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## **Quantitative genetic changes in reproductive performance of giant freshwater prawn after ten years of selection for increased growth rate**

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## Abstract

Effect of long term selection for improved growth on reproductive performance of giant freshwater prawn (GFP) *Macrobrachium rosenbergii* has not been reported in the literature. The present study aimed to measure correlated responses in reproductive traits and to estimate genetic parameters for these characters in a GFP population selected for high growth over ten generations from 2007 to 2016. A total of 959 breeding females (offsprings of 515 sires and 810 dams) had measurements for seven reproductive traits (weight before spawn WBS; weight after spawn WAS; Fecundity FEC or number of larvae per female at hatching; first age to reach post-larvae PLAGE; zoea(e) weight ZOEAWT; larval survival during hatchery phase SURV1 and survival from PL to tagging SURV2). The restricted maximum likelihood (REML) and mixed model analysis were used to estimate genetic parameters and evaluate selection responses for the seven traits studied. Our REML analysis showed that heritability for these traits ranged from 0.04 to 0.42 (s.e. 0.19 to 0.28). Female body weight either before or after spawning had strong positive phenotypic correlations with fecundity (0.52 to 0.98). By contrast, the phenotypic correlations of WBS/WAS with larval and fry survivals were not significant (-0.08 to 0.05). Genetic correlations among fecundity-related traits studied were not different from zero due to their high standard errors. Correlated responses in reproductive traits were measured by comparing least squares means of the selection line and control group. Females of the selected line for high growth had significantly greater weight before or after spawning than that of the control group. There were, however, no statistical differences between the two lines in the other traits. It is concluded that selection for high growth did not have detrimental impact on reproductive performance of breeding females in the present population of GFP.

*Keywords: Selective breeding, genetic improvement, prawn, heritability, correlation and selection response*

## 1. INTRODUCTION

Quantitative genetic inheritance of reproductive traits is not well understood in crustacean species, including giant freshwater prawn (GFP), *Macrobrachium rosenbergii*. These characters are, however, economically important for hatchery operators because the main aims of this sector are to i) produce a large quantity of post-larvae to supply seeds for commercial purpose, and ii) reduce fixed and variable costs to maximise return and revenue for aquaculture enterprises. To achieve these goals, reproductive traits can be improved through direct selection for the traits of interest or through indirect selection for growth performance. The former approach requires a knowledge of genetic parameters for these traits. For the latter, correlated responses should be estimated to measure genetic changes in reproductive traits to selection criteria, typically growth rate or harvest body weight in aquaculture breeding programs.

Genetic parameters for reproductive traits are generally dispersed in prawn/shrimp species. Earlier studies reported low to moderate heritability for days to spawn, egg/or nauplii number and hatching rate in tiger prawn *Penaeus monodon* (Macbeth et al., 2007) or egg/oocyte diameter, measures of egg quality and vitellogenin in hemolymph (Arcos, Racotta, & Ibarra, 2004; Ibarra, Famula, & Arcos, 2009) and spawning related traits in White leg shrimp *Litopenaeus vannamei* (Caballero-Zamora et al., 2015).

Furthermore, there are limited published information regarding correlated responses in reproductive traits to selection for improved growth performance in GFP or shrimp species. Only the study of Vu et al. (2017) showed that survival during grow-out phase (2 to 34g) did not change with selection for improved growth in *M. rosenbergii* (Vu, Trong, & Nguyen, 2017). To date, genetic changes in larval survival during the early phase of rearing in tank and subsequently in hapas until juvenile stage have not been estimated in any GFP populations.

The present paper had three main aims: i) to investigate effect of female body weight before or after spawning on reproductive traits, ii) to estimate genetic parameters (heritability, common full-sibs and correlations) for these characters, and iii) to measure correlated response in reproductive traits to selection for high growth. The data were collected over 10 years (or generations), with a total of 959 breeding females that produced 110,646 progenies used for performance testing during the course of selection. Our hypothesis was that selection for high growth did not impair reproductive performance of *M. rosenbergii* female.

