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Effects of selection for fast growth on survival rate during grow-out phase in giant freshwater prawn (*Macrobrachium rosenbergii*)

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Abstract

Background: Correlated genetic response in survival to selection for high growth has not been reported in giant freshwater prawn (GFP) (*Macrobrachium rosenbergii*). The main aim of this study was to measure genetic changes and estimate heritability for this character (survival rate) and its genetic associations with body traits in a GFP population selected over eight generations from 2008 to 2015. Statistical analyses were conducted on 106,696 data records, using threshold logistic mixed model.

Results: The estimated heritability for survival was 0.14 ± 0.04 and significant. Genetic associations of survival with body traits (weight, length and width) were weak, with the estimates of genetic correlations between the traits close to zero. Realised genetic changes in survival, calculated as the difference in estimated breeding values between the selection line and control group within the same generation, was in positive direction but the estimates were not significantly different from zero regardless of the expression unit used either in actual unit of measurement or genetic standard deviation unit. On the other hand, communal testing of stocks in the latest generation, namely G7 (2015), showed that the selection line had 18% higher survival rate than progeny of the wild prawns originated from Mekong river. This result suggests that inadvertent changes in survival occurred during domestication-selection.

Conclusions: It is concluded that selection for high growth had no significant effect on survival in the present population of *M. rosenbergii*.

Keywords: Survival rate, Correlated genetic changes, Selection response, Heritability and prawn

Background

In commercial aquaculture sector, productivity or production yield is simply defined as a function of body weight and survival rate (yield = body mass × % survival). In addition to body weight, survival is one of the main characters to determine profit and economic return of the sector because it is related to the number of animals to be harvested and marketed.

Majority of selective breeding programs in aquaculture species have focused mutually exclusive on improving body weight or growth [1, 2]. Genetic evaluation of these

selective breeding programs in fish showed that selection for high growth did not have significant effects on survival during grow-out, such as in tilapia [3] or common carp [4]. In some studies, improving growth performance was found to be associated with inadvertent increase in survival rate, an example can be found here in yellowtail kingfish [5]. To the best of our knowledge, there is no formal publication on correlated genetic changes in survival to selection for high growth in any shrimp species. Only the study of Campos-Montes et al. [6] reported a moderate and positive genetic correlation between body weight and survival in Pacific white leg shrimp.

Family selection programs have been initiated for giant freshwater prawn *M. rosenbergii* in China [7], India [8]

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and Vietnam [9, 10]. Selection for high growth significantly increased harvest body weight at an average rate of about 7% per generation [11]. There were also correlated changes in carcass traits (i.e. abdominal weight, telson-off weight and skeleton-off weight) by 3–4% per generation [12]. However, evaluation of possible changes in survival has not been conducted in this GFP population. To fill in the knowledge gap identified from the literature, in the present study we measured correlated response in this trait from a family selection program for GFP conducted over eight generations from 2008 to 2015. We also report heritability that estimated for survival and its genetic associations with important body traits (live weight, total length and abdominal width) as well as survival rate of the selected line in comparison with one of the founder stocks used to form the base population.

Methods

Experimental location and animals

The experiment was carried out at National Breeding Centre for Southern Freshwater Aquaculture (NABREC-SOFA) at Cai Be district, Tien Giang province (latitude: 10.3 and longitude: 105.9), Vietnam. NABREC-SOFA is one of the research centres of Research Institute for Aquaculture No. 2 (RIA2).

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. Details of the diallel cross to form the base population were described by Hung et al. [10]. In brief, the complete diallel cross involved three strains and produced 81 full-sibs families in 2008 (G0). From G1 – G7 (2009–2015), superior (highest ranking EBV, estimated breeding values) animals were selected to produce subsequent generations. In the last two generations, some males from Dong Nai and Mekong strains were mated with selected females due to high mortality of male brooders. In generation 2012 (G4), two exotic stocks imported from Thailand and Myanmar were introduced into the population at a ratio of 10% of selected breeders to produce G4.

