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Genotype by environment interactions, heritabilities and genetic correlations for productive traits of *Haliotis rufescens*

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ABSTRACT

A critical aspect of a selective breeding program is whether responses of traits of interest are similar in different environments. The magnitude of the genotype by environment interaction (GEI) together with heritability (h^2) accounts for this aspect. Despite the economic significance of abalones and the interest in genetic improvement programs for their cultivation, only one previous study has reported GEI estimations for this group of mollusks. The objective of the present study was to estimate h^2 and the existence of GEI for growth traits of *Haliotis rufescens* cultivated in Chilean farms with different environmental and management conditions. A total of 2 cohorts (2007 and 2009) of 50 and 42 families of full sibs (FS), respectively, were used. Replicates of each FS family of the 2007 cohort were distributed in two farms in the northern region of the country and were evaluated after 1 and 2 years of cultivation. For the 2009 cohort, replicates of each family were distributed in a farm in the northern region and a farm in the southern region of the country. The estimated h^2 values were significant for all traits, with the length and width of the shell and total weight varying primarily by cohort between 0.22–0.62, 0.16–0.58 and 0.40–0.53, respectively. The genetic correlations (r_G) between traits were all higher than 0.82. The expected correlated responses for improving the total weight using the shell length as a selection criterion predict a selection gain (14–51%) similar to what would be obtained by selecting directly for weight (16–51%) in all environments examined. Thus, indirect selection by shell length and the direct use of total weight as a selection criterion would yield similar effects in terms of the increase in weight. High r_G, not significantly different from 1, were observed for the analyzed traits between replicates of the families in any of the farms compared, both within the northern region and between the northern and southern regions of the country. These high r_G were indicative of non-significant GEI for the analyzed traits. Therefore, results suggest that one selective breeding program could provide improved red abalone for the industry in Chile with consistent results between farms located in different environments.

Statement of relevance: Abalones are one of the most important mollusks in aquaculture due to their commercial value in international markets, especially in Asia; as such there are several efforts to develop abalone breeding programs in different countries. In this work we addressed a critical aspect for a selective breeding program, which is to know whether responses of productive traits are similar in different environments. Considering that the magnitude of the genotype by environment interaction (GEI) together with heritability (h^2) accounts for this aspect, we estimated these genetic quantitative parameters for growth traits (total mass, shell length and width) in two cohorts of the red abalone, *Haliotis rufescens*, cultivated throughout Chile. Results indicated that the application of selection by the shell length at age of harvest has the greatest potential for improving the production of *H. rufescens*. These improvements are practical (ease and accuracy in measurement), have indirect effects on the objective trait of selection (weight), and consist of a trait that is not significantly affected by genotype-environment interactions. In addition, the results obtained suggest that a single selective breeding program would be sufficient for the red abalone industry in Chile, as the response to selection of traits associated with growth would be similar in different environments. Red abalone is naturally distributed in California and Baja California coasts, and this information can be especially useful in planning breeding programs also in the west coast of USA and México.

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1. Introduction

Abalones are marine gastropod mollusks that are valued commercially for their edible muscular foot (Hahn, 1989). The cultivation of abalones is a growing industry worldwide due to the high value of abalones particularly in Asian markets, and the reduction of abalone supply due to overfishing (Cook and Gordon, 2010; Gordon and Cook, 2013; Cook, 2014). World aquaculture production of these mollusks reached 128,208 t in 2014, with an approximate value of US $1 billion (FAO, 2016). In Chile, two abalone species have been introduced for commercial cultivation: the red abalone of California, *Haliotis rufescens*, and the Pacific abalone, *Haliotis discus hannai* (Flores-Aguilar et al., 2007). Abalone cultivation in Chile began in the 1990s and has grown at an average annual rate of nearly 20% over the last 14 years (FAO, 2016), reaching 1146 t in 2014 (FAO, 2016). The red abalone is the main species cultivated, as it represents 98% of the total national landings of this species and has the highest unit value among farmed shellfish commodities produced in the country (FAO, 2016).

Large abalones of high commercial value, such as *H. rufescens*, primarily inhabit temperate waters; thus, they are slow growing, taking 4–8 years to reach commercial size (Hahn, 1989). The red abalone cultivated in Chile reaches harvest size between 40 and 48 months of age (Flores-Aguilar et al., 2007; Enríquez and Villagrán, 2008). Several studies have shown that the growth rate is the productive factor that most impacts the profitability of abalone cultivations (Robinson and Li, 2008; Robinson et al., 2010; Zúñiga, 2010; Pérez et al., 2012; Zúñiga-Jara and Marín-Riffo, 2014). Selective breeding has been successfully applied to improve productive traits in various aquaculture species, including abalones and other species of mollusks (Gjedrem et al., 2012). However, in order for selective breeding to generate intergenerational progress in the phenotypic value of a trait, the trait must show genetic variation within the population (Falconer and Mackay, 1996; Lynch and Walsh, 1998; Gjedrem and Baranski, 2009).

Heritability (h^2) is a central parameter for estimating the response potential to selection of a trait in a population (Falconer and Mackay, 1996; Lynch and Walsh, 1998; Kruuk, 2004). h^2 has been estimated for some traits linked to production, such as the shell length or weight, in various abalone species through different methods; these values vary widely among species (Jónasson et al., 1999; Mgaya, 2000; Li et al., 2005; Lucas et al., 2006; Kube et al., 2007; Li, 2008; Choe et al., 2009; Roussel et al., 2013; Brokordt et al., 2015), in different studies on the same species (Kube et al., 2007; Li, 2008; You et al., 2010a, b; van Schalkwyk, 2011; Brokordt et al., 2015) and throughout the development of some abalone species (Jónasson et al., 1999; Brokordt et al., 2015). Differences in heritability estimates may indicate that the response potential to selection varies depending on the environment, hence affecting the economic feasibility of applying a selective breeding program. Therefore, estimations of this parameter in different environments are useful for identifying the most appropriate conditions for operating breeding programs.

