–
F_{9m}	−0.011	0.040	0.035	0.045	0.090	0.006	−0.012

* $P < .05$.

Table 5
Relative expected correlated response (CG%) to selection in *A. nucleus* after selecting on a genetically correlated traits (i = 2.06). Length (L), height (H), and width of shell (T); total wet weight (Wt), soft tissue wet weight (Wst), adductor muscle weight (Wm) and survival (S). NE = not estimable, n = 650. m: month age.

Selected trait	Correlated response in secondary trait (%)									
	$L_{3.5m}$	$H_{3.5m}$	$T_{3.5m}$	$Wt_{3.5m}$	L_{9m}	H_{9m}	T_{9m}	Wt_{9m}	Wst_{9m}	Wm_{9m}
$L_{3.5m}$ (μm)	–	28.6	18.7	48.3	6.0	5.7	5.7	18.8	7.1	27.1
$H_{3.5m}$ (μm)	28.2	–	19.4	41.8	4.4	4.5	5.7	15.1	7.2	33.3
$T_{3.5m}$ (μm)	8.2	8.7	–	19.9	2.7	2.7	2.8	8.1	3.6	15.4
$Wt_{3.5m}$ (g)	5.9	5.2	14.5	–	3.9	5.0	5.6	13.5	8.0	30.4
L_{9m} (mm)	12.0	8.9	9.2	18.4	–	NE	5.5	16.5	7.2	28.3
H_{9m} (mm)	10.7	8.6	10.1	25.8	NE	–	6.1	18.4	NE	30.0
T_{9m} (mm)	6.4	6.5	8.8	24.2	5.1	5.2	–	17.7	8.2	NE
Wt_{9m} (g)	17.1	13.9	10.2	23.6	6.1	6.2	7.1	–	NE	33.8

Table 6
Two factors ANOVA of the effect of family and culture depth on the variation of different quantitative traits in the Caribbean scallop *A. nucleus*. Length (L), height (H), and width of shell (T); total wet weight (Wt), soft tissue wet weight (Wst), adductor muscle weight (Wm), survival (S) and fecundity (F), m: month age.

Trait/stage	Source of variation	Sum of squares	df	Square means	F
$L_{3.5m}$	A: Family	29,118.10	37	1004.07	152.52*
	B: Depth	377.89	2	188.94	28.70*
	A × B interaction	2821.29	74	48.64	7.39*
$H_{3.5m}$	A: Family	21,851.50	37	753.50	112.96*
	B: Depth	418.50	2	209.25	31.37*
	A × B interaction	3046.06	74	52.52	7.87*
$T_{3.5m}$	A: Family	6890.71	37	237.61	100.76*
	B: Depth	134.54	2	67.27	28.53*
	A × B interaction	1163.51	74	20.06	8.51*
$Wt_{3.5m}$	A: Family	3955.83	37	136.41	151.07*
	B: Depth	36.71	2	18.36	20.33*
	A × B interaction	324.65	74	5.60	6.20*
L_{9m}	A: Family	80,355.90	37	2770.89	256.44*
	B: Depth	2362.15	2	1181.07	109.30*
	A × B interaction	6610.89	74	113.98	10.55*
H_{9m}	A: Family	87.95	37	3.03	165.58*
	B: Depth	2.33	2	1.16	63.56*
	A × B interaction	9.43	74	0.16	8.88*
T_{9m}	A: Family	23,912.20	37	824.56	214.89*
	B: Depth	507.45	2	253.72	66.12*
	A × B interaction	2292.12	74	39.52	10.30*
Wt_{9m}	A: Family	36,674.00	37	1264.62	45.57*
	B: Depth	4371.57	2	2185.79	78.76*
	A × B interaction	9616.65	74	165.80	5.97*
Wst_{9m}	A: Family	204.77	37	17.06	9.47*
	B: Depth	15.97	2	15.97	8.86*
	A × B interaction	36.87	74	3.07	1.71
Wm_{9m}	A: Family	33.58	37	2.80	18.71*
	B: Depth	1.75	2	1.75	11.69*
	A × B interaction	4.31	74	0.36	2.40*
S_{9m}	A: Family	50,385.90	37	2580.86	253.44
	B: Depth	2362.15	2	1021.10	111.30
	A × B interaction	6520.88	74	113.98	10.50
F_{9m}	A: Family	4.28E7	37	1.38E6	2.27
	B: Depth	1.15E6	2	576,925	0.95
	A × B interaction	4.51E7	74	726,733	1.19

* $P < .01$.

ziczac (Pérez and Alfonsi, 1999), *Mercenaria mercenaria* (Hilbish et al., 1993), *Ostrea edulis* (Toro and Newkirk, 1990), an increase of h^2 for morphometric characters with age has been reported. This has being attributed to a greater physiological adaptation to the environment at an older age, which would reduce the sensitivity to environmental conditions and, consequently, the environmental variance, thus generating an increase in the heritability of such traits (Gjedrem, 1983). In abalone, in turn, the increase of h^2 with age has been related with the decrease in the maternal/common environment effects (Brokordt et al., 2015a). Contrarily, the decline of h^2 with age in *A. nucleus* can be caused by asynchrony in the sexual maturation or partial spawning, which could cause a rise in the residual variance of the traits, or by the progressive accumulation of environmental effects that reduce the covariance among relatives. This would agree with the drastic decrease of the coefficient of genetic variation (CV_A) observed in adults versus juveniles. This is an interesting point because CV_A is considered a better estimator of the evolvability, i.e. the capability to evolve as consequence of selective pressures, of a trait than h^2, because a low h^2 can be the consequence of a large V_R instead of the absence or extremely low V_A (Houle, 1992; Brookfield, 2009). Indeed, in *A. nucleus* both, CV_A and h^2, suggest that better results to improve growth rate would be obtained if selection is applied early in the *A. nucleus* lifespan.

