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Review Article

Biology, pathogenesis and management approaches of White Spot Disease in shrimp aquaculture: A review

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Abstract

Several viruses cause devastating mortality in economically crucial shrimp species, including *Penaeus monodon*, *Litopenaeus vannamei*, and *L. stylirostris.* In this context, the white spot syndrome virus (WSSV) is a highly contagious lethal, stress-dependent virus, which belongs to the family Nimaviridae, genus *Whispovirus*, and it is responsible for deadly WSSV affecting the shrimp industry worldwide. This virus possesses a large, circular, and double-stranded DNA genome that varies in sizes (292.9–307.2 kb), where different isolates exhibit differing levels of virulence. The spread of the infection through horizontal transmission may be related to the infected shrimp and carriers such as other crustaceans, seabirds, aquatic arthropods or other vectors. There are various managerial responsibilities including biosecurity measures and the implementation of vaccination programs to control the spread of WSSV in the aquaculture shrimp sectors. There are still many challenges in the management of this disease. Probiotics and immunostimulants show promise methods for controlling WSSV. Additionally, New strains of WSSV are emerging, posing a serious threat to the shrimp aquaculture due to their genetic variation and differing virulence levels, which all complicate existing disease control strategies. This review provides an overview of the current knowledge on the biology and pathogenesis of white spot disease (WSD), including the mechanisms involved in viral replication, host immune response, epidemiology and disease progression. Moreover, it discusses the various management approaches that have been developed for the control and prevention of WSD in the shrimp aquaculture industry and also highlights the challenges faced in the management of WSD and the potential future directions for research in this field.

Introduction

As a significant component of the global aquaculture industry, shrimp farming involves cultivating shrimp in controlled environments like ponds and tanks. It serves as a critical source of food and income for many people worldwide (New and Nair, 2012). According to the Food and Agriculture Organization (FAO) of the United Nations, farmed shrimp accounted for approximately 55% of global shrimp production in 2018, with the top producing countries including China, India, Vietnam, Indonesia, and Thailand (Miao and Wang, 2020). In 2022, global shrimp production reached a record high of 9.4 million tonnes. Specifically, the production of *L. vannamei*, which is the primary species cultured worldwide, experienced significant growth and reached nearly 5 million tonnes in the same year. Ecuador emerged as the top producer of this shrimp variety, with an estimated production of 1.3 million tonnes in 2022. The shrimp industry has grown rapidly in recent decades, driven by increasing demand for shrimp in both domestic and international markets. However, like many forms of aquaculture, shrimp farming can have environmental impacts, including the depletion of mangrove forests, water pollution, and disease outbreaks (Páez-Osuna, 2001).

Global aquaculture of penaeid shrimp has grown rapidly in the last two decades and its cultivation is carried out even in saltwater aquifers, marine areas, freshwater and brackish waters. The global shrimp production exceeded 6.5 million tons in 2019 (Lee *et al.*, 2022). The main producers accounted for 6.0 million tons of this production. The overall global production from fishing and shrimp culture reached 8 million tonnes, indicating a significant increase in shrimp culture compared to worldwide catch (Kakoolaki *et al.*, 2020) (Table 1).

Table 1: Top and mid shrimp producers: Quantity (tonnes) and different species in 2019.

Country	*L. vannamei*	*P. monodon*	*P. chinensis*	*P. japonicus*	*P. indicus*	Total
	Top producers (>150,000 t)					
Ecuador	1,815,550	84,066	38,583	50,968	-	1,989,167
China	679,985	-	-	-	-	679,985
Vietnam	724,268	34,615	-	-	-	758,883
Indonesia	697,100	191,300	-	-	-	888,400
India	170,073	-	-	-	-	170,073
Thailand	365,503	17,364	-	-	-	382,867
Mexico	577,000	261,000	-	-	-	838,000
Total top prod.	5,029,479	588,345	38,583	50968	-	5,707,375
	Mid producers (> 40,000 t<150000t)					
Bangladesh	63,171	-	-	-	2,098	65,269
Iran	55,000	-	-	-	-	55,000
Myanmar	-	51,796	-	-	-	51,796
Peru	43,481	-	-	-	-	43,481
Philippines	19,152	45,733	-	-	-	64,885
Saudi Arabia	60,800	-	-	-	-	60,800
Total Mid Prod.	241,604	97,529	-	-	2,098	341,231
Total	5,271,083	685,874	38,583	50,968	2,098	5,600,000

Source: (FAO Yearbook. Fishery and Aquaculture Statistics 2019/FAO. Rome).

Based on the latest statistics from 2022, global shrimp production reached 5.6 million metric tons, marking an 11.5 percent increase from the previous year. It is projected that global shrimp supply could reach a record-breaking 6 million metric tons in 2023. As a result, the value of the global shrimp market is estimated to reach 25 billion dollars by 2026 (Jiménez-Ortega *et al*., 2025).

It has been determined that approximately 75 percent of global shrimp production comes from aquaculture which is currently almost totally dominated by two species—*P. monodon* and *L. vannamei* (Walker and Winton, 2010). Despite these challenges, shrimp farming continues to be an important source of food and livelihoods for many people around the world. With the development of more sustainable and responsible practices, the industry has the potential to continue to grow and contribute to global food security (Munasinghe *et al.*, 2010; Thornber *et al.*, 2020).

Since 1981, several new viral pathogens have emerged in succession, causing widespread mortality and threatening the economic sustainability of industries in Asia and the Americas. White spot syndrome virus (WSSV) is one of the biggest threats to shrimp aquaculture in many countries, especially Asian countries. This virus has caused a significant decrease in shrimp production, due to which many shrimp farmers and hatchery owners had to face huge economic losses (Walker and Mohan, 2009). Starting from the primary account of the outbreak in China and then in Taiwan during the years 1991 and 1992, the WSSV was recognized to be responsible for substantial financial hit in shrimp generation industry in several countries, particularly in South America and South-East Asia ((Flegel *et al.*, 1999; Escobedo-Bonilla *et al.*, 2008; Lin *et al.*, 2012). The total economic loss from WSD since the first outbreak of the disease, is estimated at $8–15B and the loss continues to upsurge by $1B annually, which is approximately 3% of global shrimp production (Oakey *et al.*, 2019 Panchal *et al.*, 2021).

Several investigations have been done to evaluate disinfectants effect on WSSV (Park *et al.*, 2004; Corre Jr *et al.*, 2012). Applying immunostimulants and vaccine-like compounds have also been investigated to control WSSV (Witteveldt *et al.*, 2004; Afsharnasab *et al.*, 2014; Amar *et al.*, 2021). To date, there have been no reported treatments for WSSV. Therefore, the implementation of preventive measures is crucial in avoiding the disease, and biosecurity actions have proven to be effective in reducing the risk of WSD outbreaks and preventing the spread of the pathogen (Tendencia *et al.*, 2011; Moss *et al.*, 2012).