One of the factors that can cause differences in the heritabilities of a trait between environments is genotype by environment interactions (GEIs). These are relative changes (*ranking*) in the performance of certain traits when different genotypes of a species are evaluated in two or more environments (Falconer, 1952; Browman, 1972; Lin and Togashi, 2002). The occurrence of GEIs causes the relative performance of a single genotype to vary unpredictably between different environments, thus requiring experimental testing (Evans and Langdon, 2006). Despite the relevance of GEIs to the design of a breeding program, there is only one study in abalones in which this parameter has been estimated (Jónasson et al., 1999). That study, which used *H. rufescens*, did not detect genotype-environment interactions for growth traits in abalones cultivated in two different farms in Iceland (Jónasson et al., 1999). However, significant GEIs have been recorded for traits associated with growth in other mollusk species, such as *Crassostrea gigas* (Langdon et al., 2003; Degremont et al., 2005; Evans and Langdon, 2006), *Crassostrea virginica* (Newkirk, 1978), *Pinctada maxima* (Kvingedal et al., 2010) and *Mercenaria mercenaria* (Rawson and Hilbish, 1991).

The cultivation of *H. rufescens* is concentrated in central-northern Chile between the Atacama (19°20′ S) and Valparaíso (33°57′ S) regions, occurring mainly in onshore facilities, and between the Los Ríos (39°15′ S) and Los Lagos (44°14′ S) regions in southern Chile, occurring primarily in suspended systems in the sea (Fig. 1). However, due to the favorable conditions of water temperature, production of juveniles is concentrated between the Atacama and Coquimbo regions (19°20′ - 32°15′ S), where juveniles are transferred to grow-out areas in the seas of the southern region (Flores-Aguilar et al., 2007). Consequently, a selective breeding program can be developed in an environment that is distinct from the grow-out area; therefore, a deep knowledge of the magnitude of GEI for traits of productive interest for red abalone is necessary. The existence of GEI can limit the diffusion of genetic progress if the selected genotypes behave differently according to the areas in which they are produced (James, 1961). In order to determine if the response to the selection for traits of productive interest are similar in different environments, this study evaluated the heritability of traits linked to abalone production (shell length and width, and total weight) and the existence of GEI for these traits upon cultivating *H. rufescens* in different farms with different environmental and management conditions.

2. Methodology

2.1. Experimental design

Two *Haliotis rufescens* cohorts were produced in 2007 (2007 cohort) and 2009 (2009 cohort) at the Center for Abalones Production of the Catholic University of the North (UCN in Spanish), Coquimbo. A nested design was used to produce abalone progenies, in which each male was crossed with 2 or 3 females to produce full (FS) and half sib (HS) families. 50 families of FS and 20 HS families were produced in 2007; and 42 FS and 18 HS families in 2009. Each family of FS was cultivated separately in 200 L tanks for 14–17 months (2007 cohort) or 36 months (2009 cohort). Later, a tag was attached to the shell of each individual with underwater epoxy putty to identify the families. Subsequently, each of the 50 families of the cohort 2007 was randomly divided into two groups (i.e., replicates of families; n = 12–34 abalones per family) that were distributed in two land based farms, one of which was located on the southern shore of the Bay of Coquimbo (CBO) (29°56′16,2″ S - 71°20′ 09,2″ W) and the other to the North of Caldera (CAL) (26°57′24,5″ S - 70°48′12,9″ W) (Fig. 1). In these farms, abalone families were cultivated together until 42 months of age in individualized baskets distributed in 20 t race-way tanks with constant water flow and aeration. The abalones were fed ad libitum twice a week with brown algae (*Lessonia* spp. and *Macrocistys pyrifera*) supplemented with small doses of *Ulva* spp. and *Gracilaria* spp. Replicates of the 42 families of the 2009 cohort (n = 5–8 abalones per family) were distributed between the Center of Abalone Cultivation of UCN located in the bay of La Herradura, in Coquimbo (UCN) (29°57′58″ S - 71°21′15,8″ W), and a commercial sea based farm located in Chiloé (CHI) (42°20′27.6″ S - 73°33′01.8″ W). At UCN, the abalones from the different families were stocked and cultured for 12 months in one 10 t race-way tank, and fed ad libitum weekly with *Lessonia* spp. In Chiloé, abalones were cultured for a year as stoked in cages suspended on *long-line* systems in the sea. These abalones were fed ad libitum weekly, mainly with *M. pyrifera* and *Gracilaria chilensis*. In each culture system densities were maintained at commercial conditions, i.e., with substrate coverture by animals that varied between 30 and 60% of the available area, depending of the age/size of the abalones. In northern farms sea temperature fluctuate between 13 and 18 °C (SHOA, 2016); and present a stable salinity of 34.5 psu (Moraga et al., 2001). In the southern farm sea temperature

