Latin American Journal of Aquatic Research, 53(1): 1-21, 2025
DOI: 10.3856/vol53-issue1-fulltext-3254

Review

Advances in genetic and genomic resources in Pacific whiteleg shrimp *Penaeus vannamei*: Towards modern and sustainable shrimp aquaculture

Adriana Max-Aguilar[1], Ana M. Ibarra[1], Diego Robledo[2,3] & Ricardo Perez-Enriquez[1]
[1]Programa de Acuicultura, Centro de Investigaciones Biológicas del Noroeste, S.C.,
La Paz, B.C.S., México
[2]The Roslin Institute and Royal (Dick) School of Veterinary Studies
The University of Edinburgh, Midlothian, United Kingdom
[3]Department of Genetics, Universidad de Santiago de Compostela, Santiago de Compostela, Spain
Corresponding author: Ricardo Perez-Enriquez (rperez@cibnor.mx)

ABSTRACT. Genetic improvement of Pacific whiteleg shrimp *Penaeus vannamei*, the most economically important crustacean worldwide, is key to ensuring shrimp aquaculture's sustainability. Maximizing the potential of this industry requires implementing well-managed, genome-enabled breeding programs. This review discusses genetic and genomic resources available for shrimp production and their application, covering topics such as population genetics, reference genomes, linkage maps, genetic markers, genome-wide association studies, and genomic selection. The genetic characterization of shrimp requires the availability of genetic marker panels, whose density depends upon the applications. Several low- and high-density marker panels, from microsatellites to single nucleotide polymorphisms, are currently used in population genetic structure, diversity, and parentage assignment studies. The challenge is the low cost per individual panel for commercial aquaculture operations. The reference genome of *P. vannamei* has been recently improved with new genome assemblies. Nevertheless, there is still room for improvement in scaffold assembly, genetic mapping, and gene annotation. This information will be useful to integrate genomic information into breeding programs to improve desired economic traits. Wild and captive populations have been well-characterized, and the genetic architectures of commercially relevant traits (i.e. growth, immune response, sex) have been studied. Future work should focus on the underlying genomic basis of productive and adaptive traits, which can be applied to modern selective breeding strategies, such as genomic selection. Developments in these areas should accelerate shrimp genetic improvement and will be key in ensuring the industry's sustainability.

Keywords: *Penaeus vannamei*; selective breeding; genomic selection; genotyping; GWAS; SNP

INTRODUCTION

The Pacific whiteleg shrimp *Penaeus vannamei* is one of the most important economic aquaculture species, representing 53% of the crustacean aquaculture production worldwide and 6.9% of the total aquaculture production, with 6.3 million metric tons in 2021 valued at approximately US$36.5 billion (FAO 2024). *P. vannamei* is native to the East Pacific Ocean from Mexico to Peru, but it is farmed in over 30 countries across the world; the 10 principal producing countries are China, Indonesia, India, Ecuador, Vietnam, Thailand, Mexico, Brazil, Saudi Arabia, and the Islamic Republic of Iran (FAO 2020).

Despite the growing trend of Pacific whiteleg shrimp aquaculture production (8% per year from 2009 to 2018; FAO 2020), the increasing demand for protein for human consumption and the current context of

Associate Editor: Carlos Alvarez

environmental emergency calls for more efficient production.

Breeding programs effectively ease aquaculture production (Gjedrem et al. 2012), permanently and cumulatively improving target traits to develop aquaculture stocks with enhanced performance (Gjedrem & Baransky 2009). According to the action plan for aquatic genetic resources for food and agriculture, selective breeding is a priority in aquaculture (FAO 2022a). Despite the advantages of breeding programs, only 55% of aquaculture countries report a significant impact from genetic improvement on their production (FAO 2022b).

In the case of *P. vannamei*, several breeding programs, mainly directed towards growth and disease resistance, have been reported (Argue et al. 2002, Gitterle et al. 2005, Neira 2010, Andriantahina et al. 2013b, Moss et al. 2013, Van der Pijl 2020, Prochaska et al. 2022). Still, it is unclear how much of the world's shrimp production comes from selective breeding programs.

Advances in sequencing technologies, such as genotyping by sequencing, have allowed the development of genomic resources in non-model species, opening the possibility of selection based on genomic information. Implementing genomic information in breeding programs while carefully controlling inbreeding can increase the rate of genetic gain through more accurate selection of broodstocks to be used in the next generation, especially for complex traits that cannot be measured directly in the candidates for selection, such as disease resistance (Castillo-Juárez et al. 2015). Access to genomics tools has also facilitated genetic diversity evaluation, stock identification, and parentage assignment or traceability, and it has allowed us to gain insight into many biological processes.

Here, we review the status of genetic and genomic resources available in Pacific whiteleg shrimp and their applications in shrimp aquaculture (Fig.1). The status and perspectives of topics such as population genetics of wild and cultivated shrimp stocks, available genomic resources, and their applications, such as genomic wide association studies (GWAS) and genomic selection (GS), are discussed.

Genetic and genomic resources

Genetic marker panels and genotyping

Genetic markers underpin most genetic studies, being fundamental to studying genetic diversity and inbreeding, population genetics and stock identification, parentage analysis, species, and hybrid identification (Liu & Cordes 2004, Chauhan & Rajiv 2010), mapping quantitative trait loci (QTL) (Miles & Wayne 2008), genetic linkage maps, GWAS (Guppy et al. 2018), and GS (Song et al. 2023). Identification and application of genetic markers have been an important focus of research in aquaculture genetics. Over time, different types of molecular markers have been developed and used in aquaculture species; detailed information about principles, molecular basis, and applications have been extensively discussed (e.g. Liu & Cordes 2004, Liu 2007, Chauhan & Rajiv 2010).

In *P. vannamei*, microsatellite markers have been traditionally the most popular due to their high polymorphism. Extensive work has been done over the last 25 years (e.g. Wolfus et al. 1997, Cruz et al. 2002, Meehan et al. 2003, Zhi-Ying et al. 2006, Garcia & Alcivar-Warren 2007, Santos et al. 2012, Perez-Enriquez et al. 2018a), focusing in the characterization of wild and cultivated population, genetic diversity and parentage analyses (see section 3). However, due to the common scoring of null alleles derived from high mutation rates (Ellegren 2000), these markers have become substituted by single nucleotide polymorphisms (SNPs) in recent years.

SNPs, genetic markers that consist in the variation of a nucleotide (A, C, G, or T) at a single site in a specific position of the genome, offer several advantages over microsatellites and other genetic markers, such as abundance and even distribution along the genome (Collins et al. 1998, Rafalski 2002), low genotyping errors, and straightforward genotyping with lower cost as many samples can be analyzed simultaneously (Vignal et al. 2002, Hayes et al. 2005). Despite being less polymorphic (SNPs are mostly bi-allelic), identification and genotyping of a large number of SNPs along the genome in many individuals, even in non-model species, has become accessible and more feasible economically. Even though several authors have shown similar capabilities for parentage assignment with few microsatellites and few hundred SNPs (e.g. Trong et al. 2013, Kaiser et al. 2017), in the Pacific whiteleg shrimp, Perez-Enriquez & Max-Aguilar (2016) showed the better performance of an SNP panel in parentage assignment than microsatellite markers.

SNP identification and genotyping have been feasible for several years. Kim & Misra (2007) review several genotyping technologies, such as those based on allele discrimination strategies (primer extension, hybridization, single-strand conformation polymerphism, mismatch repair detection) and allele detection methods (mass-based, fluorescence signal-based, and

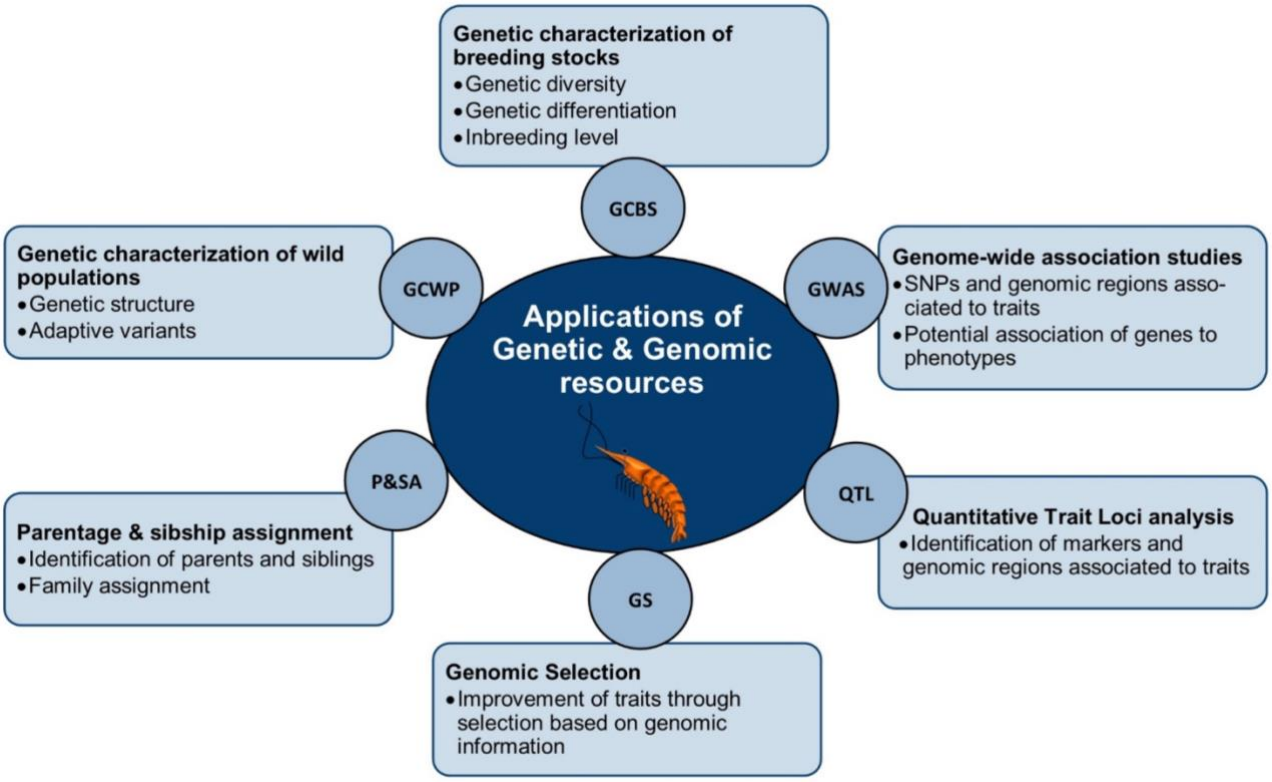

Figure 1. Applications of genetic and genomic resources.

chemiluminescence detection). However, the development of methods based on next-generation sequencing has led to the popularization of SNPs. For instance, restriction-site associated DNA sequencing (RAD-seq) (Baird et al. 2008) has been widely applied in aquaculture species (Robledo et al. 2018b).

Different variations of RAD-seq have emerged over the last 10 years, such as 2b-RAD (Wang et al. 2012), SLAF-seq (Sun et al. 2013), dd-RAD (Peterson et al. 2012), or ezRAD (Toonen et al. 2013), all based in the use of restriction enzymes, which reduces the representation of the genome and hence reduces the cost of sequencing. In addition to this cost-effectiveness, the other major advantage of RAD-like technologies is that they do not require a chromosome-level genome assembly as a reference.