However, there is currently a lack of comprehensive and well-defined information regarding the WSSV virus. Therefore, the objective of this review article is to present a comprehensive understanding of the biological and management aspects of the WSSV virus. By doing so, this article aims to contribute to crisis management strategies and address the economic implications of this virus within the shrimp aquaculture industry.

Biology

Viruses seem to be the most abundant biological organisms on the planet (Koonin and Dolja, 2013). Shrimp is one of the main aquaculture species in the world and different viruses affect them, which causes serious mortality to economically important species, such as *P. monodon*, *L. vannamei* and *L. stylirostris*, among others.

The emergence of many viral diseases has caused changes in penaeid shrimp aquaculture (Peeler, 2012). White Spot Syndrome Virus (WSSV) is one of the most devasting viral diseases affecting the shrimp farming industry which have spread rapidly across the globe through trading, mainly via live animals and potentially also commodity products during the last decade (Bateman *et al*., 2012). According to Chou *et al.* (1995) the first report of WSSV prevalence was evidenced in northern Taiwan causing massive mortality in penaeid shrimp. The viral agent was detected from Japan's outbreak in late 1993 (Inouye *et al*., 1994) and in a few years, this new pathogenic agent expanded in shrimp farms in several countries swiftly (Flegel, 1997).

Taxonomy

The WSSV was known by various names until 2005 when the international name of the virus was confirmed (Fauquet *et al*., 2005). Because of cylindrical morphology of WSSV and the histopathological effects similar to ‘‘nonoccluded’’ baculoviruses, it originally called baculovirus. Hypodermal and hematopoietic necrosis baculovirus (HHNBV) (Huang *et al*., 1995), rod-shaped nuclear virus of P. japonicus (RV-PJ) (Takahashi *et al*., 1994), Chinese baculovirus (CBV), systemic ectodermal and mesodermal baculovirus (SEMBV) (Vickers *et al*., 2000), penaeid rod-shaped DNA virus (PRDV) (Vickers *et al*., 2000), white spot baculovirus (WSBV) are the other names of the White spot Virus that was known earlier and now it called as white spot syndrome virus (WSSV) (Lightner, 2011) and WSD is almost indicated as the disease caused by WSSV. The WSSV was initially classified as the subfamily of Nudibaculoviridae (Dey *et al*., 2020), belonging to Baculoviridae. Nevertheless, they replaced it by a family called Whispoviridae (Jang *et al*., 2011). It was then listed into a new family named Nimaviridae covering a genus, Whispovirus, which has a single species, WSSV (Murphy *et al*., 1995; Sánchez-Martínez *et al*., 2007; Bateman and Stentiford, 2017).

Based on genomic structure and unique morphology of WSSV, the taxonomic position of the virus was assigned by the International Committee of Taxonomy of Viruses (ICTV) to Whispovrius as a new genus, under the family of Nimaviridae (Durand *et al*., 1997; Mayo, 2002). The reason for classifying WSSV in the family Nimaviridae was a thread-like polar extension at one end of the virus particle (Pradeep *et al*., 2012).

Morphology and Ultrastructure features

White spot syndrome virus (WSSV) is a double-stranded DNA virus with a diameter ranging from 80 to 120 nm and a length of 250 to 380 nm (Durand *et al*., 1997). The ultrastructure of WSSV has been determined through two approaches: (i) Transmission electron microscopy (TEM) analysis of isolated nucleocapsids confirmed that they consist of stacked loop segments. Each loop segment is composed of three rows of subunits connected by strands, deviating from the typical helical structure. (ii) Investigation of the morphological characteristics of virus self-assembly at different stages revealed two distinct enveloping morphologies, suggesting that the virion undergoes two separate envelopment processes. Based on these findings, a model for viral membrane assembly in WSSV is proposed (Wang *et al.*, 2000; Li *et al.*, 2020). Intact enveloped virions of WSSV have a length ranging from 210 to 380 nm and a maximum width of 70 to 167 nm (Reddy *et al.*, 2013). In negatively stained electron micrographs, some virions exhibit a tail-like and unique addendum at one end. The viral envelope is approximately 6-7 nm thick and consists of a membrane structure containing 35 different proteins. Among these proteins, VP28 and VP26 are the most abundant and play crucial roles containing pathogenicity, accounting for approximately 60% of the envelope composition (Sanchez-Paz, 2010). During the investigation of the nucleocapsid proteins of WSSV, two important proteins were listed: a basic DNA-binding protein called VP15, and a giant protein known as VP64. These proteins form the stacked ring subunits of the nucleocapsid. The virions of WSSV have a rod-shaped to oval morphology and are characterized by their large size, measuring approximately 80-120 nm in width and 250-380 nm in length (Fig. 1).

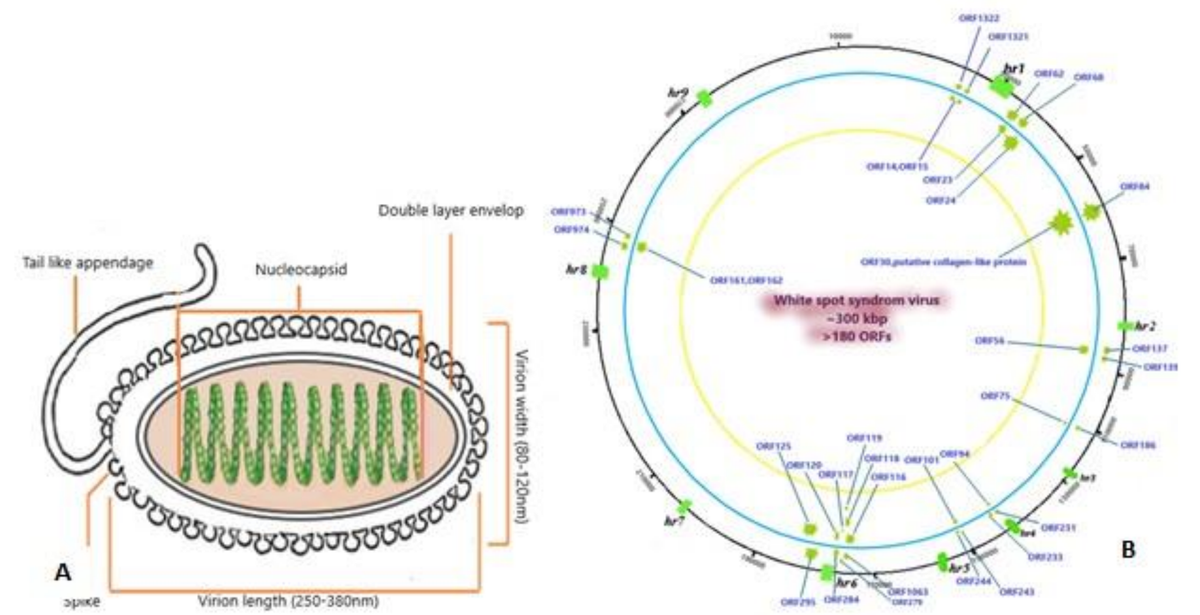

Figure 2: The general structure (A) and complete genome sequences (B) of shrimp White Spot Syndrome Virus.

