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Aquaculture

Review

Evolution of Molecular Markers Used in Genetic Studies of *Penaeus vannamei*

Evolución de los marcadores genéticos empleados en estudios genéticos de *Penaeus vannamei*

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ABSTRACT

Background: Shrimp farming is one of the pillars of aquaculture. Among the main shrimp species, *Peneaus vannamei* stands out, which represents around 70% of the world's shrimp production. The control of genetic diversity is essential to improve a selective breeding program in the shrimp industry. The volume of data on genetic markers in *Peneaus vannamei* has been growing in the last few years. **Aim.** To review and analyze the information related to genetic studies in this shrimp species using the most widely known molecular markers. Several different studies on genetic characterization through molecular markers in white-leg shrimp culture were reviewed. **Development:** This study also tackled the analysis of microsatellite and Single Nucleotide Polymorphism (SNP) markers of this Penaeus shrimp and the genetic characterization of shrimp populations in Cuba using molecular markers. This paper also includes different reviews of research studies of SNP trait-associated markers in *Peneaus vannamei* shrimp culture. **Conclusions:** Microsatellite and SNP markers were found to play an important role in the genetic characterization of *Penaeus vannamei* shrimps, as the most powerful tools for genome analysis. Furthermore, the genetic polymorphism markers associated with phenotypic traits can be used in future selective breeding applications in shrimp farming mainly in developing countries.

Keywords: shrimp, microsatellite, SNP (*Source: MESH*)

RESUMEN

Antecedentes: El cultivo intensivo del camarón es una de las principales actividades de la acuicultura. Entre las especies de camarones se destaca el *Peneaus vannamei*, que representa

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alrededor del 70% de la producción mundial. El control de la diversidad genética es fundamental para mejorar los programas de crianza selectiva dentro de la camaronicultura. En los últimos años se ha incrementado el volumen de información sobre los marcadores genéticos del *Peneaus vannamei.* **Objetivo.** Analizar la información sobre los estudios genéticos en esta especie de camarones a través de los marcadores genéticos de más amplio uso. Se valoraron diferentes estudios sobre la caracterización genética mediante el empleo de marcadores genéticos en cultivos de camarones blancos. **Desarrollo:** Se analizaron los marcadores microsatélites (SSR) y de polimorfismos de un solo nucleótico (SNP) en esta especie, así como las caracterizaciones genéticas de las poblaciones de camarón en Cuba mediante el empleo de marcadores genéticos. Por otra parte, se realizó una revisión de los SNP marcadores relacionados con rasgos fenotípicos del en cultivos de *Peneaus vannamei.* **Conclusiones:** El estudio reveló que los marcadores microsatélites y SNP son las herramientas más útiles para el análisis del genoma y desempeñan un rol significativo en la caracterización genética de *Peneaus vannamei.* Asimismo, esta revisión demostró las potencialidades de los marcadores genéticos asociados a rasgos fenotípicos para aplicar en la crianza selectiva en el cultivo de camarones, particularmente en los países en desarrollo.
Palabras clave: camarón, microsatélite, SNP (*Fuente: MESH*)

INTRODUCTION

Aquaculture is the fastest-growing sector of livestock raising, especially in recent years, with an astonishing development, accounting for a 5% annual growth rate. Aquaculture also emerged as one of the most productive industries with a potential for further expansion and development. In 2019, 86,500 tons were produced worldwide, compared to 2,500 tons in 1970 (Anderson et al., 2019; Fao., 2020).

Shrimp is among the most traded products and the second group of aquaculture species exported by its value (FAO, 2018). Shrimp farming is one of the pillars of aquaculture.(FAO, 2020; Sampantamit *et al.*, 2020). Intensive shrimp farming has increased in the last ten years faster than the same specimens in their natural environment. However, high densities of animals in the culture generate stressful conditions, which are ideal for disease outbreaks. Viral and bacterial pandemics cause the highest losses to shrimp farmers (Flegel, 2019). Among the main species, *Peneaus vannamei* stands out, which represents around 70% of the world's shrimp production (FAO, 2020; Sampantamit *et al.*, 2020). *Peneaus vannamei* is the most widely farmed species in the world. It is a euryhaline species with better tolerance in high population densities and greater availability of genetically selected viral pathogen-free domesticated broodstock (Chong-Robles *et al.*, 2014).

The increased demand for shrimp in the international market led to the development of more efficient production systems through efficient management of larval development, controlled nutrition, advances in disease diagnosis, maintenance of water quality, and genetic improvements of productive indicators (Andriantahina *et al.*, 2013). The control of genetic diversity is essential to improve a selective breeding program in the shrimp industry. A population with low genetic variability compared to others of the same species has a lower capacity to adapt to the

environment (Tiknaik *et al.*, 2020). There are several documented examples of inbreeding depression in closed cycle breeding among cultured species, *Penaeus vannamei* (Perez-Enriquez, Medina-Espinoza, *et al.*, 2018). The development and use of best practices for the domestication and management of broodstock banks should be done through genetic techniques (Cobo and Pérez, 2018).

Considering the growing volume of data on genetic markers in *Peneaus vannamei* and because of the growing relevance of this topic in recent years, this paper aimed to review and analyze the information of genetic studies in *Peneaus vannamei* shrimp cultures using the most popular molecular markers for future studies and assess the utilization of single nucleotide polymorphisms (SNP) markers in future genetic breeding programs for this shrimp species in Cuba.