Nevertheless, Robledo et al. (2018b) indicate that despite the advantages of RADseq approaches in cost and design, there are still challenges to overcome, such as laborious sample processing, complex bioinformatics analysis, long turnaround time, and medium repeatability. For instance, a comparative analysis between ddRAD and 2bRAD indicates similar results in repeatability, allelic dropout, and phylogenetic inferences but at a lower cost per SNP locus of ddRAD (Chambers et al. 2023). Furthermore, for applications requiring only a few hundred markers, 2b-RAD using selective adapters is a good alternative (e.g. Barbanti et al. 2020).

In the Pacific whiteleg shrimp, 2b-RAD (Wang et al. 2017b, 2019a,b, Dai et al. 2020, Lyu et al. 2021, Chen et al. 2022), SLAF-seq (Yu et al. 2015, 2019, Wang et al. 2017a, Peng et al. 2020), and NextRAD (Perez-Enriquez et al. 2018c) have been the most used techniques. These methods enabled genetic characterization, constructing high-density genetic linkage maps, and carrying on GWAS and GS.

Once many SNPs have been identified, it is possible to develop stable SNP high-density array genotyping platforms. The advantages of these platforms are that they overcome some of the problems described above (Robledo et al. 2018b). SNP arrays are now available for several aquaculture species [e.g. Atlantic salmon *Salmo salar* (Houston et al. 2014, Yáñez et al. 2016), European seabass *Dicentrarchus labrax* and gilthead seabream *Sparus aurata* (Peñaloza et al. 2021), Nile

tilapia *Oreochromis niloticus* (Peñaloza et al. 2020), Pacific oyster *Crassostrea gigas* (Qi et al. 2017), among others]. Two main SNP array technologies have been used in aquaculture species: Illumina BeadArray and Affymetrix Axiom. For *P. vannamei*, two high-density SNP panels are commercially available: the Illumina Infinium Shrimp LD-24 BeadChip with ~6.4k SNPs and the AQUArray HD vannamei with 50k SNPs; this last one was developed by Neogen and the Center for Aquaculture Technologies (CAT, https://aquatechcenter.com/). These technologies are being successfully used for QTL identification (Jones et al. 2020) and GWAS (Medrano-Mendoza et al. 2023); however, their application in commercial operations is still limited by the cost per individual.

For applications requiring tens to hundreds of genetic markers, such as pedigree analysis and traceability, other genotyping techniques have emerged to meet this demand: AQUArray LD vannamei (192 SNPs; CAT, https://aquatechcenter.com/), Fluidigim system (https://www.fluidigm.com/), Genotyping in-thousands by sequencing (GT-seq) (Campbell et al. 2015), Multiplexed PCR Targeted Amplicon sequencing (MTA-seq) (Onda et al. 2018), Highly Multiplexed Amplicon sequencing (HiMAP) (Dupuis et al. 2018), and Ion Ampliseq by Thermo Fisher. These are mostly based on sequencing amplicons from multiplexed PCR targeting previously identified SNPs, but the disadvantage of some of those is the need for costly equipment.

Other alternatives are based on fluorophore-labeled PCR amplicons such as KASP (Biosearch Technologies; https://www.biosearchtech.com/), TaqMan assay (Roche Molecular Systems, Inc.), and High-Resolution Melting (HRM), or those based on mass spectrometry like MassARRAY System (Sequenom, San Diego), can be more appropriate to genotype few markers. For instance, HRM has been used for genotyping a *P. vannamei* sex identification SNP (Perez-Enriquez et al. 2020), while the Sequenom MassARRAY iPLEX Gold platform has been used for genotyping 49 SNPs presumably associated with ammonia tolerance (Lu et al. 2018).

Different factors must be considered when selecting a *P. vannamei* SNP platform, such as the study's objective, their advantages and disadvantages (Table 1), and available funds. In shrimp aquaculture, with a relatively low value per animal [~US$55 per *P. vannamei* specific pathogen-free (SPF) breeder (Van der Pijl 2020)], a cost-effective SNP genotyping platform is required for routine genetic analysis in breeding programs, especially for small-medium shrimp producers. To our knowledge, the platforms with the lowest cost per individual presently available for the species are the AQUAarray HD and AQUAarray LD, respectively, for high- and low-density SNP panels. The development of low-density panels based on GT-seq (Campbell et al. 2015), 2bRAD using selective adaptors (e.g. Barbanti et al. 2020), pooled DNA genotyping (Sui et al. 2020), or target SNP sequencing (Huang et al. 2021) can decrease genotyping costs per individual.

Genome assembly

A complete genome assembly is a valuable resource for understanding the genomic characteristics of a species, facilitating the improvement of economically important traits. The assembly of the *P. vannamei* genome has been challenging due to its complexity. A large number of repetitive sequences (approximately 79-80% of the genome; Yu et al. 2015, Abdelrahman et al. 2017), high levels of heterozygosity [(Yuan et al. 2021a), and a large number of chromosomes (44 pairs by karyotype; Campos-Ramos 1997)], are the main constraints.

However, initial efforts led to the assembly of a *P. vannamei* reference genome covering ~1.66 Gb of the total genome size (2.45 and 2.6 Gb estimated with flow cytometry and *k*-mer analysis, respectively; Zhang et al. 2019), which represents 63.8-67.8%, with scaffold N50 of 605.56 Kb. A second *P. vannamei* genome assembly of 1.63 Gb with a higher scaffold N50 of 31.3 Mb was reported (Yuan et al. 2021b) but is not publicly available.

More recently, Peng et al. (2023) published an improved genome assembly using PacBio reads and Hi-C data, which spans 1.87 Gb with scaffold N50 of 39.7 Mb. The 87% of the assembly is assigned to 44 pseudo-chromosomes. Finally, Perez-Enriquez et al. (2024a) reported an even more complete reference-guided genome assembly organized into 44 pseudo-chromosomes and 15,682 scaffolds, with a genome size of 2.055 Gb, N50 of 40.14 Mb, and the longest scaffold of 65.79 Mb.

Relative to other penaeids, the *P. vannamei* genome assembly is comparable to those of *Penaeus monodon* (scaffold N50 of 44.9 Mb; longest scaffold 65.9 Mb; genome size 2.4 Gb; Uengwetwanit et al. 2021), *Fenneropenaeus chinensis* (scaffolds N50 of 36.87 Mb; longest scaffold 48.8 Mb; genome size 1.47 Gb; Wang et al. 2022), and *Penaeus indicus* (scaffolds N50 of 34.4 Mb; longest scaffold 51.6 Mb; genome size 2.4 Gb; Katneni et al. 2022). Future efforts should focus on obtaining even higher quality genome assemblies, mapping many scaffolds rich in repetitive sequences

Table 1. Genotyping methods available for different SNP panel density. Applications are based in the SNP panel density.

Genotyping method	Genotyping options for method	Advantages	Disadvantages	Applications
High density SNPs panel (thousands)				
RAD-like (Based in the use of restriction enzymes)	-2bRAD -dd-RAD -SLAF-seq	-Reduced genome representation hence reduced sequencing cost -Chromosome-level genome assembly is not necessary	-Medium repeatability -Library preparation can be laborious	-Genome-wide association studies (GWAS) -Genomic selection -QTL mapping
Custom Arrays	-Illumina services for custom arrays	-Fast genotyping workflow for many samples -High repeatability	-Require specialized high-cost equipment -Significant initial investment -Previous SNPs identification and selection are needed	
Commercially available genotyping platforms	-Illumina Infinium Shrimp LD-24 BeadChip -AQUArray HD vannamei	-Less genotyping time for large number of samples run simultaneously -High repeatability	-SNPs information is not public (e.g. SNP position in the genome) -In some countries is difficult to send samples abroad	
Low-medium density SNPs panel (tens to hundreds)				
Targeted amplicon genotyping (sequencing of multiplexed PCR amplicons)	-GT-seq -MTA-seq -HiMAP	-Low cost	-Previous SNPs identification and selection are needed -Library preparation can be laborious compared with other genotyping options	-Parentage analysis -Genetic characterization -Genetic traceability -Genotyping of few specific SNPs (such as sex identification or genes with known function)
Fluidigim system (based on integrated microfluidic circuit system)	Fluidigm	-Fast genotyping workflow for many samples	-Require the acquisition of specialized equipment -Previous SNPs identification and selection are needed	
Genotyping platform commercially available	-AQUArray LD vannamei	Less genotyping time for large number of samples run simultaneously -High repeatability	-SNPs information is not public (e.g. SNP position in the genome) -In some countries is difficult to send samples abroad	
Based on fluorophore-labeled PCR amplicons	-KASP (competitive allele-specific PCR) -Taqman -High-Resolution Melting (HRM)	-Low cost -More suitable for very few SNPs (less than tens)	-Previous SNPs identification and selection are needed	
MassARRAY system (based on mass spectofotometry)	- MassARRAY	-Fast genotyping workflow for many samples	-Require the acquisition of specialized equipment -Previous SNPs identification and selection are needed	

using new long-read sequencing strategies such as those employed in the t2t consortium (McCartney et al. 2022). Additionally, it is still necessary to map and annotate genes and functionally annotate the whiteleg shrimp genome for regulatory elements. Inter-institutional efforts towards this end (e.g. AQUA-FAANG, https://www.aqua-faang.eu/) are advisable.

Genetic linkage maps

An accurate and robust genetic linkage map is also a key tool for understanding genomic characteristics, such as recombination rates or assembling chromosome-level genomes. Linkage maps have been published in several penaeid species [e.g. black tiger shrimp *P. monodon* (Baranski et al. 2014, Guo et al. 2019), Chinese shrimp *P.* (*Fenneropeaneus*) *chinensis* (Liu et al. 2010), kuruma shrimp *P.* (*Marsupenaeus*) *japonicus* (Lu et al. 2016, Zhang et al. 2021), *P. vannamei* (Table 2)] to set up the bases to identify markers for QTL and association studies for commercially important traits. Linked markers to sex, temperature tolerance, and body weight have been identified in *P.* (*Marsupenaeus*) *japonicus* (Lu et al. 2016, Zhang et al. 2021) and nitrite tolerance in *P. vannamei* (Peng et al. 2020).

Several linkage maps in the Pacific whiteleg shrimp have been reported using genetic markers such as AFLPs, microsatellites, and SNPs (Table 2). The most recent high-density SNP linkage maps with 4,817 SNPs spanning 4,552.5 cM (Jones et al. 2017), 17,242 SNPs spanning 6,828 cM (Peng et al. 2020), and 6,146 markers spanning 4,271 cM (Yu et al. 2015), provide with increased coverage of the genome (>97%), reducing the distance between markers in the 44 expected linkage groups [principally in Peng et al. (2020)] (Table 2). All these improvements have been possible using medium- and high-density SNP panels obtained using genotyping-by-sequencing technologies.

Nevertheless, there are concerns that the linkage groups are not located within specific genomic regions; in the high-density linkage map of Peng et al. (2020), only 59.34% of the reads match the reference genome of *P. vannamei*. Moreover, the occurrence of significant local alignments between a scaffold of the reference genome and different linkage groups is of concern; for example, the Lvan-scaffold-1907 of the reference genome of Zhang et al. (2019) matches with several linkage groups from the Yu et al. (2015) map (Perez-Enriquez et al. 2020), or there are Hi-C scaffolds found in different linkage groups (Yuan et al. 2021b). Efforts on marker mapping and gene annotation over the new genome assemblies described in section 2.2 are required to clarify this issue.