## **2. MATERIALS AND METHODS**

### *2.1 Selection line and control group*

The breeding program for improved growth in giant freshwater prawn (GFP) has been conducted over 10 years (or generations) at National Breeding Centre for Southern Freshwater Aquaculture (NABRECSOFA) of Research Institute for Aquaculture No.2 (RIA2), Vietnam. NABRECSOFA is located in Cai Be district, Tien Giang province (latitude: 10.3 and longitude: 105.9). All the experimental protocols

and procedures were in accordance with commercial standard practices (Hung, Nguyen, Ponzoni, Hurwood, & Mather, 2013).

The present GFP population was established in 2007, comprising two indigenous wild strains (collected from Mekong and Dong Nai rivers that are geographically isolated) and an introduced strain from Malaysia. In 2008, a complete 3×3 diallel cross was performed and 81 full-sibs families were produced to form the base population (G0) (Hung, Nguyen, et al., 2013). Subsequent generations (G1 –G9) were produced in 2009 to 2016. In each generation, both Selection line and Control group were simultaneously produced and selected. The Selection line was selected based on estimated breeding values (EBVs) for high body weight. The average selection proportion across the nine generations was 7% in females and 6% in males. Superior selected animals (with the highest EBV ranking for body weight) were mated with unrelated individuals from the pedigree to avoid inbreeding and maintain genetic diversity of the population to ensure long term response to selection. Contemporaneously with the selection line, the Control group in each generation consisted of individuals that had a mean EBV of the population (Hung, Nguyen, et al., 2013). The actual number of parental breeders that successfully produced offspring (for both the Selection line and Control group) is given in Supplementary Table S1, ranging from 27-101 sires and 49-170 dams (averaging 57 sires and 90 dams per generation).

## 2.2 Breeding and rearing

Except for the first generation in 2007 where 81 full-sib families were produced, all subsequent generations (2008 – 2016) aimed to achieve both paternal half- and full-sib groups. Prior to mating, selected broodstocks were kept in fibre glass tanks (1 cubic meter) and fed high protein diets (44% crude protein) in combination with fresh foods (squid and flesh of trash fish). To produce half-sib families, one male was mated with two females and berried females were removed every 10 days after mating. Hatching of each family occurred in separate spawning tanks which was same as larvae stocking stage. Prawn larvae were reared in 70 litre-round plastic tank with a density of 60 larvae per litre. They reached post-larvae (PL) stage after 22 – 25 days. PL prawns were then moved to stock in 1 m<sup>3</sup> tanks (at a density of 1,000 PLs) for about 2 weeks until they were bigger than the mesh size (Hung, Nguyen, et al., 2013). Subsequently they were transferred to rear in hapas (net enclosure) installed in earthen pond. After a rearing period of about 2.0 – 2.5 months, the PLs reached a size of about 2 g for physical tagging. A random sample of 100 – 150 juveniles collected from each family were tagged using Visible Implant Elastomer (Hung & Nguyen, 2015).

The tagged prawns from all families were then conditioned in tanks for two or three days without food before they were transferred to ponds for grow-out. In the grow-out phase, the stocking densities in every generation were set at two individuals/m<sup>2</sup> (Hung, Nguyen, et al., 2013) with earthen pond sizes ranging from 2.000 to 9.000 m<sup>2</sup>. Commercial feed pellet (30% crude protein and 5% lipid) were provided three times a day at the feeding rate of 3 – 5% of the prawn biomass (Hung & Nguyen, 2014). After 3 – 4 months of grow-out, prawns were harvested using a cast-net after the pond was drained. In this study, family production, breeding, rearing and grow-

out were practised as described in our earlier studies (Hung, Nguyen, et al., 2013; Hung, Vu, et al., 2013).

### 2.3 Trait measurements

Seven traits included in this study were female body weight before spawn (WBS), female weight after spawn (WAS), fecundity FEC (i.e., number of zoea per female at hatching), first age that prawn reached post-larvae stage (PLAGE), total zoea weight (ZOEAWT), larval survival during hatchery phase (SURV1) and fry survival in the subsequent rearing period in hapas (SURV2). These traits were recorded individually for each breeding female.