DEVELOPMENT

Genetic studies on farmed shrimp began more than forty years ago. The first cultivators, who completed the life cycles of species such as *Penaeus monodon, considered the* variations in gene frequency and the alteration of the development of these animals as they were cultivated (Andriantahina *et al.*, 2013; Cobo and Pérez, 2018).

In *Penaeus vannamei*, the classification of microsatellite and polymorphism markers and their standardization in specific databases is still insufficient (Mangabeira-Silva *et al.*, 2020). Over the last ten years, sequencing the *P. vannamei* genome meant a tremendous breakthrough, with the characterization of multiple markers, such as single nucleotide polymorphisms and microsatellites, the construction of linkage maps, and the generation of transcriptomes and partial genomes. Moreover, in the last 30 years of breeding, *P. vannamei* has been subjected to high selection pressures that have profoundly affected its genome (Zhang *et al.*, 2019).

In aquaculture, these genetic markers monitor and select organisms in a culture that will be part of genetic crossbreeding programs. Through them, variability and genetic structure may determine the best crosses, minimize inbreeding and increase the selection response (Cobo and Pérez, 2018; Machado Tamayo, 2006).

Among molecular genetic markers, SSR and SNP are the most commonly recommended for analyzing genetic variability and association due to their properties (A. R. Cobo, 2016). A review of several studies on genetic diversity and population structure analysis using genetic markers SSR and SNP in *P. vannamei* shrimp to characterize populations (Table 1) revealed that the use of SNPs in recent years has been associated with advances in new-generation sequencing (NGS), SNP genotyping techniques, high levels of polymorphisms, genomic frequencies, and codominant inheritance of SNP markers. Garcia *et al.*, 2021; Medrano-Mendoza *et al.* (2023) used the largest number of SNPs as genetic markers in genetic diversity studies, 50K (50 SNPs). This marker number greatly exceeded the 35 SSR used by Garcia and Alcivar-Warren (2007). In both markers, the total size of samples used in the last five years has increased, as did the number of populations of *P. vannamei* studied. The broodstocks are the stages studied most because they

are relevant in obtaining satisfactory results in the shrimp production chain. Garcia and Alcivar-Warren (2007) obtained between 21 and 31 alleles per locus using 35 microsatellite markers, while Lu *et al.* (2018) obtained between 1.17 and 2.0 alleles per locus after genotyping 318919 SNP markers (Table 1).

Table 1. Genetic diversity and population structure analysis with Microsatellite or SSR markers and Single Nucleotide Polymorphism (SNPs) markers in *P. vannamei* shrimps to characterize populations. PL (Post-Larvas).

Marker Type	Marker number	Total sample size	Population studied	Live Stages	Quantity of alleles per locus	Reference
SSR	2	601	1	Broodstocks	7.5 - 10	(Cruz et al., 2004)
SSR	5	207	5	Adults/ Juveniles/PL	7.4 - 8.6	(Valles-Jimenez et al., 2004)
SSR	11	35	1	Adults	18	(Zhi-Ying et al., 2006)
SSR	4	310	4	Broodstocks Juveniles/PL	4.5 - 6.8	(Tamayo, 2006)
SSR	35	48	4	Adults/ juveniles	21 - 31	(Garcia and Alcivar-Warren, 2007)
SSR	6	658	13	Broodstocks	8.9	(Perez-Enriquez et al., 2009)
SSR	4	200	5	Broodstocks	1.0 - 12	(Adriana Artiles et al., 2011)
SSR	4	130	6	Broodstocks	3.5 - 6	(Pérez-Beloborodova et al., 2012)
SSR	7	192	7	Adults	4.0 - 21	(Zhang et al., 2014)
SSR	4	123	4	Broodstocks	5.0 - 9.0	(Artiles et al., 2015)
SSR	10	90	1	Juveniles	7.8	(Andriantahina et al., 2015)
SSR	4	45	3	PL	5.0 - 10	(Rezaee et al., 2016)
SSR	7	216	3	Adults/ PL	4.0 - 8.0	(Suárez, 2016)
SSR	4	360	9	Broodstocks	3.5 - 9.0	(Cobo, 2016)
SSR	5	192	81	Broodstocks	6.6	(Perez-Enriquez and Max-Aguilar, 2016)
SNP	76	192	81	Broodstocks	1.97	(Perez-Enriquez and Max-Aguilar, 2016)
SSR	6	195	7	Broodstocks	14	(Guadalupe, 2017)
SNP	192	162	7	Broodstocks	1.9 -1.91	(Guadalupe, 2017)
SNP	6	119	3	Juveniles		(Ferreira Jr et al., 2017)
SSR	7	1162	30	Broodstocks	5.8 - 12.4	(Ren et al., 2018)
SSR	14	359	5	Broodstocks	3 - 13.2	(Perez-Enriquez, Medina-Espinoza, et al., 2018)
SSR	6	500	10	Broodstocks	15.6	(Perez-Enriquez, Millán-Márquez, et al., 2018)
SNP	318919	1849	7	Juveniles	1.17 - 2.0	(Lu et al., 2018)
SNP	2619	95	21	Broodstocks	1.3 -1.5	(Perez-Enriquez, Robledo, et al., 2018)
SSR	6	952/20000	8	Broodstocks	3.0 - 12.5	(Knibb et al., 2020)
SNP	19157	952/20000	7	Broodstocks		(Knibb et al., 2020)
SSR	16	1110	36	Adults	10 - 10.6	(Jiang et al., 2021)
SNP	50 K	96	140	Adults		(Garcia et al., 2021)
SSR	12	369	37	Adults	4.4 - 17	(Ren et al., 2022)

