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Heritability, genetic correlations and genotype-environment interactions for growth and survival of larvae and post-larvae of the Caribbean scallop, *Argopecten nucleus* (Mollusca: Bivalvia)

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ABSTRACT

The Caribbean scallop *Argopecten nucleus* is a species with a great potential for commercial aquaculture in the Caribbean given its fast growth and the availability of culture technology. However, its production relies completely on hatchery-reared seed, and the survival in early stages, particularly during the settling process, is the main limitation for this activity to become cost effective. Thus, in order to assess the feasibility of improving survival of larvae and post-larvae of *A. nucleus* through genetic selection without affecting growth, it was estimated the heritability and the genotype-environment interactions for such traits, as well as the genetic correlations between them. These parameters were estimated based on intraclass correlations of 40 full-sib families (10 half-sib families) at 1, 11 and 75 days post fertilization. Heritability values were very high for the post-larvae survival (0.49), while it was low and not significant for larvae survival (≤ 0.07) and medium to high for growth traits of larvae and post-larvae (> 0.3). The traits analyzed in post-larvae exhibited significant genotype-environment interactions in relation to culture depth in the sea. No significant genetic correlations between the measured traits were found. The results suggest the existence of an important genetic component in the variation of post-larval survival, and larval and post-larval growth, as well as a high potential response to direct genetic selection, especially for post-larval survival (50% increase per generation), without affecting the growth traits.

1. Introduction

Argopecten nucleus is a pectinid species from the Caribbean sea with a great potential for commercial aquaculture in this geographical region, given its fast growth (reaches 40 mm in 10 months post fertilization) and the availability of culture technology (Velasco and Barros, 2007, 2008, 2009; Velasco et al., 2007; Velasco et al., 2009). The seed supply for this species relies completely on hatchery production, since collection of wild spat is usually very low (5 to 23 spats per collector), apparently due to the reduced density of natural populations (Castellanos and Campos, 2007). Pilot scale aquaculture trials have demonstrated that the commercial production can be limited by low survival values, particularly at 75 days post fertilization, after the settling period (post-larvae; 0.08–1.35%) (Velasco et al., 2013; Valderrama et al., 2016). This low percentage of recovered post-larvae is similar to that reported in commercial hatcheries for other scallop species, including *Argopecten purpuratus* in Chile (0.7–1.0%; Disalvo et al., 1984). However, this has not inhibited the development of commercial aquaculture of these species because the main source of spat is the collection from wild populations using artificial collectors, with an average of 64 to 1428 larvae per collector for *A. purpuratus* (Bandin and Mendo, 1999).

A. nucleus is a functional simultaneous hermaphrodite that generally release male gametes first and female gametes afterwards, through the nephridial channel (Velasco, 2008), which sometimes might result in self-fertilization, phenomena that has been previously reported for other pectinids (Ibarra et al., 1995; Winkler and Estévez, 2003; Toro et al., 2010; Concha et al., 2011; Liu et al., 2011). The larval culture of *A. nucleus* in laboratory conditions spend < 13 days, including the stages of trochophore larvae (12 h, 74 μm length), D veliger (22 h, shell

Abbreviations: 1_d, 1 day; 11_d, 11 days; 75_d, 75 days; σ_P, phenotypic standard deviation; CV_A, coefficient of additive genetic variance; CV_P, coefficient of phenotypic variance; FS, full siblings; G, potential response to directional selection; GEI, genotype-environment interactions; H, shell height; h^2, heritability; HS, half siblings; i, selection intensity; L, shell length; r_G, genotypic correlations; r_P, phenotypic correlations; S, survival; V_A, additive genetic variance; V_R, residual variance

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length $L = 100\,\mu m$), umbonate veliger (7 days, $L = 150\,\mu m$) and pediveliger (9 to 13 days, $L = 225\,\mu m$) (Velasco et al., 2007). Previous studies showed that the survival was 44% from eggs to D veliger, and 30% from veliger to pediveliger (Velasco and Barros, 2008; Velasco et al., 2013). In this species the optimal culture condition, as function of larval growth and survival, are a water temperature at 25 °C and a density of 1 larvae mL^{-1}, fed with a mix of the microalgae *Isochrysis galbana* and *Chaetoceros calcitrans* supplied by constant dripping at a daily rate of 20 cells μL^{-1}, and complete water renewal every 48 h (Velasco and Barros, 2008). The settlement begins when pediveliger larvae exhibit an eye spot and crawling behavior, moment when artificial collectors are introduced in the rearing tanks (9–13 days). The post-larvae phase begins after the settlement and extends until the animals reach a size large enough to resist manipulation and can be detached from the artificial collectors (aprox. 10 mm of shell high). Under laboratory conditions, this usually occurs at 110 days, and in the sea at 75 days, after keeping the collectors in the lab for 15 to 30 days (Velasco and Barros, 2009; Valderrama et al., 2016). The best results in terms of survival and post-larval growth has been obtained using plastic onion bags as substrate, and settlement inductors such as epinephrine (10^{-5} M) or low temperature (20 °C) for 48 h (Velasco and Barros, 2009).