Applications of genetic and genomic resources

Genetic characterization of wild populations

Wild whiteleg shrimp populations are distributed along the eastern coast of the Pacific Ocean, from Mexico to Peru (FAO 2006). Genetic studies have reported a population genetic structure through the species' distribution using mitochondrial DNA (Valles-Jimenez et al. 2006), microsatellite markers (Valles-Jimenez et al. 2005), and SNPs (Perez-Enriquez et al. 2024b) that, in the long-range, is explained by oceanographical barriers, but between northwestern and southwestern Pacific might be due to isolation-by-distance (Perez-Enriquez et al. 2024b). In addition, at a regional scale in the Gulf of California, no genetic population differentiation has been observed (Perez-Enriquez et al. 2018b). As expected, the genetic diversity analysis has consistently shown a larger diversity of the wild population over cultivated stocks (Perez-Enriquez et al. 2018a, 2024b, Knibb et al. 2020).

Further population genomics studies on the species are needed to identify adaptive genetic variants that respond to environmental changes (Matur et al. 2023). Adaptive variations have been shown in other marine invertebrates such as the American lobster *Homarus americanus* (Benestan et al. 2015), the pink abalone *Haliotis corrugata* (Mares-Mayagoitia et al. 2021), and the tiger shrimp *P. monodon* (Vu et al. 2021).

Genetic characterization of breeding stocks

The domestication of Pacific whiteleg shrimp started in the 70's in different parts of the American continent (FAO 2009, INAPESCA 2021) and consolidated in the 90's in the USA with the production of postlarvae from SPF broodstock (Wyban 2019). Since then, the established stocks have required dedicated breeding management. The genetic characterization of each breeding line and monitoring their genetic diversity and relatedness between lines are critical components of breeding programs.

Awareness of the existing genetic diversity within a closed breeding population informs decisions on stock management strategies, such as whether to increase genetic variation or cross different lines. A lack of genetic diversity can diminish the population's response to environmental stress and pathogens (Dixon et al. 2008). Similarly, inbreeding must be closely controlled to avoid inbreeding depression (Moss et al. 2007); inbreeding increases homozygosity and the probability of expression of deleterious alleles (Tave 1993).

Great interest has been shown in assessing the genetic composition and diversity of cultivated *P.*

Table 2. Linkage maps reported in Pacific whiteleg shrimp *Penaeus vannamei*. [1]Only one linkage map for both sexes was reported. [2]Two linkage maps for both sexes were reported. [3]Sex average.

Authors	Genetic Marker	Number of markers	Distance between markers (cm)	Map length (cm)	Number of linkage group	% Genome coverage
		Female/male	Female/male	Female/male	Female/male	Female/male
Pérez et al. (2004)	AFLPs	212/182	17.1/15.6	2771/2116	51/47	62/59
Alcivar-Warren et al. (2007)[1]	Microsatellites	48	22.1	663	14	-
Zhang et al. (2007)	AFLPs, microsatellites	319/267	15.1/14.5	4,134.4/3,220.9	45/45	75.9/69.6
Du et al. (2010)	SNPs	418/413	-	2,071.1/2,130.2	45/48	48.27/37.25
Andriantahina et al. (2013a)[1]	AFLPs, microsatellites	451	7.6	3,313.90	49	72.63
Gonçalves et al. (2014)[2]	AFLPs	98 and 59	-	-	14 and 4	-
Yu et al. (2015)	SNPs	4,396/4,201	1.29/1.46	5,657.42/6,143.95	44/44	97.49/97.71
Jones et al. (2017)	SNPs	4,817[3]	0.973	4,530.6/4,522.3	44/44	98.12[3]
Peng et al. (2020)	SNPs	11,543/10,276	0.60/0.60	6906.78/6164.79	44/44	-
Chen et al. (2022)	SNPs	3,335	1.186	3954.46	48	-

vannamei in the world [e.g. Brazil (De Freitas & Galetti 2005, Freitas et al. 2007, Luvesuto et al. 2007, Lisboa-Silva et al. 2022), Cuba (Artiles et al. 2011, Pérez-Beloborodova et al. 2012), China (Zhang et al. 2014, 2023, Ren et al. 2018), Ecuador (Garcia & Alcivar-Warren 2007, Garcia et al. 2021), and Mexico (Cruz et al. 2004, Perez-Enriquez et al. 2009, 2018c, 2024b, Vela-Avitúa et al. 2013)]. Most of these studies have used microsatellite markers, with only the most recent studies using SNP markers (Perez-Enriquez et al. 2018c, 2024b, Garcia et al. 2021, Lisboa-Silva et al. 2022). The results have been markedly different between studies; some hatcheries reported no significant loss of variability between generations (Cruz et al. 2004, Luvesuto et al. 2007, Perez-Enriquez et al. 2009); others reported considerable levels of inbreeding (Zhang et al. 2014) or on the contrary, low levels of the inbreeding coefficient (Ren et al. 2018). The difference in genetic diversity between hatcheries depended mainly on the diversity of the founder stock and the breeding program's management (Benzie 2009).

Considering that the decrease of genetic diversity in a Pacific whiteleg shrimp hatchery can occur in only a few generations (Dixon et al. 2008), restoring genetic diversity can be a necessary management practice. Restoring genetic diversity can be done via i) the introduction of wild animals as broodstock to the hatchery with the concomitant loss of genetic gains when it is done after the program starts, ii) crossbreeding with broodstock from a different hatchery or other genetic lines. In addition, intra-family selection schemes, in which individual pedigree is traced through molecular markers, are recommended to avoid loss of genetic variability.

Traditionally, the comparison between hatchery-reared stocks and wild populations has shown, as expected, genetic differentiation between them and higher genetic diversity in wild populations (Perez-Enriquez et al. 2009, 2018a, Mendoza-Cano et al. 2013, Vela-Avitúa et al. 2013, Knibb et al. 2020). In contrast, recent evaluations have shown high similarity among some hatchery-reared stocks and wild populations in Mexico, indicating that there might be some non-programmed introductions of wild-origin individuals into the hatcheries (Perez-Enriquez et al. 2024b). While the introduction of wild animals can rapidly increase genetic variability, the sanitary status (quarantine and specific pathogen evaluation) has to be carefully considered because the introduction and lack of control of diseases have been attributed to the use of wild broodstocks (Briggs et al. 2004). Additionally, as the introduction of wild individuals may have a detrimental effect on traits that have already been selected in cultivated stocks, potentially setting back the breeding program several generations, the use of this strategy to increase diversity should be carefully planned by selecting the broodstock that better behaves under hatchery conditions (e.g. acceptance of artificial feeds, tolerance to handling, best sperm and egg production, among others).

The alternative of crossing different aquaculture stocks also requires a previous genetic evaluation to assess if the cultured animals are sufficiently genetically divergent. Studies in *P. vannamei* have shown genetic differences between hatcheries with different possible origins (Perez-Enriquez et al. 2018c, 2024b, Ren et al. 2018). Knibb et al. (2020) considered sufficient genetic variation in aquaculture stocks available in different countries to restore genetic variation to a wild baseline. They suggested using different domesticated stocks rather than stocking organisms from the wild.

As a final note, the characterization of aquaculture and wild populations will enable stock identification for traceability purposes, either to identify escapes from farms to the wild (Perez-Enriquez et al. 2018a) or to trace shrimp products throughout the commercial chain, fundamental to enforcing biosecurity and protecting wild shrimp populations.

Genetic architecture of aquaculture relevant traits

The study of the genetic architecture refers to the study of the genomic regions and genes controlling variation in a target trait (Martínez et al. 2014). Whether a certain trait is explained by the large effects of one or few genes or has a polygenic nature, i.e. is controlled by many loci, each with a small effect, will determine the strategy for implementing genomic information into aquaculture breeding (Palaiokostas & Houston 2017).

Quantitative trait loci (QTL)

The statistical method that links phenotypic data and genotypic data is known as association analysis, and significant associations pinpoint the position of QTL (Miles & Wayne 2008). In the shrimp *P. vannamei*, QTL analyses have successfully identified candidate genetic markers/genes for relevant phenotypic traits such as low-temperature tolerance (Lu et al. 2023), growth-related traits (e.g. body weight and length, partial carapace length (PCL), first and third abdominal segment depth) (Andriantahina et al. 2013a, Huang et al. 2020, Janpoom et al. 2020, Chen et al. 2022, Lu et al. 2023), nitrite tolerance (Peng et al. 2020), ammonia

tolerance (Janpoom et al. 2020, Zeng et al. 2020), high pH tolerance (Huang et al. 2020), low-salinity tolerance (Chen et al. 2022), and sex-related traits (Du et al. 2010, Yu et al. 2017, Jones et al. 2020, Perez-Enriquez et al. 2020). Although no specific QTL has been reported for disease resistance in *P. vannamei*, Yin et al. (2023) reported that the length of a (CT)n microsatellite located in the *P. vannamei* interferon regulatory factor gene (*LvIRF*) influences the resistance against bacterial and viral pathogens. Even though disease resistance in aquaculture species is usually described as of polygenic nature, noteworthy exceptions have been reported such as for infectious pancreatic necrosis (IPN) in Atlantic salmon (Houston et al. 2008, 2010, Moen et al. 2009) or tilapia lake virus (TiLV) in Nile tilapia (Barría et al. 2021) where major QTL was detected; in the case of IPN, successful selection of resistant individuals has heavily diminished IPN-associated mortality in breeding programs (Houston et al. 2010, Moen et al. 2015). Whether QTLs can be present in *P. vannamei* for any relevant diseases is a topic that deserves further investigation.

Genome-wide association studies (GWAS)

GWAS are useful for understanding the genetic basis of traits of interest (i.e. the genetic architecture of the trait). A GWAS test for the statistical association of genetic markers distributed along the genome with a trait showing variation in a population will highlight the most important genomic regions controlling that trait. The availability of high-density SNP panels has allowed the popularization of these studies in aquaculture. GWAS reveals whether the genomic architecture of a trait is polygenic, controlled by many genetic variants with small effects, or mono/oligogenic, with a few QTL with major effects (Hayes & Goddard 2010). Knowing the genetic architecture of a trait can lead to selection strategies within a breeding program. Monogenic or oligogenic traits can be selected using marker-assisted selection, while genomic selection is better for traits with polygenic architecture (Hayes & Goddard 2010, Palaiokostas & Houston 2017, Zenger et al. 2019).

In the Pacific whiteleg shrimp, recent GWAS have focused on growth traits, resistance to pathogens and environmental factors, and sex determination (Table 3). Growth traits studies have shown a polygenic architecture with medium-high heritability and identified various potentially associated markers in several genomic regions, such as the *PCK-delta* and *Rap-2a* genes (Yu et al. 2019), a class C scavenger receptor gene (*LvSRC*) (Wang et al. 2019b), the *deoxycytidylate deaminase* (*dCMPD*) and the non-receptor protein tyrosine kinase (NPTK) genes (Lyu et al. 2021).

A GWAS for resistance to white spot syndrome disease (WSSV) (survival and time of death) showed a polygenic architecture and identified several SNPs, some of them potentially associated with immune response genes (e.g. *arylsulfatase B-like*, *D-beta-hydroxybutyrate dehydrogenase mitochondrial-like*, the putative mediator of RNA polymerase II transcription subunit 26). These SNPs explained 0.17 and 0.36% of the genetic variance for survival and time of death traits, respectively (Medrano-Mendoza et al. 2023).

A GWAS for ammonia nitrogen tolerance, another economically important trait in *P. vannamei* aquaculture, revealed seven candidate genes (*PDI*, *OZF*, *UPF2*, *VPS16*, *TMEM19*, *MYCBP2*, and *HOX7*), which may be useful for future breeding programs of the species (Fu & Liu 2022).