SNP	96	615	19	Broodstocks		(Silva et al., 2022)
SNP	192	311	6	Broodstocks	1.7 - 1.8	(Casado et al., 2022)
SNP	50 K	6160	176	Juveniles		(Medrano-Mendoza et al., 2023)

The review of studies on different applications of Microsatellite and Single Nucleotide Polymorphism genetic markers used in *P. vannamei* shrimp studies to characterize populations (Table 2) showed that 80.5% of the papers published targetted SNPs as genetic markers mainly for genetic linkage maps and association studies through quantitative trait loci (QTL). Medina Gonzaléz (2006) used the largest quantity of microsatellite markers (120 SSR) to design a genetic linkage map for the white shrimp *Penaeus vannamei*using codominant markers. Moreover, (Jones, Jerry, Khatkar, Raadsma, Van Der Steen, *et al.* (2017) designed a comprehensive comparative gene-based linkage and linkage disequilibrium map for the Pacific white shrimp using a high-density marker with 234452 SNPs. Lu *et al.* (2018) used 318919 SNP high-density markers as MAS to identify SNP markers associated with tolerance to ammonia toxicity by selective genotyping from *de novo* assembled transcriptome in *Penaeus vannamei*. The high-density linkage maps are necessary to conduct genetic studies and identify the desired QTL Shekhar *et al.* (2021) and Sui *et al.* (2022) used the highest density marker (629748 SNP) as GWAS for genomic signatures of artificial selection in the fecundity of the Pacific white shrimp (Table 2). The assembled shrimp genome and a large amount of SNP markers provide a useful resource for the application of genome-wide association studies and genomic selection. That way, genetic breeding will take place at a faster rate in shrimp culture (Zhang *et al.*, 2019).

Table 2. Different applications of Single Nucleotide Polymorphisms (SNPs) and microsatellite genetic markers in *P. vannamei* shrimp studies to characterize populations in the loci with quantity traits (QTL), genetic selection (GS), marker-assisted selection (MAS), and genome-wide association study (GWAS).

Marker Types	Markers Application	Marker number	Reference
SNP	Genetic linkage map and QTL	5	(Glenn *et al.*, 2005)
SNP	Association Studies (QTL)	6	(Yu *et al.*, 2006)
SSR	Genetic linkage map	120	(Medina González, 2006)
SSR	Genetic linkage map and GS	35	(Garcia and Alcivar-Warren, 2007)
SSR	Genetic linkage map	30	(Zhang *et al.*, 2007)
SNP	Association Studies (QTL)	5	(Zeng *et al.*, 2008)
SNP	Association Studies (QTL)	211	(Ciobanu *et al.*, 2010)
SNP	Genetic linkage map	1344	(Du *et al.*, 2010)
SNP	Association Studies (QTL)	18	(Liu *et al.*, 2014b)
SNP	Association Studies (QTL)	38	(Liu *et al.*, 2014a)
SNP	Genetic linkage map	25140	(Yu *et al.*, 2015)
SSR	Genetic Selection (GS)	10	(Andriantahina *et al.*, 2015)
SSR	Parentage assignment	5	(Perez-Enriquez and Max-Aguilar, 2016)
SNP	Parentage assignment	76	(Perez-Enriquez and Max-Aguilar, 2016)

SNP	Genetic linkage map	234452	(Jones, Jerry, Khatkar, Raadsma, Van Der Steen, *et al.*, 2017)
SNP	Association Studies (QTL)	6	(Ferreira Jr *et al.*, 2017)
SNP	Genetic Selection (GS)	3.2K	(Wang *et al.*, 2017)
SNP	Association Studies (QTL)	2619	(Perez-Enriquez, Robledo, *et al.*, 2018)
SNP	Marker Assisted Selection (MAS)	318919	(Lu *et al.*, 2018)
SNP	Association Studies (QTL)	7000	(Santos *et al.*, 2018)
SNP	Parentage assignment and QTL	76	(Nolasco-Alzaga *et al.*, 2018)
SNP	Association Studies (QTL)	30	(X. Zhang *et al.*, 2019)
SNP	Genetic Selection (GS)	6	(Lien *et al.*, 2019)
SNP	Genetic linkage map and QTL	17242	(Peng *et al.*, 2020)
SNP	Genetic linkage map and QTL	17338	(Zeng *et al.*, 2020)
SNP	Genetic Selection (GS)	3	(Perez-Enriquez *et al.*, 2020)
SNP	Genetic linkage map	3567	(Huang *et al.*, 2021)
SNP	Association Studies (QTL)	582	(Mangabeira-Silva *et al.*, 2020)
SNP	Association Studies (QTL)	1	(Kaewduang *et al.*, 2021)
SNP	Association Studies (QTL)	9	(Kongchum *et al.*, 2022)
SNP	Genome-wide association study (GWAS)	94113	(Lyu *et al.*, 2021)
SSR	Parentage assignment	16	(Jiang *et al.*, 2021)
SSR	Genetic Selection (GS)	12	(Ren *et al.*, 2022)
SNP	Genome-wide association study (GWAS)	629748	(Sui *et al.*, 2022)
SNP	Parentage assignment	96	(Silva *et al.*, 2022)
SNP	Genome-wide association study (GWAS)	50K	(Medrano-Mendoza *et al.*, 2023)

DNA microsatellites have quickly become popular molecular markers for advanced biotechnology applications. The availability and use of microsatellites facilitate the collection of information on important functional traits such as survival and growth traits at the family level. High polymorphism and easiness of labeling are two of its main characteristics that apply to numerous genetic studies in shrimp (Machado Tamayo, 2006). SNP panels, on the other hand, are widely used to analyze genetic diversity in specific phenotypic elements from certain populations(Ciobanu *et al.*, 2010).

