



Genetic parameters for growth and morphological traits of the Pacific white shrimp *Penaeus vannamei* from a selective breeding programme in the industrial sector of Ecuador

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ABSTRACT

This study aimed to estimate the genetic parameters of growth-related traits (weight and length), morphological traits (cephalothorax, abdomen, length, height, segment width and volume), and the correlated response of weight traits via the selection for morphological traits to evaluate the relative efficiency of indirect selection in *P. vannamei* from a selective breeding growth programme, PMG-BIOGEMAR®, under industrial production conditions in Ecuador. A total of 595 shrimps from 89 full-sibling families were reared under an extensive culturing system (estuaries) (PRODUMAR, Duran, Ecuador), and were evaluated for genetic parameters at harvest size. The heritability of growth traits was moderate-medium (0.25–0.34), whereas it was quite variable for morphological traits (0.01–0.77). Among the morphological traits, Sixth Segment Width (SW6) (0.77) and Sixth Segment Volume (SV6) (0.35) had medium-high heritability, and genetic correlations between almost all morphological and growth traits were high and positive, except those corresponding to the fourth segment. According to these genetic parameters, SW6 and SV6 as the correlated response to weight are 9.7% and 5.8%, respectively, being more efficient than direct selection for weight. Thus, the sixth segment should be considered an indirect selection criterion for growth in future breeding programmes as it is a precise, non-invasive, and low-cost morphological trait for growth improvement in the industrial sector.

Abbreviations: h^2 , Heritability estimate; h , Square root of heritability as an accuracy estimation of trait; r_g , Genetic correlation; CR_{weight} , Indirect selection response of indicator trait; R_{weight} , Direct selection response of weight; CR_{weight}/R_{weight} , Ratio of indirect response to direct response (%); TLF, Total length in fresh; TL, Total length after freezing; CL, Cephalothorax length after freezing; AL, Abdomen length; SL1, 1st segment length; SL2, 2nd segment length; SL3, 3rd segment length; SL4, 4th segment length; SL5, 5th segment length; SL6, 6th segment length; CW, Cephalothorax width; SW1, 1st segment width; SW2, 2nd segment width; SW3, 3rd segment width; SW4, 4th segment width; SW5, 5th segment width; SW6, 6th segment width; CH, Cephalothorax height; SH1, 1st segment height; SH2, 2nd segment height; SH3, 3rd segment height; SH4, 4th segment height; SH5, 5th segment height; SH6, 6th segment height; SV1, 1st segment volume; SV2, 2nd segment volume; SV3, 3rd segment volume; SV4, 4th segment volume; SV5, 5th segment volume; SV6, 6th segment volume; ATV, Abdomen total volume.

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1. Introduction

The Pacific white shrimp, *Penaeus vannamei*, in economic terms, is the most valuable farmed aquaculture species with an annual global production of 5.8 million tons (FAO, 2022).

Ecuador is the leader in farmed *P. vannamei*, producing more than 1.2 million tons in 2022 (CNA, 2022) using an extensive culturing system (estuaries) of 250 thousand hectares (Gonzabay-Crespin et al., 2021). Currently, breeding programmes in Ecuador are essentially based on mass selection processes with no genealogy traceability because this was easy to implement in the industrial sector.

Industrial *P. vannamei* culture can be substantially profitable because of the high selection response of growth traits— ten per cent per generation (Thanh et al., 2009), its short generation interval, and high fecundity (Andriantahina et al., 2012). Thus, the most important trait groups for the Ecuadorian industry are growth (weight, length, condition factor), morphological (deformity, biometry of segments related to growth), meat quality (lipid, protein, moisture, ash), robustness (survival at harvest size), and disease resistance (survival against pathogenic agents) (Shin et al., 2020). Since 2017, BLUP (Best Linear Unbiased Prediction) methodology has been established in Ecuador to increase production and minimise the production interval time at an industrial scale (PMG-BIOGEMAR® breeding programme, Shin et al., 2020).

The primary selection focus in *P. vannamei* is growth enhancement as its improvement results in shorter production times. Generally, weight at a fixed age as the growth trait criterion is much easier to measure and has a lower error than length. There are many genetic parameter studies on shrimp weight (Pérez-Rostro et al., 1999; Argue et al., 2002; Pérez-Rostro and Ibarra, 2003a; b; Gitterle et al., 2005a; b; Castillo-Juárez et al., 2007; Campos-Montes et al., 2009, 2013; Sui et al., 2016), however, there are few studies estimating the genetic parameters of morphological traits (Andriantahina et al., 2012; Singh et al., 2017). Genetic parameters are important to increase the selection response, which itself affords information regarding traits of interest that are easy, cost-effective measures to incorporate into breeding programmes (Farfán et al., 2002).

Morphometric characteristics are related to animal health and welfare under culture conditions. Changes in morphometric characteristics and their relationship to different body segments are indicators of unhealthy *P. vannamei* growth (Singh et al., 2017). Andriantahina et al. (2012) reported a high genetic correlation between body weight and length (0.84–0.85) in *P. vannamei*. In shrimp, the muscle is located in the abdomen part of the body and represents about 90% of total shrimp meat, which in turn represents 48% of the total animal, the cephalothorax 39%, exoskeleton 11%, and the tail is only 2.3% (Cesar et al., 2008; Andriantahina et al., 2012; Dang et al., 2018).