Potentially associated markers have been reported for sex. Yu et al. (2017) reported a large region in LG18 with significant association; however, none of the markers in this region showed complete association with sex in other populations. Jones et al. (2020) reported a monogenetic architecture with a high heritability ($h^2 = 0.84$) and 11 SNPs associated with sex in one linkage group (LG42,44). The most significantly associated SNP presented genotypes very consistent with the sex-determination system of *P. vannamei*, with heterozygote females and homozygote males, which indicates proximity to a sex-determination locus; nevertheless, none of the sex-related genes that are known to be present in the *P. vannamei* [*fem-1* and *Sxl*; (López-Cuadros et al. 2018, Galindo-Torres et al. 2019)] are located in the QTL region (Jones et al. 2020).

Fecundity is particularly important to hatcheries for the commercial production of postlarvae (Arcos et al. 2004, Sui et al. 2022). Sui et al. (2022) identified several significant SNPs in 20 different chromosomes and 121 potentially associated genes with fecundity regulation.

Future work on GWAS should certainly be directed towards disease resistance due to the great impact on production [e.g. the WSSV and the AHND cost > US$11 million and > US$26 million, respectively, to the Asian shrimp industry in 2015 (Shinn et al. 2018)]. Commonly described as polygenic traits (Wang et al. 2017, Gutierrez et al. 2018, Holborn et al. 2018, Robledo et al. 2018a, 2019, Medrano-Mendoza et al. 2023), GWAS can be a useful approach to understand their genetic basis and implement better breeding pro-

Table 3. Genes associated to relevant traits from genome-wide association studies (GWAS) in *P. vannamei*. [1]Suggestively associated markers, non-significant after Bonferroni correction. [2]Significant at genomic level. [3]Significant at chromosome level.

Trait	Reference	SNPs associated	Genes of interest
Body weight	Yu et al. (2019)	47 SNPs[1]	-Hypothetical protein X975_01911 -Protein FAM186A isoform X1 -E3 ubiquitin-protein ligase HECW2 -Glutaminase kidney isoform, mitocondrial -Ras-related protein Rap-2a -Protein kinase C delta type
	Wang et al. (2019b)	226 SNPs[1]	-*LvSRC* (Class C scavenger receptor SRC)
	Lyu et al. (2021)	4 SNPs	-Deoxycytidylate deaminase (dCMPD) -Non-receptor protein tyrosine kinase (NPTK)
Body length	Yu et al. (2019)	52 SNPs[1]	-Beta-2 adrenergic receptor
Sex	Jones et al. (2020)	11 SNPs	None identified
	Garcia et al. (2024)	21 SNPs	-Oplophorus-luciferin 2-monooxygenase -Serine/arginine repetitive matrix protein -Spermine oxidase
Disease resistance (white spot syndrome virus)	Medrano-Mendoza et al. (2023)	2 SNPs[2]	-Arylsulfatase B-like -GDNF-inducible zinc finger protein 1-like -D-beta-hydroxybutyrate dehydrogenase mitochondrial-like -Putative mediator of RNA polymerase
		9 SNPs[3]	-Histone acetyl transferase KAT6A-like -Zinc finger protein 346-like -Proline-rich protein PRCC-like -Leucine-rich repeat transmembrane neuronal protein 4-like -Beta-1,3-galactosyltransferase 5-like -Selenocysteine lyase-like -Protein SMG9-like -26S proteasome non-ATPase regulatory subunit 2-like -Zinc finger protein 395-like -THO complex subunit 2-like -Glycine, alanine and asparagine-rich protein-like -Glycine-rich protein 5-like -Keratin, type I cytoskeletal 10-like -Risilkin-39-like -Keratin, type II cytoskeletal 3-like -Acanthoscurrin-1-like -RNA polymerase II elongation factor ELL-like -Filaggrin-2-like -Exocyst complex component 1-like - Putative uncharacterized protein YHR217C
Ammonia nitrogen tolerance	Fu & Liu (2022)	6 SNPs	-E3 ubiquitin-protein ligase MYCBP2-like -Protein disulfide-isomerase-like -Zinc finger protein OZF-like -Regulator of nonsense transcripts 2-like -Vacuolar protein sorting-associated protein 16 homolog -Transmembrane protein 19-like -Homeobox protein Hox-B7-like

grams for its improvement. Nevertheless, disease resistance has been commonly measured as a binary trait (survival) and time of death, which may not be the best measurement parameters. For this reason, other quantitative variables, such as viral load (Phuthaworn et al. 2016) or immune-response-associated parameters, should be explored.

In addition, other relevant traits for aquaculture production, such as those associated with environmental tolerance (e.g. temperature and hypoxia), need further investigation.

Genomic selection (GS)

Traditional breeding programs use individual selection, family selection, or combined selection schemes where the selection of candidates is based on phenotypic data of pedigreed records, which are used to obtain estimated breeding values (EBV); the EBVs are used to rank animals and select the best for breeding (taking into account relatedness to minimize inbreeding). In traits that cannot be measured directly on candidates, for example, disease resistance or carcass traits, the EBVs of the selected candidates are based on phenotypic data of their relatives (e.g. full siblings or progenitors), and all the members of a family share the same EBV.

In recent years, genomic data, generally high-density SNP panels, has been used for calculating EBVs in selection programs, a strategy known as GS (Meuwissen et al. 2001). A training population, formed by relatives of the selected candidates with genotypic and phenotypic data, is used to calculate the genomic estimated breeding values (GEBV) of the candidates only using genotypic data.

GS has several advantages for breeding programs: it increases the rate of genetic gain due to a more accurate prediction of breeding values, allows a higher intensity of selection by harnessing the genetic variation within families, reduces the rate of inbreeding per generation (Daetwyler et al. 2007), and enables early selection using phenotypic data of the relatives of the candidates. Song et al. (2023) thoroughly reviewed the research progress on GS in aquaculture breeding, suggesting improved strategies based on better phenotyping techniques, reducing costs, considering genotype by environment interactions, and integrating multi-omics data.

In *P. vannamei*, the reliability and feasibility of GS have been studied. For growth traits (body weight and body length), different factors that could affect the accuracy of GS have been tested, such as selection models, marker density, or population structure (Wang et al. 2017a,b), finding that different genomic selection models show similar results; on the other hand, the genetic relatedness between the reference and the validation population has a large impact on GS accuracy (Wang et al. 2017b). Regarding marker density, Wang et al. (2017b) concluded that for growth traits with moderate or high heritability (0.321-0.452), a set of 3,200 SNPs distributed along the genome can be sufficient to estimate breeding values accurately using GS.

Another study focusing on one growth trait and two feed efficiency traits (Dai et al. 2020) demonstrated that genomic-based methods obtain more accurate breeding values than pedigree-based methods. Furthermore, the prediction accuracy was even higher when the model included the common environmental effect, from 11.6 to 69.4%, depending on the trait.

As previously mentioned, disease resistance is an important trait for *P. vannamei*. The implementation of GS is even more relevant for traits that cannot be measured in the selection candidates (e.g. carcass quality) or are not recommended for breeding, such as disease-challenged animals due to the risk of introducing pathogens into SPF stocks (Villanueva et al. 2011, Castillo-Juárez et al. 2015, Zenger et al. 2019). The potential of GS for disease resistance in *P. vannamei* was first determined with simulated data, where the survival estimates in a disease challenge can be presumably 2.6× better with GS than with only phenotypic data, which was attributed to an increase in selection accuracy (Castillo-Juárez et al. 2015). When GS was applied with experimental data, the prediction accuracy was increased for resistance against *Vibrio parahaemolyticus* (6.8 and 3.5% for survival time and survival rates, respectively; Wang et al. 2019a) and WSSV (Campos-Montes et al. 2023). In addition, improvement of survival against WSSV by GS in one generation has been demonstrated to range from 38 to 51% (Lillehammer et al. 2020).

For environmental traits, tolerance to high salinity (survival time, lethal salinity, and survival status) showed an increase of 1.4-12.1% in prediction accuracy (Luo et al. 2022).

Even though the application of GS in *P. vannamei* has been evaluated on experimental conditions and simulated data for some economic traits and showed great potential for enhanced production, its application in the shrimp industry seems to be limited; it is unclear how many companies currently apply GS in shrimp production conditions, but some have already reported its use, specifically Benchmark Genetics (https://bmkgenetics.com/services/shrimp/; Lillehammer et al.

Table 4. Summary of genomics resources applications, status, and future perspectives in *P. vannamei.*

Genomic resource	Applications	Status	Future perspectives
SNPs markers and genotyping	Genetic markers are basic resources for most of the genetic studies such as genetic diversity, genetic characterization, parentage assignment, genome-wide association studies (GWAS), genomic selection, and more.	SNPs markers are available with different genotyping techniques that have been used for genetic characterization of wild populations (3.1) and breeding stocks (3.2), identification of quantitative trait loci (QTL) (3.3.1), GWAS (3.3.2), and potential application of genomic selection (3.4).	-Identification of adaptative variants -SNPs markers for genetic traceability. -Further studies focus on understanding the genetic basis of important traits, such as disease resistance and environmental tolerance are still needed. -Efforts on cost-effective genotyping tools for genomic selection in breeding programs.
Reference genome	Tool for genetic studies to understand the genetic architecture of traits, the function of sequences in the genome, evolutionary studies, among others.	Important improvement has been achieved in the construction of a new genome assembly, but a complete genome reference is still needed (the most complete genome assembly covers 79-84% of the genome).	-Focus on a complete genome assembly using new long-read sequencing projects. -Inter-institutional collaboration for a genome assembly project. -Map and annotate genes in the genome for regulatory elements.
Genetic linkage map	To understand recombination rates, the genetic architecture of traits for example to identify potential quantitative trait loci (QTL), aid in assembling chromosome-level genomes.	High-density linkage maps distributed over the 44 expected linkage groups (LG) that aim in the identification of potential QTL are available. Nevertheless, some inconsistencies are present between genome assembly chromosomes.	-Improve marker mapping and gene annotation over the more recent genome assemblies.

2020), Kona Bay (https://www.konabayshrimp.com/en/shrimp-breeding; Van der Pijl 2020) and Texcumar (http://www.texcumar.com/). Further official reports on this matter are advisable.

A critical limitation to the widespread application of GS is the cost of genotyping many animals. It can represent a substantial cost for shrimp aquaculture because, unlike other species, the individual value of the animals is low. For example, the approximate price for a specific pathogen-free shrimp breeder in 2019 was ~US$55 (Van der Pijl 2020).

Another issue is the limited incorporation of specialized personnel within the shrimp industry, principally in medium-sized producers. Nevertheless, to cope with demand in the current sociopolitical and environmental context, the shrimp industry must overcome these limitations and embrace genomic selection to maximize production efficiency and minimize environmental impact.

CONCLUSIONS

Despite being one of the most important aquaculture species worldwide, the development and application of advanced genomic resources in *P. vannamei* is a field that requires attention (Table 4). Particularly, a new high-quality genome assembly would be massively beneficial for both research and production efforts, contributing to the continued understanding of the genetic architecture of relevant traits in aquaculture production (e.g. growth, disease resistance, feed efficiency) by genome-wide association studies. The genetics of wild and domesticated populations have been well studied, but reviewing the genetic structure

of wild populations with high-density SNPs, including adaptive loci, will clarify their genetic structure and enable stock identification for traceability purposes. Likewise, even though the genetic architecture of several traits of interest has been studied, genome association studies for disease resistance and environmental tolerance are needed to understand the biological processes involved and to improve these traits in breeding programs. Despite that the potential for selection using genomic tools has been demonstrated, genomic selection is not yet widely applied, and novel, cost-effective genotyping tools, especially for small-medium producers, are still needed to ensure its rapid implementation, resulting in benefits for food security and the environment.