Additionally, these virions possess a trilaminar envelope. (Van Hulten *et al.*, 2001). Morphologically, the virions have three distinct layers and are composed of at least 45 structural proteins(Tsai *et al*., 2004). The most important histological sign of WSSV infection is the enlargement of cell nuclei. WSSV predominantly infects tissues derived from the ectodermal (cuticular epidermis, foregut and hindgut, gills, and nervous tissues) and mesodermal (connective tissue lymphoid organ, antennal gland, and hemopoietic tissue) origins (Wongteerasupaya *et al*., 1995).

Genome and structural protein

The study of the genome and structural proteins of White spot syndrome virus (WSSV) is essential for understanding the biology of this virus and developing strategies to control its spread and impact on shrimp and other crustacean populations. The WSSV genome is a large, circular double-stranded DNA molecule that is approximately 300 kilobases (kb) in length (Oakey and Smith, 2018). It contains over 180 open reading frames (ORFs) that encode various proteins, including enzymes involved in viral replication and proteins that interfere with the host immune response. Only a small percentage (6%) of the WSSV ORFs have putative homologues in databases, primarily representing genes encoding enzymes for nucleotide metabolism, DNA replication, and protein modification (Huang *et al*., 1995; Van Hulten *et al*., 2001). The majority of the ORFs remain unassigned, with the exception of five that encode structural virion proteins. Notable features of the WSSV genome include a very elongated ORF of 18,234 nucleotides with an unidentified role, a collagen-like ORF, and nine regions dispersed throughout the genome that each contain a variable number of 250-base pair tandem repeats (Zhang *et al*., 2004). The genome of White spot syndrome virus (WSSV) spans approximately 300,000 base pairs (bp) in length. WSSV possesses a relatively large genome and harbors more than 180 open reading frames (ORFs) responsible for encoding a diverse array of viral proteins. WSSV also produces several structural proteins that constitute the virus particle. Among these, the major structural proteins encompass VP24, VP26, VP28, VP37, and VP51 (Verbruggen *et al*., 2016; Kawato *et al*., 2019b), which collectively form the viral capsid. Additionally, the envelope protein VP19 and tegument proteins including VP39 and VP41 contribute to the assembly and release of the virus particle. These structural proteins play crucial roles in facilitating WSSV's ability to infect host cells and induce disease. Specifically, VP26, an envelope protein, acts as a matrix-like linker protein between the viral envelope and nucleocapsid, thus playing a pivotal role in the envelopment of the WSSV virion (Wang *et al*., 2021). VP28, another major structural protein of WSSV, has garnered considerable attention from researchers and the aquaculture industry. It exhibits high immunogenicity and has been utilized in the development of WSSV vaccines. VP28 is also being investigated as a potential tool for the diagnosis and surveillance of WSSV in shrimp populations (Raguraman *et al*., 2020).

Replication and metabolism

White spot syndrome virus (WSSV) exhibits a broad host range among decapod crustaceans, particularly in shrimp. In the absence of clinical signs, the virus commonly persists as a low-level infection.

However, under certain environmental stress factors such as changes in salinity or lower temperatures, there can be rapid increases in viral load, leading to mass mortalities in ponds (Vidal *et al.*, 2001; Granja *et al.*, 2006; Reyes *et al.*, 2007). There is evidence suggesting that higher water temperatures can serve as a crucial factor in preventing the onset of disease. (Rahman *et al.*, 2006). The most efficient replication of WSSV occurs within the temperature range of 23-28°C (Guan *et al.*, 2003; Kakoolaki *et al.*, 2014).

The replication and metabolism of White spot syndrome virus (WSSV) involve several distinct steps. Upon entry into the host organism, the virus attaches to cells in the shrimp's digestive system (Verma *et al.*, 2017; Zheng *et al.*, 2019), subsequently delivering its genetic material into the host cell. Subsequently, the viral genetic material commandeers the host cell's machinery, compelling it to synthesize additional copies of the virus (Sanchez-Paz, 2010; Verma *et al.*, 2017). With remarkable speed, the virus undergoes rapid replication, generating thousands of new virus particles within a few hours. As the virus disseminates throughout the host's body, it impairs tissues and organs, giving rise to the characteristic white spots on the shrimp's shell (Chen *et al.*, 2016). WSSV is a DNA virus, thereby relying on the host cell's DNA replication machinery to generate new virus particles. The virus is also reliant on a range of host cell factors, including enzymes and proteins, to facilitate completion of its life cycle (Sanchez-Paz, 2010; Zheng *et al.*, 2019). In terms of metabolism, WSSV is an energetically demanding virus, necessitating a constant supply of nutrients and energy for replication. The virus is capable of utilizing a diverse array of carbon and nitrogen sources such as glucose, amino acids and nucleotides to sustain its replication (Alfaro *et al.*, 2021).

Epidemiology and geographical distribution

WSSV is a lethal virus and highly contagious that poses a significant threat to global shrimp aquaculture in various regions worldwide (Flegel, 2006b). The virus is particularly prevalent in Asia, with notable occurrences reported in countries such as China (Xu *et al.*, 2021b), Thailand (Flegel, 2006b), and Vietnam (Duc *et al.*, 2015). Additionally, WSSV has been reported in other countries, including India, Indonesia, Japan, Malaysia, the Philippines, and Taiwan (Flegel, 2006a; Thitamadee *et al.*, 2016). The evolutionary history of WSSV has long remained a mystery, partly due to the limited knowledge of WSSV relatives, or nimavirus. However, Kawato *et al.* (2019a) conducted a study revealing that WSSV belongs to a diverse family of large DNA viruses called Nimaviridae, which specifically infect crustaceans. They also found that WSSV possesses a unique set of host-viral interaction-related genes, which contribute to its efficient infection and replication within shrimp and other crustaceans. These genes play a crucial role in the pathogenesis of WSSV and its ability to evade the host immune response (Dhar *et al.*, 2003).