- Weight before spawn (WBS): Breeding candidate females that carried brown to grey eggs were chosen and weighed using a digital scale. Those ripen females were then brought into the hatchery. Their eggs were hatched within 2 or 3 days. Immediately after hatching, females were weighed to obtain weight after spawn (WAS)
- Fecundity (FEC): FEC was defined as total number of larvae per female per spawning at hatching and estimated from the total number of zoea collected from three 250 ml samples taken within 3-5 h after hatching (Coman, Arnold, Wood, & Preston, 2013).
- First age that prawn reached post-larvae stage (PLAGE) was measured as days from hatching until first post-larvae were observed
- Zoea(e) weight (ZOEAWT) was determined by volumetric methods of larval numbers whereby five subsamples of larvae were counted and weighed

(about 1g for 4500 zoea) and the average used to determine the total zoea weight per spawn.

- Larval survival (SURV1) was the number of post-larvae divided by 3.6 (corresponding to 0.8 g nauplii in 70l-tank, water volume of 60 L).
- Fry survival (SURV2) was calculated as the percent difference in the number of shrimps at tagging and stocking in hapas submerged in earthen pond for a rearing period of about two months.

The reproductive traits are, however, not available in all generations. Female weight before and after spawning as well as fecundity were recorded in the first (2009) and the last three generations (2014-2016) only. Survival traits (SURV1 and SURV2) and first PL age were collected throughout the 10-year period (Supplementary Table S3).

#### *2.4 Statistical analysis*

Genetic parameters were estimated for reproductive traits recorded on 959 breeding females produced from 515 sires and 810 dams over 10 generations of selection from 2007 to 2016. First, general linear model (GLM) was used to examine significance of fixed effects (SAS Institute Inc., 2005) and they were also verified by Wald statistics in ASReml (Gilmour, Gogel, Cullis, Thompson, & Butler, 2009). The fixed effects included in statistical models were generation ( $G = 1$  to 9), line ( $L =$  selection and control) and a covariable (Cov) of female weight or age during larval rearing phase in tank and subsequently in hapas (Supplementary Table S2). These effects were fitted together with the random effects of sire and dam in the final model (Equation 1)(Thoa et al., 2015) to estimate genetic parameters for reproductive traits.



$$y_{iklmno} = \mu + G_i + L_k + Cov_l + s_m + d_n + e_{iklmno} \quad (\text{Equation 1})$$

where,  $y_{iklmno}$  is an observation for traits;  $\mu$  is the overall mean;  $s_m$  is the random effect of the  $m^{\text{th}}$  sire;  $d_n$  is the random effects of maternal and common environment to full-sibs;  $e_{iklmno}$  is the random residual effect associated with individual  $iklmno$ .

Heritabilities for traits studied were estimated from a univariate model (Equation 1).

PL first age was log transformed before analysis. Survival traits approximated normal distribution (Supplementary Figure F1) and they were analysed on original scale.

The genetic variance ( $\sigma_A^2$ ) was calculated as  $4 \times \sigma_s^2$  where  $\sigma_s^2$  is sire variance

(Falconer & Mackay, 1996). The dam variance component ( $\sigma_D^2$ ), in this case, was a combination of the maternal, dominant and common environmental effects, also

named as common full-sib effects ( $\sigma_D^2 = \sigma_C^2$ ). The "and(dam)" option used in ASReml

assumed equal sire and dam variances ( $\sigma_s^2 = \sigma_D^2$ ) (Gilmour et al., 2009). The

phenotypic variance ( $\sigma_P^2$ ) was calculated as the sum of the additive genetic sire

variance ( $\sigma_s^2$ ), the dam variance ( $\sigma_D^2$ ), the common full-sib ( $\sigma_C^2$ ) and the residual

variance ( $\sigma_e^2$ ), as  $\sigma_P^2 = \sigma_s^2 + \sigma_D^2 + \sigma_C^2 + \sigma_e^2$  or  $\sigma_P^2 = 2\sigma_s^2 + \sigma_C^2 + \sigma_e^2$ . Then the heritability

was calculated as  $h^2 = \frac{\sigma_A^2}{\sigma_P^2}$ . The common environmental effect was calculated as

$$c^2 = \frac{\sigma_C^2}{\sigma_P^2}.$$

Genetic and phenotypic correlations were estimated from a two-trait sire and dam

model with the same fixed effects as described above (Equation 1). The correlations

were calculated as the covariance divided by the product of the standard deviations

of traits:  $r = \frac{\sigma_{XY}}{\sqrt{\sigma_X^2} \sqrt{\sigma_Y^2}}$  where  $\sigma_{XY}$  was the estimated additive genetic or phenotypic

covariance between the two traits, and  $\sigma_X^2$  and  $\sigma_Y^2$  are the additive genetic or phenotypic variances of traits  $X$  and  $Y$ , respectively. As genetic correlations among female weights, fecundity and nauplii weight were not estimable, simple Pearson correlations were also calculated. The data were then corrected for the fixed and covariate effects to obtain residual correlations that are approximately as genetic correlations.