The future competitiveness of the industrial *P. vannamei* sector is based on the incorporation of genetic improvement tools that allow us to use the best animals each generation to generate offspring with greater growth potential and quality, minimising production times, and improving the profitability of the entire productive sector. It must be highlighted that genetic achievements are permanent, cumulative, and extendable to the entire production chain, even when selection is no longer applied (López-Fanjul and Toro, 2007).

In the present study, the objective is to analyse and provide new genetic estimates for some morphological and growth traits and suggest indirect selection traits by estimating the correlated response of weight as the target trait using their genetic parameters. Then, we compare the genetic correlation between traits with high relative efficiency to indirect selection responses and other morphological traits in a *P. vannamei* population from the second generation of an industrial-scale selective breeding programme for growth in an extensive culturing system of Ecuador (estuaries).

2. Materials and methods

2.1. Biological material and traceability

The *P. vannamei* used in this study belonged to the second generation (F2) of a PGM-BIOGEMAR® breeding programme and came from F1 broodstock, located at BIOGEMAR S.A., San Pablo, Ecuador. The selection of candidates (249 males and 1213 females) and mating (172 males and 275 females) of F1 broodstock was performed according to the Optimal Contribution Selection method (Meuwissen, 1997). Each male was mated with a single or two females through artificial insemination under an industrial operating protocol including broodstock acclimation, spawning, etc., as described by Lorenzo et al. (2010). A total of 238 families (14.4 ± 4.02 offspring per family) were generated along four consecutive days to maximise the number of families produced because of different sexually mature breeders per day; their viable offspring were cultured in the same tank to minimise the common environment as a source of resemblance between relatives. To obtain a balanced number of descendants per family, the same number of nauplius (nauplius 5, N5) were taken from each family. When their descendants reached the PL12 stage (F2), they were sent to the selection nucleus (BIOGEMAR S.A., San Pablo, Ecuador) and on-growing commercial population (PRODUMAR, Duran, Ecuador). Environmental conditions differed greatly between the nucleus (≥ 35 psu for salinity, ~ 300 animals/m³) and the on-growing commercial population (2–10 psu for salinity, ~ 30 animals/m³). At harvest size, a random sample of individuals was tagged with eye rings and, at that point, a sample of pleopods was taken from each *P. vannamei* and stored in RNAlater® (Sigma-Aldrich) for genotyping and parental assignment.

2.2. Growth and morphological analysis

A total of 595 *P. vannamei* individuals from PRODUMAR (on-growing company) were sampled at harvest size (130–133 days, 18.7 g, and 13.2 cm on average) by slaughtering in ice. Traits were characterised according to standardised methodologies defined in AquaExcel-ATOL (AQUAEXCEL, 2013). Whole body weight was measured by ATOL:0000351 (including cephalothorax), length by ATOL:0001660 (from rostrum until telson), and first-segment width by vernier calliper under fresh conditions. Then, whole bodies of 595 *P. vannamei* were frozen at -20 °C and transferred to BIOGEMAR, until morphological analysis.

Total length was measured from the anterior end of the cephalothorax carapace to the tip of the telson under fresh conditions (TLF), once thawed the total length of each animal (TL) was measured again. The length of the cephalothorax was measured from the anterior end of the cephalothorax to the beginning of the 1st segment (CL), the total length of the abdomen (AL) from the end of the cephalothorax to the beginning of the telson. The length of each of the six segments constituting the abdomen (SL1, SL2, SL3, SL4, SL5, and SL6), the height of the cephalothorax (CH), and the height of each of the six segments constituting the abdomen (SH1, SH2, SH3, SH4, SH5, and SH6) (side views, Fig. 1 A and Table 1) were measured. Cephalothorax width (CW) and the width of each of the six segments constituting the abdomen (SW1, SW2, SW3, SW4, SW5, and SW6) (superior view, Fig. 1B and Table 1) were also measured. The width and height of the cephalothorax and each abdomen segment were measured at the central point of their parts. All measurements were recorded in centimetres (cm).

With the length, width, and height data of each segment, the total volume of the abdomen (ATV) and of each of its segments (SV1, SV2, SV3, SV4, SV5, and SV6) (cm³) were calculated as follows:

$$ATV \text{ (cm}^3\text{)} (i) = \sum (AS_{ji} * HS_{ji} * LS_{ji})$$

where i is the measured individual and j each of the segments.