Finally, we expect this review to be useful for academics and shrimp producers who want to improve their production using available genetic and genomic resources.

Credit author contribution

A. Max-Aguilar: conceptualization, analysis, writing-original draft; R. Perez-Enriquez: conceptualization, supervision, review, and editing; A.M. Ibarra & D. Robledo: validation, supervision, review. All authors have read and accepted the published version of the manuscript.

Conflict of interest statement

The authors declare no conflict of interest.

ACKNOWLEDGMENTS

A. Max-Aguilar is the recipient of a Ph.D. scholarship from CONAHCYT (Nº413201). R. Perez-Enriquez is the recipient of CONAHCYT (grant Nº319686). D. Robledo acknowledges funding by the Axencia Galega the Innovación (GAIN, Xunta de Galicia) as part of the Oportunius Programme and also by BBSRC Institute Strategic Grants to the Roslin Institute (BBS/E/ 20002172, BBS/E/D/30002275, BBS/E/D/10002070, and BBS/E/RL/230002A).

REFERENCES

Abdelrahman, H., ElHady, M., Alcivar-Warren, A., Allen, S., et al. 2017. Aquaculture genomics, genetics and breeding in the United States: Current status, challenges, and priorities for future research. BMC Genomics, 18: 1-23. doi: 10.1186/s12864-017-3557-1

Alcivar-Warren, A., Meehan-Meola, D., Se, W.P., Xu, Z., et al. 2007. ShrimpMap: A low-density, microsatellite-based linkage map of the Pacific whiteleg shrimp, *Litopenaeus vannamei*: Identification of sex-linked markers in linkage group 4. Journal of Shellfish Research, 26: 1259-1277. doi: 10.2983/0730-8000 (2007)26[1259:SALMLM]2.0.CO;2

Andriantahina, F., Liu, X. & Huang, H. 2013a. Genetic map construction and quantitative trait locus (QTL) detection of growth-related traits in *Litopenaeus vannamei* for selective breeding applications. Plos One, 8: e75206. doi: 10.1371/journal.pone.0075206

Andriantahina, F., Liu, X., Huang, H. & Xiang, J. 2013b. Selection for growth performance of tank-reared Pacific white shrimp, *Litopenaeus vannamei*. Chinese Journal of Oceanology and Limnology, 31: 534-541. doi: 10.1007/s00343-013-2220-1

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: 151-165. doi: 10.1016/j.aquaculture.2004.03.003

Argue, B.J., Arce, S.M., Lotz, J.M. & Moss, S.M. 2002. Selective breeding of Pacific white shrimp (*Litopenaeus vannamei*) for growth and resistance to Taura syndrome virus. Aquaculture, 204: 447-460. doi: 10.1016/S0044-8486(01)00830-4

Artiles, A., Rodríguez, I., Pérez, A., Pérez, L., et al. 2011. Low genetic variability in the fifth introduction of *Litopenaeus vannamei* in Cuba, as estimated with microsatellite markers. Biotecnología Aplicada, 28: 147-150.

Baird, N.A., Etter, P.D., Atwood, T.S., Currey, M.C., et al. 2008. Rapid SNP discovery and genetic mapping using sequenced RAD markers. Plos One, 3: e3376. doi: 10.1371/journal.pone.0003376

Baranski, M., Gopikrishna, G., Robinson, N.A., Katneni, V.K., et al. 2014. The development of a high density linkage map for black tiger shrimp (*Penaeus monodon*) based on cSNPs, Plos One, 9: e85413. doi: 10.1371/journal.pone.0085413

Barbanti, A., Torrado, H., Macpherson, E., Bargelloni, L., et al. 2020. Helping decision making for reliable and cost-effective 2b-RAD sequencing and genotyping analyses in non-model species. Molecular Ecology Resources, 20: 795-806. doi: 10.1111/1755-0998.13 144

Barría, A., Trịnh, T.Q., Mahmuddin, M., Peñaloza, C., et al. 2021. A major quantitative trait locus affecting resistance to tilapia lake virus in farmed Nile tilapia (*Oreochromis niloticus*). Heredity, 127: 334-343. doi: 10.1038/s41437-021-00447-4

Benestan, L., Gosselin, T., Perrier, C., Sainte-Marie, B., et al. 2015. RAD genotyping reveals fine-scale genetic structuring and provides powerful population assignment in a widely distributed marine species, the American lobster (*Homarus americanus*). Molecular Ecology, 24: 3299-3315. doi: 10.1111/mec.13245

Benzie, J.A.H. 2009. Use and exchange of genetic resources of penaeid shrimps for food and aquaculture. Reviews in Aquaculture, 1: 232-250. doi: 10.1111/j.1753-5131.2009.01018.x

Briggs, M., Funge-Smith, S., Subasinghe, R. & Phillips, M. 2004. Introductions and movement of *Penaeus vannamei* and *Penaeus stylirostris* in Asia and the Pacific. RAP publication 2004/10. FAO Regional Office for Asia and the Pacific, Bangkok.

Campbell, N.R., Harmon, S.A. & Narum, S.R. 2015. Genotyping-in-thousands by sequencing (GT-seq): A cost effective SNP genotyping method based on custom amplicon sequencing. Molecular Ecology Resources, 15: 855-867. doi: 10.1111/1755-0998.12357

Campos-Montes, G.R., Garcia, B.F., Medrano-Mendoza, T., Caballero-Zamora, A., et al. 2023. Genetic and genomic evaluation for resistance to white spot syndrome virus in post-larvae of Pacific white shrimp (*Litopenaeus vannamei*). Aquaculture, 575: 739-745. doi: 10.1016/j.aquaculture.2023.739745

Campos-Ramos, R. 1997. Chromosome studies on the marine shrimps *Penaeus vannamei* and *P. californiensis* (Decapoda). Journal of Crustacean Biology, 17: 666-673.

Castillo-Juárez, H., Campos-Montes, G.R., Caballero-Zamora, A. & Montaldo, H.H. 2015. Genetic improvement of Pacific white shrimp [*Penaeus* (*Litopenaeus*) *vannamei*]: perspectives for genomic selection. Frontiers in Genetics, 6: 93. doi: 10.3389/fgene.2015.00093

Chambers, E.A., Tarvin, R.D., Santos, J.C., Ron, S.R., et al. 2023. 2b or not 2b? 2bRAD is an effective alternative to ddRAD for phylogenomics. Ecology and Evolution, 13: e9842. doi: 10.1002/ece3.9842

Chauhan, T. & Rajiv, K. 2010. Molecular markers and their applications in fisheries and aquaculture. Advances in Bioscience and Biotechnology, 1: 281-291. doi: 10.4236/abb.2010.14037

Chen, B., Zhong, P., Wu, X., Peng, K., et al. 2022. Construction of a genetic linkage map, QTLs mapping for low salinity and growth-related traits and identification of the candidate genes in Pacific white shrimp (*Litopenaeus vannamei*). Aquaculture Reports, 22: 100978. doi: 10.1016/j.aqrep.2021.100978

Collins, F.S., Brooks, L.D. & Chakravarti, A. 1998. A DNA polymorphism discovery resource for research on human genetic variation. Genome Research, 8: 1229-1231. doi: 10.1101/gr.8.12.1229

Cruz, P., Mejia-Ruiz, C.H., Perez-Enriquez, R. & Ibarra, A.M. 2002. Isolation and characterization of microsatellites in Pacific white shrimp *Penaeus (Litopenaeus) vannamei*. Molecular Ecology Notes, 2: 239-241. doi: 10.1046/j.1471-8286.2002.00211.x

Cruz, P., Ibarra, A.M., Mejia-Ruiz, H., Gaffney, P.M., et al. 2004. Genetic variability assessed by microsatellites in a breeding program of Pacific white shrimp (*Litopenaeus vannamei*). Marine Biotechnology, 6: 157-164. doi: 10.1007/s10126-003-0017-5

Daetwyler, H.D., Villanueva, B., Bijma, P. & Woolliams, J.A. 2007. Inbreeding in genome-wide selection. Journal of Animal Breeding and Genetics, 124: 369-376. doi: 10.1111/j.1439-0388. 2007.00693.x

Dai, P., Kong, J., Liu, J., Lu, X., et al. 2020. Evaluation of the utility of genomic information to improve genetic evaluation of feed efficiency traits of the Pacific white shrimp *Litopenaeus vannamei*. Aquaculture, 527: 735421. doi: 10.1016/j.aquaculture.2020.735421

De Freitas, P.D. & Galetti, P.M. 2005. Assessment of the genetic diversity in five generations of a commercial broodstock line of *Litopenaeus vannamei* shrimp. African Journal of Biotechnology, 4: 1362-1367. doi: 10.4314/ajb.v4i12.71450

Dixon, T.J., Coman, G.J., Arnold, S.J., Sellars, M.J., et al. 2008. Shifts in genetic diversity during domestication of black tiger shrimp, *Penaeus monodon*, monitored using two multiplexed microsatellite systems. Aquaculture, 283: 1-6. doi: 10.1016/j.aquaculture.2008.07.009

Du, Z.-Q., Ciobanu, D.C., Onteru, S.K., Gorbach, D., et al. 2010. A gene-based SNP linkage map for Pacific white shrimp, *Litopenaeus vannamei*. Animal Genetics, 41: 286-294. doi: 10.1111/j.1365-2052.2009.02002.x

Dupuis, J.R., Bremer, F.T., Kauwe, A., San Jose, M., et al. 2018. HiMAP: Robust phylogenomics from highly multiplexed amplicon sequencing. Molecular Ecology Resources, 18: 1000-1019. doi: 10.1111/1755-0998.12783

Ellegren, H. 2000. Microsatellite mutations in the germline: implications for evolutionary inference. Trends in Genetics, 16: 551-558. doi: 10.1016/S0168-9525(00)02139-9

Food and Agriculture Organization (FAO). 2006. Programa de información de especies acuáticas.

Penaeus vannamei. In: Briggs, M. (Ed.). Programa de información de especies acuáticas. FAO, Rome.

Food and Agriculture Organization (FAO). 2009. *Penaeus vannamei*. FAO, Rome. [https://www.fao. org/fishery/docs/DOCUMENT/aquaculture/CulturedSpecies/file/en/en_whitelegshrimp.htm]. Reviewed: March 12, 2024.

Food and Agriculture Organization (FAO). 2020. Fishery and aquaculture statistics. Global aquaculture production 1950-2018 (FishstatJ). FAO, Rome.

Food and Agriculture Organization (FAO). 2022a. Global plan of action for the conservation, sustainable use and development of aquatic genetic resources for food and agriculture. FAO, Rome.

Food and Agriculture Organization (FAO). 2022b. The state of world fisheries and aquaculture 2022. Towards blue transformation. FAO, Rome.

Food and Agriculture Organization (FAO). 2024. Fishery and aquaculture statistics - Yearbook 2021. FAO, Rome.