Correlated responses were measured as the differences in least squares means between the selection line and control group. The mixed model approach (Equation 1) was used to account for family structure because the error variance is often underestimated with general linear fixed model. Tukey test was used to control type-I errors and to determine significant differences between the selection line and control ( $P < 0.05$ ).

### **3. RESULTS**

#### *3.1 Pedigree and data*

The number of breeding females, sires and dams for the Selection line and Control group is given in Table 1. The average female weight before and after spawning were 45.6 and 39.0g, respectively (Table 2). The relative fecundity or average number of larvae at hatching per female was 24,816. The total zoea weight per female per spawning was 4.8g. Larvae reached post-larvae (PL) stage after 23 days. The survival rate during the hatchery phase from hatching to PL was low (only 10%).

However, the survival rates during subsequent period in hapas assembled in ponds were moderate (50%).

### *3.2 Family variation in reproductive traits*

There were substantial variations among families for all reproductive traits ( $P < 0.05$  to  $0.001$ ). Amongst those, fecundity had the largest data range from 1,005 to 76,950 nauplii ( $CV = 57\%$ ), as expected for reproductive traits that are strongly influenced by a range of genetic and environmental factors. This was followed by total zoea weight (ranging from 0.02 to 10g,  $CV = 51\%$ ). Large variation was also observed for larval survival during the hatchery phase (from hatching to PL),  $CV = 80\%$  compared with those in subsequent rearing periods in hapas of 43%. Our preliminary general linear model analysis showed that the sire and dam variances were significant for PLAGE and survival rates ( $P < 0.05$ ). They were included as the random factors in statistical models to estimate heritability for these traits (section 'Heritability' 3.4 below).

### *3.3 Relationship between female body weight before spawning and fecundity, nauplii weight and first PL age*

Regression analysis showed linear relationship between female body weight before spawning (WBS) and fecundity (fecundity =  $568.4 + 535.5 \times WBS$ ) (Supplementary Figure F2). High body weight females are also expected to produce big zoea (zoea weight =  $0.1266 + 0.119 \times WBS$ ) (Supplementary Figure F3). Interestingly, larvae prawn is expected to reach PL stage at an earlier age when they were produced from bigger females (PL first age =  $29.193 - 0.1185 \times WBS$ ) (Figure 1). There was no

association between female weights and larval or fry survivals (Supplementary Figure S4).

### *3.4 Heritability and common full-sib effects*

The heritability for PL first age (PLAGE) and survival rates (SURV1 and SURV2) ranged from 0.04 to 0.42 but the estimates had high standard errors (s.e. = 0.16 to 0.29). The heritability was not estimable for female weights, fecundity and zoea weight, likely due to the limited data records for these traits in the present study. The maternal and common full-sib effects were significant for larval survival (from hatching to PL), accounting for 15% of total phenotypic variance (Table 3).

### *3.5 Correlations*

Phenotypic and genetic correlations among PL first age and survival traits were not significant, due to their high standard errors (Supplementary Table S4). Simple Pearson correlations showed that female weights had moderate to high positive correlations with fecundity and zoea weight (Supplementary Table S5). However, the correlations of female weights with PL first age were negative. The phenotypic associations between female weights and larval (SURV1) or fry survival (SURV2) were weak; the simple Pearson correlations, albeit negative, were low and not significant.

### 3.6 Line difference

Correlated response in reproductive traits to selection for high growth was measured as the differences in least squares means (LSMs) between the selection line and control group. Except for female weight before spawning, the differences between the two lines were not statistically significant for the other traits ( $P > 0.05$ ) (Table 4).