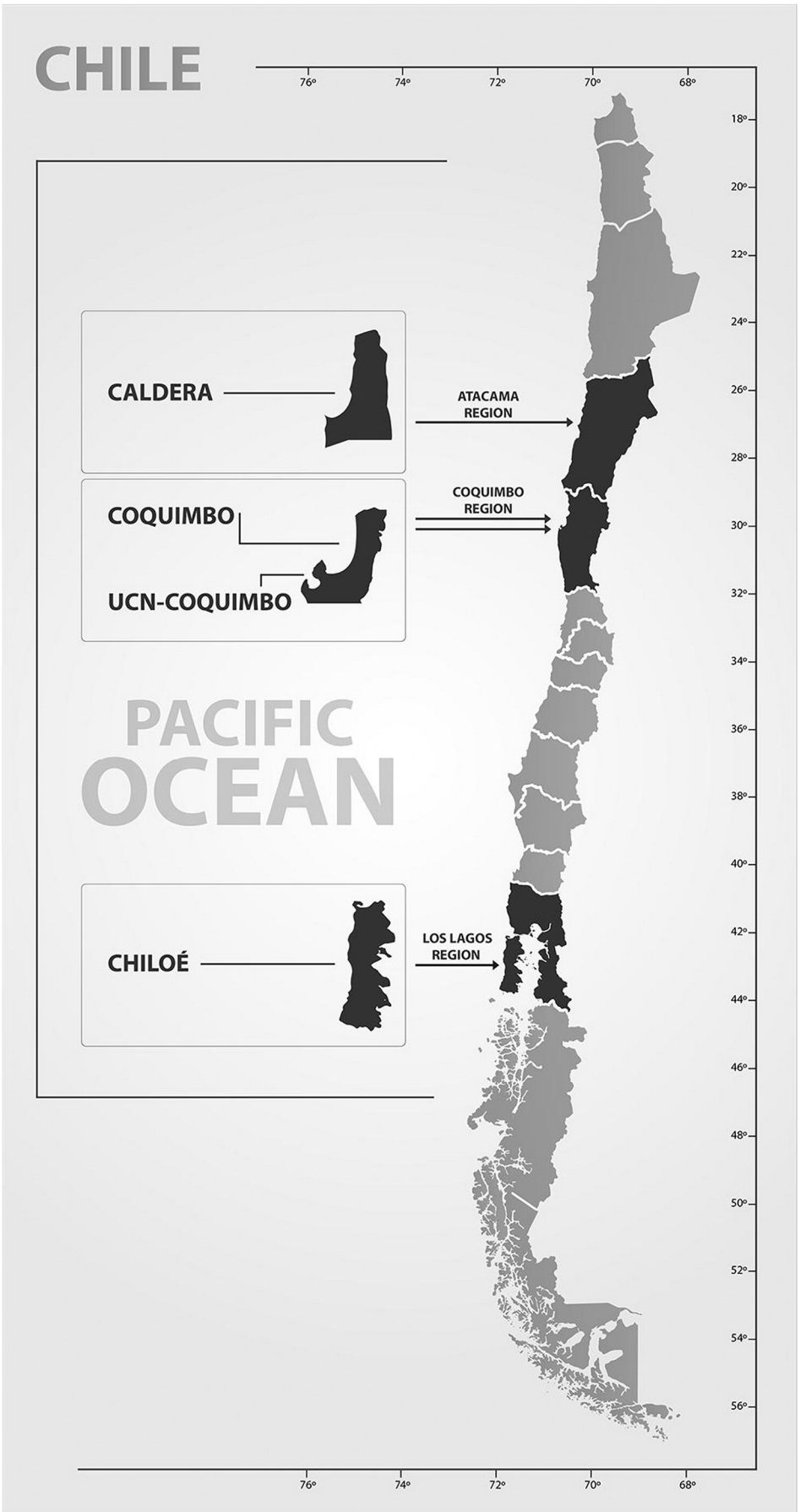

Fig. 1. Geographic localization of the farms used in the present study for red abalone *Haliotis rufescens* cultivation.

fluctuated between 8 and 14 °C; and salinity between 32.5 and 34.1 psu (Carrasco and Silva, 2008).

2.2. Phenotypic analysis of productive traits

After the growth period in each environment, the following parameters from each individual coming from replicates of the FS families were taken: total weight were measured using a digital balance (±0.01 g); and the shell length and width using a digital caliper (±0.01 mm). Measurements on the 2007 cohort were made at 32 (n = 1571) and 42 months of age (n = 1165). For the 2009 cohort, abalones were measured at 48 months of age (n = 469), i.e., 12 months after distribution to the farms.

Differences in weight and size (length and width of the shell) suggested the existence of possible growth allometries between farms; thus, these were analyzed by an analysis of covariance (ANCOVA) (Choo and Liew, 2006). The allometry equation using untransformed data is $y = ax^2$; allometries were estimated through analysis of linear regression using length as the independent variable and by calculating the regression curve as $log_y = \log a + b\ log_x$, where y is the dependent variable, x is the independent variable, a is the intercept and b is the slope of the growth coefficient (Choo and Liew, 2006).

2.3. Estimation of the components of phenotypic variance

Additive genetic variances of the productive traits were estimated through intraclass correlations using the restricted maximum likelihood (REML) model (Johnson and Thompson, 1995). The ASReml v.3.0 program was used (Gilmour et al., 2009), and mixed linear models of analysis of variance were implemented according to the general model:

$$Y = Xb + Za + e$$

where Y is a vector of observations of all individuals, b is the fixed effects vector, a is the vector of additive genetic effects and e is the error. X and Z are the corresponding incidence matrices. Prior to the estimation of quantitative genetic parameters, the fixed, random or covariate factors that could significantly affect the phenotypic variance were analyzed. When these parameters and factors showed statistically significant effects, they were incorporated into the model used to estimate the components of phenotypic variance.