White Spot Disease has a significant economic impact on the shrimp industry due to its ability to cause high mortality rates in infected shrimp populations, leading to substantial financial losses for farmers (Kakoolaki *et al.*, 2011). Therefore, comprehending the geographical distribution of WSD is crucial for preventing its distribution and controlling outbreaks. WSD is commonly observed in shrimp farming regions worldwide, including Asia, South America, and Australia (Oakey *et al.*, 2019). The prevalence of the disease can vary depending on environmental conditions and specific regions. Factors such as water temperature (Rahman *et al.*, 2007b; Barajas-Sandoval *et al.*, 2023) and salinity (Yin *et al.*, 2023), levels can contribute to the transmission of the disease. Generally, regions characterized by warm-water conditions and high shrimp densities are at the greatest risk of experiencing outbreaks.

In the Americas, WSD has been reported in several countries, including Mexico (Hill, 2002; Galavíz-Silva *et al.*, 2004; López-Téllez *et al.*, 2020), Ecuador (Rodriguez *et al.*, 2003), and Brazil (Cavalli *et al.*, 2008). A study conducted in Mexico in 2018 revealed the presence of WSD in imported shrimp broodstock, emphasizing the importance of implementing biosecurity measures to prevent the spread of the WSSV (Hill, 2002). In Brazil, WSD outbreaks have been documented in various regions, prompting researchers to study the virus extensively to develop effective control measures (Cavalli *et al.*, 2008). In 2016, WSD was initially identified in shrimp farms located in Australia. This outbreak had severe consequences, resulting in the widespread loss of millions of shrimp and necessitating the enforcement of rigorous biosecurity measures to impede the transmission of the disease (Oakey *et al.*, 2019). In response to this crisis, the Australian government has engaged in close collaboration with the shrimp industry to establish a comprehensive national management plan specifically designed to address the challenges posed by WSD (Loynes, 2017).

The WSD epidemics originated in China and subsequently spread to Taiwan between 1991 and 1992 (Flegel, 2012). From there, the disease rapidly distributed to various Asian countries. By the end of the decade, WSD had also reached Korea (Park *et al.*, 1998), Japan (Inouye *et al.*, 1994), SE Asia (Vietnam, Thailand, Malaysia, Indonesia) and India (Mohan *et al.*, 1998). In particular, Thailand has faced substantial economic losses in recent years as a result of outbreaks of WSD (Chantanachookin *et al.*, 1993). The rapid spread of WSD may be attributed to the international trade of infected prawns, including brood-stock and post-larvae (PLs). By 1999, WSD had reached South America (Lightner *et al.*, 2012). In Asia, countries like Thailand have faced significant challenges due to multiple outbreaks in recent years. In 2015, an outbreak of WSD in Thailand resulted in the destruction of millions of shrimp and incurred losses exceeding 10 billion baht (Yaemkasem *et al.*, 2022). Researchers in Thailand have been actively studying WSD and working on the development of new diagnostic methods. These efforts aim to assist shrimp farmers in the early detection of white spot disease, enabling them to take preventive measures and limit its spread. (Sampantamit *et al.*, 2020). The analysis of Thailand isolates collected between 2007 and 2014 has revealed that the most prevalent genotype (MPG) is similar to those found in Saudi Arabia, Madagascar, Mozambique, Japan, and India. Additionally, in 2001, WSD was reported in shrimp farms in the northern part of the Persian Gulf, specifically in the Khuzestan province of Iran, and subsequently spread to other shrimp farming areas within the country (Afsharnasab *et al.*, 2014). In 2010, the emergence of WSD was observed in Saudi Arabia, affecting *P. indicus*, similar to the species affected in Iran. As a result, both countries transitioned to the cultivation of a new species, specific pathogen-free (SPF) *L. vannamei*, which was imported in 2013-2014 (Afsharnasab *et al.*, 2016; Alday-Sanz *et al.*, 2020). Between 1996 and 2001, the cumulative mortality caused by WSD worldwide amounted to one million tonnes. This suggests that the source of the white spot syndrome virus (WSSV) in Saudi Arabia, Madagascar, and Mozambique may be linked to Southeast Asia, where broodstocks and post-larvae (PLs) were supplied for their farms. According to Zeng (2021), WSSV isolates from Iran exhibited unique sequencing information in variable region (VR) 75. Most of the isolates were classified into two groups: G.I, characterized by a first 8-repeat unit (RU) motif (a-L-b-c-M-b-c-d), and G.II, characterized by a first 11-RU motif (a-L-b-c-d-c-Q-f-T-f-c). These findings were based on the analysis of the open reading frame (ORF) 75, without considering the VR14-15 and VR23-24 regions. In contrast to Iran, other isolates were categorized into four sub-genotypes. Sub-genotype I displayed a first 11- repeat unit (RU) motif (a-L-b-c-d-c-M-c-e-N-f), sub-genotype IIa (Van Hulten *et al.*, 2001) had a 6-RU motif (a-L-g-h-N-f-f-P-f-c), sub-genotype IIb had a 6-RU motif (a-L-g-h-i-N-f), and sub-genotype II encompassed other isolates with smaller RU motifs (p-f-c or a-L-b-c-d-c-M-g-h). Based on the ORF23/24 locus map (Pereira *et al.*, 2019) PCR amplification and sequencing of a 400-bp fragment revealed differences between the isolates from Indonesia, Iran, and the Philippines. These isolates showed 100% similarity to the WSSV-TH isolate, with a deletion of 13,210 bp compared to WSSV-TW (Zwart *et al.*, 2010). The source of WSD in Iran, including Abadan and Khouzestan isolates was reported to originate from Southeast Asia (Simrouni *et al.*, 2014). Moreover, these isolates exhibited a close genetic relationship to a cluster of isolates from Vietnam (Table 2), characterized by shorter genotypes. Additionally, the older samples from India2 (pre-2005) and isolates from Thailand2 and Thailand3 showed genetic similarity to the USA genotype (Shekar *et al.*, 2012). Based on the VR23/24 analysis, WSSV-VN isolates Tv and Kg displayed deletions of 11,450 bp and 12,166 bp, respectively, compared to the WSSV-TW genome. Isolate Kg was suggested to be more closely related to WSSV-CN and WSSV-TH rather than WSSV-TW (Table 2).

Table 2: The occurrence of WSD in different countries: Concerning attributes.