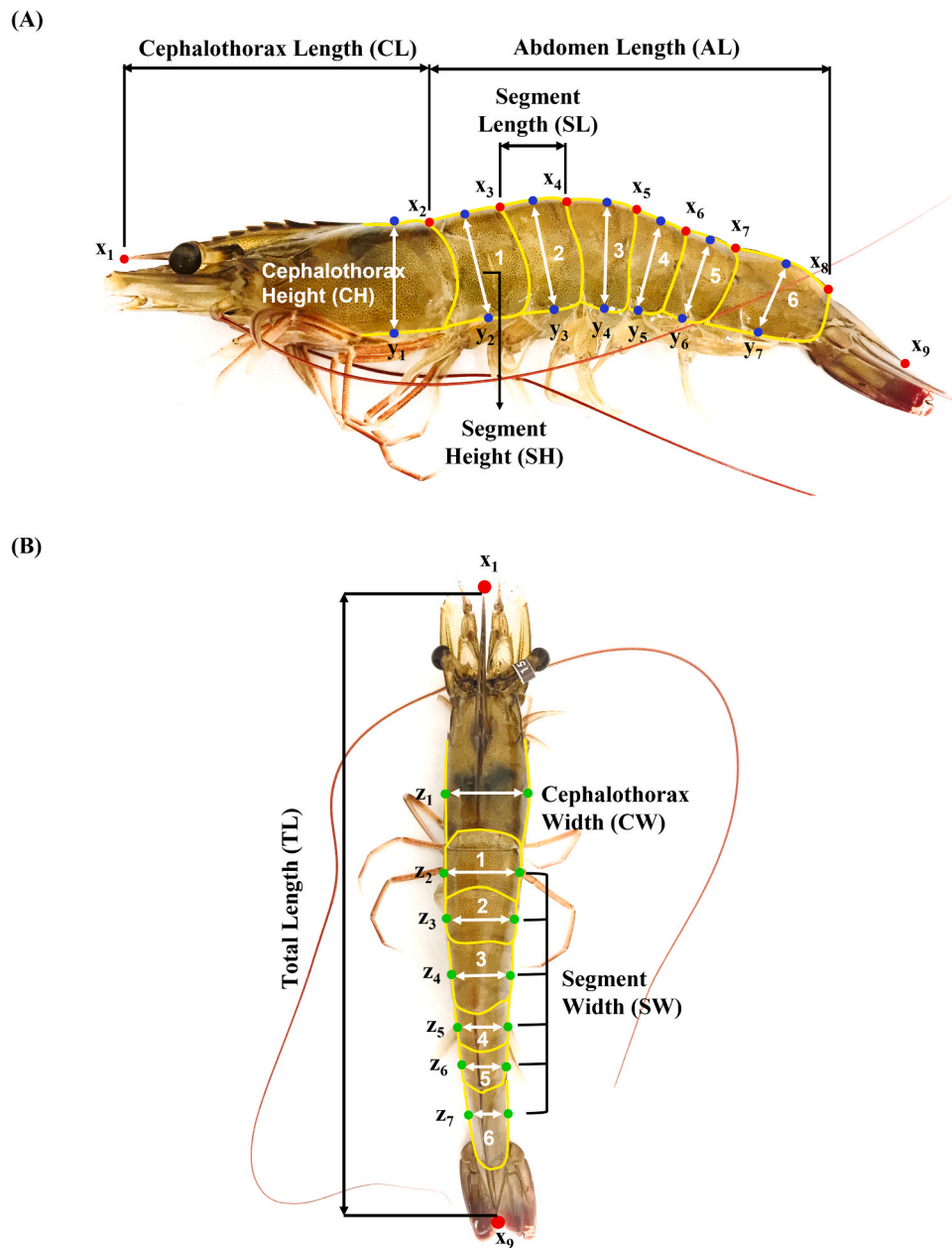


Fig. 1. (A) Lateral view of a *P. vannamei* individual with the measurements of the morphological analysis carried out in this view, (B) Dorsal view of a *P. vannamei* individual with the measurements of the morphological analysis carried out in this view.

2.3. Genotyping

A pleopod was cut from each animal and stored in *RNAlater*[®] (Sigma-Aldrich) until analysis. DNA extraction was performed in the SABE-IUECOAQUA laboratory (University of Las Palmas de Gran Canaria, ULPGC). DNA was extracted from each sample using the BIOSPRINT[®] 96 DNA Blood kit (QIAGEN[™]) via a BIOSPRINT[®] robot, following the manufacturer’s protocol. ASSIST-PLUS (INTEGRA[™]) was used for volume dosing in S-Block with kit contents, NANODROP-8000[™] (Thermo Fisher Scientific[™]) for DNA concentration and quality, and the FREEDOM EVO[®] (TECAN) platform for DNA normalisation. Finally, genotyping consisted of 143 SNP-arrays (AQUAArray, CAT) by the services of the Centre for Aquaculture Technologies (CAT), which allowed parental assignment of known gender using the exclusion method with CAT’s non-commercial software.

2.4. Statistic data analysis

All data regarding different characteristics were tested for normality and homogeneity of variance using a General Linear Model analysis with the SPSS v27 programme (SPSS, Chicago, USA). Variance components were estimated to obtain estimates of genetic parameters via Restricted Maximum Likelihood (REML) using the following model (two by two traits, three by three traits, and four traits),

$$y = X\beta + Zu + e$$

where *y* is the phenotype of the trait studied, β is the fixed effect (sex, age, on-growing environment, spawning origin), *u* is the random animal effect, and *e* is the residual error. All estimates were carried out using the VCE programme (v 6.0) (Neumaier and Groeneveld, 1998; Groeneveld et al., 2010). For managing input data and automating processes, VCE-Executer (v3.0) (developed by Álvaro Lorenzo-Felipe with Ruby programming language) was run followed by VCE-analysis (v1.0)

Table 1
P. vannamei morphology measurements from lateral-side images based on detected points depicted in Fig. 1. Morphological traits obtained were named according to the calculation method in the table.

