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Estimation of genetic parameters for survival to multiple isolates of Taura syndrome virus in a selected population of Pacific white shrimp *Penaeus* (*Litopenaeus*) *vannamei*

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ABSTRACT

Taura syndrome virus (TSV) is an economically important pathogen of the Pacific white shrimp, *Penaeus* (*Litopenaeus*) *vannamei*. To date, >40 unique TSV isolates have been identified and phylogenetic analyses of these isolates have revealed four distinct genetic groups named according to their geographic origin: Americas, Belize, South East Asia, and Venezuela. Although there is evidence that virulence varies among different TSV isolates, little is known about how shrimp survival is correlated among isolates (i.e. genetic correlations). In addition, estimates of genetic correlation between TSV survival and other commercially important traits are limited. The objectives of this study were to (1) estimate genetic correlations for shrimp survival to a genetically diverse suite of TSV isolates and (2) estimate genetic correlations between isolate-specific TSV survival and growout performance traits (i.e. growth and growout survival). A total of 180 full-sib families were challenged with TSV: 130 families challenged with Americas and Belize group isolates and 50 families challenged with isolates from all four genetic groups. In addition, 100 of these families were tested for growout performance in a recirculating aquaculture system (RAS) at intensive stocking densities (>230 shrimp/m^2). All families were from a shrimp line selected for TSV resistance and growth over multiple generations. Genetic correlations for survival among TSV isolates were positive and of moderate to high magnitude (r_G = 0.35–0.99). Genetic correlations for TSV survival and RAS growth were all negative, but of low magnitude (r_G = −0.07 to −0.29). Correlations between TSV survival and RAS survival varied from slightly negative to moderately positive. These results indicate that breeding for survival to any one of the four TSV isolates evaluated in this study should, in general, improve survival to the other isolates. Results also suggest that there are no significant costs associated with selection for TSV resistance relative to growout performance.

1. Introduction

Taura syndrome virus (TSV) is an economically important pathogen of Pacific white shrimp, *Penaeus* (*Litopenaeus*) *vannamei*, which is the most commonly cultured shrimp species worldwide (Food and Agriculture Organization, 2011). TSV was first identified in Ecuador in 1992 (Hasson et al., 1995; Lightner, 1995) and has since spread to all major shrimp farming regions of the Americas and Asia (Hasson et al., 1999; Tang and Lightner, 2005; Tu et al., 1999; Yu and Song, 2000). TSV is highly virulent and TSV-associated mortalities in unselected, naïve populations of *P. vannamei* can range from 40 to 95% (Lightner, 1999).

Selective breeding of *P. vannamei* for TSV resistance began in the mid-1990s and several research and commercial breeding programs have developed lines of shrimp which exhibit varying degrees of TSV resistance (Argue et al., 2002; Bienfang and Sweeney, 1999; Clifford and Preston, 2006; Wyban, 1999); note: the terms “resistant” and “resistance” have been adopted by many stakeholders in the shrimp farming industry to refer to a shrimp's ability to survive viral exposure. Although heritability for TSV resistance is considered low to moderate, significant improvements in TSV resistance have been made (Argue et al., 2002; Fjalestad et al., 1997; Gitterle, 1999; White et al., 2002), including the establishment of some selectively bred stocks which exhibit >80% survival to TSV in *per os* laboratory challenges (Moss et al., 2011; Srisuvan et al., 2006; Wyban, 2000).

TSV has a single-stranded, positive-sense RNA genome comprised of two open reading frames (ORFs), with ORF1 coding for non-structural proteins (helicase, protease, and RNA polymerase) and ORF2 coding for structural proteins, including three capsid proteins (Bonami et al., 1997; Mari et al., 2002). As is common with RNA viruses, TSV is prone to mutation due to a lack of proofreading enzymes (Holland et al., 1982). A comparison of 40 TSV isolates, based on the deduced amino

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acid sequence of a highly variable region of the capsid-2 protein, identified 31 unique sequences (Tang and Lightner, 2005). Phylogenetic analysis of these sequences revealed three distinct genetic groups of TSV named according to their geographic origin: Americas, Belize, and South East Asia. A more recent analysis, including newly collected isolates, identified a fourth genetic group originating from Venezuela (Côté et al., 2008).

Shrimp survival after TSV exposure has been documented for only a few isolates, so the virulence of most isolates is unknown. However, there is evidence that virulence varies among isolates. Erickson et al. (2005) conducted four *per os* laboratory challenges, using isolates BLZ02 (Belize group) and USHI94 (Americas group), and found that survival of Kona shrimp (an unselected, reference population of *P. vannamei*; see Hennig et al., 2004) was lower when shrimp were exposed to the Belize-group isolate. Shrimp survival to BLZ02 ranged from 0 to 35%, whereas shrimp survival to USHI94 ranged from 20 to 70%. Similar results were reported by Tang and Lightner (2005) for Kona shrimp exposed to USHI94 and a different Belize-group isolate (BZ01). Srisuvan et al. (2006) reported survival for two populations of *P. vannamei* (Kona shrimp and a population selected for TSV resistance) when exposed to isolates USHI94, BZ01, TH04 (South East Asia group), and VE05 (Venezuela group). Survival patterns for Kona shrimp and the selected population were similar with survival to USHI94 being the highest for both populations (21.5% and 100%, respectively). Survival to VE05 (11.4% and 95.3%) was the next highest, followed by TH04 (5.3% and 82.7%), and BZ01 (0.0% and 77.5%).