Country	Year	VR	Genotype	Characteristics or Similar Isolates	References
Thailand	2007-2014	14-15, 23-24	5950, 10971	WSSV. Ja, 95- WSSV. CB, 06- WSSV.In, 05- WSSV. SA, 2010- WSSV. MA 11- WSSV. MZ, 12-	(Pradeep *et al*., 2009; Zwart *et al*., 2010; Tang *et al*., 2013; Piamsomboon *et al*., 2018)
Thailand	2007-2014	14-15*, 23-24	6031*, N/K	WSSV. TH-S, 96- WSSV.PHI, 99- WSSV. INDO, 08-	(Zwart *et al*., 2010; Piamsomboon *et al*., 2018)
Iran	unknown	ORF75	Three genotypes: S, T and Q	unique sequences	(Dieu *et al*., 2004; Zeng, 2021)
Globally	unknown	ORF75	Four sub-genotypes	I:WSSV-TH, TH-96-II, KX686117-CN, KU216744-MX; IIa: WSSV-CN, KT995472-CN, KR083866-EG, MX-F&C&G&H, AF403004-SG, MN-840357-US, MH090824-EC; IIb: WSSV-TW, MG264599-BR, Mx12-1; II: MG432482-MX, MH883319-IN, KX650068-IR,KT995470-CN,KX694239-IR	(Zeng, 2021)
Japan and Cambodia	<2010	ORF23/24	isolates	Indian isolate (ACC. No. EU 327499) with a deletion of about 10,970 bp compared to WSSV-TW.	(Zwart *et al*., 2010)
Japan, Iran and Cambodia	<2010	ORF23/24	isolates	Have the same 5,950 bp deletion present in VN-X and VN-S	(Zwart *et al*., 2010)
Iran	2012	ORF94	IRWSSVBU1 and 2, IRWSSVKH3 and 6	WSSV-TW, WSSV-TH, WSSV-CN with 6, 6, and 12 RUs, respectively and no similarities with Saudi Arabia due to different RUs (7-13)	(Simrouni *et al*., 2014)
Mexico	2005	ORF23/24	ACF2, ACF4, LC1, LC10, DVI, AC1, LG, GVE05, JP,	China (LC1, LC10, DVI) and Korea (ACF2, ACF4)	(Parrilla-Taylor *et al*., 2018)
Vietnam	2003-4	a-ORF94 b-ORF23/24	a-WSSV-VN-central: S, X. K, T and L had a deletion b- WSSV-VN-Kg	a-number of RUs was varied between the isolates (7-17). WSSV-VN- central 100% identity with WSSV-TW and WSSV-TH. WSSV-TH and WSSV-VN-T are highly homologous. b- Identity with WSSV-CN and WSSV-TH rather than WSSV-TW	(Dieu *et al*., 2004)
Vietnam	2004	a-ORF14/15 b-RF14/15, 23/24	a-VN-HT b-VN-BR	a-Maybe recombination between directly introduced WSSV-TW and existing Vietnamese genotypes. b-Identical to WSSV-TH in both the ORF23/24 and ORF14/15 loci, suggesting perhaps introduced from Thailand.	(Dieu *et al*., 2010)
India	1990s-2010s	36 locus in 6 PCRs with STR markers	1:OTN1-3 (*P. monodon*), 2:NTN1-4 (*L. vannamei*)	1: Major genotypes closed to Vietnam cluster and finally to USA cluster. 2: Major genotypes closed to Ecuador cluster and major genotypes of the Thailand and China clusters.	(Oakey *et al*., 2019)
India	2005-2006	a-ORF94 b-ORF125	13 genotypes	a-RUs showed 2-16. The most prevalent genotype with 4 RUs (47.1%). No observed 6 and 13 RUs. b-Similarities of tandem repeats in ORF 125 among WSSV infected carriers (wild shrimp Acetes sp., crabs) and cultured shrimp (Horizontal transmission)	(Pradeep *et al*., 2008)
China	1998-99	a-ORF23/24 b-ORF14/15	a-WSSV98NB2 (with three genotypes 6, 9 and 14 RUs), W WSSV98SZ3*, SSV99GZ*. b- 3genotypes:1) WSSV98NB2; 2)WSSV98SZ1,3 ,WSSV98NB; 3)WSSV98SZ2,4 and WSSV99GZ	a- compared to WSSV-TW. *identical to WSSV-CN (1996). b- compared to WSSV-TH-96-II.	(Tan and Shi, 2011)

Host susceptibility

The susceptibility of shrimp to the WSSV is influenced by various factors, including both genetic and environmental factors (Chen and He, 2019). Genetic factors play a significant role in determining the susceptibility of shrimp to WSSV. Genetic factors play a crucial role in determining the susceptibility of shrimp to WSSV. Different shrimp species exhibit varying levels of resistance to the virus, with certain populations demonstrating higher resistance compared to others (McLean *et al.*, 2020). For instance, certain shrimp populations in Asia have shown greater resistance to WSSV than populations in other regions. Furthermore, a study conducted by Robalino *et al.* (2011) identified a specific allele of the PmRab7 gene that was associated with increased resistance to WSSV in shrimp. This finding suggests that selective breeding aimed at enhancing genetic traits could potentially enhance resistance to WSD.

In addition to genetic factors, environmental criteria also play a significant role in determining the susceptibility of shrimp to WSSV. In addition to water quality, temperature, and stress levels can all influence the ability of shrimp to resist the virus, age, size, and nutritional status are other factors that can impact susceptibility to WSSV. Typically, juvenile and smaller shrimp are more susceptible to the virus compared to larger, more mature shrimp (Qayoom *et al.*, 2023). High stocking densities and inadequate nutrition can increase stress levels in shrimp, making them more vulnerable to WSSV (Apún-Molina *et al.*, 2017).

Furthermore, malnourished or underfed shrimp often exhibit weakened immune systems, rendering them more susceptible to WSD. Inadequate nutrition can compromise the shrimp's ability to fight off the virus (Sánchez-Paz *et al.*, 2012). Poor water quality and higher or lower temperatures can also have detrimental effects on the immune system of shrimp, making them more vulnerable to WSSV (Lehmann *et al.*, 2016). Factors such as low dissolved oxygen levels and elevated levels of ammonia and nitrite in the water can increase stress levels in shrimp, further contributing to their susceptibility to WSSV (Kakoolaki *et al.*, 2011).

Water temperature is a crucial environmental factor that can influence the susceptibility of shrimp to WSSV. Zhang *et al.* (2016)) reported that water quality and temperature have an impact on the susceptibility of shrimp to WSSV. In a study, You *et al.* (2010) demonstrated that high water temperatures (above 30°C) increase the vulnerability of shrimp to WSSV. This is because elevated temperatures can compromise the shrimp's immune system, rendering them more susceptible to infections. Furthermore, heightened levels of stress can weaken the shrimp's immune system, making them more prone to WSD. For instance, factors such as overcrowding and poor water quality can elevate stress levels in shrimp result in their vulnerability to WSD (Islam *et al.*, 2023).