Trait category	Acronym	Trait	Calculation method
Length (cm)	TLF	Fresh Total length	From x ₁ to x ₉ within the longitudinal axis (LA)
	TL	Total Length	From x ₁ to x ₉ within the LA
	AL	Abdomen Length	From x ₂ to x ₈ within the LA
	CL	Cephalothorax Length	From x ₁ to x ₂ within the LA
	SL1	First Segment Length	From x ₂ to x ₃ within the LA
	SL2	Second Segment Length	From x ₃ to x ₄ within the LA
	SL3	Third Segment Length	From x ₄ to x ₅ within the LA
	SL4	Fourth Segment Length	From x ₅ to x ₆ within the LA
	SL5	Fifth Segment Length	From x ₆ to x ₇ within the LA
	SL6	Sixth Segment Length	From x ₇ to x ₈ within the LA
Height (cm)	CH	Cephalothorax Height	Axis y ₁
	SH1	First Segment Height	Axis y ₂
	SH2	Second Segment Height	Axis y ₃
	SH3	Third Segment Height	Axis y ₄
	SH4	Fourth Segment Height	Axis y ₅
	SH5	Fifth Segment Height	Axis y ₆
	SH6	Sixth Segment Height	Axis y ₇
Width (cm)	CW	Cephalothorax Width	Axis z ₁
	SW1	First Segment Width	Axis z ₂
	SW2	Second Segment Width	Axis z ₃
	SW3	Third Segment Width	Axis z ₄
	SW4	Fourth Segment Width	Axis z ₅
	SW5	Fifth Segment Width	Axis z ₆
	SW6	Sixth Segment Width	Axis z ₇
Volume (cm³)	ATV	Abdomen Total Volume	Sum [(SL1 (i) * SH1 (i) * SW1 (i)) + ... (SLn (i) * SHn (i) * SWn (i))]
	SV1	First Segment Volume	SL1 (i) * SH1 (i) * SW1 (i)
	SV2	Second Segment Volume	SL2 (i) * SH2 (i) * SW2 (i)
	SV3	Third Segment Volume	SL3 (i) * SH3 (i) * SW3 (i)
	SV4	Fourth Segment Volume	SL4 (i) * SH4 (i) * SW4 (i)
	SV5	Fifth Segment Volume	SL5 (i) * SH5 (i) * SW5 (i)
	SV6	Sixth Segment Volume	SL6 (i) * SH6 (i) * SW6 (i)

(developed by Javier Lorenzo with Java programming language) to process output data. The magnitudes of the heritability estimates were established following the classification of Cardellino and Rovira (1987), where they are considered low between 0.05 and 0.15, medium between 0.2 and 0.4, high between 0.45–0.6, and very high > 0.65. Correlations were classified as low (0–0.40), medium (0.45–0.55), and high (0.60–1) (Navarro et al., 2009), regardless of their sign.

The direct genetic selection response of the target trait ($R_x = i_x \cdot h_x \cdot \sigma_{A-x}$), and the indirect genetic selection response as a correlated response

of the trait were calculated ($CR_x = r_g \cdot i_y \cdot h_y \cdot \sigma_{A-x}$). The ratio of indirect to direct genetic selection response [CR_x/R_x (%) = $(r_g \cdot i_y \cdot h_y \cdot \sigma_{A-x}) / (i_x \cdot h_x \cdot \sigma_{A-x}) \cdot 100$] (Falconer and Mackay, 1996) was calculated as the relative efficiency of the correlated response of the target trait with the percentage of gain possible from direct genetic selection. The proportioned selection intensity was 8% for all selection traits.

3. Results

3.1. Genotyping and parental assignment

A total of 78 sire and 86 dam (F1) breeders constituted 89 full-sibling families, with 74 full-sib families and 15 half-sibling families (12 paternal and 3 maternal). A sample of 595 individual *P. vannamei* offspring (F2) were characterised by 143 SNP-array genotyping chips at the Centre for Aquaculture Technologies (CAT, San Diego, California). The assignment rate was 37.48%, presenting a low percentage of parental assignment due to low-quality DNA, transport issues, and different SNP-array genotyping chips between F1 breeders and F2 descendants.

3.2. Phenotyping

Total length was 13.16 ± 0.03 cm under fresh conditions and 13.21 ± 0.03 cm after freezing. Therefore, no significant changes in length were observed due to the freezing process.

The coefficient of variation (CV) for both traits was similar and lower than for other morphological traits (see Supplementary Material). Thus, abdominal segment height presented low and homogeneous CVs. As for the CVs of each morphological trait, volume had higher a CV than other morphological traits.