Our results suggest that selection for high growth did not impair reproductive performance of giant freshwater prawn.

## 4. DISCUSSION

*Correlated changes in reproductive traits:* Long term selection programs are sparse in aquaculture species. Our study has been conducted over ten years from 2007 to 2016 and achieved significant improvement in prawn body weight (the sole selection criterion) by 56% compared with the control group or 1.85 genetic standard deviation units (Hung, Vu, et al., 2013). There was also concomitant increase in female body weight before or after spawning. Interestingly, selection for high growth, however, did not impair reproductive performance of *M. roseinbergii*. A 17-generation selection study for improved harvest body weight in Nile tilapia also reported that there were no significant changes in five important reproductive characteristics (Hamzah et al., 2016). Currently there is no comparative results in any prawn/shrimp species. However, our findings are in line with those reported in crustacean (McPhee, Jones, & Shanks, 2004) and fish species (Hamzah et al., 2014) as well farmed animals (Kerr & Cameron, 1995; N. Nguyen, MCPhee, & Wade, 2006). This suggests that selection for high growth does not have any adverse impacts on reproductive characteristics.

*Heritability:* Existence of heritable genetic components were observed for reproductive traits in the present population of giant freshwater prawn (GFP).

However, the heritability estimates had large standard errors, indicating that a larger sample size is needed to obtain accurate genetic parameter estimates. Across aquaculture species, there is very limited information regarding heritability for reproductive characteristics. The  $h^2$  estimates for reproductive or fitness-related traits are generally low and not different from zero (Arcos et al., 2004; Gall & Neira, 2004; Hung & Nguyen, 2015; Nguyen H. Nguyen et al., 2018; Su, Liljedahl, & Gall, 2002). The weighted mean heritability from a meta-analysis of nine studies (N H Nguyen, Submitted) was  $0.14 \pm 0.12$  for fecundity,  $0.09 \pm 0.13$  for fry weight or  $0.08 \pm 0.14$  for fry survival.

*Common full-sibs ( $c^2$ ):* The  $c^2$  is a combination of maternal and common full-sib effects that were significant ( $c^2 = 0.15 \pm 0.05$ ) for larval survival during the early phase of rearing in hatchery. In Nile tilapia, Hamzah et al. (2016) obtained close to zero  $c^2$  for number of fry at hatching, total fry weight or number of dead fry. Thoa et al. (2017) also found that the  $c^2$  effects were not significant for these reproductive characteristics. Other studies in the literature (Gima et al., 2014; Ibarra, Arcos, Famula, Palacios, & Racotta, 2005; Macbeth et al., 2007; Trọng, van Arendonk, & Komen, 2013) did not report the maternal and common full-sib effects for reproductive performance of shrimp or fish species.

### *Phenotypic and genetic correlations*

Phenotypically, female body weight either before or after spawning exhibited positive correlations with fecundity and negative correlations with first PL age. In other words, fecundity is increased with female body weight and selection for high growth shortened larval rearing time from hatching to PL. On the other hand, the phenotypic correlations between female weight and survival rates were not significant. Due to incomplete data recording of reproductive traits and the small genetic variances, genetic correlations of female weight with fecundity, total zoea weight and PL first age were not estimable. In White leg shrimp, genetic correlations of female weight with fecundity or fry weight estimated were positive but all the estimates were associated with high standard errors (Caballero-Zamora et al., 2015). Further study is needed to better understand genetic relationship between growth and the traits measured here.

### *Practical implications*

Results from the present study re-affirmed those reported previously in the literature (Hamzah et al., 2016; Thoa, Hamzah, & Nguyen, 2017) that except for female body weight, other reproductive traits were not altered by selection for high growth. Thus, there is no concern regarding the negative impact of selection for high growth on reproductive performance of GFP. Existence of heritable genetic variation in reproductive traits suggests that there are possibilities for improving these characters in commercial breeding programs. Our study, however, also pointed that a routine data collection of reproductive traits should be practised in selective breeding programs to obtain accurate estimates of genetic parameters and breeding values

for these traits. Accumulation of reproductive data is needed because in each generation only a limited number of breeding females were used to produce progenies for subsequent performance testing in selection programs for high growth.