Yu *et al.* (2003) revealed that changes in salinity can induce alterations in total haemocyte count (THC), phenoloxidase (PO) activities and WSD outbreak in the kuruma shrimp (*Marsupenaeus japonicus*), with salinity serving as a significant environmental factor that impacts the immune responses. Moreover, they observed that shrimp maintained at salinity levels different from their original habitat exhibited weakened immune responses (Kakoolaki *et al*., 2011), rendering them more susceptible to WSSV under salinity-induced stress (Table 3).

Table 3: Host susceptibility of WSSV.

Host	Region	Infection type	Infection severity	Environmental stressors	References
L. vannamei *L. stylirostris* *P. setiferus* *P.aztecus* *P.duorarum*	America	trial and pond	Serious mortality in post-larvae and juvenile stage	different	Lightner *et al*., 1997
P. monodon, *P. japonicus* *P. monodon*	Taiwan India	trial trial	• 40% mortality during 14 days • 100% mortality within 5-7 days in shrimps, survival of two species of mud crab (*Scylla* sp.) for 30 days and three species of lobsters (*Panulirus* sp.) and *Macrobrachium rosenbergii* for 70 days	ammonia	Wang *et al*., 1997; Rajendran *et al*., 1999
F. chinensis				tem: 30°C, S.: 35%, pH: 8.0 become worst at tem: 15°C, S.: 35%, pH: 9.0	Gao *et al*., 2011
L. vannamei	Mexico	trial	To reduce false-negative PCR	Tem:29°C for 48 h before collecting samples to PCR analysis	Moser *et al*., 2012
Macrobrachium rosenbergii	India	trial	Mortality and cannibalism range: - in post-larvae= up to 28% and 28–40%, respectively - in juveniles=10–20% and 6.7–30.0%, respectively - in sub-adults= 2.8-6.7%, and up to 20%, respectively		Kiran *et al*., 2002
Marsupenaeus japonicus	China	trial	Mortality: mild-severe	Salinity variations from the optimum rate (33ppt) decrease THC and increase PO activities.	Yu *et al*., 2003
P. indicus	Iran	trial and pond	Mortality: 36 hpi*	Tem:25°C Salinity: 50 ppt	Kakoolaki *et al*., 2015
L. vannamei	Vietnam	trial	Mortality: reduce in the early stages of wssv infection	Tem:33°C	Rahman *et al*., 2007a

*hpi= hours post incubation.

In another experimental study by Rajendran *et al.* (1999), various crustacean species were exposed to white spot syndrome virus (WSSV) obtained from infected *P. monodon* shrimp. The findings demonstrated that all species tested, including shrimp, freshwater prawns, crabs, and lobsters, were susceptible to the virus. The infected shrimp displayed identical clinical symptoms and histopathological characteristics to naturally infected *P. monodon*. Shrimp injected with WSSV experienced a 100% cumulative mortality rate within 5-7 days, while those fed infected tissue succumbed within 7-9 days. Notably, two species of mud crab (*Scylla* sp.) survived the infection for 30 days without exhibiting any symptoms, and all three species of lobsters (*Panulirus* sp.) and the freshwater prawn (*Macrobrachium rosenbergii*) survived for 70 days without clinical signs. However, bioassay and histological analyses using healthy *P. monodon* indicated that crabs, prawns, and lobsters could potentially serve as asymptomatic carriers or reservoir hosts of WSSV. These findings shed light on the carrier/reservoir capacity of these hosts through detailed histological and bioassay investigations.

Kakoolaki *et al.* (2015) conducted a study on shrimp farms in Iran to investigate the relationship between water temperature and salinity levels and the occurrence of white spot syndrome virus (WSSV). The researchers discovered a significant correlation between the occurrence of WSSV and elevated water temperature and salinity levels. These findings suggest that these environmental factors may contribute to the spread of the virus within shrimp farms in Iran. The study concluded that fluctuations in salinity and a decrease in water temperature are crucial factors in the occurrence of WSSV and the resulting high mortality rates in shrimp culture sites. Rahman *et al.* (2007a) investigated the impact of high-water temperature (33°C) at different stages of infection with highly virulent (WSSV Thai-1) and low virulent (WSSV Viet) strains of WSSV in *L. vannamei* juveniles. The researchers demonstrated that temperatures exceeding 33°C effectively reduced mortality and inhibited WSSV replication, thereby leading to a decrease in infection severity depending on the stage of infection. Moser *et al.* (2012) evaluated the influence of thermal stress on the replication rate of WSSV in shrimps exposed to warm water (29±0.5°C) compared to those held in cooler water (18±0.5°C). The study aimed to enhance virus detection in epidemiological programs. The results indicated that water temperature exerted a significant and profound effect on the replication rate of WSSV in *L. vannamei*. Therefore, considering environmental temperature as a key management strategy for selecting WSSV-free spawning shrimp is crucial for the shrimp farming industry in all producing countries, based on the research findings of these scientists.

The cumulative mortality in post-larvae reached a maximum of 28%, with cannibalism accounting for a significant loss of up to 68% while the corresponding brood stock was introduced to WSSV (Kiran *et al.*, 2002). The juveniles exhibited mortality rates ranging from 10% to 20% and cannibalism rates between 6.7% and 30.0%, resulting in a maximum loss of

50%. Sub-adults displayed mortality rates varying from 2.8% to 6.7%, cannibalism of up to 20%, and an overall loss of up to 26.7%. Furthermore, the study observed that sub-adults and adults exhibited greater tolerance to WSSV infection, as evidenced by the mortality patterns.

Induced the disease in the brood stock, and subsequently tested the eggs and larvae for WSSV infection. The results showed that all stages, except for the eggs, tested positive for WSSV infection through histopathology, cross infection bioassay, and polymerase chain reaction (PCR) analysis. Post-larvae and juveniles that were experimentally infected exhibited high mortality rates and increased cannibalism. The cumulative mortality in post-larvae reached up to 28%, with cannibalism contributing to a maximum loss of 68%. Juveniles experienced mortality rates of 10-20% and cannibalism rates of 6.7-30.0%, resulting in a maximum loss of 50%. Sub-adults showed mortality ranging from 2.8% to 6.7%, cannibalism of up to 20%, and a total loss of up to 26.7%. It was observed that sub-adults and adults displayed greater tolerance to the infection based on the mortality pattern. A nested (two-step) PCR analysis successfully yielded a 570-bp product specific to WSSV in all stages except for the eggs.