3.3. The relative efficiency of the correlated selection response

The correlated response of the weight trait to the selection of morphological traits predicts gain from indirect selection and could be used to quantify the relative efficiency of indirect selection in improving the target trait, weight. The ratio of indirect to direct responses was assessed under the same proportioned selection intensity for all traits (Table 2). Two traits, SW6 and SV6, as correlated responses for weight were 9.7% and 5.8%, respectively. SW6 and SV6 have a positive relative efficiency as indirect selection traits to improve weight as the target trait; the other morphological traits had a negative relative efficiency.

3.4. Heritability and correlations

The heritability and genetic correlation of growth and morphological traits involving length measurements at harvest size are shown in Table 2. Heritability values for weight and TLF were medium (0.34 and 0.27, respectively) and higher than for most morphological traits. However, TL heritability was lower than for TLF (0.25 vs. 0.34). Furthermore, among the morphological traits, the heritability of CL and SL4 was the highest with medium levels (0.25–0.32). The genetic correlation between weight and morphological traits presented high correlations except with SL4 (0.18). Of the morphological traits, SH5 and SH6 showed medium levels (0.20–0.21), SH2 and SH3 a little lower (0.15 and 0.17), and other heights yielded very low heritability (<0.05). Correlations between weight and all segment heights were high/positive (0.62–1). Regarding morphological traits involving width measurements at harvest size, the heritability of CW and SW1 showed medium levels (0.26 and 0.25, respectively), however, SW6 yielded a high level (0.77). Volume heritability (SV1–SV6) at harvest size was < 0.17, except for SV6, which was medium-high (0.35).

According to correlated response results, the genetic correlation between weight as the target trait, SW6 and SV6 as indicator traits, which have a positive relative efficiency, and the other morphological

Table 2
Direct and indirect selection responses of weight as the target trait.

Traits	h^2	h	r_g	CR _{weight} /R _{weight} (%)
TLF	0.34	0.58	0.69	-23
TL	0.25	0.50	0.89	-14
CL	0.25	0.50	0.96	-8
AL	0.06	0.24	0.95	-55
SL1	0.07	0.26	0.97	-51
SL2	0.03	0.17	0.93	-69
SL3	0.18	0.42	0.65	-47
SL4	0.32	0.57	0.18	-80
SL5	0.07	0.26	0.46	-77
SL6	0.13	0.36	0.65	-55
CW	0.26	0.51	0.94	-8
SW1	0.25	0.50	0.86	-17
SW2	0.19	0.44	0.94	-21
SW3	0.09	0.30	0.97	-44
SW4	0.01	0.10	-0.64	-112
SW5	0.04	0.20	0.77	-70
SW6	0.77	0.88	0.65	10
CH	0.01	0.10	0.88	-83
SH1	0.04	0.20	0.62	-76
SH2	0.15	0.39	0.88	-34
SH3	0.17	0.41	0.86	-32
SH4	0.05	0.22	0.98	-58
SH5	0.2	0.45	0.85	-27
SH6	0.21	0.46	0.91	-20
SV1	0.12	0.35	0.99	-34
SV2	0.09	0.30	0.99	-43
SV3	0.16	0.40	0.93	-28
SV4	0.17	0.41	0.28	-78
SV5	0.14	0.37	0.71	-49
SV6	0.35	0.59	0.93	6
ATV	0.15	0.39	1	-25

traits, are shown in Tables 3 to 6. The genetic correlation between weight and morphological traits was positive and high, except for SW4, which had a negative correlation, and SV4, which had a low though positive correlation (Tables 3–6). Of these results, the correlation between weight and abdomen total volume is noteworthy, being much higher than the other traits (Table 6). The genetic correlation between SW6 and the other morphological traits was medium-high, except for SW3, which was low (Table 5); the correlation between SV6 and the other morphological traits was medium-high, except for SL3, SL4, SH2, SH3, and SH5, which had low correlations with SV6 (Tables 3 and 4).

4. Discussion

The use of morphological traits as alternatives to growth traits for indirect selection in aquaculture selective breeding programmes has been studied mainly in fish (Kause et al., 2007; Navarro et al., 2016; Vandeputte et al., 2020; León-Bernabeu et al., 2021). Most breeding programmes for *P. vannamei* have focused on growth and disease resistance (Hetzl et al., 2000; Gitterle et al., 2006), however, only weight has been used to measure phenotypes to improve *P. vannamei* growth in breeding programmes. Also, various studies (Oscos et al., 2005; Simon et al., 2009; Andriantahina et al., 2012; Fernandes et al., 2017; León-Bernabeu et al., 2021) reported a high genetic correlation between body weight and length (0.84–0.91) in *P. vannamei* and fish. Therefore, in the present study, various morphological traits measuring length, height,

Table 3

Genetic correlation between indicator traits with positive relative efficiency of the indirect selection response, and length-type morphological traits, including weight, in *P. vannamei* from the PMG-BIOGEMAR® programme, at harvest size.