D. K. Garcia and Alcivar-Warren, 2007 characterized 35 new microsatellite genetic markers in the Pacific white-leg shrimp to know their usefulness in the study of the genetic diversity of wild and cultured stocks, tracing pedigree in breeding programs, and linkage mapping. Genotypes and productive traits have been associated with several shrimp species, including the description of an SSR region linked to genetic diversity and growth breeding selection in Penaeus vannamei (Andriantahina *et al.*, 2015). Another example is the description of SNPs associated with survival and disease resistance in *Penaeus vannamei* (Martin Marti *et al.*, 2010). Furthermore, Medrano-Mendoza *et al.* (2023) evaluated the genetic diversity, population structure, and linkage

disequilibrium and performed a genome-wide association study (GWAS) to search for single nucleotide polymorphisms (SNPs) that might be associated with the Pacific white shrimp (*Penaeus vannamei*) resistance to the White Spot Syndrome Virus (WSSV).

The identification of SNP markers in white shrimp was possible thanks to previously-reported coding regions in Genbank, using information analysis software (Du *et al.*, 2010). Zhang *et al.* (2019) identified 31,993,474 single nucleotide polymorphisms (SNPs) in the genome of *P. vannamei.* These were the first data published about the alignment of the genome of these species, and the largest set of high-quality SNPs obtained from *P. vannamei*, in addition to the fact that it is a valuable resource for genetic research and selection. A limited number of research studies use genome-wide association studies (GWAS) in shrimp, which could be a potential resource for obtaining large numbers of SNP markers useful for the genomic selection of various traits in aquaculture species, but future development of low-cost, high-density markers in shrimp may be required to maximize the GWAS potential (Yu *et al.*, 2014).

In Cuba, Artiles *et al.* (2011) estimated the genetic variability and the relatedness index between the five founding stocks of this same species, introduced and cultivated in Cuba in different years. In the fifth and last introduction, the authors detected the lowest heterozygosity values concerning the previous broodstock importations. The authors suggested the need to cross them with broodstock from different origins to improve the gene pool and production yields. Likewise, Pérez-Beloborodova *et al.* (2012) characterized the first descendants of four founder stocks and two crosses of *P. vannamei* introduced in Cuba for aquaculture, using four microsatellite loci. The authors observed the beginning of a drop in their genetic variables. Besides, Artiles *et al.* (2015) evaluated the genetic variation and productive markers of four progenies from the first cultured shrimp stock introduced in Cuba (*Penaeus vannamei*), and four microsatellite regions were explored to characterize the four populations cultured. Casado *et al.* (2022) made the first report on SNP use for the genetic characterization of an exotic shrimp species cultured in Cuba.

Recent advances in analytical methods and high throughput genotyping might contribute to simpler breeding schemes and increase genetic gain, particularly for complex traits or characteristics that are difficult to measure. Specifically, quantitative trait loci (QTL) mapping, or genes with a higher effect, may have an immediate application in marker-assisted selection (MAS) (Khatkar *et al.*, 2017).

As a result of the rapid development of high-throughput sequencing and genotyping techniques, it is possible to identify multiple causative genes of phenotypic variants of *P. vannamei* (Lukwambe *et al.*, 2019; Lyu *et al.*, 2021; Wang, Yu, Zhang, Zhang, Yuan, *et al.*, 2019).

At present, genomic data are used for shrimp farming; advances in genetics are expected to speed up over time. SNP use will contribute to genome selection and other relevant studies of the entire genome, depending on the amount of linkage disequilibrium (LD) determined (Garcia *et al.*, 2021). So far, little genome-wide research has been done on this species.

CONCLUSION

This paper examined and analyzed information about genetic studies in *Peneaus vannamei* shrimp cultures based on the most widely used molecular markers. Microsatellite and Single Nucleotide Polymorphism markers play a critical role in the genetic characterization of *Penaeus vannamei* shrimp. These two molecular genetic markers represent the most powerful tools for genome analysis, and they permit the association of genetic traits with an underlying gene variation.

The inclusion of novel molecular biology techniques, and their optimization helped decrease the costs of SNP-assisted genetic determination, thus making the use of this technique in the genetic characterization of shrimp farming populations in Cuba possible. Nevertheless, this genetic study fails to meet the needs of Cuban shrimp culture. The knowledge about the presence of trait-associated single nucleotide polymorphism (SNP) markers in *Peneaus vannamei* shrimp culture could favor the implementation of a genetic management program for this shrimp species in Cuba.

Further studies on genetic marker-based penaeid shrimp genome could increase shrimp production substantially worldwide. The advantages of the knowledge acquired on diversity and the genetic structure of *Peneaus vannamei* populations permit the monitoring and decision-making concerning these populations to maximize diversity and manage genetic improvements and assess the genetic traits of new stocks. Single nucleotide polymorphism markers associated with phenotypic traits could be used in future selective breeding applications in shrimp farming, mainly in developing countries.