Family production, breeding, rearing and grow-out

In all generations (G0 – G7), family production, breeding, rearing and grow-out were practised as described in Hung et al. [10]. Indoor fibre glass tanks (1 cubic meter) were used for stocking selected broodstocks and mating. To produce half-sib families, 6–8 females were mated with one male, berried females were removed every 10 days after mating. Hatching of each family occurred in separate spawning tanks which was the same as larvae stocking stage. Rearing of prawn larvae were conducted

in 70 l-round plastic tank with a density of 60 larvae per litre. After 25–30 days of rearing, post-larvae (PL) were stocked in 1 m³ tanks (at a density of 500–1000 PLs) for about 2 weeks until PL prawns were bigger than the mesh size. After a rearing period of about 2.0–2.5 months in hapas (net enclosure) installed in earthen pond where the PLs reached a size of larger than 1 g in body weight, 100–150 animals randomly sampled from each family were tagged using Visible Implant Elastomer [13].

All the tagged animals were then conditioned in tanks for two days without food before they were transferred to ponds for grow-out. In the grow-out phase, the stocking densities in every generation were from two to seven individuals/m² with earthen pond sizes ranging from 2,000 to 9,000 m². Industrial feed pellet (30% crude protein and 5% of fat) for black tiger shrimp (*P. monodon*) was used in the experiments with a diet of 3–5% biomass stocking rate [14]. We harvested the animals after 3–4 months of grow-out.

Measurements and data collection

A detailed description of data recording for body traits (body weight, total body length, cephalothorax length, abdominal length and abdominal width), male prawn morphotypes and female reproduction status were given in Hung et al. [11].

In the present study, survival rate was recorded by the end of communal growing period, that is, at the time of harvest. The tag loss across generations were around 1% and animals that did not recognize family were assumed dead. Survival rate was recorded as a binary trait, coded as 1 for shrimp that survived at harvest or 0 for those that were not present or missing.

Statistical analysis

Co-variance component analysis

Survival rate during grow-out was analysed using generalised linear mixed model (GLMM) with a logit link function. Under this model, the assumption was that the data followed a binomial distribution, and a logit link function ($\hat{p} = e^x / (1 + e^x)$) was used where p is the probability of animal survival recorded at harvest and x is a linear predictor. The fixed effects (F) included in the model were generation (spawning seasons, 2008 to 2015), line (selection or control) and pond (two grow-out ponds used per generation), the second order interaction between generation and line, and a linear covariate (i.e. number of days or age from stock to harvest) fitted within ponds and generation subclasses. The threshold logistic mixed model included individual prawn (a) as the random term effect [Eq. 1]. The mathematical form of the nonlinear

(generalised) mixed models used to estimate variance components for survival rate is as the followings:

$$\log\left(\frac{p_{ijk}}{1-p_{ijk}}\right) = \mu + \mathbf{F} + \mathbf{a} + \mathbf{e} \quad (1)$$

With the GLMM model [1], heritability was calculated using the variance of the logit link function, which implies a correction of the residual variance by factor $\pi^2/3$.

$$h^2 = \frac{4\sigma_a^2}{\sigma_a^2 + \sigma_e^2 \frac{\pi^2}{3}}$$

where σ_a^2 is the additive genetic variance and $\sigma_e^2 = 1$

The estimates of h^2 on the liability scales (logit) for binomial characters can be transformed to observed (0/1) scale using the formula of Robertson and Lerner [15] as follows:

$$h_O^2 = h_L^2 \frac{z^2}{p(1-p)}$$

where h_O^2 is the heritability on the observed (0/1) scale, h_L^2 is the estimated heritability on the liability (logit or probit) scale, p is a proportion of survival in the data, and z is the height of the ordinate of normal distribution corresponding to a truncation point applied to p proportion of survival during grow-out phase.