The heritability (h^2) of each productive trait was calculated separately for each farm as the ratio of the additive genetic variance with respect to phenotypic or total variance (Falconer and Mackay, 1996; Kruuk, 2004). The statistical significance of the fixed effects (date of birth and sampling order) and covariates (age at the time of measurement) were estimated using the Wald F Statistic. The statistical significances of non-additive random effects of common environment/maternal effects and random additive effects (heritability) were estimated using *log-likelihood* ratio tests (log-LR tests) (Lynch and Walsh, 1998).

The phenotypic and genotypic correlations between the productive traits (total weight, length and width of the shell) were estimated separately for each farm. The yield correlations of the same genotypes (families) between environments (i.e., genotype-environment interactions, GEI) were estimated with a bivariate animal model using the ASReml 3.0 program (Gilmour et al., 2009). The statistical significance of the genotypic correlations between traits was estimated using the *log-LR* test (Lynch and Walsh, 1998). The *z*-score test was used to calculate the significance of GEI and phenotypic correlations (Nguyen et al., 2007; Tan et al., 2016):

$$z = \frac{x_i - x_j}{\left(\sigma_i^2 + \sigma_j^2\right)^{0.5}},$$

where x_i and x_j are the genetic correlations of the traits, and σ_i and σ_j are their respective standard errors. x_j was set to one or zero to test whether an estimate was significantly different from one or zero, respectively. The resulting *z*-scores were then tested against a large sample with a normal distribution. GEIs were considered significant when they differed from 1 (Nguyen et al., 2007; Tan et al., 2016), whereas the phenotypic correlations were considered significant when they differed from 0.

The direct response to selection was estimated as $G = ih^2\sigma_P$, in which i is the intensity of selection, h^2 is heritability and σ_P is the phenotypic standard deviation of the trait (Falconer and Mackay, 1996). The correlated response was estimated as $CR_y = ih_x h_y r_A \sigma_{Py}$, in which h_x and h_y are the square roots of the heritabilities for the selected trait (x) and correlated traits (y), respectively, r_A is the additive genetic correlation between x and y traits, and σ_P is the standard deviation of the y trait (Lande and Arnold, 1983; Falconer and Mackay, 1996). For the estimations, $i = 2.063$ was used, which resulted from selecting 5% of the reproductive population with the best yield.

2.4. Animal research

This study was carried out in strict accordance with the recommendations made by the Canadian Council on Animal Care. The protocol was approved by the Committee of Bio-ethics of the Chilean National Council for Science and Technology (CONICYT).

3. Results

3.1. Phenotypic analysis of productive traits

Age-matched abalones belonging to the same families of FS showed differences in the mean size after growth in distinct farms (Table 1; $P < 0.01$). Shell length and width of abalones at 32 months of age was approximately 11% higher in Caldera (CAL) than in Coquimbo (CBO) ($P < 0.001$), both farms located in the northern part of Chile. During the second year, the animals maintained in CAL increased their length by 42%, while the lengths of the animals in CBO increased by only 24%. Thus, growth in CAL was practically double that obtained in CBO in this period ($P < 0.001$). The relative increase in the width of the shell followed the same trend, although this difference was less pronounced ($P < 0.001$). Moreover, the weight gain during the second year in CAL was 79% higher than in CBO ($P < 0.001$).

Interestingly, the growth differences in the width and length of the shells between abalones maintained at Coquimbo (UCN) and Chiloé (CHI) were lower than those observed between farms in the northern region (Table 1). Only the width of the shell was significantly greater (5.7%) in UCN than in CHI (Table 1: $P < 0.05$). However, the total mass achieved in UCN was 24% greater than that obtained in CHI ($P < 0.001$).

Allometry analysis in the 2007 cohort showed that the relationships between the length of the shell and weight were similar between the two farms in northern Chile (CAL and CBO), both in the measurements at 32 months and 42 months of age ($P > 0.05$; Fig. 2). In contrast, the relationship between the length of the shell and weight in individuals of the 2009 cohort differed (allometric) between the farms of northern (UCN) and southern (CHI) Chile ($P < 0.0001$; Fig. 2). In the 2009 cohort, abalones with equal shell lengths in UCN were heavier than those in CHI (Table 1: Fig. 2). The same trends were confirmed upon relating the width of the shell with weight.

Table 1
Mean shell length and width, and total weight (±SD) of *Haliotis rufescens* abalone reared by cohorts in different farms in northern (CAL: Caldera; CBO: Coquimbo Bay; UCN: Universidad Católica del Norte – Coquimbo at La Herradura Bay) and southern Chile (CHI: Chiloé).

Trait	Cohort 2007				Cohort 2009	
	32 month		42 month		48 month	
	CAL	*CBO*	*CAL*	*CBO*	*UCN*	*CHI*
Length (mm)	54.99 (5.32)[a]	49.34 (6.43)[b]	78.17 (6.17)[a]	60.97 (7.73)[b]	67.11 (11.34)[a]	65.41 (9.37)[a]
Width (mm)	38.12 (4.70)[a]	34.07 (4.64)[b]	54.55 (4.57)[a]	44.20 (5.85)[b]	48.17 (8.46)[a]	45.57 (6.87)[b]
Weight (g)	26.83 (7.57)[a]	20.71 (7.79)[b]	85.67 (19.96)[a]	53.61 (17.54)[b]	57.26 (26.49)[a]	45.89 (20.61)[b]

Different letters in superscript mean statistical differences ($P < 0.05$).