Selective breeding is one of the most effective tools for improving productive traits in bivalve mollusks (Newkirk and Haley, 1983; Ibarra et al., 1999), since its effects are cumulative along several generations. The potential success can be inferred if the genetic-quantitative parameters of interest in a population, such as phenotypic variance, heritability (h^2), genotype-environment interactions (GEI) and genetic correlations between traits (r_G) are known (Gjedrem, 2005). The heritability is the proportion of phenotypic variance of a trait that can be explained by the additive effects of the genes (Falconer and MacKay, 2006; Gjedrem and Baranski, 2009). Genetic correlations estimate the heritable association between the variance of two traits, being useful predictors about the consequences on different traits of selection applied to improve one trait (Falconer and MacKay, 2006; Gjedrem and Baranski, 2009). The genotype by environment interactions (GEI), on the other hand, represent the relative genetic performance of different genotypes over different environments, and can variate from 1 (no GEI) to 0 (Falconer and MacKay, 2006; Gjedrem and Baranski, 2009).

The heritability for larval and post-larval growth has been studied in different bivalve species, including *Crassostrea virginica* (Newkirk et al., 1977), *Crassostrea gigas* (Ernande et al., 2003), *Mercenaria mercenaria* (Hilbish et al., 1993) and *Mytilus chilensis* (Toro and Paredes, 1996; Toro et al., 2004). However, heritability estimations for survival during larval and post-larval stages have been reported only in *C. gigas* (Lannan, 1972; Ernande et al., 2003). In pectinids, the realized heritability for larval growth has been estimated for *Argopecten irradians irradians* (Zheng et al., 2004) and in post-larval growth in *Euvola ziczac* (Pérez and Alfonsi, 1999). In general, h^2 values reported in bivalve mollusks are higher than 0.2, depending on age, trait and species. Lacks of genetic correlations between survival and growth have been reported for larvae and post-larvae in *C. gigas* (Ernande et al., 2003) as well as among larval growth at different ages in *M. mercenaria* (Hilbish et al., 1993). Finally, there are a few published studies that estimate genotype-environment interactions in mollusk species (Rawson and Hilbish, 1991; Evans and Langdon, 2006; Dégremont et al., 2007; Farías et al., 2017), but none of them in pectinids.

For *A. nucleus,* estimations of genetic-quantitative traits, including growth, survival and fecundity in juveniles and adults, have been previously reported (Barros et al., 2018). The heritability values were medium to high ($h^2 \geq 0.29$) for most of the growth-related traits, and low for adult survival and fecundity ($h^2 \leq 0.18$). Moreover, positive genetic correlation between growth-related traits were found ($r_G \geq 0.69$), but not significant genetic correlations between those traits and survival or fecundity were detected. Genotype-environment interactions associated to the culture depth were also reported for growth traits. Nevertheless, is unknown the feasibility for improving productive traits in *A. nucleus* larvae and post-larvae by artificial selection, as well as the expected correlated response between traits. The aims of this work were to evaluate the potential to improve larval and post-larval survival through selective breeding, and to estimate the potential impact of a selective breeding program for growth at these stages. With this objective, heritability, genetic correlations, genotype-environment interactions and the potential of response to artificial selection were estimated.

2. Materials and methods

2.1. Collection and conditioning of broodstock

A hundred and fifty adults of *A. nucleus*, with average shell length of 42 ± 4 mm, were used as broodstock. These animals were derived from a wild population, originally collected as spats from Neguanje Bay, Santa Marta, Colombia (Lat. 11° 20′ 03″ N, Long. 74° 09′ 24″ W), and donated at the time of the study by Instituto de Investigaciones Marinas y Costeras-INVEMAR (Santa Marta). The animals were transferred to the Laboratorio de Moluscos y Microalgas of the Universidad del Magdalena in Taganga, Santa Marta, into containers with sponges soaked in seawater at 18 °C. Subsequently, they were conditioned to promote gonad maturation, keeping them in rectangular tanks with seawater at 25 ± 1 °C, microfiltered at 1 μm, sterilized with UV, salinity of 37 ± 2‰, constant aeration, daily water renewal of 80% and daily feed by dripping using a algal mixture of *Isochrysis galbana* and *Chaetoceros calcitrans* (1:1) at a concentration of 40 cells μL^{-1} in the culture tank (Velasco, 2006, 2007; Velasco and Barros, 2007).