Transmission

Once the WSSV enters a susceptible host, it undergoes rapid replication and spreading throughout the animal body. The virus invades and destroys different tissues and organs, resulting in a spectrum of clinical manifestations, such as lethargy, loss of appetite, and the formation of white spots on the carapace (Cheng *et al.*, 2021; Lee *et al.*, 2022). The severity of the disease is influenced by several factors, including the host age and species, the virulence of the virus strain, and prevailing environmental conditions (Jayasree *et al.*, 2006; Millard *et al.*, 2021).

One of the most important modes of transmission (Lee *et al.*, 2023) is through the movement of infected animals from one area to another . This can occur through the trade of live animals, the transport of infected animal, or the movement of contaminated water (Lightner *et al.*, 1997). International trade of live shrimp and shrimp products has been identified as the primary pathway for the spread of WSSV to new areas (Soowannayan and Phanthura, 2011). The virus can also be transmitted through the release of infected wastewater or by contaminated equipment, such as nets or tanks (Alavandi *et al.*, 2014; Ng *et al.*, 2018; Xu *et al.*, 2021b).

To prevent the transmission of WSSV, many countries have implemented strict regulations and biosecurity measures, such as screening for the virus prior to importation of live animals or products, and disinfection of equipment and facilities (Ng *et al.*, 2018; Wan *et al.*, 2023). Additionally, oral vaccination and improved management practices are being developed to reduce the impact of the virus on the aquaculture industry (Yogeeswaran *et al.*, 2012). However, the effectiveness of these measures can be limited by various factors, including the lack of a reliable diagnostic test and the difficulty in controlling the spread of the virus in open systems (Peeler and Taylor, 2011; Flegel, 2019).

Managerial measures

In order to prevent and control the spread of the WSSV, various managerial measures have been developed and implemented (Kakoolaki *et al.*, 2015; Lee *et al.*, 2023). These measures can be categorized into three main categories: biosecurity measures, hygiene measures, and management strategies (Lightner *et al.*, 1997).

Biosecurity measures are designed to prevent the introduction of the virus into shrimp farms and to minimize the risk of transmission within farms. This can include measures such as use of SPF animal stock (Alday-Sanz *et al.*, 2020), screening of shrimp entering the site and ponds (Amar *et al.*, 2021), quarantine procedures (Lightner, 2005; Delphino *et al.*, 2022), and strict controls on the movement of people and equipment onto and off of the farm (Munasinghe *et al.*, 2010; Kakoolaki *et al.*, 2022). Additionally, farms can implement measures such as the use of closed systems to prevent contact with external sources of infection (Lorgen-Ritchie *et al.*, 2023), and the use of herbal medicine to reduce the risk of contamination (Zhang *et al.*, 2023). These measures have been shown to be effective in reducing the incidence of WSD in shrimp farms (Moss *et al.*, 2012; Delphino *et al.*, 2022).

Hygiene measures are focused on reducing the risk of transmission of the virus within a farm. This includes measures such as maintaining clean and well-maintained equipment (Widiasa *et al.*, 2023), and the use of protective clothing and equipment by workers (Desrina *et al.*, 2022). Regular cleaning and disinfection of ponds or tanks, equipment and facilities can also help to reduce the risk of transmission. In addition, farms can implement measures such as the use of probiotics to promote healthy shrimp (Sharifuzzaman and Adhikari, 2013; Sumon *et al.*, 2022).

Management strategies are designed to reduce the impact of the virus on shrimp farms. This includes measures such as the use of selective breeding to develop disease-resistant variants (Islam *et al.*, 2023), and the implementation of probiotic programs (Lightner, 2005). Additionally, farms can implement measures such as the use of alternative feed sources to reduce stress on the shrimp, which can make them more un-susceptible to infection (Zhang *et al.*, 2023). These measures have been shown to be effective in reducing the incidence and impact of WSD in shrimp farms (Walker and Mohan, 2009).

Disinfections

Disinfection is an important aspect of controlling and managing WSSV in shrimp farms. The virus can survive for extended periods of time in both water and sediment, which makes it difficult to eradicate once it has become established in a shrimp farm (Islam *et al.*, 2023). Disinfection can help to prevent the spread of the virus between ponds and farms, and can also help to reduce the viral load within individual ponds (da Silva *et al.*, 2021).

Some effective disinfection compounds have been used in shrimp farming include potassium permanganate, chlorine (He *et al.*, 2024), hydrogen peroxide, and ozone (Ghosh, 2023). Chlorine is a commonly used disinfectant that is effective against WSSV, but it can be corrosive and toxic at high concentrations (Islam *et al.*, 2023), and its efficacy can be reduced by organic matter in the water.

Hydrogen peroxide is another effective disinfectant that can be used to treat both water and sediment, but it can also be toxic at high concentrations and may require special equipment to apply (Ghosh, 2023). Ozone is a powerful oxidizing agent that can be used to disinfect water, but it is expensive and can be difficult to apply in shrimp farm settings (Widiasa *et al.*, 2023). In addition to disinfection, other management strategies for controlling WSSV in shrimp farms include stocking healthy shrimp (Cox *et al.*, 2023), using proper water management practices, and implementing biosecurity measures to prevent the introduction of the virus into the farm (Corsin *et al.*, 2001). This includes maintaining appropriate water quality parameters. Acidic pH is usually hinder survival or transmission of WSSV. Therefore, it may overcome this inactivation through vectors present in the environment including microplastic (Shan *et al.*, 2023), zooplankton or phytoplankton (Cox *et al.*, 2023). temperature, and salinity, as well as ensuring adequate water exchange and circulation. Biosecurity measures, such as screening new stock for the virus and preventing the introduction of contaminated water or equipment, can also be effective in preventing the spread of WSSV within a farm (Lightner, 2005).

Environmental control

Environmental control is an important aspect of managing WSSV in shrimp farms. The virus can survive for extended periods of time in both water and sediment, making it critical to control the aquatic environment in and around shrimp farms to prevent the spread of the virus.

Maintaining appropriate water quality parameters is an important aspect of environmental control for WSSV management. Proper water quality can help to reduce stress on shrimp and improve their immune function, making them less susceptible to WSSV infection. This includes maintaining appropriate pH, temperature, and salinity levels, as well as adequate water exchange and circulation to prevent the buildup of organic matter that can provide a breeding ground for WSSV and other pathogens (Flegel, 2012).