To enable a large-scale routine recording of reproductive traits, separate breeding programs could be conducted to develop specialised maternal genetic lines when the breeding objective is aimed at improving reproductive performance for the hatchery sector. Developing both maternal and paternal lines would require extra resources but different breeding objectives can be targeted for specific niche markets and production systems.

## **5. CONCLUSIONS**

Selection for high growth increased female body weight before or after spawning but there were no unintended effects on other reproductive traits in this giant freshwater prawn population. Heritable genetic variation was observed for larval and fry survivals, although they should be re-estimated when more data is cumulated.

Fecundity was strongly associated positively with female weight. Phenotypically, female body weight exhibited negative correlations with PL first age. Genetic correlations among reproductive traits were not estimable. Further study is needed to understand genetic relationships between reproductive traits and growth performance in this population of giant freshwater prawn.



## Declarations

**List of abbreviations:** WBS = Female weight before spawn, WAS = Female weight after spawn, FEC= Fecundity (number of larvae per female at hatching), PLAGE = PL first age, NAUWT = Nauplii weight, SURV1 = Larval survival during hatchery phase, SURV2 = fry survival in hapas

**Ethics approval and consent to participate:** Animal ethics approval was not required for crustacean species. This study was conducted in accordance with commercial standard practices.

**Consent to publish:** Not Applicable

**Availability of data and materials:** The data will be made available upon request after publication of the manuscript

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**Author Contributions:** N.T.V and N.H.N. conceived and designed the experiments, analysed the data, and prepared and approved the manuscripts.

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## References

- Arcos, F. G., Racotta, I. S., & Ibarra, A. M. (2004). Genetic parameter estimates for reproductive traits and egg composition in Pacific white shrimp *Penaeus (Litopenaeus) vannamei*. *Aquaculture*, 236(1), 151-165. doi:<https://doi.org/10.1016/j.aquaculture.2004.03.003>
- Caballero-Zamora, A., Cienfuegos-Rivas, E. G., Montaldo, H. H., Campos-Montes, G. R., Martínez-Ortega, A., & Castillo-Juárez, H. (2015). Genetic parameters for spawning and growth traits in the Pacific white shrimp (*Penaeus (Litopenaeus) vannamei*). *Aquaculture Research*, 46(4), 833-839.
- Coman, G. J., Arnold, S. J., Wood, A. T., & Preston, N. P. (2013). Evaluation of egg and nauplii production parameters of a single stock of domesticated *Penaeus monodon* (Giant Tiger Shrimp) across generations. *Aquaculture*, 400-401, 125-128. doi:<https://doi.org/10.1016/j.aquaculture.2013.03.015>
- Falconer, D., & Mackay, T. (1996). *Introduction to quantitative genetics* (Vol. 4): Longmans Green, Harlow, Essex, UK.
- Gall, G. A., & Neira, R. (2004). Genetic analysis of female reproduction traits of farmed coho salmon (*Oncorhynchus kisutch*). *Aquaculture*, 234(1), 143-154.
- Gilmour, A. R., Gogel, B., Cullis, B., Thompson, R., & Butler, D. (2009). ASReml user guide release 3.0. *VSN International Ltd, Hemel Hempstead, UK*.
- Gima, M. E., Gima, A., Hutson, A., Chaimongkol, A., Beam, R., Perera, D. A., & Dunham, R. A. (2014). Realized heritability and response to selection for fecundity, hatching rate and fry/Kg for channel catfish females (*Ictalurus punctatus*) induced to ovulate and fertilized with blue catfish (*Ictalurus furcatus*) males for the production of hybrid catfish embryos. *Aquaculture*, 420, S36-S41.
- Hamzah, A., Nguyen, N. H., Mekkawy, W., Khaw, H. L., Yee, H. Y., Abu Bakar, K. R., . . . Mohd Nor, S. A. (2014). Genetic parameters and correlated responses in female reproductive traits in the GIFT strain. *Aquaculture Research*, doi: 10.1111/are.12608. doi:10.1111/are.12608
- Hamzah, A., Nguyen, N. H., Mekkawy, W., Khaw, H. L., Yee, H. Y., Bakar, A., . . . Azizah, S. (2016). Genetic parameters and correlated responses in female reproductive traits in the GIFT strain. *Aquaculture Research*, 47(5), 1488-1498.
- Hung, D., & Nguyen, H. N. (2014). Genetic inheritance of female and male morphotypes in giant freshwater prawn *Macrobrachium rosenbergii*. *PLoS One*, 9(2), e90142.
- Hung, D., & Nguyen, N. H. (2015). Are female reproductive status and male morphotypes of the giant freshwater prawn *Macrobrachium rosenbergii* altered by selection for high growth? *Marine and Freshwater Behaviour and Physiology*, 48(5), 299-308. doi:10.1080/10236244.2015.1073457
- Hung, D., Nguyen, N. H., Ponzoni, R. W., Hurwood, D. A., & Mather, P. B. (2013). Quantitative genetic parameter estimates for body and carcass traits in a cultured stock of giant freshwater prawn (*Macrobrachium rosenbergii*) selected for harvest weight in Vietnam. *Aquaculture*, 404, 122-129.