The expected selection gains in *A. nucleus* goes from moderate to very high (4.6 to 56.2% per generation) for the measured productive traits, which suggests it would be feasible to improve such characters through artificial selection. The predicted selection response per generation for juvenile shell length is close to the upper limit of the range reported for *C. nobilis* (28–35% per generation; Liu and Liu, 2012), but higher than those reported for the same trait in *M. edulis* (13–19%; Strömgren and Nielsen, 1989) or *A. irradians* (7–10%; Zhang et al., 2007). In turn, the potential for genetic gain in body weight is much higher than those reported in *A. ventricosus* (17%; Ibarra et al., 1999).

Growth related traits showed high and positive genetic correlations among them both in juveniles and adults. Similar results have been reported for other mollusk species such as *P. maxima* ($r_G > 0.82$, Kvingedal et al., 2010), *O. edulis* ($r_G > 0.96$, Toro and Newkirk, 1990) and *Haliotis rufescens* ($r_G > 0.82$, Brokordt et al., 2015b; Farías et al., 2017). Genetic correlations arise because of the pleiotropic effects of the same set of genes affecting different traits or due to gametic phase disequilibrium between loci controlling different characters (Falconer and Mackay, 2006). *A. nucleus* displays a low population density in natural environments and is a functional hermaphrodite (Lodeiros et al., 1993; Castellanos and Campos, 2007). Evidence from microsatellite markers show high levels of homozygosis, which suggest the existence of high levels of inbreeding, at individual level, in wild populations, although the intra-population genetic variability is high (Barros et al., in prep.). Therefore, although the influence of gametic phase disequilibrium cannot be excluded as a cause of the high levels of genetic correlation found between traits, it is very unlikely since in this study the mating was doing using scallops haphazardly took from the same population, that exhibit high levels of genetic variability.

The high genetic correlations estimated between traits, in addition to the heritability values, allow inferring a high potential of correlated response to selection for productive traits in this species. The adductor muscle weight is the commercially most important trait in scallops, since it is the body part most consumed (Pacheco-Aguilar et al., 2001). As this trait cannot be measured in live animals and it cannot be directly selected regardless its high heritability (74%) and expected response (56% per generation), it is necessary to apply indirect selection, using as selection criteria another trait genetically correlated to it. Our results indicate that the best selection criteria to improve adductor muscle weight would depend on the age at which the potential broodstock be selected. If selection is applied in 3.5 months old

juveniles, the best correlated response would be obtained selecting for the shell height (CG = 33.3% per generation), but in adults would be total weight, with an expected correlated responses of around 33.8% per generation ($i = 2.06$). On the contrary, the expected gain for the remaining soft tissues would be lower (≤8% per generation) and relatively similar using any of the morphometric traits of the shell or total weight as selection criteria.

The survival at adult age of *A. nucleus* did not show significant genetic correlations with any morphologic and gravimetric trait, being similar to results previously reported in *C. gigas* at 6 months old (Ernande et al., 2003). In adults, it was not possible to estimate some genetic correlations, a phenomenon that has been observed in other mollusk species as well (Brokordt et al., 2015b; Farías et al., 2017) which is attributable to a lineal dependence between analyzed traits, resulting in a lack of information for the estimation of such effect (Gilmour et al., 2009).

Genotype-environment interactions (GEI) were founds for most of the measured traits in *A. nucleus*. Reports of GEI in mollusks are scarce (Farías et al., 2017), and is a relevant factor to consider for the design of selective breeding programs, since it means that the relative performance of different genotypes will depend on the environments in which they are expressed (Falconer and Mackay, 2006). Environmental conditions in the Caribbean Sea are less variable than in higher latitudes (Miloslavich et al., 2010), but the results show that different genotypes are sensitive to variations related to depth. Previous measures have not shown differences in mean temperature nor in seston within the deep range used in this study (unpubl. data). That suggest that some other unidentified factors are affecting growth rate in the commercial culture systems. From an evolutive point of view, if growth related traits are under natural selection, the existence of GEI can be a factor that contributes to maintain genetic diversity within natural populations, and can explain the high levels of CV_A and h^2 found, especially in juveniles of a species with apparently high inbreeding levels (Barros et al., in prep).

In conclusion, this study is the first report of heritability for productive traits in *A. nucleus*, confirming the potential for improving commercially important traits in this species through selective breeding. The natural populations of this species have high levels of additive genetic variability and potential selection response for the measured traits, with the exception of survival and fecundity, assets that can be exploited to improve such traits and hence productivity. Most of the measured traits exhibited significant GEI in relation to culture depth, a factor that will be important to consider when designing selective breeding programs.

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