In addition to the GLMM procedure, the linear mixed model was also used to analyse body traits (weight, length and width). The fixed effects (\mathbf{F}) were the same as described above in Eq. 1 but the random factors were the additive genetic effect of individual animal (\mathbf{a}) and the common full-sib effect (\mathbf{c}) [Eq. 2].

$$y = \mu + \mathbf{F} + \mathbf{a} + \mathbf{c} + \mathbf{e} \quad (2)$$

Genetic and phenotypic correlations between survival and body traits were estimated using a series of two-trait linear mixed model [Eq. 2]. All computation was conducted in ASReml 3.0 [16]. Significance of the heritability and genetic (phenotypic) correlation estimates was tested using z-score against a large random normal distribution [17].

Selection response

Correlated genetic changes in survival rate were calculated using two methods: i) as the differences in estimated breeding values (EBVs) between the selection line and control group within the same generation, and ii) as the differences in the EBVs between successive generations. The responses for the trait studied were expressed in actual units (i.e. % for survival), genetic standard deviation unit (SD_A) and percentage of the base population.

The statistical model used to estimate EBVs for body weight and other traits were the same as those used to estimate the heritability.

Results

Pedigree information, data structure and basic statistics

Survival rate during grow-out of this giant freshwater prawn population (GFP) ranged from 20 to 44%, averaging 32.5% across generations (Table 1). One exception was generation 2014 (G6) where mass mortality occurred due to testing of different tagging methods. The survival rate in this generation was only about 15%.

In all generations, there was significant variation in survival rate among families ($P < 0.001$). An example of family variation in the latest generation 2015 (G7) is graphically presented in Fig. 1. Analysis of variance showed that survival rate differed significantly among 88 families in this generation. For instance, the highest survival family was 31%, whereas the poorest survival family was only 8.6%.

Heritability

The heritability estimated from logistic generalised model for survival rate during grow-out was 0.14 ± 0.04 and differed significantly from zero (Table 2). When the estimate on the underlying liability was transformed to the observed scale (0, 1), it had similar magnitude to the heritability obtained from threshold model.

Further, the heritability estimate obtained for body traits (weight, length and width) from linear mixed model analysis was generally moderate, ranging from 0.09 to 0.21. The proportion of maternal and common environmental effects accounted for 4 to 9% of total phenotypic variation in morphometric body traits (Table 2).

Table 1 Number of sires, dams and offspring and survival rate over eight generations of selection

Generation	Line	Sires	Dams	Progeny	Survival rate (%)
G0 (2008)	Base population	81	81	1870	26.7
G1 (2009)	Selection	76	89	3060	40.2
	Control	17	17	711	32.4
G2 (2010)	Selection	60	96	4464	45.4
	Control	20	20	1256	40.4
G3 (2011)	Selection	65	144	5520	31.3
	Control	42	42	1324	38.5
G4 (2012)	Selection	74	93	2306	35.1
	Control	27	34	734	24.9
G5 (2013)	Selection	60	60	5743	33.8
G6 (2014)	Selection	34	54	504	20.4
	Control	7	15	162	10.0
G7 (2015)	Selection	56	87	3862	44.4
	Control	25	31	788	31.6