3.2. Components of the phenotypic variance, heritabilities and genetic correlations

In the analysis of factors that could significantly affect phenotypic variance, it was observed for the 2007 cohort that regardless of the farm, the fixed (birth date and sampling order), covariate (age at the time of measurement) and random effects (common environment/maternal effects) at 32 months of age were not statistically significant ($P < 0.05$). At 42 months, however, age showed a significant covariate effect on growth ($P < 0.05$). In the 2009 cohort, the fixed factors of sampling order and age were statistically significant in the UCN cultivation ($P < 0.05$). In the CHI cultivation, in turn, no fixed, covariate or random effects were detected ($P > 0.05$).

Thus, in estimating the heritabilities (h^2), genetic correlations and genotype interactions for the 2007 cohort at 32 months of age, the simple statistical model described in the methodology was used. To estimate those parameters at 42 months in the 2007 cohort, age was incorporated as a covariate; in the 2009 cohort, the model included sampling order as a fixed factor and age as a covariate.

All estimated heritabilities were significantly different from zero ($P < 0.05$) but varied between traits and, in some cases, between farms within the same cohort (Table 2). In general, the mean values of estimated h^2 were 0.38, 0.30 and 0.39 for the length and width of the shell and total weight, respectively. The estimated h^2 for the three traits in the replicates of families cultivated in the north (CAL vs CBO) showed somewhat greater values in Coquimbo than in Caldera at both 32 and 42 months, except for total weight at 42 months of age (Table 2). In contrast, the estimated h^2 for the total weight in the replicates of families maintained in northern (UCN) and southern (CHI) Chile were the same (0.53). However, the h^2 values for the length and width of the shell were markedly greater in replicates maintained in the south (CHI) (Table 2).

The coefficient of additive genetic variation (CV_A) for shell dimensions showed values ranging from 4.38 (2007 cohort at 42 months in CAL) to 11.49 (2009 cohort at 48 months in CHI) for length and from 3.55 (2007 cohort at 42 months in CAL) to 11.72 (2009 cohort at 48 months in CHI) for width. For the weight, CV_A varied between 15.08 (2007 cohort at 42 months in CAL) and 33.84 (2009 cohort at 48 months in UCN). For most of the traits, the lowest and highest CV_A were observed in CAL and CHI, respectively (Table 2).

In general, no significant effect of the farm factor (cultivation environment) was observed upon comparing the genetic gain potential by direct selection (G%) for the three productive traits between replicates of families in different farms (Table 2). Weight was the trait with the highest gain potential, with expected responses of 16% to 51% per generation if the highest 5% of the reproducing population is selected to form the following generation (Table 2). Expected gain by selection using the same intensity of selection for length or width of the shell would be lower, with a range of 3 to 19% per generation.

High and positive phenotypic ($r_P = 0.75–0.98$) and genetic ($r_A = 0.82–0.98$) correlations were observed among all the examined traits regardless of age and environment in which they were estimated (Table 3; $P < 0.05$). Particularly relevant were the genetic correlations of total weight with the length and width of the shell, which were all higher than 0.82. Upon selecting the 5% of abalones with the largest shell lengths, the estimations of correlated gain in weight varied between 14 and 51% per generation, which were similar to those values expected upon directly selecting for weight. The use of width of the shell as selection criterion would produce much lower expected correlated responses, varying from 11 to 45%.

3.3. Genotype-environment interactions

High correlations were observed for the three analyzed traits ($r_G = 0.95–1.10$) between replicates of the families in the 2007 cohort (in both examined ages) maintained at two farms of northern Chile (CBO vs CAL). These correlations were not significantly different from 1 ($P > 0.05$), which was indicative of the absence of GEI for the three analyzed traits (Fig. 3). The correlations for the three analyzed traits among replicates of the families in the 2009 cohort maintained at UCN and CHI were smaller than the correlations found for the 2007 cohort ($r_G = 0.55–0.76$) but not statistically different from 1 ($P > 0.05$; Fig. 3). Therefore, a GEI was also undetected in comparing environments of northern vs southern Chile.

4. Discussion

In a selective breeding program, it is essential that target production traits possess heritable genetic variation in order to favorably respond to selection. In programs involving rearing individuals in different environments, it is very important to know whether the response to selection is similar between these individuals. For the red abalone, *H. rufescens*, we found that some traits associated with growth had significant levels of heritability and potentially important correlated responses. In addition, we observed that there were no GEIs for these traits; in other words, the relative performance of these traits in the genotypes was similar between different cultivation environments.

On the other hand, although the abalones compared in this study consisted of duplications of the same families in two environments, a clear trend towards better growth rates in both weight and shell measurements was observed in abalones cultivated at farms in the northern Chile compared to their genotypic replicates cultivated further south. Among the environmental factors that influence the growth of abalones, the quantity and quality of food (Britz et al., 1997; Gilroy and Edwards, 1998; Nidoo et al., 2006; Hernández et al., 2009; Cho and Kim, 2012), water temperature (Leighton, 1974; López et al., 1998; Britz et al. 1997; Kelly and Owen, 2002; Steinarsson and Imsland, 2003; Searle et al., 2006), stress levels (Hooper et al., 2007), population density (Capinpin et al., 1999; Wu et al., 2009), oxygen concentration (Harris et al., 1999), dissolved ammonia (Harris et al., 1998), and other factors (Brown and Quinn, 1998) have been identified. In the farms in northern Chile (Caldera and Coquimbo), the water temperatures are higher, with an annual average temperature of 15.6 °C; by contrast, in the south (Chiloé), the annual average temperature is notably lower (12.8 °C) (SHOA, 2016). This factor may at least partially explain the variation observed in growth. However, the effects of cultivation

