GENOTYPE X ENVIRONMENT INTERACTION IN SHRIMP BREEDING: A REVIEW AND PERSPECTIVES

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SUMMARY

Genotype by environment interactions (GxE) can effectively suppress the response to selection in shrimp breeding programs. In order to understand the magnitude of GxE, we conducted a systematic review of literature on GxE in shrimp aquaculture. A departure from unity in the genetic correlation between the same trait measured in different environments indicated a GxE. Significant GxE was detected for survival and growth traits. The mean genetic correlation estimates for survival (n=22) and growth (n=26) traits were 0.53 (ranged -0.99 to 0.99) and 0.65 (range 0.47 to 0.99) across environments, indicating genetic improvement in one environment may not be fully realized in other environments.

INTRODUCTION

Global shrimp aquaculture has increased from 1 million metric ton in 1995 to almost 5 million metric ton in 2018, with further prediction of growing demand (Global Aquaculture Alliance 2018). Sustainable increased production of shrimp requires the development of genetically improved high-quality seed stock. Globally, breeding programs have been implemented for a number of shrimp species in particular for *Penaeus vannamei*. Despite the development of such breeding programs, realised genetic gains for different traits have been limited (Nguyen 2016). This may be due to several factors that limit response to selection, including genotype x environment interactions (GxE). GxE is the difference in phenotypic expression of traits in different environments by genetically similar organisms that result in inconsistent performance of superior genotypes across different environments. Evidence of GxE is observed by a re-ranking of breeding values of individuals for each environment. Moreover, as compared to plant and livestock production such phenomena are more obvious in aquaculture breeding programmes, where the majority of the commercial grow-out conditions can be very diverse e.g., ponds, outdoor net and cages, raceways compared to the breeding and selection environments under which brood stock are raised and selected. Given such large variability in production environments, a critical understanding of the importance of GxE is vital for the design of optimal breeding programmes for aquaculture species, including shrimp. Evidence of substantial GxE may require shrimp breeders to develop environment-specific strains. Furthermore, in the era of high throughput phenomics and genomic selection, novel selection strategies may present themselves to mitigate the impact of GxE by making environment specific selection decisions at a central location (i.e., measure performance under diverse commercial environments and link back through genomics to central seed stock providers). The purpose of this study is to review and characterise the magnitude of GxE for important health and production traits within shrimp species, and to discuss the possible knowledge gaps and the implications of these findings in shrimp breeding programmes.

MATERIALS AND METHODS

Publically available GxE studies of shrimp species were selected using the 'PubMed' search

engine with the 'topic' search terms 'genotype', 'environment', 'interaction', 'shrimp/prawn' and 'aquaculture'. This search gave 20 published articles, which were selected for this review. For each selected GxE study, we recorded the publication date, species name, breeding design, pedigree, number of individuals/families sampled, type of study (e.g., marker/pedigree based), traits, environment type and presence of GxE. Information about the publication year, country of study, commonly used species, pedigree information and extent of GxE were assembled. Various traits and environmental conditions were categorized into three broad trait groups and three environmental groups, (Table 1). The extent of GxE among the selected studies was determined using two approaches. Firstly, estimates of genetic correlation between the same trait across different environments (r_g) was taken as a measure of GxE. Among the selected studies on GxE interaction, a total of 15 studies reported such genetic correlation between environments. Secondly, the proportion of variance accounted for by interactions between families (genotype) and environments, as reported in six different studies, were compiled. All data were analysed in the R statistical environment (version: 3.5.0) (R Core Team 2013).

Table 1. Definition of trait groups and environments

Traits	Definition
Growth	Body weight, growth rate, body length
Survival	Overall or in a challenge test
Body composition	Protein, lipid, carbohydrate contents
Environment	**Definition**
Habitat	Pond vs. pond (location), pond vs. tank or cage
Feed	Feed type and feeding regimes.
Stress	Salinity, ammonia concentration, temperature, density (high vs. low), pathogens.

RESULTS AND DISCUSSION

The most commonly reported species in the GxE studies was *P. vannamei* followed by *P. japonicus*. Growth and survival were the most commonly studied traits in family-based breeding populations. The earliest GxE study on shrimp was conducted in 2002. There was no specific trend found in terms of the number of studies per year, although highest number of studies were reported in 2018, and most of the studies were conducted in Australia. We recorded a total of 62 genetic correlation estimates primarily focussed on growth, whilst some studies also reported on body composition and feeding efficiency. Habitat type was the most common environmental factor studied reported in the GxE studies for shrimp.