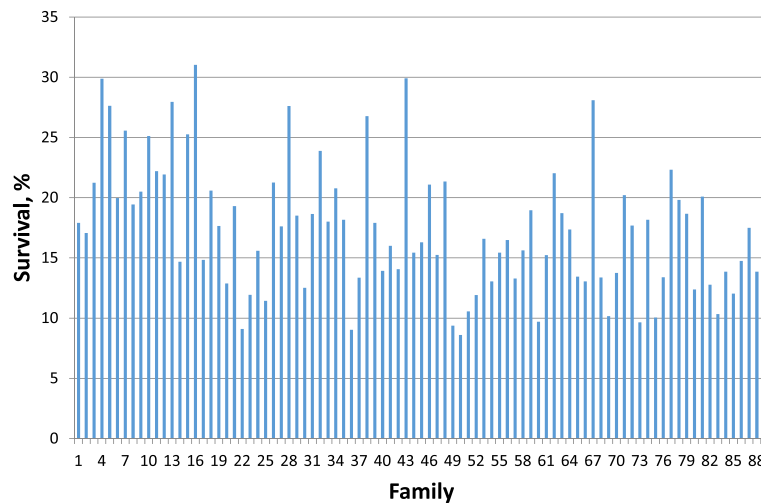


Fig. 1 Variation in survival rate among 88 families in the latest generation 2015

Phenotypic and genetic correlations

Table 3 presents phenotypic and genetic correlations between survival and body traits. All the estimates of genetic and phenotypic correlations were low and not significantly different from zero ($P > 0.05$).

Correlated genetic response in survival

Correlated genetic changes in survival to selection for high growth measured as the differences in EBV between the selection line and control (method 1) and between successive generations (method 2) are shown in Table 4. Consistently across the two methods, the estimated correlated responses in survival were close to zero and not significant, regardless of the expression units used either in actual unit of measurements or genetic standard deviation unit (i.e. 0.009 to 0.046SD_A). When the response in survival was expressed as percentage of the population mean, it ranged from 0.03 to 0.13% across generations of selection.

Survival of the selected line compared with wild stocks

Communal testing of the selected line together with its counterparts from the wild was conducted in ponds in 2015. Least squares means obtained from generalised logistic mixed model show that the selected line had

Table 2 Heritability and common full-sib effects for survival and body traits

Traits	Model	Heritability	Full-sib effects
Survival	1	0.14 ± 0.04	
Weight	2	0.12 ± 0.02	0.07 ± 0.01
Length	2	0.09 ± 0.02	0.09 ± 0.01
Width	2	0.21 ± 0.03	0.04 ± 0.01

Model 1 = Threshold logistic model, Model 2 = The animal model with common full-sib effect

significantly higher survival rate than the stock from Mekong river ($P < 0.05$) (Fig. 2).

Discussion

The main finding of our study was that the selection program for high growth did not result in adverse effects on survival of GFP during grow-out phase. The correlated responses in survival, although in positive direction, were small and not significant. The negligible changes in survival during the course of eight generations of selection for high growth in this population of GFP are in accordance with the results reported in the literature from long term genetic improvement programs for other aquaculture species, such as tilapia [3, 18, 19], common carp [4] or salmonids [1]. Our present results taken collectively with those reported in other species suggest that improvement in survival rate by selection on body traits could be achieved but at a slow rate.

The small changes in survival here are consistent with the weak genetic associations between survival and body traits obtained in the present study, with the genetic correlation estimate between the two traits close to zero (Table 3). A similar trend was reported in fish and crustacean species, such as rainbow trout [20], tilapia [3], common carp [4] or Pacific white leg shrimp [6]. There are however estimates of the genetic correlations

Table 3 Phenotypic (r_p) and genetic (r_g) correlations between survival rate and body traits

Traits	r_p	r_g
Weight	-0.01 ± 0.007	-0.10 ± 0.09
Length	-0.01 ± 0.006	-0.04 ± 0.09
Width	-0.02 ± 0.006	-0.10 ± 0.09

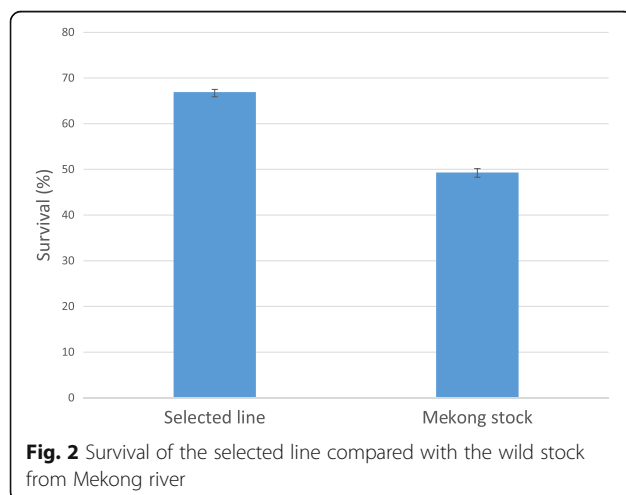
Table 4 Correlated genetic changes in survival rate measured as the differences in EBV between the selection line and control group (method 1) or between successive generations (method 2)