	TLF	TL	AL	CL	SL1	SL2	SL3	SL4	SL5	SL6
Weight	0.68 ± 0.14	0.91 ± 0.10	0.86 ± 0.31	0.97 ± 0.08	0.99 ± 0.03	1.00 ± 0.03	0.80 ± 0.42	0.13 ± 0.32	0.23 ± 0.46	0.60 ± 0.40
SW6	0.74 ± 0.21	0.64 ± 0.19	0.91 ± 0.24	0.67 ± 0.26	0.97 ± 0.09	0.98 ± 0.05	0.50 ± 0.29	0.43 ± 0.21	0.69 ± 0.30	0.49 ± 0.37
SV6	0.99 ± 0.05	0.93 ± 0.21	0.99 ± 0.15	0.95 ± 0.16	0.96 ± 0.08	0.99 ± 0.09	0.10 ± 0.41	0.25 ± 0.40	0.55 ± 0.44	0.88 ± 0.22

Abbreviations; TLF: Total length in fresh; TL: Total length after freezing; AL: Abdomen length; CL: Cephalothorax length; SL1: 1st segment length; SL2: 2nd segment length; SL3: 3rd segment length; SL4: 4th segment length; SL5: 5th segment length; SL6: 6th segment length.

width, cephalothorax volume, abdomen, and each segment were evaluated with *P. vannamei* weight.

4.1. Growth trait as a goal

The heritability value of a parameter is used as an indicator of the population's ability to respond to selection (Falconer and Mackay, 1996). It is generally assumed that traits with high heritability ($h^2 > 0.4$) are suitable for phenotypic selection, while traits with low heritability ($h^2 < 0.2$) need family selection or within-family selection to get acceptable response levels (He et al., 2011). Most of the heritability reported for *P. vannamei* weight at harvest size is within the medium-high range of heritability estimates (0.17–0.42) (Carr et al., 1997; Pérez-Rostro and Ibarra, 2003a; b; Gitterle et al., 2005a; Castillo-Juárez et al., 2007). In the present study, the growth traits measured, particularly weight, presented phenotypic values of 18.7 ± 0.13 g and heritability of 0.27 ± 0.12 at harvest size, which is in agreement with results previously reported for *P. vannamei* (Pérez-Rostro and Ibarra, 2003a; b; Campos-Montes et al., 2009; 2013). However, Pérez-Rostro et al. (1999) and Argue et al. (2002) report weight heritability ranging from 0.89 ± 0.18 – 1.32 ± 0.18 and 0.84 ± 0.43 – 1.0 ± 0.4 , respectively, including estimates outside the parameter space (i.e., >1). These discrepancies may be explained by the use of different estimation methods, numbers of families, and possibly overestimations that include the common environment (Tan et al., 2017; Zhang et al., 2017). Furthermore, it must be recalled that heritability estimates are specific for a particular population and, thus, affected by the genetic background of the base population of the breeding programme, the number of generations under selection, the familial structure of the population, among others (Castillo-Juárez et al., 2007; Luan et al., 2012).

P. vannamei length is one of the important criteria for size growth traits and for calculating the condition factor with weight and length in selective breeding programmes. The heritability estimates for length (TLF: 0.34 ± 0.16 and TL: 0.25 ± 0.14) were consistent with previous studies (Pérez-Rostro and Ibarra, 2003a; Andriantahina et al., 2012; Zhang et al., 2017). In this study, two types of length were measured, fresh (TLF) and frozen conditions (TL), and their heritability had different values (0.34 and 0.25, respectively). The reasons why frozen length is less useful for selection include problems related to different morphological conditions, such as broken rostrum or telson, muscle contraction, position when frozen, etc.; nevertheless, the correlation between TLF and TL was not low (0.68). Furthermore, in our study, the phenotypic correlation between weight and the two types of total length, TLF and TL, was 0.82 (weight-TL)-and 0.78 (weight-TLF), which is in agreement with Singh et al. (2017) who reported linear relationship values of 0.88 between weight and body length. This is true even though the average body weight in the study by Singh et al. (2017) was lower than in the present study, which may be due to shorter culture days, different agroclimatic conditions, and that the studied individuals were not from a growth breeding programme.

4.2. Morphological traits

In the present study, the genetic estimates of parameters for traits

Table 4

Genetic correlation between indicator traits with positive relative efficiency of the indirect selection response, with weight as the target trait and **height**-type morphological traits in *P. vannamei* from the PMG-BIOGEMAR® programme, at harvest size.

	CH	SH1	SH2	SH3	SH4	SH5	SH6
Weight	0.88 ± 0.50	0.62 ± 1.03	0.88 ± 0.26	0.86 ± 0.31	0.98 ± 0.16	0.85 ± 0.26	0.91 ± 0.23
SW6	0.85 ± 0.45	0.96 ± 0.32	0.58 ± 0.30	0.41 ± 0.32	0.81 ± 0.54	0.49 ± 0.31	0.55 ± 0.20
SV6	0.90 ± 0.26	0.80 ± 0.33	0.18 ± 0.51	0.32 ± 0.51	0.97 ± 0.14	0.37 ± 0.40	0.57 ± 0.32

Abbreviations; CH: Cephalothorax height; SH1: 1st segment height; SH2: 2nd segment height; SH3: 3rd segment height; SH4: 4th segment height; SH5: 5th segment height; SH6: 6th segment height.

Table 5

Genetic correlation between indicator traits with positive relative efficiency of the indirect selection response, with weight as the target trait and **width**-type morphological traits in *P. vannamei* from the PMG-BIOGEMAR® programme, at harvest size.