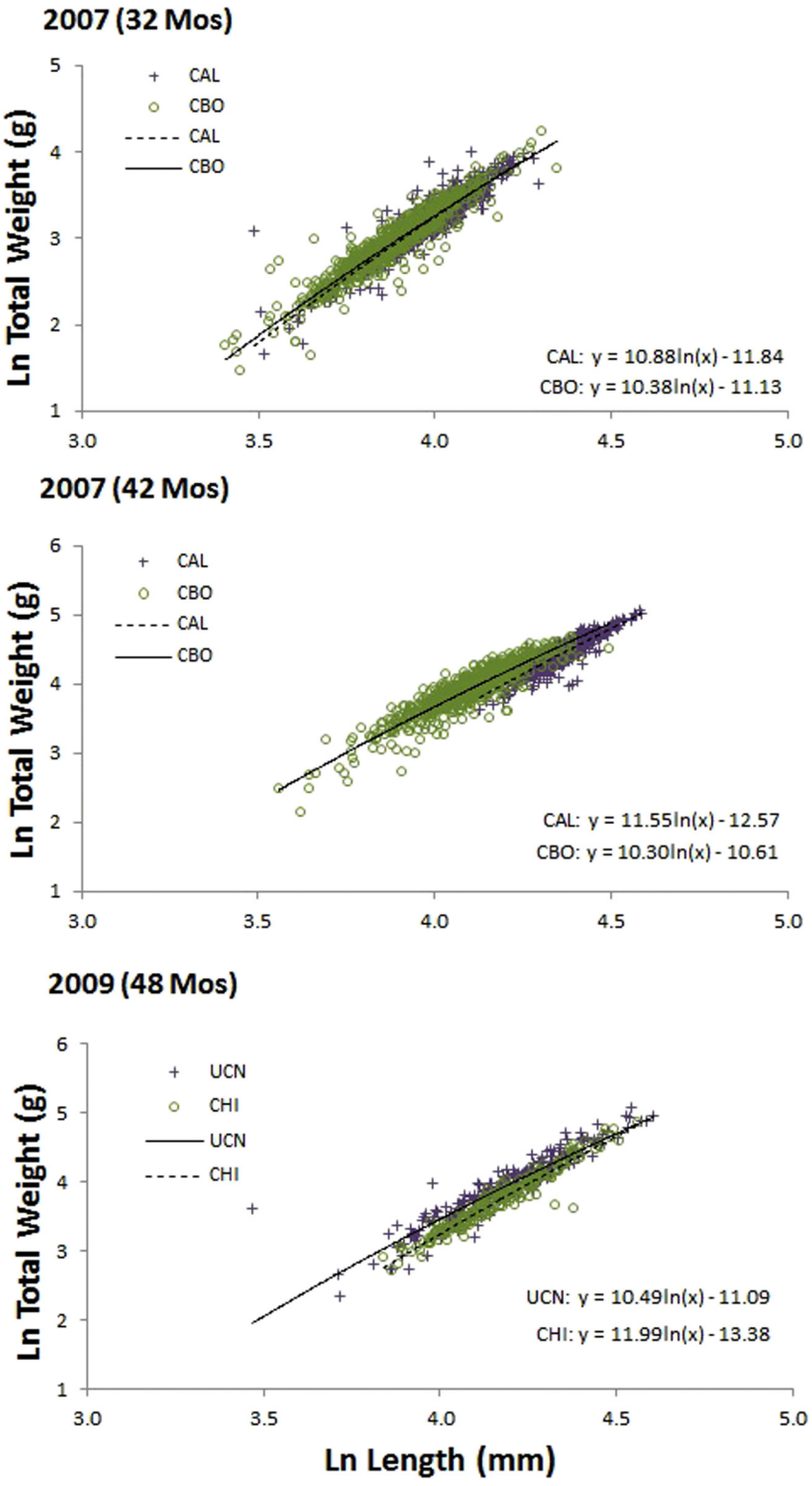

Fig. 2. Allometric comparisons between the length of the shell and total weight in *Haliotis rufescens* individuals of the 2007 cohort (measured at 32 and 42 months of age) and the 2009 cohort (measured at 48 months of age). Abalones from the 2007 cohort were maintained at the Caldera (CAL) and Coquimbo (CBO) farms; the 2009 cohort was maintained at the Catholic University of the North - Coquimbo (UCN) and Chiloé (CHI) farms.

techniques (e.g., baskets in tanks vs baskets at sea) and the general management of cultivation and feeding cannot be excluded; though animals were preferably fed with *Macrocystis pyrifera*, other algae species were incorporated into their feed depending on the availability of the main species.

A notable aspect of the results is the evidence of allometry in growth upon comparing populations maintained in the northern (UCN) and southern country (CHI). This phenomenon has been described when comparing diploid and triploid abalones (Liu et al., 2009) or when cultivating abalones at high densities (Mgaya and Mercer, 1995). Our results

Table 2
Estimated quantitative genetic parameters [heritabilities (h^2); coefficients of additive (CV_A), residual (CV_R) and phenotypic (CV_P) variation; absolute (G) and relative (G%) responses to selection] for the shell length and width, and total weight in two cohorts (2007 and 2009) of red abalone evaluated in different farms: CAL = Caldera; CBO = Coquimbo; UCN = Catholic University of the North - Coquimbo; and CHI = Chiloé. The 2007 cohort was evaluated at two ages (32 and 42 months) in the respective environments (CAL and CBO).