2.2. Induction to spawning and fertilization

Fifty-six individuals with maximum gonadal ripeness (state IV; Sastry, 1963) were cleaned of epibionts, pat dried, and individualized with a tag stick on the shell with epoxy glue. Subsequently, spawn was induced and fertilization was completed according to the protocols described by Velasco et al. (2007). The animals were left for 30 min without any water, and then placed in a container with seawater and microalgae (560 ± 20 cells μL^{-1}) at 22 °C. After 30 min, they were transferred to a different container with clean seawater at 30 °C for an additional 30 min. The cycle was repeated by 3 h or until the animals spawned. When animals began to spawn, they were individually placed in 8 L containers with microfiltered seawater. From each container, a 10-mL water sample of unfertilized eggs was taken, and incubated for 4 h to estimate the self-fertilization percentage, as described Winkler and Estévez (2003). Crosses were done using a nested design, such as the sperms of one male were used to fertilize the eggs of 4 females haphazardly chosen from the population, to produce 40 full-sibs (FS) and 10 half-sibs (HS) families.

2.3. Embryo and larval culture

Each FS family was divided into two groups containing approximately the same quantity of embryos, and placed in cylindrical tanks (500 L) at an approximate density of 3 embryos mL^{-1}. The culture of embryos, larvae and post-larvae was done following the methods described by Velasco and Barros (2008, 2009). Water renewal was done every second day, collecting larvae using 40 and 65 μm mesh sieves in the first and second halves of the culture period, respectively. Before water renewal, the content of each tank was homogenized using aeration and two independent 10-mL samples were taken and fixed with a drop of lugol in a Petri dish. The larvae were counted twice per tank under a microscope with a 4× magnification. The survival (S) was estimated at 1 and 11 days post fertilization as the proportion of live D larvae and pediveliger larvae in each tank with respect to the initial number of embryos and D larvae, respectively. Larvae with damaged or

empty shells were considered dead. Between days 1 and 9, the culture density was 2 larvae mL^{-1}, and later it was reduced to 0.7 larvae mL^{-1} by adjusting the volume of water in the tanks. Shell length (*L*) and height (*H*) was measured under microscope using a graded grid in 30 larvae haphazardly chosen from each tank at 1 and 11 days post fertilization.

2.4. Settlement and post-larval culture

When 50% or more of the pediveliger larvae exhibited the eye spot (11 day post-fertilization), 24 polypropylene onion bags (70 × 90 cm and ∅ = 1 cm), previously conditioned for 5 days with a microalgal mixture of *I. galbana* and *C. calcitrans*, were introduced in each cylindrical tank (500 L) as substrate for settlement. Settling process was conducted with an initial density of 0.7 larvas mL^{-1}, fed with a 1:1 mixture of *I. galbana* and *C. calcitrans* at 40 cell μL^{-1} day^{-1}. Settlement was induced reducing water temperature to 20 ± 1 °C for 48 h, and increasing it to 25 ± 1 °C afterward, for 15 days. During settling and initial period post-larvae, water was completely renewed every 24 h without removing the collectors from the tanks, maintaining the water level constant while discarded water was slowly released through the bottom tank drain as new water was added to the tank. Unsettled larvae were retained in a 65 µm mesh sieves and returned to the same tank.

The collectors with attached spats from each FS family were placed individually inside of polypropylene bags (30 × 80 cm and ø = 1 mm). Eight haphazardly chosen bags with spat from each FS family were tied in pairs at the end of 4 culture rope lines of three lengths (1, 3 and 5 m) and transferred in wet conditions to the sea, in Taganga Bay. The ropes were suspended in 4 zones along a 100 m *long line*, with each FS family distributed at 3 different depths (6, 8 and 10 m). After 1.5 months (75 days post fertilization) the scallops were manually removed from the collectors and counted. The survival (or post-larvae recovered) was estimated for each family and depth as the percentage of post-larvae recovered with the respect to pediveliger larvae seeded of each family group. A random sample of 30 individuals was taken from each family and depth, and the shell length (*L*) was measured with a caliper (± 0.1 mm). During the culture period in the sea (January to October 2015), water temperature fluctuated between 26 and 29 °C. Salinity was between 35 and 37 ppt; the total seston concentration was between 2 and 8 mg L^{-1} and its organic content was between 21 and 61%.