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REFERENCES

Andriantahina, F., Liu, X., Feng, T., and Xiang, J. (2013). Current status of genetics and genomics of reared penaeid shrimp: information relevant to access and benefit sharing. *Marine Biotechnology*, *15*(4), 399-412. https://www.proquest.com/openview/69e195494f46d52d6f63766c2b09e305/1?pqorigsite=gscholar&cbl=55468

Andriantahina, F., Liu, X., and Huang, H. (2015). Using microsatellite markers to identify heritability of Pacific white leg shrimp *Litopenaeus vannamei*. *Acta Oceanologica Sinica, 34*, 59-65. https://www.infona.pl/resource/bwmeta1.element.springer-a344b87d-11b7-38a0-83a2-bf9ad279598e

Artiles, A., Cobo, R., Benítez, L., and Espinosa, G. (2015). Assessment of genetic variation and productive markers through four progenies of the first introduced stock of cultured shrimp Penaeus (Litopenaeus) vannamei in Cuba. *International Journal of Aquaculture, 5*. https://aquapublisher.com/index.php/ija/article/view/1842

Artiles, A., Rodríguez, I., Pérez, A., Pérez, L., and Espinosa, G. (2011). Low genetic variability in the fifth introduction of *Litopenaeus vannamei* in Cuba, as estimated with microsatellite markers. [Limitada variabilidad genética de la quinta introducción en Cuba de *Litopenaeus vannamei* estimada con el uso de marcadores microsatélites]. *Biotecnología Aplicada, 28*(3), 147-150. Retrieved from http://scielo.sld.cu/scielo.php?script=sci_arttext&pid=S1027285220110003000003&lang=en

Casado, E., Cabrera, H., González, M., Espinosa, G., Reyes, Y., Artiles, A., . . . Arenal, A. (2022). Genetic diversity and growth-related traits in Penaeus vannamei after ten years without introducing new stocks into Cuba. *Aquaculture, 554*, 738097. https://www.sciencedirect.com/science/article/abs/pii/S0044848622002137

Chong-Robles, J., Charmantier, G., Boulo, V., Lizárraga-Valdéz, J., Enríquez-Paredes, L. M., and Giffard-Mena, I. (2014). Osmoregulation pattern and salinity tolerance of the white shrimp *Litopenaeus vannamei* (Boone, 1931) during post-embryonic development. *Aquaculture, 422*, 261-267. https://www.sciencedirect.com/science/article/abs/pii/S0044848613006467

Ciobanu, D. C., Bastiaansen, J. W., Magrin, J., Rocha, J., Jiang, D. H., Yu, N., . . . Gong, H. (2010). A major SNP resource for the dissection of phenotypic and genetic variation in Pacific white shrimp (*Litopenaeus vannamei*). *Animal genetics, 41*(1), 39-47. https://doi.org/10.1111/j.1365-2052.2009.01961.x

Cobo, A. R. (2016). Parámetros genéticos y desempeño productivo en lotes de camarón *Litopenaeus vannamei* (Boone, 1931) cultivados en Cuba. https://aquadocs.org/handle/1834/14093

Cobo, R., and Pérez, L. (2018). Aspectos generales del cultivo y la genética del camarón blanco del Pacífico *Litopenaeus vannamei* (Boone, 1931). https://aquadocs.org/handle/1834/15129

Cruz, P., Ibarra, A. M., Mejia-Ruiz, H., Gaffney, P. M., and Pérez-Enríquez, R. (2004). Genetic variability assessed by microsatellites in a breeding program of Pacific white shrimp (*Litopenaeus vannamei*). *Marine Biotechnology, 6*, 157-164. https://pubmed.ncbi.nlm.nih.gov/14595549/

Du, Z.-Q., Onteru, S. K., Gorbach, D., and Rothschild, M. F. (2010). A SNP Genetic Map for Pacific White Shrimp (*Litopenaeus vannamei*). *Animal Industry Report, 656*(1), 35. doi:https://doi.org/10.31274/ans_air-180814-604

FAO. (2018). Meeting the sustainable development goals. *The State of World Fisheries and Aquaculture 2018* Retrieved from https://www.fao.org/documents/card/es/c/I9540ES

FAO. (2020). Sustainability in action. *The State of World Fisheries and Aquaculture 2020*. Retrieved from http://www.fao.org/3/ca9229en/online/ca9229en.html

Ferreira Jr, A., Maggioni, R., ConceiÃ, D., Perazzolo, L., and Petersen, R. (2017). Hsp70 gene polymorphisms in farmed marine shrimp *Litopenaeus vannamei* populations exposed to white spot disease and infectious myonecrosis. *Genetics and Molecular Research, 16*(2). doi:DOI http://dx.doi.org/10.4238/gmr16029668

Flegel, T. W. (2019). A future vision for disease control in shrimp aquaculture. *Journal of the World Aquaculture Society, 50*(2), 249-266. https://onlinelibrary.wiley.com/doi/abs/10.1111/jwas.12589

Garcia, B. F., Bonaguro, Á., Araya, C., Carvalheiro, R., and Yáñez, J. M. (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. https://www.sciencedirect.com/science/article/pii/S2352513421001071

Garcia, D. K., and 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*(4), 1203-1216. https://doi.org/10.2983/0730-8000(2007)26[1203:CONMGM]2.0.CO;2

Glenn, K., Grapes, L., Suwanasopee, T., Harris, D., Li, Y., Wilson, K., and Rothschild, M. (2005). SNP analysis of AMY2 and CTSL genes in *Litopenaeus vannamei* and Penaeus monodon shrimp. *Animal genetics, 36*(3), 235-236. https://doi.org/10.1111/j.1365-2052.2005.01274.x