	Cohort	Farm	Age (month)	h^2 (SE)	CV_A	CV_R	CV_P	G	G%
Shell length	2007	*CAL*	32	0.33 (0.09)*	5.70	8.05	9.87	3.69	6.71
		CBO	32	0.36 (0.09)*	8.03	10.7	13.4	4.90	9.94
		CAL	42	0.30 (0.10)*	4.38	6.76	8.05	3.89	4.98
		CBO	42	0.22 (0.08)*	6.08	11.3	12.9	3.55	5.83
	2009	*UCN*	48	0.46 (0.16)*	11.0	12.1	16.4	10.4	15.5
		CHI	48	0.62 (0.17)*	11.5	9.06	14.6	12.2	18.7
Shell width	2007	*CAL*	32	0.21 (0.07)*	5.76	11.0	12.4	2.05	5.38
		CBO	32	0.35 (0.09)*	8.26	11.3	14.0	3.44	10.1
		CAL	42	0.18 (0.08)*	3.55	7.64	8.43	1.70	3.12
		CBO	42	0.16 (0.07)*	5.36	12.2	13.3	1.94	4.39
	2009	*UCN*	*48*	0.33 (0.15)*	9.74	13.9	17.0	5.55	11.5
		CHI	*48*	0.58 (0.17)*	11.7	10.0	15.4	8.40	18.4
Total weight	2007	*CAL*	32	0.34 (0.09)*	16.7	23.2	28.6	5.37	20.0
		CBO	32	0.31 (0.08)*	21.4	32.0	38.5	5.09	24.6
		CAL	42	0.40 (0.11)*	15.1	18.5	23.8	16.8	19.6
		CBO	42	0.24 (0.08)*	16.1	28.8	33.0	8.74	16.3
	2009	*UCN*	48	0.53 (0.17)*	33.8	31.9	46.5	29.1	50.8
		CHI	48	0.53 (0.16)*	33.4	31.3	45.7	22.9	49.9

* Significantly different from zero ($P < 0.05$).

suggest a distinct distribution of the metabolic energy in abalone under different environmental conditions, favoring the increase in size over the accumulation of biomass in the southern region.

The estimated heritabilities for weight, length and width were medium to high. These results are consistent with prior observations made in this species (Jónasson et al., 1999) and are within the ranges reported for other abalone species (Roussel et al., 2013; Lucas et al., 2006; You et al., 2010a). Unlike the heritabilities observed by Brokordt et al. (2015), all h^2 values were distinct from zero, and no significant maternal or common environmental effects were detected.

Genetic correlations between traits, which were high and significant in all environments, were similar to those reported by Brokordt et al. (2015) for the same species. Similar results have been obtained for these same traits in different abalone species by other authors (Lucas et al., 2006; Li, 2008; Choe et al., 2009; Brokordt et al., 2015). This suggests a high potential of positively correlated responses over the other studied traits upon selection for one of these traits. However, the objective of a commercial selective breeding program in abalones is to increase the biomass at harvest. In this study, the expected correlated responses for improving the total weight using the length of the shell as a selection criterion predict a selection gain (14–51%) similar to what would be obtained by selecting directly for weight (16–51%) in all environments examined. In this way, indirect selection by length of the shell and the direct use of total weight as a selection criterion would yield similar effects in terms of the increase in weight. The use of shell length as a selection criterion, however, would have the advantage to be more easily and accurately measured than the weight.

Discrimination on the existence or absence of GEIs can be based on statistical or conventional criteria. When the correlation of the yield of several tested genotypes in two environments is 1, it is understood that there is no GEI (Falconer and Mackay, 1996). The conventional way of determining the presence of GEIs (Robertson, 1959) suggests that if the correlation value is higher than 0.8, the GEIs are considered negligible, but if the correlation value is lower, GEIs are assumed to exist. Upon comparing the Coquimbo and Chiloé farms, the correlations were lower than 0.8, but not upon comparing the farms in the northern region (Coquimbo-Caldera). However, the statistical means of identifying the existence of a GEI is by verifying the significance of the statistical deviation of the correlation coefficient obtained relative to 1 (Nguyen et al., 2007). In this study, none of the analyses showed significantly distinct differences from 1, which can be interpreted as the absence of a GEI, as observed by Jónasson et al. (1999) for the same species in Iceland.

In conclusion, this is the first study in evaluating the effect of contrasting real farming environments in terms of management conditions and large geographic distance, on the estimation of heritability and GEI for productive traits. Results indicate that the application of selection by the shell length at age of harvest has the greatest potential for improving the production of *H. rufescens*. These improvements are practical (ease and accuracy in measurement), have indirect effects on the

Table 3
Genetic (above the diagonal) and phenotypic (below the diagonal) correlations between total weight and length and width of the shell in red abalone, estimated in the 2007 cohort grow-out in Caldera (CAL) and Coquimbo (CBO), at 32 and 42 months, and 2009 cohort evaluated at the Catholic University of the North - Coquimbo (UCN) and Chiloé (CHI) farms, at 48 months.