	CW	SW1	SW2	SW3	SW4	SW5
Weight	0.94 ± 0.14	0.86 ± 0.14	0.94 ± 0.20	0.97 ± 0.23	-0.64 ± 1.84	0.77 ± 0.34
SW6	0.59 ± 0.19	0.80 ± 0.19	0.84 ± 0.26	0.35 ± 0.25	0.81 ± 0.87	0.96 ± 0.10
SV6	0.85 ± 0.20	0.65 ± 0.29	0.76 ± 0.32	0.66 ± 0.64	1.00 ± 0.03	0.79 ± 0.40

ABBREVIATIONS; CW: Cephalothorax width; SW1: 1st segment width; SW2: 2nd segment width; SW3: 3rd segment width; SW4: 4th segment width; SW5: 5th segment width; SW6: 6th segment width.

Table 6

Genetic correlation between indicator traits with positive relative efficiency of the indirect selection response, with weight as the target trait and **volume**-type morphological traits in *P. vannamei* from the PMG-BIOGEMAR® programme, at harvest size.

	ATV	SV1	SV2	SV3	SV4	SV5
Weight	1.00 ± 0.00	0.99 ± 0.06	0.99 ± 0.03	0.93 ± 0.18	0.28 ± 0.38	0.71 ± 0.31
SW6	0.86 ± 0.14	0.79 ± 0.20	0.97 ± 0.15	0.58 ± 0.23	0.68 ± 0.32	0.76 ± 0.17
SV6	0.83 ± 0.14	0.89 ± 0.18	0.88 ± 0.26	0.54 ± 0.27	0.66 ± 0.32	0.77 ± 0.18

Abbreviations; ATV: Abdomen total volume; SV1: 1st segment volume; SV2: 2nd segment volume; SV3: 3rd segment volume; SV4: 4th segment volume; SV5: 5th segment volume; SV6: 6th segment volume.

measuring length, width, height, and volume of partial sections of the animals (i.e., cephalothorax, each segment, and abdomen) are reported for the first time in *P. vannamei*. Penaeid growth follows a sigmoidal pattern (Dall et al., 1990). The analysis of multi-pronged morphological traits is necessary for the prediction of carcass yield without the cephalothorax and including carapace, telson, and uropod. Moreover, estimated additive genetic variation values suggest that genetic selection is feasible for these characters (Zhang et al., 2017) and, therefore, the response will be positive in future generations.

The results obtained show that CL (0.25 ± 0.14) and CW (0.26 ± 0.13) have a medium-high heritability. Tan et al. (2017) and P é rez-Rostro et al. (2003b) also reported slightly lower heritability (0.21 ± 0.06 and 0.22 ± 0.17 , respectively) under low-density conditions. Diaz et al. (2001) found that the cephalothorax, the part of the body containing major portions of the gonads, grew faster relative to the abdomen in sub-adults than in juveniles of *Farfantepenaeus duorarum*. The hepatopancreas of *P. vannamei* is located in the cephalothorax, being the organ or tissue where most reserves accumulate in the animal (Ramos-Trujillo and Fernández-Luna, 1981; Spaargaren and Haefner, 1994; Allen et al., 2001; Pérez-Rostro et al., 2003b). According to these studies, cephalothorax size could be the measurable factor for growth traits in *P. vannamei*.

The heritability of SW1, SL4, and SH5 in our study was medium and

these results partially agree with P é rez-Rostro et al. (2003a) who reported a slightly lower heritability (0.22 ± 0.17) for SW1 than we did. Andriantahina et al. (2012) reported an SW1 heritability of 0.42 ± 0.02 ; this much higher heritability may be caused by the different number of full-sib families, which affect the accuracy of genetic parameter estimates and, thus, increase the selection response, even though measures were taken at similar ages in both studies.

These values highlight the importance of the sixth segment (not studied as yet in works on morphological characters), which showed medium-high heritability (SH6, SW6, SV6), over the other segments that make up the abdomen. It is assumed that the sixth segment has a harder exoskeleton than the other segments, resulting in lower measurement variations as it is not affected by various conditions, such as the freeze/thaw process or any physical or personal effect. Therefore, its measurement is simpler, affording a more precise and reliable value for genetic estimates.

On the other hand, from a sex maturation perspective, the phenomenon that mature females are heavier than immature females of the same body or carapace length might be related to the high energy requirement of female reproduction (Chu et al., 1995). From the behavioural perspective, these larger sizes may reflect better nutrition and/or less competition in the wild compared with culture ponds (Primavera et al., 1998). From this hypothesis arises the idea to analyse different body weights with the same body length, and different body lengths with the same body weight in the future, which could provide useful data for selective breeding programmes for growth in the industrial sector.

4.3. Genetic correlation and correlated response

The genetic correlation between parameters indicates how the two parameters are genetically determined by some common genes. Therefore, if selection is placed on one, the correlated response in the other trait can be predicted (Falconer and Mackay, 1996; Andriantahina et al., 2012).