Guadalupe, B. (2017). *Caracterización genética de líneas de reproductores de camarón blanco Penaeus (Litopenaeus) vannamei en cultivo.* (Maestro en Ciencias en Acuicultura). https://cicese.repositorioinstitucional.mx/jspui/handle/1007/1876

Huang, Y., Zhang, L., Ge, H., Wang, G., Huang, S., and Yang, Z. (2021). SNP Development in Penaeus vannamei via Next-Generation Sequencing and DNA Pool Sequencing. *Fishes, 6*(3), 36. https://www.mdpi.com/2410-3888/6/3/36

Jiang, H. G., Channarong, J., Ngernsiri, L., and Swatdipong, A. (2021). Microsatellite Techniques in Guam's Specific-Pathogen-Free Penaeus Vannamei Stock: Genetic Variance and Parentage Identification. *Fisheries and Aquaculture Journal*. *S, 2*. https://hal.science/hal-03629030/

Jones, D. B., Jerry, D. R., Khatkar, M. S., Raadsma, H. W., van der Steen, H., Prochaska, J., . . . Zenger, K. R. (2017). A comparative integrated gene-based linkage and locus ordering by linkage disequilibrium map for the Pacific white shrimp, *Litopenaeus vannamei*. *Scientific reports*, *7*(1), 1-16. DOI:10.1038/s41598-017-10515-7

Kaewduang, M., Prasertlux, S., Janpoom, S., Rongmung, P., Ratdee, O., Lirdwitayaprasit, T., . . . Khamnamtong, B. (2021). Differential expression following ammonia stress and growth-related SNP of ferritin: Applications for establishment of stress-tolerant stocks with high growth performance of Pacific white shrimp *Litopenaeus vannamei* in Thailand. *Regional Studies in Marine Science*, *42*, 101656. https://www.sciencedirect.com/science/article/abs/pii/S2352485521000487

Khatkar, M., Zenger, K., Jones, D., Prochaska, J., van der Steen, H., Jerry, D., and Raadsma, H. W. (2017). Quantitative genomic analyses in the pacific whiteleg shrimp *Litopenaeus vannamei*. In *Proc. Assoc. Advmt. Anim. Breed. Genet*. 22, 121-124. https://www.cabdirect.org/cabdirect/abstract/20203385280

Knibb, W., Giang, C., Premachandra, H., Ninh, N., and Dominguez, B. (2020). Feasible options to restore genetic variation in hatchery stocks of the globally important farmed shrimp species, *Litopenaeus vannamei*. *Aquaculture*, *518*, 734823. https://www.sciencedirect.com/science/article/abs/pii/S0044848619321738

Kongchum, P., Chimtong, S., and Prapaiwong, N. (2022). Association between single nucleotide polymorphisms of nLvALF1 and PEN2-1 genes and resistance to Vibrio parahaemolyticus in the Pacific white shrimp *Litopenaeus vannamei*. *Aquaculture and Fisheries*, *7*(4), 373-381. https://www.sciencedirect.com/science/article/pii/S2468550X21000964

Lien, N. T. K., Van Tung, N., Thanh, D. C., Hien, N. T., Ngoc, N., Lan, N. T. T. N., . . . Hung, N. H. (2019). Evaluate the potential SNPs for breeding selection of white spot syndrome virus resistance in *Litopenaeus vannamei*. *Journal of Biotechnology*, *17*(4), 637-643. https://vjs.ac.vn/index.php/vjbt/article/view/13555

Liu, J., Yu, Y., Li, F., Zhang, X., and Xiang, J. (2014a). A new ALF from *Litopenaeus vannamei* and its SNPs related to WSSV resistance. *Chinese Journal of Oceanology and Limnology*, *32*(6), 1232-1247. https://pubag.nal.usda.gov/catalog/914167

Liu, J., Yu, Y., Li, F., Zhang, X., and Xiang, J. (2014b). A new anti-lipopolysaccharide factor (ALF) gene with its SNP polymorphisms related to WSSV-resistance of *Litopenaeus vannamei*. *Fish & Shellfish Immunology*, *39*(1), 24-33. https://www.sciencedirect.com/science/article/abs/pii/S1050464814001156

Lu, X., Kong, J., Meng, X., Cao, B., Luo, K., Dai, P., and Luan, S. (2018). Identification of SNP markers associated with tolerance to ammonia toxicity by selective genotyping from de

novo assembled transcriptome in *Litopenaeus vannamei*. *Fish & Shellfish Immunology, 73*, 158-166. DOI:10.1016/j.fsi.2017.12.005

Lukwambe, B., Nicholaus, R., Zhang, D., Yang, W., Zhu, J., and Zheng, Z. (2019). Successional changes of microalgae community in response to commercial probiotics in the intensive shrimp (*Litopenaeus vannamei* Boone) culture systems. *Aquaculture, 511*, 734257. https://doi.org/10.1016/j.aquaculture.2019.734257

Lyu, D., Yu, Y., Wang, Q., Luo, Z., Zhang, Q., Zhang, X., . . . Li, F. (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. https://www.frontiersin.org/articles/10.3389/fgene.2021.611570/full

Machado Tamayo, R. (2006). Assessment of genetic variability in two lots of white shrimp, *Litopenaeus vannamei* (Boone, 1931) introduced to Cuba. https://munin.uit.no/handle/10037/344

Mangabeira-Silva, I. S., Soares, P. E. T., and Lanza, D. C. F. (2020). Single nucleotide polymorphism associated with disease resistance in Penaeus vannamei. *Journal of Invertebrate Pathology, 177*, 107498. https://www.sciencedirect.com/science/article/abs/pii/S0022201120302044