Generation	Method 1			Method 2		
	Actual unit	SD _A	% of the mean	Actual unit	SD _A	% of the mean
1	0.00037					
2	0.000119	0.02927	0.07827	0.000405	0.000000	0.00000
3	0.000267	0.00942	0.02518	0.000634	0.031983	0.085516
4	0.000492	0.02113	0.05650	0.000614	0.050087	0.133924
5	0.000395	0.03890	0.10400	0.000466	0.048517	0.129725
6	0.00091	0.03123	0.08350	0.001671	0.036872	0.098589
7	n.a.	n.a.	n.a.	n.a.	n.a.	n.a.
8	0.00540	0.00000	0.00000	0.002915	0.00000	0.000000

Actual unit (%), genetic standard deviation unit (SD_A), n.a. = not available due to limited data records

between the two traits which are moderate and either positive [21, 22] or negative [23].

In this study, the analysis of variance using threshold logistic mixed model showed that there was additive genetic component for survival during grow-out phase in ponds ($h^2 = 0.14 \pm 0.04$). This suggests that genetic improvement through direct selection for this trait (survival rate) should be possible. In a different population of GFP, Luan et al. [7] reported a low heritability for this character. Studies in other species pointed out that survivals in the early phase of development or during grow-out are lowly heritable such as in shrimp [6], freshwater fish (tilapia and common carp) [3, 4] or abalone [22]. On the other hand, a number of studies also reported moderate heritability for survival under field grow-out conditions for Atlantic salmon [24] or another population of common carp [25] and tilapia [18].

**Fig. 2** Survival of the selected line compared with the wild stock from Mekong river

Despite the existence of the heritable additive genetic variation for survival in the present population of GFP, it is well known that this trait is strongly influenced by environmental factors. Among factors recorded in the present study, the effect of generations, grow-out pond, sex/morphotype on survival were all statistically significant ($P < 0.05$ to 0.001). Several other factors such as diseases or inbreeding may have had impacts on this trait; however, they were not examined in the present research. Our results also pointed out that there is a need to maintain the control group since it enabled the separation of the domestication-selection effect. Owing to the non-significant difference between the selection line and control group in this study, any increase in the survival rate in the selected line relative to its counterparts from the wild was likely a result from long-term domestication. The higher survival rate in the selected line compared with the wild stock would bring about greater economic benefits and returns to prawn farmers.

Conclusion

- Selection for high growth did not cause significant changes in survival rate during grow-out phase in the present population of GFP
- The genetic correlations between survival and body traits were weak and not significant
- There is heritable additive genetic component for survival during grow-out
- Survival during grow-out was largely influenced by environmental factors
- Possible effect of selection for high growth on survival rate during the early phase of rearing in this GFP population deserves future research.

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Availability of data and materials

The data may be available upon request with permission of the Research Institute for Aquaculture No.2, Vietnam.

Authors' contributions

NHN and NTV conceived and designed the experiments, analysed the data and prepared the manuscript; TQT contributed the study materials and overseen the breeding program. NTV, NHN and TQT participated in data and tissue sample collection. All authors read and approved the manuscripts.

Competing interests

The authors declare no competing interests.

Consent for publication

Not Applicable.

Ethics approval

All the methods and experimental protocols of this study were performed in accordance with guidelines and regulations endorsed by the local government of Vietnam. Animal ethics approval was not required for crustacean species.

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