While there is evidence that virulence varies among TSV isolates at the shrimp population level, little is known about how within-population variation for survival is correlated across TSV isolates (i.e. phenotypic and genetic correlations). Moss et al. (2005) reported a positive phenotypic correlation ($r_P = 0.52$) for survival among families ($n = 80$) of selectively bred *P. vannamei* exposed to two TSV isolates (USHI94 and BLZ02). However, additional estimates of phenotypic or genetic correlations for survival to multiple TSV isolates have yet to be reported.

Estimates of phenotypic and genetic correlations between TSV survival and other commercially important traits are also limited. Argue et al. (2002) found no correlation between pond survival and survival to TSV isolate USTX95 (Americas group) in *P. vannamei*, but did find a negative genetic correlation ($r_G = -0.46$) between growth and TSV survival. More recently, Moss et al. (2005) reported a negative correlation ($r_P = -0.15$) between harvest weight and TSV survival (USHI94 or USTX95) for the same *P. vannamei* population.

For selective breeding programs to operate effectively, information about genetic correlations between important traits is needed to properly define selection goals and optimize selection/breeding protocols. Specifically with regard to breeding for TSV resistance, it is unknown if survival to TSV isolates are unique traits or represent a single survival trait. Furthermore, it is unknown how isolate-specific TSV survival is related to other commercially important traits. The objectives of this study were to (1) estimate genetic correlations for shrimp survival to a genetically diverse suite of TSV isolates and (2) estimate genetic correlations between isolate-specific TSV survival and growout performance traits (i.e. growth and growout survival).

2. Materials and methods

2.1. Breeding population

Shrimp for this study came from Oceanic Institute's (OI; Waimanalo, HI, USA) selective breeding program. There are complete pedigree records for the breeding population and it is comprised of eight founder populations of *P. vannamei* collected from the wild at different geographic locations within the natural range of this species. Since the inception of the breeding program, shrimp have been specific pathogen free (SPF) for all pathogens listed by the US Marine Shrimp Farming Program (for most current list, see USMSFP, 2010), including those pathogens that are International Office of Epizootics (OIE) notifiable (OIE, 2012).

The breeding population has been artificially selected for growth for 14 generations and a portion of the population has also been selected for TSV resistance (or survivability) for the last 10 generations. Each year, 40–160 families were produced (one generation/year) and, after evaluation, about 40 families were chosen as broodstock to produce the next generation. The population was separated into two lines with each line consisting of 20–80 families per generation. One line, referred to as Growth Line, was primarily selected for growth and the other line, referred to as TSV Line, was selected for a combination of TSV resistance and growth. Founder populations were the same for both lines and germplasm (typically in the form of broodstock) was moved between lines periodically to maintain pedigree connectedness and to manage inbreeding (goal of <1% per generation).

Selection for TSV resistance was based on shrimp survival during laboratory, *per os* challenges. For early generations (1–6), TSV challenges and selection decisions were based on single-isolate challenges using either USHI94 or USTX95. In later generations (7–11), several multi-isolate challenges were conducted and selection decisions incorporated BZ01 challenge data when available. This was done because phenotypic variability was highest for BZ01 and allowed for increased selection intensity. Growth evaluations were originally conducted (generations 1–8) in an earthen pond at stocking densities <100 shrimp/m^2. However, growout evaluations of the later three generations were conducted in a recirculating aquaculture system (RAS) at super-intensive stocking densities (>235 shrimp/m^2). For further details on OI's founder stocks and breeding program see Wyban et al. (1993), Carr et al. (1997), and Argue et al. (2002).

2.2. Production and evaluation of shrimp families

Performance data for 180 full-sib families (offspring of 177 sires and 175 dams) were used for this study and represent generations 7 (G7), 9 (G9), and 11 (G11) of the TSV Line. These generations were chosen because families within each generation were challenged with multiple isolates of TSV (allows for estimation of genetic covariance using multi-trait animal model), challenges for two isolates (USTX95 and BZ01) were conducted in multiple generations (allows for estimation of genetic covariance both within and across generations), and TSV evaluations (both within and across generations) were conducted at the same disease-challenge facility. Families in G9 and G11 were also evaluated for growout performance in RAS. It should be noted that families in G8 and G10 were challenged and selected for TSV resistance. However, only a single TSV isolate was used (USHI94) and challenges were conducted at a different facility than that used for G7, G9, and G11. Although performance data from G8 and G10 were excluded from this study, pedigree information from these generations was used.

Families for each generation were produced over 5–9 d using artificial insemination (Arce et al., 2000). Mated females were placed in individual tanks for spawning. After hatching, ~15,000 nauplii from each family were randomly selected and transferred to family-specific, 100-l larval rearing tanks. Shrimp hatchery techniques similar to those described by Wyban and Sweeney (1991) were used for rearing shrimp to 10-day postlarvae (PL-10).

After larval rearing, 1000 PL-10 were randomly selected from each family and stocked into family-specific, 500-l nursery tanks. Nursery tanks were connected to a common recirculation system to minimize water quality and temperature difference among tanks. When shrimp reached 1–2 g wet weight, randomly selected juveniles (300–500) from each family were tagged with a fluorescent elastomer (Godin et al., 1996). Each family received a unique tag code and, after tagging, shrimp were returned to their respective nursery tanks until all families were tagged (≤5 d). Nursery tanks were then harvested and shrimp