Medina Gonzaléz, M.K. (2006). *Elaboración de un mapa genetico del ligamiento para el camanón blanco Penaeus vannamei empleando marcadores codominantes.* (Tesis de grado). Universidad estatal Penñsula de Santa Elena, Facultad de Ciencias del Mar Escuela de Biolocía Marina, Ecuador. https://repositorio.upse.edu.ec/handle/46000/826

Martin Marti, S., Onteru, S. K., Du, Z.-Q., and Rothschild, M. F. (2010). SNP analyses of the 5HT1R and STAT genes in Pacific white shrimp, *Litopenaeus vannamei*. *Spanish Journal of Agricultural Research, 8*(1), 53. DOI:10.5424/sjar/2010081-1162

Medrano-Mendoza, T., García, B. F., Caballero-Zamora, A., Yáñez, J. M., Montoya-Rodríguez, L., Quintana-Casares, J. C., . . . Campos-Montes, G. R. (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. https://www.sciencedirect.com/science/article/abs/pii/S0044848622009528

Nolasco-Alzaga, H. R., Perez-Enriquez, R., Enez, F., Bestin, A., Palacios-Mechetnov, E., and Haffray, P. (2018). Quantitative genetic parameters of growth and fatty acid content in the hemolymph of the Whiteleg shrimp *Litopenaeus vannamei*. *Aquaculture, 482*, 17-23. https://www.sciencedirect.com/science/article/abs/pii/S0044848616309668

Peng, M., Zeng, D., Zhu, W., Chen, X., Yang, C., Liu, Q., . . . Liang, J. (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. https://www.frontiersin.org/articles/10.3389/fgene.2020.571880/full

Pérez-Beloborodova, A., Artiles-Valor, A., Pérez-Jar, L., Hernández-Martínez, D., Guerra-Aznay, M., and Espinosa-López, G. (2012). Genetic Characterization of Six Stocks of *Litopenaeus vannamei* used in Cuba for Aquaculture by means of Microsatellite Loci. *International Journal of Zoology, 2012*. https://aquadocs.org/handle/1834/5347?locale-attribute=es

Perez-Enriquez, R., Hernández-Martínez, F., and Cruz, P. (2009). Genetic diversity status of White shrimp Penaeus (Litopenaeus) vannamei broodstock in Mexico. *Aquaculture, 297*(1), 44-50. doi:https://doi.org/10.1016/j.aquaculture.2009.08.038

Perez-Enriquez, R., Llera-Herrera, R., Torres, P. G., and Avila, S. (2020). A fast sex detection method for the Whiteleg shrimp *Litopenaeus vannamei* by post-PCR high resolution melting (HRM). *Aquaculture, 520*, 734784. https://www.sciencedirect.com/science/article/abs/pii/S004484861932664X

Perez-Enriquez, R., and Max-Aguilar, A. (2016). Pedigree traceability in whiteleg shrimp (*Litopenaeus vannamei*) using genetic markers: A comparison between microsatellites and SNPs. *Ciencias marinas, 42*(4), 227–235-227–235. doi:http://dx.doi.org/10.7773/cm.v42i4.2662

Perez-Enriquez, R., Medina-Espinoza, J. A., Max-Aguilar, A., and Saucedo-Barrón, C. J. (2018). Genetic tracing of farmed shrimp (Decapoda: Penaeidae) in wild populations from a main aquaculture region in Mexico. *Revista de Biología Tropical, 66*(1), 381-393. https://www.scielo.sa.cr/scielo.php?script=sci_arttext&pid=S003477442018000-100381

Perez-Enriquez, R., Robledo, D., Houston, R. D., and Llera-Herrera, R. (2018). SNP markers for the genetic characterization of Mexican shrimp broodstocks. *Genomics, 110*(6), 423-429. https://doi.org/10.1016/j.ygeno.2018.10.00

Ren, S., Mather, P. B., Tang, B., and 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. https://www.sciencedirect.com/science/article/abs/pii/S0044848617-325358

Ren, S., Mather, P. B., Tang, B., and Hurwood, D. A. (2022). Standardized microsatellite panels for pedigree management of farmed white-leg shrimp (Penaeus vannamei) stocks validated in a VIE tagged family selection line. *Aquaculture, 551*, 737946. https://www.sciencedirect.com/science/article/abs/pii/S0044848622000606

Rezaee, S., Farahmand, H., and Nematollahi, M. A. (2016). Genetic diversity status of Pacific white shrimp (*Litopenaeus vannamei*) using SSR markers in Iran. *Aquaculture international, 24*(2), 479-489. https://link.springer.com/article/10.1007/s10499-015-9939-y

Sampantamit, T., Ho, L., Lachat, C., Sutummawong, N., Sorgeloos, P., and Goethals, P. (2020). Aquaculture production and its environmental sustainability in Thailand: Challenges and potential solutions. *Sustainability, 12*(5), 2010. https://www.mdpi.com/2071-1050/12/5/2010

Santos, C. A., Andrade, S. C., and Freitas, P. D. (2018). Identification of SNPs potentially related to immune responses and growth performance in *Litopenaeus vannamei* by RNA-seq analyses. *PeerJ, 6*, e5154. DOI: 10.7717/peerj.5154

Shekhar, M. S., Katneni, V. K., Jangam, A. K., Krishnan, K., Kaikkolante, N., and Vijayan, K. K. (2021). The Genomics of the farmed shrimp: Current status and application. *Reviews in Fisheries Science & Aquaculture, 29*(4), 654-665. https://doi.org/10.1080/23308249.2020.1858271