By analysing six studies on variance attributed to GxE, we detected that habitat type and stress had significant interaction for the shrimp growth and survival traits at a family level (genotype). On an average, the habitat x family interaction for growth accounted for 7% of the variation in the model, and the stress environment accounted for 0.5% and 9% of the variation for the growth and survival traits. A higher level of variability in GxE interaction was observed for survival traits compared to growth traits (Figure 1).
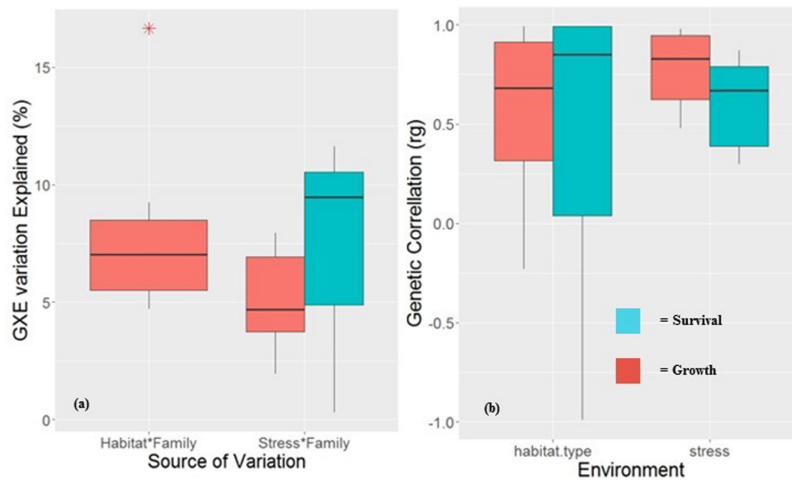
Figure 1. (a) Percent of GxE variation accounted for in ANOVA models; and (b) mean rg values across traits by environments

Growth traits were most commonly reported across all the studies. This might be due to the fact that these traits are directly correlated with economic return in shrimp farming. Moreover, these traits are also easier to record as compared to other traits. The mean r_g value for growth trait was 0.65 with a range of 0.47 to 0.99 (Figure 1b). This positive r_g value implies that selection for improved growth performance in one environment is likely to lead to a genetic response in the same direction in other environments but will result in re-ranking of genotypes. Survival as another economically important trait in shrimp aquaculture, was the second most reported traits for GxE interaction studies in shrimp. The mean r_g value for survival was 0.53 for all the studies with an extreme range of -0.99 to 0.99. This indicates that the re-ranking of candidates available for selection for survival is potentially of great importance pending the environmental conditions in which their progeny are expected to perform. This extreme level of re-ranking for survival traits can be as a result of different causative mortality factors in different environments. Furthermore, there might be limited additive genetic variation for resilience against these factors and making changes in co-variance across environments relatively more important.

Opportunities for genomic selection in overcoming GxE. Traditionally, GxE is viewed as a problem in breeding programs. Where commercial animals are raised in a different environment compared to that where the original selection of breeding animals is carried out, which may result in GxE. Consequently, genetic gain made in the nucleus breeding environment may not be fully realized in the production environment. This scenario is most likely in shrimp and other aquaculture species. Firstly, since aquatic animals are immersed in their water environments which greatly affect physiological activities and overall production can vary significantly across different locations/farms. Secondly, like in poultry and pigs, selection and breeding of broodstock in shrimp species is usually conducted in the hatchery/nucleus which is often pathogen free, but the actual breeding objective usually is to improve the performance of family lines (or their crosses) in commercial environments. Compared to traditional selection breeding program, which rely on pedigree information of family line-bred animals, genomic selection with reference populations of animals grown in several environments

can be far more effective. Such multi-environment reference populations could be combined with high-throughput genomics and phenomics using machine learning. For instance, high-throughput image-based phenotyping of very large numbers has been reported for several genomic selection studies with plants and animals (Leiboff 2015; Zenger *et al.* 2017). The large datasets from high-throughput phenotyping can be utilized to improve resilience of animals across environments. Multi-environment reference population could facilitate the computation of more accurate genomic breeding values (GEBV) for all genotyped and pedigreed selection candidates in their ranking for performance and resilience in specific environments. This also opens the possibility of creating specialized lines by genomic selection. Creating such specialized lines would also facilitate maintenance of broader genetic diversity across lines (Mulder 2017).

Developing breeding programmes by incorporating environmental information. Variable environmental factors, including disease and pathogen challenge, salinity, temperature and occurrence of severe weather events, are potentially major constraints to profitable shrimp farming and may limit sustainable and uniform production. Moreover, in the face of climate change, these factors may have profound impact depending on climatic zones, geographic locations and type of aquaculture systems (e.g., intensive vs. extensive). In such situations, animals bred for one specific set of conditions may not perform well in other environment. Moreover, climatic instability may facilitate physiological stress, as well as outbreaks of existing pathogens or may promote dispersal of new diseases. However, combined spatial modelling of all risk factors and selective breeding strategies can be applied to tackle these issues. Environment specific genetic lines can be established by identification of genotypes that perform optimally in specific locations or specific conditions. For example, using detailed environmental data, prevalence of both short and long-term pathogen attack can be predicted (Singh *et al.* 2006). Based on current weather forecast data, such predictions can potentially be carried out for coming year or season, in combination with historical data on disease, pathogens and climatic factors. It is important to develop genotypes resilient to disease and pathogens and suited for a range of environments to minimize the effect of GxE. Although no experiments have been carried out with shrimp, studies with wheat and barley have shown that specific disease outbreaks can be successfully predicted and adapted resistant cultivars used to suit local conditions (Singh *et al.* 2006; Gillberg *et al.* 2017). Similar approaches can be applied to shrimp breeding and production by developing locally adapted and resilient shrimp lines for specific environments, providing a possible means to achieve yield improvement.

CONCLUSIONS

This review shows substantial GxE of importance for a number of economic traits of commercially farmed shrimp species and that such GxE effects warrant consideration in the development of shrimp breeding programmes. Furthermore, it also suggested the potential for genomic selection combined with large scale phenomics across diverse environments to overcome limitations imposed by GxE in advanced shrimp breeding programmes.

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