Freitas, P.D., Calgaro, M.R. & Galetti, P.M. 2007. Genetic diversity within and between broodstocks of the white shrimp *Litopenaeus vannamei* (Boone, 1931) (Decapoda, Penaeidae) and its implication for the gene pool conservation. Brazilian Journal of Biology, 67: 939-943. doi: 10.1590/S1519-69842007000500019

Fu, S. & Liu, J. 2022. Genome-wide association study identified genes associated with ammonia nitrogen tolerance in *Litopenaeus vannamei*. Frontiers in Genetics, 13: 961009. doi: 10.3389/fgene.2022.961009

Galindo-Torres, P., Ventura-López, C., Llera-Herrera, R. & Ibarra, A.M. 2019. A natural antisense transcript of the *fem-1* gene was found expressed in female gonads during the characterization, expression profile, and cellular localization of the *fem-1* gene in Pacific white shrimp *Penaeus vannamei*. Gene, 706: 19-31. doi: 10.1016/j.gene.2019.04.066

Garcia, D.K. & Alcivar-Warren, A. 2007. Characterization of 35 new microsatellite genetic markers for the Pacific whiteleg shrimp, *Litopenaeus vannamei*: Their usefulness for studying genetic diversity of wild and cultured stocks, tracing pedigree in breeding programs, and linkage mapping. Journal of Shellfish Research, 26: 1203-1216. doi: 10.2983/0730-8000(2007)26[1203:CONMGM]2.0.CO;2

Garcia, B.F., Bonaguro, Á., Araya, C., Carvalheiro, R., et al. 2021. Application of a novel 50K SNP genotyping array to assess the genetic diversity and linkage disequilibrium in a farmed Pacific white shrimp (*Litopenaeus vannamei*) population. Aquaculture Reports, 20: 100691. doi: 10.1016/j.aqrep.2021.100691

Gitterle, T., Rye, M., Salte, R., Cock, J., et al. 2005. Genetic (co)variation in harvest body weight and survival in *Penaeus* (*Litopenaeus*) *vannamei* under standard commercial conditions. Aquaculture, 243: 83-92. doi: 10.1016/j.aquaculture.2004.10.015

Gjedrem, T. & Baransky, M. 2009. Selective breeding in aquaculture: an introduction. Springer, Dordrecht.

Gjedrem, T., Robinson, N. & Rye, M. 2012. The importance of selective breeding in aquaculture to meet future demands for animal protein: a review. Aquaculture, 350-353: 117-129. doi: 10.1016/j.Aquaculture.2012.04.008

Gonçalves, M.M., Regitano, L.C. de A., Cruz, C.D., Salgado, C.C., et al. 2014. Inheritance of AFLP markers and genetic linkage analysis in two full-sib families of the marine shrimp *Litopenaeus vannamei* (Crustacea, Decapoda). Advances in Bioscience and Biotechnology, 5: 273-281. doi: 10.4236/abb.2014.53034

Guo, L., Xu, Y.-H., Zhang, N., Zhou, F.-L., et al. 2019. A high-density genetic linkage map and QTL mapping for sex in black tiger shrimp (*Penaeus monodon*). Frontiers in Genetics, 10: 326. doi: 10.3389/fgene.2019.00326

Guppy, J.L., Jones, D.B., Jerry, D.R., Wade, N.M., et al. 2018. The state of "omics" research for farmed penaeids: Advances in research and impediments to industry utilization. Frontiers in Genetics, 9: 282. doi. 10.3389/fgene.2018.00282

Gutierrez, A.P., Bean, T.P., Hooper, C., Stenton, C.A., et al. 2018. A genome-wide association study for host resistance to ostreid herpesvirus in Pacific oysters (*Crassostrea gigas*). G3: Genes Genomes Genetics, 8: 1273-1280. doi: 10.1534/g3.118.200113

Hayes, B. & Goddard, M. 2010. Genome-wide association and genomic selection in animal breeding. Genome, 53: 876-883. doi: 10.1139/G10-076

Hayes, B., Sonesson, A.K. & Gjerde, B. 2005. Evaluation of three strategies using DNA markers for traceability in aquaculture species. Aquaculture, 250: 70-81. doi: 10.1016/j.aquaculture.2005.03.008

Holborn, M.K., Ang, K.P., Elliott, J.A.K., Powell, F., et al. 2018. Genome wide association analysis for bacterial kidney disease resistance in a commercial North American Atlantic salmon (*Salmo salar*) population using a 50 K SNP panel. Aquaculture, 495: 465-471. doi: 10.1016/j.aquaculture.2018.06.014

Houston, R.D., Haley, C.S., Hamilton, A., Guy, D.R., et al. 2008. Major quantitative trait loci affect resistance to infectious pancreatic necrosis in Atlantic salmon (*Salmo salar*). Genetics, 178: 1109-1115. doi: 10.1534/genetics.107.082974

Houston, R.D., Haley, C.S., Hamilton, A., Guy, D.R., et al. 2010. The susceptibility of Atlantic salmon fry to freshwater infectious pancreatic necrosis is largely explained by a major QTL. Heredity, 105: 318-327. doi: 10.1038/hdy.2009.171

Houston, R.D., Taggart, J.B., Cézard, T., Bekaert, M., et al. 2014. Development and validation of a high-density SNP genotyping array for Atlantic salmon (*Salmo salar*). BMC Genomics, 15: 90. doi: 10.1186/1471-2164-15-90

Huang, W., Cheng, C., Liu, J., Zhang, X., et al. 2020. Fine mapping of the high-pH tolerance and growth trait-related quantitative trait loci (QTLs) and identification of the candidate genes in Pacific white shrimp (*Litopenaeus vannamei*). Marine Biotechnology, 22: 1-18. doi: 10.1007/s10126-019-09932-8

Huang, Y., Zhang, L., Ge, H., Wang, G., et al. 2021. SNP development in *Penaeus vannamei* via next-generation sequencing and DNA pool sequencing. Fishes, 6: 36. doi: 10.3390/fishes6030036

Instituto Nacional de la Pesca (INAPESCA). 2021. Carta nacional acuícola. Diario Oficial de la Federación, Ciudad de Mexico. [https://www.gob.mx/imipas/documentos/carta-nacional-acuicola-2021]. Reviewed: April 15, 2024.

Janpoom, S., Kaewduang, M., Prasertlux, S., Rongmung, P., et al. 2020. A SNP of the hemocyanin gene (*LvHc*) is a marker for high growth and ammonia tolerance in Pacific white shrimp *Litopenaeus vannamei*. Fish and Shellfish Immunology, 106: 491-501. doi. 10.1016/j.fsi.2020.07.058

Jones, D.B., Jerry, D.R., Khatkar, M.S., Raadsma, H.W., et al. 2017. A comparative integrated gene-based linkage and locus ordering by linkage disequilibrium map for the Pacific white shrimp, *Litopenaeus vannamei*. Scientific Reports, 7: 10360. doi: 10.1038/s41598-017-10515-7

Jones, D.B., Nguyen, H.T., Khatkar, M.S., Simma, D.B., et al. 2020. The identification of a major sex QTL in the white-leg shrimp, *Litopenaeus vannamei*. Aquaculture, 529: 735673. doi: 10.1016/j.aquaculture.2020.735673

Kaiser, S.A., Taylor, S.A., Chen, N., Sillett, T.S., et al. 2017. A comparative assessment of SNP and microsatellite markers for assigning parentage in a socially monogamous bird. Molecular Ecology Resources, 17: 183-193. doi: 10.1111/1755-0998.12589

Katneni, V.K., Shekhar, M.S., Jangam, A.K., Krishnan, K., et al. 2022. A superior contiguous whole genome assembly for shrimp (*Penaeus indicus*). Frontiers in Marine Science, 8: 808354. doi: 10.3389/fmars.2021.808354

Kim, S. & Misra, A. 2007. SNP genotyping: technologies and biomedical applications. Annual Review of Biomedical Engineering, 9: 289-320. doi: 10.1146/annurev.bioeng.9.060906.152037

Knibb, W., Giang, C.T., Premachandra, H.K.A., Ninh, N.H., et al. 2020. Feasible options to restore genetic variation in hatchery stocks of the globally important farmed shrimp species, *Litopenaeus vannamei*. Aquaculture, 518: 734823. doi: 10.1016/j.aquaculture.2019.734823

Lillehammer, M., Bangera, R., Salazar, M., Vela, S., et al. 2020. Genomic selection for white spot syndrome virus resistance in whiteleg shrimp boosts survival under an experimental challenge test. Scientific Reports, 10: 20571. doi: 10.1038/s41598-020-77580-3

Lisboa-Silva, N.M., Ianella, P., Beleza-Yamagishi, M.E., Rocha, J.L., et al. 2022. Development and validation of a low-density SNP panel for paternity and kinship analysis and evaluation of genetic variability and structure of commercial Pacific white shrimp (*Litopenaeus vannamei*) populations from Brazil. Aquaculture, 560: 738540. doi: 10.1016/j.aquaculture.2022.738540

Liu, Z.J. 2007. Aquaculture genome technologies. Blackwell Publishing Ltd., Oxford.

Liu, Z.J. & Cordes, J.F. 2004. DNA marker technologies and their applications in aquaculture genetics. Aquaculture, 238: 1-37. doi: 10.1016/j.aquaculture.2004.05.027

Liu, B., Wang, Q., Li, J., Liu, P., et al. 2010. A genetic linkage map of marine shrimp *Penaeus (Fenneropenaeus) chinensis* based on AFLP, SSR, and RAPD markers. Chinese Journal of Oceanology and Limnology, 28: 815-825. doi: 10.1007/s00343-010-9915-3

López-Cuadros, I., García-Gasca, A., Gomez-Anduro, G., Escobedo-Fregoso, C., et al. 2018. Isolation of the sex-determining gene *Sex-lethal* (*Sxl*) in *Penaeus* (*Litopenaeus*) *vannamei* (Boone, 1931) and characterization of its embryogenic, gametogenic, and tissue-specific expression. Gene, 668: 33-47. doi: 10.1016/j.gene.2018.05.024

Lu, H., Chen, W., Liu, F., Huang, M., et al. 2023. A genetic linkage map of the Pacific white shrimp

(*Litopenaeus vannamei*): QTL mapping for low-temperature tolerance and growth-related traits and identification of the candidate genes. Aquaculture, 562: 738834. doi: 10.1016/j.aquaculture.2022.738834

Lu, X., Kong, J., Meng, X., Cao, B., et al. 2018. Identification of SNP markers associated with tolerance to ammonia toxicity by selective genotyping from *de novo* assembled transcriptome in *Litopenaeus vannamei*. Fish and Shellfish Immunology, 73: 158-166. doi: 10.1016/j.fsi.2017.12.005

Lu, X., Luan, S., Hu, L.Y., Mao, Y., et al. 2016. High-resolution genetic linkage mapping, high-temperature tolerance and growth-related quantitative trait locus (QTL) identification in *Marsupenaeus japonicus*. Molecular Genetics and Genomics, 291: 1391-1405. doi: 10.1007/s00438-016-1192-1

Luo, Z., Yu, Y., Bao, Z., Xiang, J., et al. 2022. Evaluation of genomic selection for high salinity tolerance traits in Pacific white shrimp *Litopenaeus vannamei*. Aquaculture, 557: 738320. doi: 10.1016/j.aquaculture.2022.738320

Luvesuto, E., de Freitas, P.D. & Galetti, P.M. 2007. Genetic variation in a closed line of the white shrimp *Litopenaeus vannamei* (Penaeidae). Genetics and Molecular Biology, 30: 1156-1160. doi: 10.1590/S1415-47572007000600021

Lyu, D., Yu, Y., Wang, Q., Luo, Z., et al. 2021. Identification of growth-associated genes by genome-wide association study and their potential application in the breeding of Pacific white shrimp (*Litopenaeus vannamei*). Frontiers in Genetics, 12: 611570. doi: 10.3389/fgene.2021.611570