Silva, N. M. L., Ianella, P., Yamagishi, M. E. B., Rocha, J. L., Teixeira, A. K., Farias, F. G., . . . Caetano, A. R. (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. https://www.sciencedirect.com/science/article/abs/pii/S0044848622006561

Suárez, V. (2016). *Uso de marcadores genéticos para la diferenciación genética de poblaciones cultivadas de camarón blanco.*

Sui, J., Luan, S., Cao, J., Dai, P., Meng, X., Luo, K., . . . Kong, J. (2022). Genomic signatures of artificial selection in fecundity of Pacific white shrimp, Penaeus vannamei. *Frontiers in genetics, 13*, 929889. https://www.frontiersin.org/articles/10.3389/fgene.2022.929889/full

Tiknaik, A., Khedkar, C., Khedkar, G., Prakash, B., Mamatha, D. M., Sangale, D., and Kalyankar, A. (2020). Microsatellite Genotyping Corroborated Loss of Genetic Diversity in Clarias batrachus as a Result of Lack of Regulatory Reforms in Aquaculture. *Biochemical genetics, 58*(4), 595-616. https://link.springer.com/article/10.1007/s10528-020-09963-0

Valles-Jimenez, R., Cruz, P., and Perez-Enriquez, R. (2004). Population genetic structure of Pacific white shrimp (*Litopenaeus vannamei*) from Mexico to Panama: microsatellite DNA variation. *Marine Biotechnology, 6*(5), 475-484. doi:DOI: 10.1007/s10126-004-3138-6. https://link.springer.com/article/10.1007/s10126-004-3138-6

Wang, Q., Yu, Y., Yuan, J., Zhang, X., Huang, H., Li, F., and Xiang, J. (2017). Effects of marker density and population structure on the genomic prediction accuracy for growth trait in Pacific white shrimp *Litopenaeus vannamei*. *BMC genetics, 18*(1), 1-9. https://pubmed.ncbi.nlm.nih.gov/28514941/

Wang, Q., Yu, Y., Zhang, Q., Zhang, X., Yuan, J., Huang, H., . . . Li, F. (2019). A novel candidate gene associated with body weight in the Pacific white shrimp *Litopenaeus*

vannamei. *Frontiers in genetics*, *10*, 520. https://www.frontiersin.org/articles/10.3389/fgene.2019.00520/full

Yu, M., Cheng, Y., and Rothschild, M. F. (2006). SNP analysis of Molting related genes in Penaeus monodon and *Litopenaeus vannamei* shrimp (Brief report). *Archives Animal Breeding*, *49*(4), 411-412. https://aab.copernicus.org/articles/49/411/2006/

Yu, Y., Wei, J., Zhang, X., Liu, J., Liu, C., Li, F., and Xiang, J. (2014). SNP discovery in the transcriptome of white Pacific shrimp *Litopenaeus vannamei* by next generation sequencing. *PloS one*, *9*(1). DOI:10.1371/journal.pone.0087218

Yu, Y., Zhang, X., Yuan, J., Li, F., Chen, X., Zhao, Y., . . . Xiang, J. (2015). Genome survey and high-density genetic map construction provide genomic and genetic resources for the Pacific White Shrimp *Litopenaeus vannamei*. *Scientific reports*, *5*(1), 1-14. DOI: 10.1038/srep15612

Zeng, D., Chen, X., Li, Y., Peng, M., Ma, N., Jiang, W., . . . Li, M. (2008). Analysis of Hsp70 in *Litopenaeus vannamei* and detection of SNPs. *Journal of Crustacean Biology*, *28*(4), 727-730. http://dx.doi.org/10.1651/08-3019.1

Zeng, D., Yang, C., Li, Q., Zhu, W., Chen, X., Peng, M., . . . Liu, H. (2020). Identification of a quantitative trait loci (QTL) associated with ammonia tolerance in the Pacific white shrimp (*Litopenaeus vannamei*). *BMC Genomics*, *21*(1), 1-12. https://bmcgenomics.biomedcentral.com/articles/10.1186/s12864-020-07254-x

Zhang, L., Yang, C., Zhang, Y., Li, L., Zhang, X., Zhang, Q., and Xiang, J. (2007). A genetic linkage map of Pacific white shrimp (*Litopenaeus vannamei*): sex-linked microsatellite markers and high recombination rates. *Genetica*, *131*, 37-49. https://link.springer.com/article/10.1007/s10709-006-9111-8

Zhang, X., Yuan, J., Sun, Y., Li, S., Gao, Y., Yu, Y., . . . Zhang, X. (2019). Penaeid shrimp genome provides insights into benthic adaptation and frequent molting. *Nature communications*, *10*(1), 356. https://www.nature.com/articles/s41467-018-08197-4

Zhi-Ying, J., Xiao-Wen, S., Li-Qun, L., Da-Yu, L., and Qing-Quan, L. (2006). Isolation and characterization of microsatellite markers from Pacific white shrimp (*Litopenaeus vannamei*). *Molecular Ecology Notes*, *6*(4), 1282-1284. https://onlinelibrary.wiley.com/doi/abs/10.1111/j.1471-8286.2006.01515.x

AUTHOR CONTRIBUTION STATEMENT

Research conception and design: ECS, HCA, AAC; redaction of the manuscript: ECS, AAC.

DECLARATION OF COMPETING INTEREST

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.