2.5. Genetic and statistical analysis

The components of the phenotypic variance (V_P), heritabilities for the different traits in larvae and post-larvae, and genetic correlations (r_G) between those traits were estimated using an Animal Model (Lynch and Walsh, 1998), based on the restricted maximum likelihood model (REML) (Johnson and Thompson, 1995). Survival was treated as a threshold trait and analyzed after probit transformation (Falconer and MacKay, 2006). The following general model was used:

$$y = X\beta + Za + Zd + e \quad (1)$$

where *y* is the vector for observations in all individuals, β is the vector for fixed and covariate effects, *a* is the vector for additive genetic effects (random), *d* is the effect of the random non-genetic quantitative variables and *e* is the vector for residual errors. Both *X* and *Z* are known incidence design matrices (Lynch and Walsh, 1998). Those fixed and covariate effects that were statistically significant were included in the model for the analysis of the components of the phenotypic variance. For all the traits, maternal/common environment effects were analyzed by including the mothers as a random effect in the model.

The components of the phenotypic variance, h^2 and r_G values were estimated using the software ASReml V4.0 (Gilmour et al., 2009). The statistical significance of fixed (birth date, culture tank, position of the collectors in the long-line and culture depth in the sea, for post-larvae) and covariate (self-fertilization percentage, water temperature and seston) effects were estimated using Wald-F statistic. The significance of random effects (maternal effects) and h^2 were tested using a log-*likelihood ratio test* (LRT test) (Lynch and Walsh, 1998). r_G values were estimated only for traits with $h^2 \geq 0$. Phenotypic correlations (r_P) between traits were estimated as the Pearson correlation using the software Statgraphics Centurion XVII X64.

The hoped selection response for each trait was estimated in absolute (*G*) and relative (% *G*) units as:

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

$$\%G = 100\ G/u \quad (3)$$

where *i* is the selection intensity, σ_P is the standard phenotypic deviation of the trait and *u* is the phenotypic media of the trait. All estimations were done assuming the selection of the upper 5% of the population as broodstock ($i = 2.06$) (Falconer and MacKay, 2006).

Factorial ANOVAs (Truberg and Hühn, 2000; Mohammadi and Amri, 2008) followed by a Bonferroni multiple comparison test were used to assess genotype-environment interactions (GEI) for every trait in post-larvae, considering FS families and culture depth as factors. Prior to ANOVA and genetic analysis, the normality and homoscedasticity of all data were assessed using Kolmogorov-Smirnov for goodness of fit and C of Cochran tests, respectively. All the analyses were performed using the statistical software Statgraphics Centurion XVII ×64, with an alpha of 0.05.

3. Results

3.1. Survival and growth

By the end of the first day, 43.3 ± 9.0% of fertilized oocytes reached the D veliger stage. The pediveliger larval survival, in turn, was of 29.9 ± 5.5% (Fig. 1A), with a survival ranged from 17.0 to 35.3% among FS families. Zero to 0.45% of pediveliger larvae per family were recovered as post-larvae after 75 days of grow-up (Fig. 2A). One day after fertilization, the larvae of *A. nucleus* had a shell length between 90 and 100 µm, with an average of 98.6 ± 3.4 µm. After 11 days, they

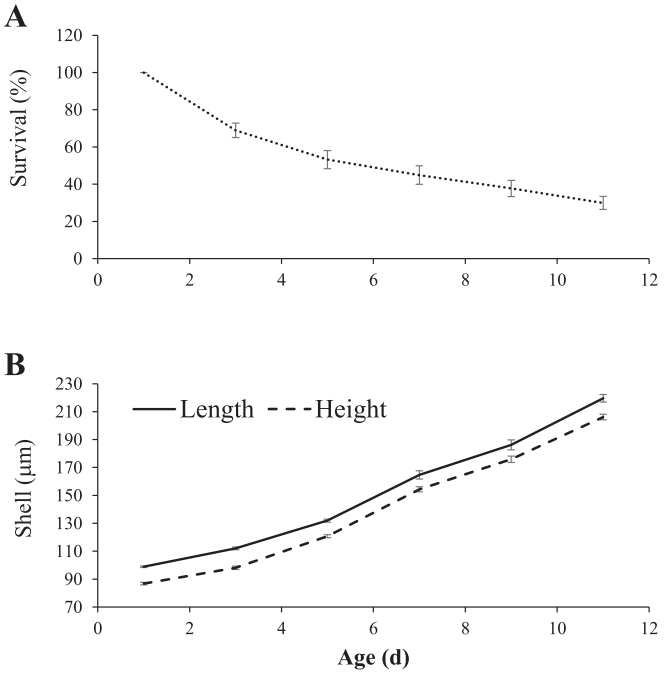

Fig. 1. Changes in survival (A), length and height (B) averages (± se) along the larval culture period in an *A. nucleus* population under laboratory conditions (µ ± se).