- Hung, D., Vu, N. T., Nguyen, N. H., Ponzoni, R. W., Hurwood, D. A., & Mather, P. B. (2013). Genetic response to combined family selection for improved mean harvest weight in giant freshwater prawn (*Macrobrachium rosenbergii*) in Vietnam. *Aquaculture*, *412*, 70-73.
- Ibarra, A. M., Arcos, F. G., Famula, T. R., Palacios, E., & Racotta, I. S. (2005). Heritability of the categorical trait 'number of spawns' in Pacific white female shrimp *Penaeus* (*Litopenaeus*) *vannamei*. *Aquaculture*, *250*(1), 95-101.  
doi:<https://doi.org/10.1016/j.aquaculture.2005.03.018>
- Ibarra, A. M., Famula, T. R., & Arcos, F. G. (2009). Heritability of vitellogenin in hemolymph, a pre-spawning selectable trait in *Penaeus* (*Litopenaeus*) *vannamei*, has a large genetic correlation with ovary maturity measured as oocytes mean diameter. *Aquaculture*, *297*(1), 64-69.  
doi:<https://doi.org/10.1016/j.aquaculture.2009.09.015>
- Kerr, J. C., & Cameron, N. D. (1995). Reproductive performance of pigs selected for components of efficient lean growth. *Animal Science*, *60*(02), 281-290.  
doi:[doi:10.1017/S1357729800008444](https://doi.org/10.1017/S1357729800008444)
- Macbeth, M., Kenway, M., Salmon, M., Benzie, J., Knibb, W., & Wilson, K. (2007). Heritability of reproductive traits and genetic correlations with growth in the black tiger prawn *Penaeus monodon* reared in tanks. *Aquaculture*, *270*(1), 51-56.  
doi:<https://doi.org/10.1016/j.aquaculture.2007.03.018>
- McPhee, C. P., Jones, C., & Shanks, S. A. (2004). Selection for increased weight at 9 months in redclaw crayfish (*Cherax quadricarinatus*). *Aquaculture*, *237*(1), 131-140.
- Nguyen, N., McPhee, C., & Wade, C. (2006). Genetic variation and responses in reproductive performance of sows in lines selected for growth rate under restricted feeding. *Animal Science*, *82*(1), 7-12.
- Nguyen, N. H. (Submitted). A systematic review and meta-analysis of genetic parameters for quantitative complex traits in aquatic animal species.
- Nguyen, N. H., Fitzgibbon, Q. P., Quinn, J., Smith, G., Battaglione, S., & Knibb, W. (2018). Can metamorphosis survival during larval development in spiny lobster *Sagmariasus verreauxi* be improved through quantitative genetic inheritance? *BMC Genetics*, *19*(1), 27.
- Su, G.-S., Liljedahl, L.-E., & Gall, G. A. (2002). Genetic correlations between body weight at different ages and with reproductive traits in rainbow trout. *Aquaculture*, *213*(1), 85-94.
- Thoa, N. P., Hamzah, A., & Nguyen, N. H. (2017). Genetic variation and correlated changes in reproductive performance of a red tilapia line selected for improved growth over three generations. *Animal Reproduction Science*, *184*, 94-101.
- Thoa, N. P., Knibb, W., Ninh, N. H., Van Dai, N., Nhat, P. H., Toan, L. M., & Nguyen, N. H. (2015). Genetic variation in survival of tilapia (*Oreochromis niloticus*, Linnaeus, 1758) fry during the early phase of rearing in brackish water environment (5–10 ppt). *Aquaculture*, *442*, 112-118.  
doi:<http://dx.doi.org/10.1016/j.aquaculture.2015.02.040>
- Trọng, T. Q., van Arendonk, J. A. M., & Komen, H. (2013). Genetic parameters for reproductive traits in female Nile tilapia (*Oreochromis niloticus*): II. Fecundity and fertility. *Aquaculture*, *416-417*(Supplement C), 72-77. doi:<https://doi.org/10.1016/j.aquaculture.2013.08.031>
- Vu, N. T., Trọng, T. Q., & Nguyen, N. H. (2017). Effects of selection for fast growth on survival rate during grow-out phase in giant freshwater prawn (*Macrobrachium rosenbergii*). *BMC Genetics*, *18*(1), 56.