Mares-Mayagoitia, J.A., De-Anda-Montañez, J.A., Perez-Enriquez, R., Mejía-Ruíz, P., et al. 2021. Neutral and adaptive population structure of pink abalone (*Haliotis corrugata*): fishery management implications. ICES Journal of Marine Science, 78: 1909-1919. doi: 10.1093/icesjms/fsab098

Martínez, P., Viñas, A.M., Sánchez, L., Díaz, N., et al. 2014. Genetic architecture of sex determination in fish: applications to sex ratio control in aquaculture. Frontiers in Genetics, 5: 340. doi: 10.3389/fgene.2014.00340

Matur, F., Keskin, E. & Sezgin, E. 2023. Population genomics and adaptation to novel environments: challenges and opportunities. Frontiers in Ecology and Evolution, 11: 1190218. doi: 10.3389/fevo.2023.1190218

McCartney, A.M., Shafin, K., Alonge, M., Bzikadze, A.V., et al. 2022. Chasing perfection: validation and polishing strategies for telomere-to-telomere genome assemblies. Nature Methods, 19: 687-695. doi: 10.1038/s41592-022-01440-3

Medrano-Mendoza, T., García, B.F., Caballero-Zamora, A., Yáñez, J.M., et al. 2023. Genetic diversity, population structure, linkage disequilibrium and GWAS for resistance to WSSV in Pacific white shrimp (*Litopenaeus vannamei*) using a 50K SNP chip. Aquaculture, 562: 738835. doi: 10.1016/j.aquaculture.2022.738835

Meehan, D., Xu, Z., Zuniga, G. & Alcivar-Warren, A. 2003. High frequency and large number of polymorphic microsatellites in cultured shrimp, *Penaeus* (*Litopenaeus*) *vannamei* (Crustacea: Decapoda). Marine Biotechnology, 5: 311-330. doi: 10.1007/s10126-002-0092-z

Mendoza-Cano, F., Grijalva-Chon, J.M., Pérez-Enríquez, R., Ramos-Paredes, J., et al. 2013. Genetic diversity of mitochondrial DNA from *Litopenaeus vannamei* broodstock used in northwestern Mexico. Ciencias Marinas, 39: 401-412.

Meuwissen, T.H.E., Hayes, B.J. & Goddard, M.E. 2001. Prediction of total genetic value using genome-wide dense marker maps. Genetics, 157: 1819-1829. doi: 10.1093/genetics/157.4.1819

Miles, C.M. & Wayne, M. 2008. Quantitative trait locus (QTL) analysis. Nature Education, 1: 208.

Moen, T., Baranski, M., Sonesson, A.K. & Kjøglum, S. 2009. Confirmation and fine-mapping of a major QTL for resistance to infectious pancreatic necrosis in Atlantic salmon (*Salmo salar*): Population-level associations between markers and trait. BMC Genomics, 10: 368. doi: 10.1186/1471-2164-10-368

Moen, T., Torgersen, J., Santi, N., Davidson, W.S., et al. 2015. Epithelial cadherin determines resistance to infectious pancreatic necrosis virus in Atlantic salmon. Genetics, 200: 1313-1326. doi: 10.1534/genetics.115.175406

Moss, D.R., Moss, S.M. & Lotz, J.M. 2013. Estimation of genetic parameters for survival to multiple isolates of Taura syndrome virus in a selected population of Pacific white shrimp *Penaeus* (*Litopenaeus*) *vannamei*. Aquaculture, 416-417: 78-84. doi: 10.1016/j.aquaculture.2013.07.037

Moss, D.R., Arce, S.M., Otoshi, C.A., Doyle, R.W., et al. 2007. Effects of inbreeding on survival and growth of Pacific white shrimp *Penaeus* (*Litopenaeus*) *vannamei*. Aquaculture, 272: 30-37. doi: 10.1016/j.aquaculture.2007.08.014

Neira, R. 2010. Breeding in aquaculture species: genetic improvement programs in developing countries. 9th

World Congress on Genetics Applied to Livestock Production, August 1 to August 6, 2010, Leipzig.

Onda, Y., Takahagi, K., Shimizu, M., Inoue, K., et al. 2018. Multiplex PCR targeted amplicon sequencing (MTA-Seq): Simple, flexible, and versatile SNP genotyping by highly multiplexed PCR amplicon sequencing. Frontiers in Plant Science, 9: 201. doi: 10.3389/fpls.2018.00201

Palaiokostas, C. & Houston, R.D. 2017. Genome-wide approaches to understanding and improving complex traits in aquaculture species. CAB Reviews, 12: 55. doi: 10.1079/PAVSNNR201712055

Peñaloza, C., Manousaki, T., Franch, R., Tsakogiannis, A., et al. 2021. Development and testing of a combined species SNP array for the European seabass (*Dicentrarchus labrax*) and gilthead seabream (*Sparus aurata*). Genomics, 113: 2096-2107. doi: 10.1016/j.ygeno.2021.04.038

Peñaloza, C., Robledo, D., Barría, A., Trinh, T.Q., et al. 2020. Development and validation of an open access SNP array for Nile Tilapia (*Oreochromis niloticus*). G3: Genes, Genomes, Genetics, 10: 2777-2785. doi: 10.1534/g3.120.401343

Peng, M., Chen, X., Yang, C., Liu, Q., et al. 2023. A high-quality genome assembly of the Pacific white shrimp (*Litopenaeus vannamei*) provides insights into its evolution and adaptation. Aquaculture Reports, 33: 101859. doi: 10.1016/j.aqrep.2023.101859

Peng, M., Zeng, D., Zhu, W., Chen, X., et al. 2020. Construction of a high-density genetic map and identification of quantitative trait loci for nitrite tolerance in the Pacific white shrimp (*Litopenaeus vannamei*). Frontiers in Genetics, 11: 571880. doi: 10.3389/fgene.2020.571880

Pérez, F., Erazo, C., Zhinaula, M., Volckaert, F., et al. 2004. A sex-specific linkage map of the white shrimp *Penaeus* (*Litopenaeus) vannamei*) based on AFLP markers. Aquaculture, 242: 105-118. doi: 10.1016/j.aquaculture.2004.09.002

Pérez-Beloborodova, A., Artiles-Valor, A., Pérez-Jar, L., Hernández-Martínez, D., et al. 2012. Genetic characterization of six stocks of *Litopenaeus vannamei* used in Cuba for aquaculture by means of microsatellite loci. International Journal of Zoology, 2012: 352165. doi: 10.1155/2012/352165

Perez-Enriquez, R. & Max-Aguilar, A. 2016. Pedigree traceability in whiteleg shrimp (*Litopenaeus vannamei*) using genetic markers: a comparison between microsatellites and SNPs. Ciencias Marinas, 42: 227-235. doi: 10.7773/cm.v42i4.2662

Perez-Enriquez, R., Hernández-Martínez, F. & Cruz, P. 2009. Genetic diversity status of white shrimp *Penaeus* (*Litopenaeus*) *vannamei* broodstock in Mexico. Aquaculture, 297: 44-50. doi: 10.1016/j.aquaculture.2009.08.038

Perez-Enriquez, R., Llera-Herrera, R., Galindo-Torres, P. & Avila, S. 2020. A fast sex detection method for the whiteleg shrimp *Litopenaeus vannamei* by post-PCR high resolution melting (HRM). Aquaculture, 520: 734784. doi: 10.1016/j.aquaculture.2019.734784

Perez-Enriquez, R., Magallón-Barajas, F.J. & Llera-Herrera, R. 2024b. Bases to inform a genetic line of whiteleg shrimp *Penaeus (Litopenaeus) vannamei* of Mexican origin. Latin American Journal of Aquatic Research, 52: 150-162. doi: 10.3856/vol52-issue1-fulltext-3066

Perez-Enriquez, R., Medina-Espinoza, J.A., Max-Aguilar, A. & Saucedo-Barrón, C.J. 2018a. Genetic tracing of farmed shrimp (Decapoda, Penaeidae) in wild populations from a main aquaculture region in Mexico, Revista de Biología Tropical, 66: 381-393. doi: 10.15517/rbt.v66i1.27112

Perez-Enriquez, R., Millán-Márquez, A.M., Cruz-Hernández, P. & Saucedo-Barrón, C.J. 2018b. Population genetics of whiteleg shrimp *Litopenaeus vannamei* in Sinaloa, Mexico. Revista Mexicana de Biodiversidad, 89: 290-297. doi: 10.22201/ib.20078706e.2018.1.2070

Perez-Enriquez, R., Robledo, D., Houston, R.D. & Llera-Herrera, R. 2018c. Genomics SNP markers for the genetic characterization of Mexican shrimp broodstocks. Genomics, 110: 423-429. doi: 10.1016/j.ygeno.2018.10.001

Perez-Enriquez, R., Juárez, O.E., Galindo-Torres, P., Vargas-Aguilar, A.L., et al. 2024a. Improved genome assembly of the whiteleg shrimp *Penaeus* (*Litopenaeus*) *vannamei* using long- and short-read sequences from public databases. Journal of Heredity, 115: 302-310. doi: 10.1093/jhered/esae015

Peterson, B.K., Weber, J.N., Kay, E.H., Fisher, H.S., et al. 2012. Double digest RADseq: An inexpensive method for *de novo* SNP discovery and genotyping in model and non-model species. Plos One, 7: e37135. doi: 10.1371/journal.pone.0037135

Phuthaworn, C., Nguyen, N.H., Quinn, J. & Knibb, W. 2016. Moderate heritability of hepatopancreatic parvovirus titre suggests a new option for selection against viral diseases in banana shrimp (*Fenneropenaeus merguiensis*) and other aquaculture species. Genetics Selection Evolution, 48: 64. doi: 10.1186/s12711-016-0243-8

Prochaska, J., Poompuang, S., Koonawootrittriron, S., Sukhavachana, S., et al. 2022. Evaluation of a commercial SPF *Litopenaeus vannamei* shrimp breeding program: Resistance to infectious myonecrosis virus (IMNV), Taura syndrome virus (TSV), and white spot syndrome virus (WSSV) from laboratory challenges. Aquaculture, 554: 738145. doi: 10.1016/j.aquaculture.2022.738145

Qi, H., Song, K., Li, C., Wang, W., et al. 2017. Construction and evaluation of a high-density SNP array for the Pacific oyster (*Crassostrea gigas*). Plos One, 12: e0174007. doi: 10.1371/journal.pone.0174007

Rafalski, J.A. 2002. Novel genetic mapping tools in plants: SNPs and LD-based approaches. Plant Science, 162: 329-333. doi: 10.1016/S0168-9452(01)00587-8

Ren, S., Mather, P.B., Tang, B. & Hurwood, D.A. 2018. Levels of genetic diversity and inferred origins of *Penaeus vannamei* culture resources in China: Implications for the production of a broad synthetic base population for genetic improvement. Aquaculture, 491: 221-231. doi: 10.1016/j.aquaculture.2018.03.036

Robledo, D., Matika, O., Hamilton, A. & Houston, R.D. 2018a. Genome-wide association and genomic selection for resistance to amoebic gill disease in Atlantic salmon. G3: Genes, Genomes, Genetics, 8: 1195-1203. doi: 10.1534/g3.118.200075

Robledo, D., Gutiérrez, A.P., Barría, A., Lhorente, J.P., et al. 2019. Discovery and functional annotation of quantitative trait loci affecting resistance to sea lice in Atlantic salmon. Frontiers in Genetics, 10: 56. doi: 10.3389/fgene.2019.00056

Robledo, D., Palaiokostas, C., Bargelloni, L., Martínez, P., et al. 2018b. Applications of genotyping by sequencing in aquaculture breeding and genetics. Reviews in Aquaculture, 10: 670-682. doi: 10.1111/raq.12193