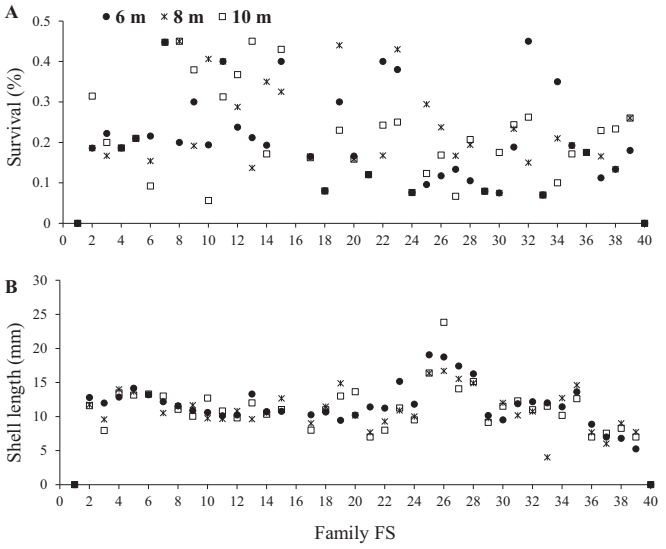

Fig. 2. Average survival (A) and length (B) of *A. nucleus* post-larvae in FS families cultured at different depths at Taganga Bay.

reached an average shell length of 219 μm (Fig. 1B). The shell height exhibited a similar trend. The family mean shell length of the recovered post-larvae ranged from 4 to 24 mm, depending on the culture depth and the family, with a population average of 11.9 ± 3.9 mm (Fig. 2B). The phenotypic coefficient of variation (CV_P) of those traits ranged from 3.5 to 50.0% (Table 1).

3.2. Genetic parameter evaluation

Significant effect of the tanks within the FS families were detected for shell length in pediveliger larvae at 11 days ($P < 0.05$). The self-fertilization percentage had a co-variated effect on the shell length in 11 days old larvae and on post-larvae ($P < 0.05$), as well as on survival at 75 days ($P < 0.05$). No maternal effects were found for any of the analyzed traits ($P > 0.05$).

The coefficients of genetic variation (CV_A) of the studied traits were higher in post-larvae ($CV_A \geq 21.1\%$) than in larvae ($CV_A \leq 8.3\%$; Table 1). The heritabilities for the larval survival were low and not statistically significant ($P > 0.05$), but the value for post-larvae was high ($h^2 = 0.49$), with an estimated response to selection of 50% per generation. The estimated h^2 for size traits in larvae and post-larvae were medium to high (≥ 0.31; $P < 0.05$), with an estimated response to selection between 3 and 21% per generation (Table 1). The heritabilities for shell height of larvae were somewhat higher than those for shell length. The heritability values for length tend to decrease with age, while those of shell height tend to increase.

No significant genetic correlations were found between survival and the growth-related traits in larvae or post-larvae, or between growth traits ($P > 0.05$) (Table 2). Only phenotypic correlations for some traits in larvae were found to be significant and positive ($P < 0.05$; Table 2).

3.3. Genotypic by environment interaction

Culture depth did not show significant effect on growth nor survival of post-larvae ($P > 0.05$) but significant effect of FS families ($P < 0.01$) and the interaction between FS families and culture depth were observed ($P < 0.05$). Higher growth values were obtained at 10 m of depth in the 26 family genotypes, while the higher survival values occurred at 10 m of depth in the 8 and 13 families genotypes, and at 6 m of depth in the 32 family genotypes (Fig. 2; $P < 0.05$).

4. Discussion

Our results indicate that the heritability for survival in larvae stage was not significant, although it was high for post-larvae, with a high potential response to selection. In addition, the levels of genetic variability were medium to high for growth traits in both larvae and post-larvae. No significant genetic correlations between traits were detected. Also, nor significant effects of culture depth in the sea on survival or growth were detected. However, significant GEI was detected associated to culture depth on the survival and growth of post-larvae.