Trait	Weight	Length	Width	Weight	Length	Width
2007 (32 months)		CAL		2007 (32 months)		CBO
Weight	.....	0.95 (0.02)*	0.86 (0.06)*	.....	0.97 (0.02)*	0.94 (0.03)*
Length	0.98 (0.02)*	.....	0.90 (0.05)*	0.93 (0.01)*	.....	0.98 (0.01)*
Width	0.75 (0.02)*	0.76 (0.02)*	.....	0.91 (0.01)*	0.94 (0.01)*	.....
2007 (42 months)		CAL		2007 (42 months)		CBO
Weight	.....	0.82 (0.05)*	0.87 (0.07)*	.....	0.89 (0.04)*	0.94 (0.03)*
Length	0.90 (0.02)*	.....	0.95 (0.04)*	0.91 (0.02)*	.....	0.97 (0.02)*
Width	0.84 (0.02)*	0.83 (0.03)*	.....	0.91 (0.02)*	0.95 (0.01)*	.....
2009 (48 months)		UCN		2009 (48 months)		CHI
Weight	.....	0.97 (0.03)*	0.88 (0.05)*	.....	0.96 (0.03)*	0.88 (0.05)*
Length	0.93 (0.02)*	.....	0.98 (0.01)*	0.95 (0.02)*	.....	0.98 (0.01)*
Width	0.92 (0.02)*	0.94 (0.02)*	.....	0.94 (0.02)*	0.98 (0.01)*	.....

* Significantly different from zero ($P < 0.05$).

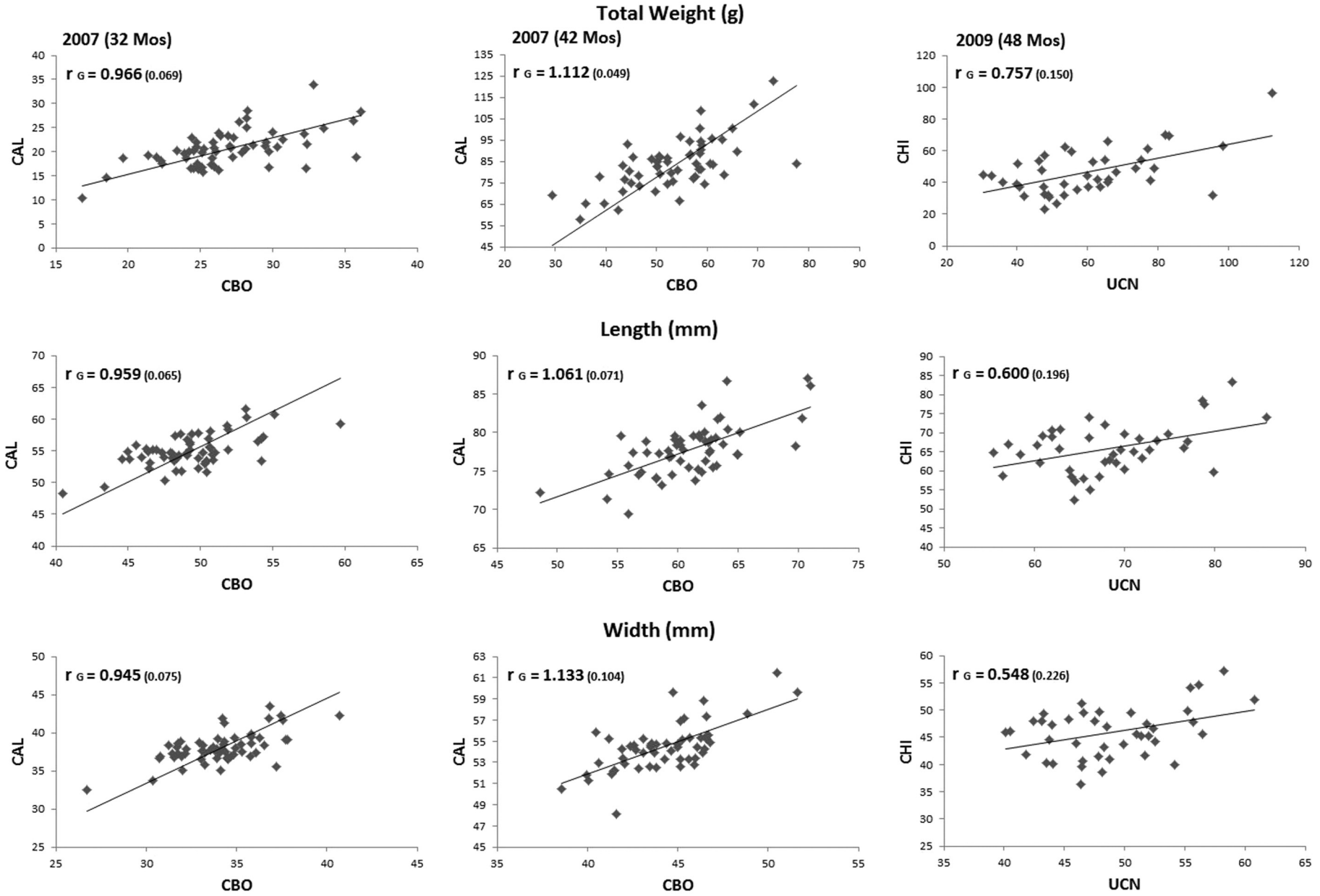

Fig. 3. Coefficients of genetic correlation ($r_G \pm$ SE) for total weight, length and width of the shell between replicates of families of two cohorts (2007 and 2009) of the red abalone *Haliotis rufescens* cultivated in different farms on the coast of Chile (CAL = Caldera; CBO = Coquimbo; UCN = Catholic University of the North - Coquimbo; and CHI = Chiloé). The 2007 cohort was evaluated at two ages (32 and 42 months) in the CAL and CBO environments; the 2009 cohort was evaluated at 48 months of age in the UCN and CHI environments.

objective trait of selection (weight), and consist of a trait that is not significantly affected by genotype-environment interactions. In addition, the results obtained suggest that a single selective breeding program would be sufficient for the red abalone industry in Chile, as the response to selection of traits associated with growth would be similar in different environments.

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