Santos, C.A., Rossini, B.C., Marques, C.G., Galetti, P.M., et al. 2012. Characterization and genomic annotation of polymorphic EST-SSR loci in *Litopenaeus vannamei* shrimp. Aquaculture Research, 43: 1567-1570. doi: 10.1111/j.1365-2109.2011.02956.x

Shinn, A.P., Pratoomyot, J., Griffiths, D., Trong, T.Q., et al. 2018. Asian shrimp production and the economic costs of disease. Asian Fisheries Science, 31: 29-58. doi: 10.33997/j.afs.2018.31.S1.003

Song, H., Dong, T., Yan, X., Wang, W., et al. 2023. Genomic selection and its research progress in aquaculture breeding. Reviews in Aquaculture, 15: 274-291. doi: 10.1111/raq.12716

Sui, J., Luan, S., Cao, J., Dai, P., et al. 2022. Genomic signatures of artificial selection in fecundity of Pacific white shrimp, *Penaeus vannamei*. Frontiers in Genetics, 13: 929889. doi: 10.3389/fgene.2022.929889

Sui, J., Luan, S., Dai, P., Fu, Q., et al. 2020. High accuracy of pooled DNA genotyping by 2b-RAD sequencing in the Pacific white shrimp, *Litopenaeus vannamei*. Plos One, 15: e0236343. doi: 10.1371/journal.pone.0236343

Sun, X., Liu, D., Zhang, X., Li, W., et al. 2013. 'SLAF-seq: An efficient method of large-scale *de novo* SNP discovery and genotyping using high-throughput sequencing. Plos One, 8: e58700. doi: 10.1371/journal.pone.0058700

Tave, D. 1993. Genetics for fish hatchery managers. Springer, Berlin.

Toonen, R.J., Puritz, J.B., Forsman, Z.H., Whitney, J.L., et al. 2013. ezRAD: A simplified method for genomic genotyping in non-model organisms. PeerJ, 1: e203. doi: 10.7717/peerj.203

Trong, T.Q., van Bers, N., Crooijmans, R., Dibbits, B., et al. 2013. A comparison of microsatellites and SNPs in parental assignment in the GIFT strain of Nile tilapia (*Oreochromis niloticus*): The power of exclusion. Aquaculture, 388-391: 14-23. doi: 10.1016/j.aquaculture.2013.01.004

Uengwetwanit, T., Pootakham, W., Nookaew, I., Sonthirod, C., et al. 2021. A chromosome-level assembly of the black tiger shrimp (*Penaeus monodon*) genome facilitates the identification of growth-associated genes. Molecular Ecology Resources, 21: 1620-1640. doi: 10.1111/1755-0998.13357

Valles-Jimenez, R., Cruz, P. & Perez-Enriquez, R. 2005. Population genetic structure of Pacific white shrimp (*Litopenaeus vannamei*) from Mexico to Panama: Microsatellite DNA variation. Marine Biotechnology, 6: 475-484. doi: 10.1007/s10126-004-3138-6

Valles-Jimenez, R., Gaffney, P.M. & Perez-Enriquez, R. 2006. RFLP analysis of the mtDNA control region in white shrimp (*Litopenaeus vannamei*) populations from the eastern Pacific. Marine Biology, 148: 867-873. doi: 10.1007/s00227-005-0122-2

Van der Pijl, W. 2020. SPF *L. vannamei* broodstock', shrimp insights report series. Shrimp insights. [https://shrimpinsights.com/report-series/vannamei-broodstock]. Reviewed: January 20, 2024.

Vela-Avitúa, S., Montaldo, H.H., Márquez-Valdelamar, L., Campos-Montes, G.R., et al. 2013. Decline of genetic variability in a captive population of Pacific

white shrimp *Penaeus* (*Litopenaeus*) *vannamei* using microsatellite and pedigree information. Electronic Journal of Biotechnology, 16: 11. doi: 10.2225/vol16-issue4-fulltext-11

Vignal, A., Milan, D., San Cristobal, M. & Eggen, A. 2002. A review on SNP and other types of molecular markers and their use in animal genetics. Genetics Selection Evolution, 34: 275-305. doi: 10.1051/gse:2002009

Villanueva, B., Fernández, J., García-Cortés, L.A., Varona, L., et al. 2011. Accuracy of genome-wide evaluation for disease resistance in aquaculture breeding programs. Journal of Animal Science, 89: 3433-3442. doi: 10.2527/jas.2010-3814

Vu, N.T.T., Zenger, K.R., Silva, C.N.S., Guppy, J.L., et al. 2021. Population structure, genetic connectivity, and signatures of local adaptation of the giant black tiger shrimp (*Penaeus monodon*) throughout the Indo-Pacific region. Genome Biology and Evolution, 13: 1-17. doi: 10.1093/gbe/evab214

Wang, S., Meyer, E., Mckay, J.K. & Matz, M.V. 2012. 2b-RAD: A simple and flexible method for genome-wide genotyping. Nature Methods, 9: 808-810. doi: 10.1038/nmeth.2023

Wang, L., Liu, P., Huang, S., Ye, B., et al. 2017. Genome-wide association study identifies loci associated with resistance to viral nervous necrosis disease in Asian seabass. Marine Biotechnology, 19: 255-265. doi: 10.1007/s10126-017-9747-7

Wang, Q., Ren, X., Liu, P., Li, J., et al 2022. Improved genome assembly of Chinese shrimp (*Fenneropenaeus chinensis*) suggests adaptation to the environment during evolution and domestication. Molecular Ecology Resources, 22: 334-344. doi: 10.1111/1755-0998.13463

Wang, Q., Yu, Y., Li, F., Zhang, X., et al. 2017a. Predictive ability of genomic selection models for breeding value estimation on growth traits of Pacific white shrimp *Litopenaeus vannamei*. Chinese Journal of Oceanology and Limnology, 35: 1221-1229. doi: 10.1007/s00343-017-6038-0

Wang, Q., Yu, Y., Yuan, J., Zhang, X., et al. 2017b. Effects of marker density and population structure on the genomic prediction accuracy for growth trait in Pacific white shrimp *Litopenaeus vannamei*. BMC Genetics, 18: 45. doi: 10.1186/s12863-017-0507-5

Wang, Q., Yu, Y., Zhang, Q., Zhang, X., et al. 2019a. Evaluation on the genomic selection in *Litopenaeus vannamei* for the resistance against *Vibrio parahaemolyticus*. Aquaculture, 505: 212-216. doi: 10.1016/j.aquaculture.2019.02.055

Wang, Q., Yu, Y., Zhang, Q., Zhang, X., et al. 2019b. A novel candidate gene associated with body weight in the pacific white shrimp *Litopenaeus vannamei*. Frontiers in Genetics, 10: 520. doi: 10.3389/fgene.2019.00520

Wolfus, G.M., Garcia, D.K. & Alcivar-Warren, A. 1997. Application of the microsatellite technique for analyzing genetic diversity in shrimp breeding programs. Aquaculture, 152: 35-47. doi: 10.1016/S0044-8486(96)01527-X

Wyban, J. 2019. Selective breeding of *Penaeus vannamei*: Impact on world aquaculture and lessons for future. Journal of Coastal Research, 86: 1. doi: 10.2112/SI86-001.1

Yáñez, J.M., Naswa, S., López, M.E., Bassini, L., et al. 2016. Genome-wide single nucleotide polymorphism discovery in Atlantic salmon (*Salmo salar*): validation in wild and farmed American and European populations. Molecular Ecology Resources, 16: 1002-1011. doi: 10.1111/1755-0998.12503

Yin, B., Wang, H., Weng, S., Li, S., et al. 2023. A simple sequence repeats marker of disease resistance in shrimp *Litopenaeus vannamei* and its application in selective breeding. Frontiers in Genetics, 14: 1144361. doi: 10.3389/fgene.2023.1144361

Yu, Y., Wang, Q., Zhang, Q., Luo, Z., et al. 2019. Genome scan for genomic regions and genes associated with growth trait in Pacific white shrimp *Litopeneaus vannamei*. Marine Biotechnology, 21: 374-383. doi: 10.1007/s10126-019-09887-w

Yu, Y., Zhang, X., Yuan, J., Li, F., et al. 2015. Genome survey and high-density genetic map construction provide genomic and genetic resources for the Pacific white shrimp *Litopenaeus vannamei*. Scientific Reports, 5: 15612. doi: 10.1038/srep15612

Yu, Y., Zhang, X., Yuan, J., Wang, Q., et al. 2017. Identification of sex-determining loci in Pacific white shrimp *Litopeneaus vannamei* using linkage and association analysis. Marine Biotechnology, 19: 277-286. doi: 10.1007/s10126-017-9749-5

Yuan, J., Zhang, X., Li, F. & Xiang, J. 2021a. Genome sequencing and assembly strategies and a comparative analysis of the genomic characteristics in Penaeid shrimp species. Frontiers in Genetics, 12: 658619. doi: 10.3389/fgene.2021.658619

Yuan, J., Zhang, X., Wang, M., Sun, Y., et al. 2021b. Simple sequence repeats drive genome plasticity and promote adaptive evolution in penaeid shrimp. Communications Biology, 4: 186. doi: 10.1038/s42003-021-01716-y

Zeng, D., Yang, C., Li, Q., Zhu, W., et al. 2020. Identification of a quantitative trait loci (QTL) associated with ammonia tolerance in the Pacific white shrimp (*Litopenaeus vannamei*). BMC Genomics, 21: 857. doi: 10.1186/s12864-020-07254-x

Zenger, K.R., Khatkar, M.S., Jones, D.B., Khalilisamani, N., et al. 2019. Genomic selection in aquaculture: Application, limitations and opportunities with special reference to marine shrimp and pearl oysters. Frontiers in Genetics, 9: 693. doi: 10.3389/fgene.2018.00693

Zhang, Z., Lu, C., Lin, K., You, W., et al. 2023. Genetic diversity and genetic structure among four selected strains of whiteleg shrimp (*Litopenaeus vannamei*) using SSR markers. Fishes, 8: 544. doi: 10.3390/fishes8110544

Zhang, K., Wang, W., Li, W., Zhang, Q., et al. 2014. Analysis of genetic diversity and differentiation of seven stocks of *Litopenaeus vannamei* using microsatellite markers. Journal of Ocean University of China, 13: 647-656. doi: 10.1007/s11802-014-2208-2

Received: April 3, 2024; Accepted: August 8, 2024

Zhang, L., Yang, C., Zhang, Y., Li, L., et al. 2007. A genetic linkage map of Pacific white shrimp (*Litopenaeus vannamei*): sex-linked microsatellite markers and high recombination rates. Genetica, 131: 37-49. doi: 10.1007/s10709-006-9111-8

Zhang, X., Yuan, J., Sun, Y., Li, S., et al. 2019. Penaeid shrimp genome provides insights into benthic adaptation and frequent molting. Nature Communications, 10: 356. doi: 10.1038/s41467-018-08197-4

Zhang, Y., Zhang, C., Yao, N., Huang, J., et al. 2021. Construction of a high-density linkage map and detection of sex-specific markers in *Penaeus japonicus*. PeerJ, 9: e12390. doi: 10.7717/peerj.12390

Zhi-Ying, J., Xiao-Wen, S., Li-Qun, L., Da-Yu, L., et al. 2006. Isolation and characterization of microsatellite markers from Pacific white shrimp (*Litopenaeus vannamei*). Molecular Ecology Notes, 6: 1282-1284. doi: 10.1111/j.1471-8286.2006.01515.x