The average values for survival and growth in pediveliger larvae (S_{11d} = 30%; L_{11d} = 219 μm, respectively) and post-larvae recovered in this study (S_{75d} = 0.2%; L_{75d} = 12 mm, respectively) are similar to those previously registered for this specie at these same ages (S_{11d} = 6–54%; L_{11d} = 190–230 μm; S_{75d} = 0.08–1.35%; L_{75d} = 7–12 mm) (Velasco and Barros, 2008; Carreño et al., 2012; Gómez-León et al., 2010; Velasco et al., 2013; Valderrama et al., 2016). *A. nucleus* exhibit lower survival but higher growth rate than those reported for other small pectinid species, such as *Argopecten ventricosus* (=*circularis*) ($L_{15\text{-}18d}$ = 140–173 μm and $S_{15\text{-}18d}$ = 32–73%; Ibarra et al., 1995, 1997) or *Argopecten gibbus* (L_{14d} = 184–203 μm and S_{14d} = 17.8–55.4%, L_{60d} = 3.5 mm, S_{60d} = 20%; Sarkis and Lovatelli, 2007). This could be attributed to differences in the culture conditions, including stocking density (Ibarra et al., 1997; Velasco and Barros, 2008), water temperature (Ibarra et al., 1995, 1997; Laing, 2000; Sarkis and Lovatelli, 2007), culture management techniques (Parsons and Robinson, 2006), or inter-specific differences (Velasco and Barros, 2008, 2009; Mazón-Suástegui et al., 2011). This similarity with previously reported results for this species suggests that the culture methods used result in consistent outcomes, and thus can be extrapolated to similar studies.

The estimated heritabilities for larval survival in *A. nucleus* were low and not different from zero, suggesting a low potential for improving this trait by directional selection. The survival is a trait highly related to

Table 1
Averages, genetic additive variances (V_A), residual variances (V_R), heritabilities (h^2) ± standard error (se), phenotypic coefficient of variance (CV_P), additive genetic coefficient of variance (CV_A) and expected selection response (G) for traits in larvae and post-larvae of *A. nucleus*.

Traits	*n*	Average ± SD	V_A	V_R	h^2 ± se	CV_P (%)	CV_A (%)	G	G (%)
S_{1d} (%)	80	43.3 ± 9.0	0.01	1.00	0.01 ± 0.03	20.8	0.2	–	–
L_{1d} (μm)	1230	98.6 ± 3.4	4.51	5.98	0.43 ± 0.09*	3.5	2.2	3.01	3
H_{1d} (μm)	1230	85.9 ± 6.9	5.15	5.86	0.47 ± 0.11*	8.1	2.6	6.68	8
S_{11d} (%)	80	29.9 ± 5.5	0.01	1.00	0.07 ± 0.05	18.3	0.2	–	–
L_{11d} (μm)	1230	219.0 ± 22.0	151.56	255.25	0.33 ± 0.12*	10.0	5.6	14.96	7
H_{11d} (μm)	1230	205.2 ± 20.5	288.60	129.26	0.69 ± 0.12*	10.0	8.3	29.14	14
S_{75d} (%)	80	0.2 ± 0.1	0.01	1.00	0.49 ± 0.07*	50.0	59.1	0.10	50
L_{75d} (mm)	1230	11.9 ± 3.9	6.29	13.78	0.31 ± 0.08*	32.8	21.1	2.49	21

Length (L); height (H); survival (S); d: day; value was not calculated since it was non-significant.
* $P < 0.05$.

Table 2
Genetic (above the diagonal) and phenotypic (under the diagonal) correlations between productive traits in larvae and post-larvae of *A. nucleus*. n = 1765.

	S_{1d}	L_{1d}	H_{1d}	S_{11d}	L_{11d}	H_{11d}	S_{75d}	L_{75d}
S_{1d}	–	−0.1705	−0.2803	−0.3403	0.4865	0.0720	NE	NE
L_{1d}	0.0723	–	NE	0.4165	−0.0196	0.0173	−0.1974	0.2157
H_{1d}	0.1726	0.9881*	–	−0.3143	0.0057	−0.3177	−0.1842	0.1507
S_{11d}	0.0795	0.3111	0.3119	–	NE	0.1328	NE	NE
L_{11d}	0.2014*	0.6840*	0.6984*	0.0218	–	−0.6555	−0.0860	−0.1048
H_{11d}	0.3042*	0.7654*	0.7830*	−0.0235	0.9832*	–	−0.1155	−0.1327
S_{75d}	0.0281	0.1855	0.0312	0.0213	0.3631	0.0051	–	0.3050
L_{75d}	0.1024	0.1225	0.0651	0.2235	0.0130	0.4700	0.1130	–

d: day, NE: not estimable. Survival (*S*), shell length (*L*) and shell height (*H*).
* $P < 0.05$.