In this study, the high positive genetic correlation between weight, TLF, and all morphological traits, except the fourth segment, suggests that selection for CL, CW, SH5, SH6, SW1, SW6, and SV6, due to their medium-high heritability, would improve the weight of the animal. P é rez-Rostro et al. (2003a) reported a high positive genetic correlation between weight and SW1 (0.96) and between body length and SW1 (0.98); Andriantahina et al. (2012) reported a high genetic correlation between weight and SH1 and SH3 (0.66 and 0.67, respectively), and SW1 (0.77), their results agreeing with those of this study. Due to the high genetic correlation between sixth segment width and weight, and the high additive genetic variation of sixth segment width, an indirect selection response for weight via the SW6 trait was 9.8% and for the volume trait was 5.8% more efficient than direct weight selection. This result indicates weight, SW6, and SV6 traits seem likely to be regulated by the same genes associated with these traits. Kause et al. (2003) reported that selection for increased body weight indirectly resulted in fish with greater body weight and height with a rounded shape in rainbow trout. Generally, weight at harvest size as a selection trait is being used for breeding programmes in the industrial sector; however, the animal should be thoroughly dried for weight measurement to minimise the

error, and this measurement is complicated for live animals. In this sense, SW6 is almost 10% more efficient for growth and can be measured with a vernier calliper, being a simple, cost-effective method with lower error and mortality due to less handling in the industrial sector. Our results not only indicate weight as a growth trait but also provide an alternative measurable factor, with SW6 as an indirect selection factor for growth improvement.

Furthermore, *P. vannamei* muscle is located in the abdominal part of the body and represents about 90% of total prawn meat (Cesar et al., 2008; Andriantahina et al., 2012). *P. vannamei* meat represents 48% of the total animal, the cephalothorax 39%, exoskeleton 11%, and the tail is only 2.3% (Dang et al., 2018). The genetic correlation between weight, SW6, SV6, and ATV had a positive high correlation, and this result suggests that using SW6 and SV6 as indicator traits could improve the meat yield in the abdomen. In commercial terms, AL and ATV seem to be very interesting traits, representing the edible part of the shrimp, being productivity criteria traits for the company. The trend in recent years to market exoskeleton-free product reinforces the importance of industrial peeling according to economic value and consumer preferences (Dang et al., 2018). Consumers prefer to increase meat yield or uniformly shaped shrimp may also be preferred by retailers and consumers (Mehtar et al., 2020). The meat yield highlights the commercial value of the total volume of the abdomen and its segments, and the meat value without the head is generally less costly than whole shrimp including the head; thus, it is important to increase the meat yield to increase the cost of shrimp without heads. Consequently, it is important to estimate the genetic parameters of abdomen segments to predict the carcass yield trait.

These results provide useful data for developing a non-invasive system to predict carcass yield without the cephalothorax and afford the possibility of easily selecting shrimp for growth via an exact measurement method resulting in more precise genetic estimates. This data could then be used to study indirect selection for growth in the future and become a useful practical tool under industrial conditions for improving growth in their population. In the near future, artificial intelligence (machine learning, deep learning, etc) could play a role in the analysis to predict growth traits, including carcass yield, feed efficiency, morphology, and disease detection (Venkateswara Rao et al., 2016; Ramamohan and Kasa, 2022).

5. Conclusion

This study estimates additive genetic variations of morphological traits and the genetic correlation and correlated response of growth traits in *P. vannamei* from a selective breeding programme. Among the width-type morphological traits, the cephalothorax and first and sixth segments had medium-high heritability and high/positive genetic correlations with growth traits and ATV. Also, SW6 and SV6 as indirect traits could improve weight by 9.7% and 5.8%, respectively. Therefore, this result indicates that including these morphological traits in a breeding programme might improve growth traits, especially taking into account the positive genetic correlation with growth traits. In addition, two indirect traits are more efficient than direct selection for weight. These are useful data for developing a non-invasive method to evaluate genetic parameters using these selected morphological traits, which would then help predict carcass yield, being an easier, more practical method with the developed image analysis software in the industrial sector for increasing output benefits as an aspect of economic impact in the future.

CRediT authorship contribution statement

Hyun Suk Shin: Conceptualization, Formal analysis, Writing - Original Draft, Writing - Review & Editing. **Magaly Elizabeth Montachana Chimborazo:** Investigation. **Jakie Melissa Escobar Rivas:** Investigation. **Álvaro Lorenzo-Felipe:** Software, Formal

analysis. **Marina Martínez Soler:** Investigation. **María Jesús Zamorano Serrano:** Writing - Review & Editing. **Jesús Fernández Martín:** Software. **Juan Sebastián Ramírez Artilles:** Software. **Adrián Peña Sánchez:** Software. **Javier Lorenzo Navarro:** Software. **Walter Intriago Díaz:** Funding acquisition. **Ricardo Torres:** Project administration. **Eduardo Reyes Abad:** Funding acquisition, Project administration. **Juan Manuel Afonso López:** Conceptualization, Supervision, Project administration, Writing - Review & Editing.

Declaration of Competing Interest

The authors declare no conflict of interest. The funders had no role in the design of the study; in the collection, analyses, or interpretation of data; in the writing of the manuscript, or in the decision to publish the results.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.aqrep.2023.101649.

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