**Table 1** Number of breeding females, sires and dams for the Selection line and Control group

Generation	Year	Selection line			Control group		
		Breeding female	Sire	Dam	Breeding female	Sire	Dam
0	2007	-	-	-	-	-	-
1	2008	77	-	-	-	-	-
2	2009	89	66	80	17	17	17
3	2010	96	41	96	21	18	21
4	2011	144	65	144	26	26	26
5	2012	93	74	93	34	27	34
6	2013	60	54	54	n.a.	n.a.	n.a.
7	2014	83	16	35	n.a.	n.a.	n.a.
8	2015	75	34	71	38	11	14
9	2016	89	66	80	38	19	33
<b>Total</b>		<b>640</b>	<b>350</b>	<b>573</b>	<b>174</b>	<b>118</b>	<b>145</b>

Data not available in G0 (2007), n.a. = not recorded

**Table 2** Number of data records (*n*), mean, standard deviation (*SD*) and coefficient of variation (*CV*, %) for reproductive traits studied in giant freshwater prawn

Trait	Unit	n	Mean	SD	CV	Min	Max
WBS	g	379	44.9	15.1	33.6	15.1	92.3
WAS	g	381	38.6	13.1	33.9	13.7	97.6
FEC	no	391	24815.5	14078.9	56.7	1005	76950
ZOEAWT	g	354	4.9	2.5	51.0	0.22	10
PLAGE	day	867	23.4	5.7	24.6	10	80
SURV1	%	706	11.4	11.6	80.5	0	65.0
SURV2	%	988	48.2	20.8	43.0	2	99.0

WBS = Female weight before spawn, WAS = Female weight after spawn, FEC= Fecundity (number of larvae per female at hatching), PLAGE = PL first age, ZOEAWT = Total zoea weight, SURV1 = Larval survival during hatchery phase, SURV2 = fry survival in hapas

**Table 3** Heritability ( $h^2 \pm se$ ) and common full-sib effects ( $c^2$ ) for reproductive traits in giant freshwater prawn

Traits	$h^2$	$c^2$
PLAGE	$0.30 \pm 0.28$	$0.03 \pm 0.03$
SURV1	$0.05 \pm 0.19$	$0.15 \pm 0.05$
SURV2	$0.43 \pm 0.25$	$0.00 \pm 0.00$

PLAGE = log transformed

**Table 4** Least square means difference between the selection line and control group of giant freshwater prawn

Trait	Control (n=134)	Selection (n=595)	Significant probability
WBS	32.0 ± 2.35	37.3 ± 1.33	0.0492
WAS	26.1 ± 2.18	31.2 ± 1.24	0.0348
FEC	21974.2 ± 2580	22127.0 ± 1464	NS
ZOEAWT	4.5 ± 0.46	4.6 ± 0.27	NS
PLAGE	21.3 ± 0.46	22.1 ± 0.27	NS
SURV1	17.4 ± 1.22	17.9 ± 0.78	NS
SURV2	51.4 ± 1.77	50.3 ± 0.98	NS

NS = non-significance. Trait abbreviations given in Table 2

Figure 1 Relationship between female body weight before spawning and PL first age  
( $y = 29.193 - 0.1185 \times wbs$ ) in giant freshwater prawn