individual fitness, and such traits usually have low heritabilities (Mousseau and Roff, 1987; Houle, 1992; Falconer and MacKay, 2006). The low coefficient of genetic additive variance ($CV_A = 0.2\%$), a meaningful estimator of evolvability (Houle, 1992), in larvae survival is consistent with this hypothesis. Contrarily to the findings of our study, estimated h^2 values in *C. gigas* for larval survival are medium to high (0.31–0.55; Lannan, 1972; Ernande et al., 2003). The observed differences could be related to different reproductive strategies between *A. nucleus* and *C. gigas*. *A. nucleus* is a hermaphrodite species with partial self-fertilization (Barros et al., 2018) and low density in natural populations (Castellanos and Campos, 2007), but *C. gigas* is a protandric hermaphrodite with cross-fertilization that can reach high densities in natural populations (Diederich et al., 2005; Escapa et al., 2004; Cognie et al., 2006; Troos, 2010), which may favors exogamy. Thus, lower additive genetic variance in *A. nucleus* could be caused by selective mortality, but also by effects of genetic drift due to a low effective population size in the wild and the self-fertilization.

The high values of heritability ($h^2 = 0.49$) and phenotypic coefficient of variance (50%) let to expect a large selection response for *A. nucleus* post-larvae survival ($\%G = 50\%$, per generation), ie. after two generations of directional selection to improve the survival ($i = 2.06$), it could be close to be twice the initial one ($S_{75d} \approx 0.4\%$). The survival of post-larvae recovered from the collectors is a complex trait since involves, besides survival *per se*, the losses caused by larvae that were not able to properly settle and the detachment of post-larvae from the collectors. Factors like the substrate composition of benthic microalgae and bacteria (Hadfield, 2011), the maturity of these communities (Leyton and Riquelme, 2008), and the effects of handling the collectors during transport and set up in the long-lines, can affect the amount of recovered post-larvae. Thus, the recovery percentage of post-larvae from the collectors would be less related to biological fitness than larvae survival, and therefore higher heritability can be expected. This is consistent with the higher CV_A values for *A. nucleus* in the post-larvae stage ($CV_A = 59.1\%$) in comparison with the larval stage ($CV_A = 0.2\%$). Intermediate to high heritability values for post-larvae survival have also been reported for *C. gigas* ($h^2 = 0.45$–0.62; Dégremont et al., 2007, 2015; Azéma et al., 2017). The high h^2 values and the potential response for post-larvae survival suggest that this trait, which is considered one of the major bottlenecks in pectinid aquaculture (Bourne et al., 1989; Avendaño et al., 2001; Uriarte et al., 2001; Sarkis and Lovatelli, 2007), can be improved by selective breeding.

The medium to high values of h^2 for the growth-related traits in larvae and post-larvae of *A. nucleus* ($h^2 = 0.31$–0.69), were within the range of prior estimations for these traits in other mollusks species, such as *C. virginica* ($h^2_{6\text{-}16d} = 0.51$–$0.60$; Newkirk et al., 1977), *M. chilensis* ($h^2_{10\text{-}40d} = 0.2$–$0.8$; Toro and Paredes, 1996; Toro et al., 2004), *M. edulis* ($h^2_{14\text{-}75d} = 0.2$–$0.8$; Strömgren and Nielsen, 1989) and *M. mercenaria* ($h^2_{4\text{-}10d} = 0.58$–$0.82$; Hilbish et al., 1993). Self-fertilization is a factor that can spuriously increase the estimations of the genetic additive variance, and hence, also the heritability of the traits (Falconer and MacKay, 2006; Gjedrem and Baranski, 2009; Toro et al., 2009). It showed a significant covariated effect on the length variance of 11-day old larvae. However, this covariate effect was included in the analysis model to estimate the variance components of such traits.

The potential of genetic gains by selection for growth traits in larvae were relatively low ($3 < G < 14\%$ per generation), notwithstanding that heritability's were medium to high. This is caused by the low phenotypic variance of those traits ($CV_P = 3.5$–10.0%) that prevent to apply large selection differentials. In turn, post-larvae selection potential response was relatively high ($G = 21\%$ per generation), mostly explained for the larger phenotypic variance. In commercial scallop hatcheries, larvae are usually collected during the water renewal using sieves with increasing mesh aperture with the purpose of to selectively eliminates the slow grower larvae and retains the fast growers. As the shell size of the *A. nucleus* larvae have a relatively high heritability and expected response to selection, this practice produce a selection pressure that would tend to increase the larval growth rate along successive generations in scallop populations maintained under close reproduction in hatchery.

The heritability estimations exhibited different trends for shell length and height during the larval development of *A. nucleus*. While the heritability for shell length reduced with age, similarly to results previously reported for *M. chilensis* (Alcapán et al., 2007) and *Pinctada martensii* (Deng et al., 2009), the heritability for shell height increased, similarly to findings in *C. gigas* (Ernande et al., 2003) and *M. mercenaria* (Hilbish et al., 1993). Some of the factors that can affect h^2 estimations at different ages are the maternal effects and those of common environment (Falconer and MacKay, 2006; Gjedrem and Baranski, 2009; Brokordt et al., 2015). The maternal effects can be more noticeable in traits measured at early stages of development (Mallet and Haley, 1984), as indicated by the results in larvae of *C. virginica* (Mallet and Haley, 1984) and *A. circularis* (Cruz and Ibarra, 1997). However, maternal effects on the traits included in this study were not significant. On the other hand, the common environment effects tend to increase with time in full and half sib families if share the same tank or culture unit (Falconer and MacKay, 2006; Gjedrem and Baranski, 2009), as has been demonstrated for shell length of larvae of *M. chilensis* (Alcapán et al., 2007) and *Pinctada martensii* (Deng et al., 2009). In this study, the tank showed a significant effect on the length variance of 11 days old larvae, however, this effect was included in the analysis model to estimate the variance components of such trait. Therefore, the impact of maternal and common environment effects on the heritability estimations for growth related traits is unlikely, and any observed difference in the h^2 trends for those traits during larval development probably were associated to ontogenic factors.

The lack of significant genetic correlations between larval and post-larval traits in *A. nucleus* coincides with previous reports for larval growth in *C. gigas* (Ernande et al., 2003) and *M. mercenaria* (Hilbish et al., 1993). The larval settlement in marine invertebrates involves complex ontogenic processes, with morphogenetic changes and histolytic and histogenic processes (Burke, 1983), and there is evidence of

qualitative and quantitative changes in the expression of different set of genes along this process (Degnan and Morse, 1995; Degnan et al., 1997; Rutherford et al., 2007; Coba De La Peña et al., 2016). Therefore, the low and non-significant genetic correlations for the larval and post-larval traits in this study are consistent with the hypothesis of changes in the expression in the set of genes responsible for the variation of such traits at population level. On the other hand, the occurrence of phenotypic correlations between larval and post-larval traits, that did not show genetic correlations, suggests that non-additive genetic factors would be responsible for them (Gjedrem and Baranski, 2009). Consequently, selection to improve the growth rate of *A. nucleus* at the larval stage could have scarce or no impact on growth rate or the remaining studied traits in later developmental stages. Nevertheless, in the Chinese pearl oyster, *Pinctada martensii*, a correlated improvement has been reported in growth rate of larvae derived from selected broodstock with respect to controls (Deng et al., 2009), suggesting the existence some genetic correlations between the growth rate in larvae and post-larvae. Thus, further research is necessary before drawing more specific conclusions about potential of correlate response to selection between larval and post-larval traits in bivalve mollusks.

The variation in the relative performance in terms of survival and growth in different FS families of *A. nucleus* post-larvae in relation to culture depth indicates the existence of genotype-environment interactions (GEI). This phenomenon has been previously observed in juveniles and adults of this species (Barros et al., 2018), as well as in larvae of *M. chilensis* in association with the feeding rate (Toro and Paredes, 1996) and in *C. gigas* associated to culture conditions and geographical location (Evans and Langdon, 2006; Dégremont et al., 2015). This interaction has being related with the different genotypes sensitivity to environmental conditions (Falconer and MacKay, 2006). GEI is an important factor to consider when planning a selective breeding program, since it conditions the design of the breeding program (Falconer and MacKay, 2006; Evans and Langdon, 2006; Gjedrem and Baranski, 2009). To face up this problem, a strategy could be to select genotypes with low sensitivity to environmental conditions, thus keeping a relatively stable performance over a broad set of culture environmental conditions. Alternatively, those genetic differences can be exploited to generate strains adapted to specific environmental conditions (Falconer and MacKay, 2006). The best choice would depend on the objectives of the selection program, as well as on economic and technical factors related to production. In the present study, considering that the FS family genotypes will segregate and recombine during the reproduction process to produce the next generation, no useful information could be obtained identifying the more or the less sensitive genotypes. In turn, to assess the more relevant factors to explain GEI could be an interesting challenge in future studies, using a proper experimental design.

In conclusion, the results of this study suggest that selection would be an effective tool to improve the post-larval survival and growth in *A. nucleus*. In addition, the use of selection could also improve larval growth, although the expected response is low and hence would not have positive effects in post-larvae growth. However, our results suggest that larvae survival have low potential to be improved by selection. Finally, when trying to improve the post-larval survival, it is necessary to consider genotype-environment interactions related to culture depth, since it would directly affect the selection response.

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