Biosecurity measures are also important for environmental control of WSSV. Preventing the introduction of the virus into a shrimp farm is critical to controlling its spread. This can be achieved through measures such as screening new stock for the virus and implementing strict quarantine procedures for new animals. Additionally, preventing the introduction of contaminated water or equipment can help to prevent the spread of the virus within a farm (Turkmen and Toksen, 2010).

The management of sediment in shrimp ponds is also an important aspect of environmental control for WSSV management. The virus can survive for extended periods of time in sediment and can be transmitted to shrimp populations through ingestion of contaminated sediment. Managing the sediment in shrimp ponds through practices such as regular removal and replacement of sediment can help to reduce the viral load in the environment and prevent the spread of the virus (Avnimelech and Ritvo, 2003; Jackson *et al.*, 2003).

Probiotics

Probiotics are live microorganisms that can provide health benefits to their host, such as improving gut health and enhancing immune function. The use of probiotics has gained attention as an important strategy for controlling and managing diseases in shrimp farming, including the White Spot Syndrome Virus (WSSV). In the case of shrimp farming, probiotics are administered to the shrimp to improve gut health, enhance immune function, and reduce the pathogenic load in the gut. This can help to reduce the risk of WSSV infection, as well as other diseases that can affect shrimp (Peraza-Gómez *et al.*, 2009; Abdollahi-Arpanahi *et al.*, 2018; Sumon *et al.*, 2022).

Several studies have investigated the use of probiotics to control WSSV in shrimp. For example, one study found that the administration of a probiotic mixture containing Bacillus spp. to shrimp resulted in improved survival rates and reduced WSSV infection rates (Sánchez-Ortiz *et al.*, 2016). Another study found that the administration of a probiotic mixture containing Lactobacillus spp. to shrimp resulted in a significant reduction in WSSV mortality rates (Naiel *et al.*, 2021). Probiotics can also improve the overall health and growth of shrimp, making them less susceptible to WSSV infection. One study found that the administration of a probiotic mixture containing Bacillus spp. to shrimp resulted in improved growth performance and immune function (Zokaeifar *et al.*, 2012). The mechanisms by which probiotics confer protection against WSSV are not fully understood. However, it is believed that probiotics can help to maintain a healthy gut microbiome, which in turn can enhance the immune response of shrimp and reduce the pathogenic load in the gut (Scott *et al.*, 2015; Xu *et al.*, 2021a).

In conclusion, the use of probiotics is a promising approach for controlling and managing WSSV in shrimp farming. Probiotics can improve the overall health and growth of shrimp, making them less susceptible to WSSV infection, and can also directly reduce the viral load in infected shrimp. Further research is needed to determine the optimal probiotic strains and dosages for WSSV control in different shrimp farming systems.

SPF Brood stocks

One approach to controlling WSSV in shrimp farming is to use specific pathogen-free (SPF) brood stocks. SPF brood stocks are shrimp that have been selectively bred and raised in a controlled environment to be free of specific pathogens, including WSSV. By using SPF brood stocks, farmers can reduce the risk of introducing WSSV into their farms and prevent the spread of the disease (Lightner, 2005; Eswaran, 2022). By using SPF brood stocks, farmers can reduce the risk of introducing WSSV into their farms. SPF brood stocks are selectively bred and raised in a controlled environment to be free of specific pathogens, including WSSV. This reduces the likelihood of introducing WSSV into the shrimp farm through brood stock or larvae (Kumar and Paul, 2022). The use of SPF brood stocks can improve overall biosecurity on the shrimp farm. Farmers who use SPF brood stocks often have stricter biosecurity protocols, such as disinfection of equipment and facilities and monitoring and testing for the presence of diseases. This can help prevent the spread of WSSV within the farm (Lotz, 1997). There have been several studies that have demonstrated the effectiveness of using SPF brood stocks as a managerial measure to control WSSV in shrimp farming. For example, Ekmaharaj (2018) found that using SPF brood stocks resulted in significantly lower mortality rates and higher survival rates compared to using conventional brood stocks that were not selected for disease resistance. Another study in Bangladesh similarly found that using SPF brood stocks led to a significant reduction in WSSV incidence and mortality rates compared to using conventional brood stocks (Chakrobortty *et al.*, 2020). Also Cock *et al.* (2017) found that using SPF brood stocks resulted in significantly lower mortality rates and higher survival rates compared to using conventional brood stocks in both laboratory and field trials . The study also found that the offspring of SPF brood stocks had a higher resistance to WSSV compared to the offspring of conventional brood stocks.

These studies provide strong evidence that using SPF brood stocks is an effective measure for controlling diseases, particularly WSSV, in shrimp farming. However, it is important to note that the effectiveness of SPF brood stocks may vary depending on factors such as the specific pathogen being targeted, the environmental conditions, and the management practices used by the farmers (Turkmen and Toksen, 2010).

Pathogenesis

The pathogenesis of WSSV involves a complex interplay between the virus and the host shrimp, leading to a range of clinical signs and symptoms, including white spots on the exoskeleton, lethargy, and ultimately death. WSSV targets various tissues and organs in the shrimp, including the lymphoid organ, hepatopancreas, and gills, among others. Upon infection, the virus replicates rapidly and spreads throughout the host, leading to systemic infection and ultimately death (Zheng *et al.*, 2019). The exact mechanisms by which WSSV causes disease in shrimp are not fully understood. However, several studies have shed light on the pathogenesis of the virus. For example, it has been shown that WSSV can induce apoptosis, or programmed cell death, in infected shrimp cells, which can lead to tissue damage and inflammation. Additionally, the virus can trigger an immune response in the shrimp, leading to the production of various cytokines and immune effectors that can help to control the infection. However, WSSV has also been shown to be able to evade the host's immune response, allowing the virus to continue to replicate and spread (Wang *et al.*, 2008). Furthermore, WSSV produces a range of virulence factors, including several enzymes and structural proteins, that can aid in virus replication and pathogenesis. For example, the WSSV envelope protein VP28 has been shown to be essential for virus attachment and entry into host cells. Meanwhile, the viral protein WSSV453 has been shown to be involved in suppressing the host's immune response, allowing the virus to avoid detection and clearance by the host's immune system (Verbruggen *et al.*, 2016).

Clinical signs

The clinical signs of WSSV infection can vary depending on the severity and duration of the infection, as well as the species and age of the infected shrimp. One of the most characteristic clinical signs of WSSV infection is the appearance of white spots on the exoskeleton because of the altered metabolism and physiology of the infected shrimp. in acute condition, the shrimp mortality of WSSV infection is occurred without any clinical sign (Fig. 2). Accordingly, white spot with concentric circles are not visible to naked eyes (Kakoolaki *et al.*, 2011).

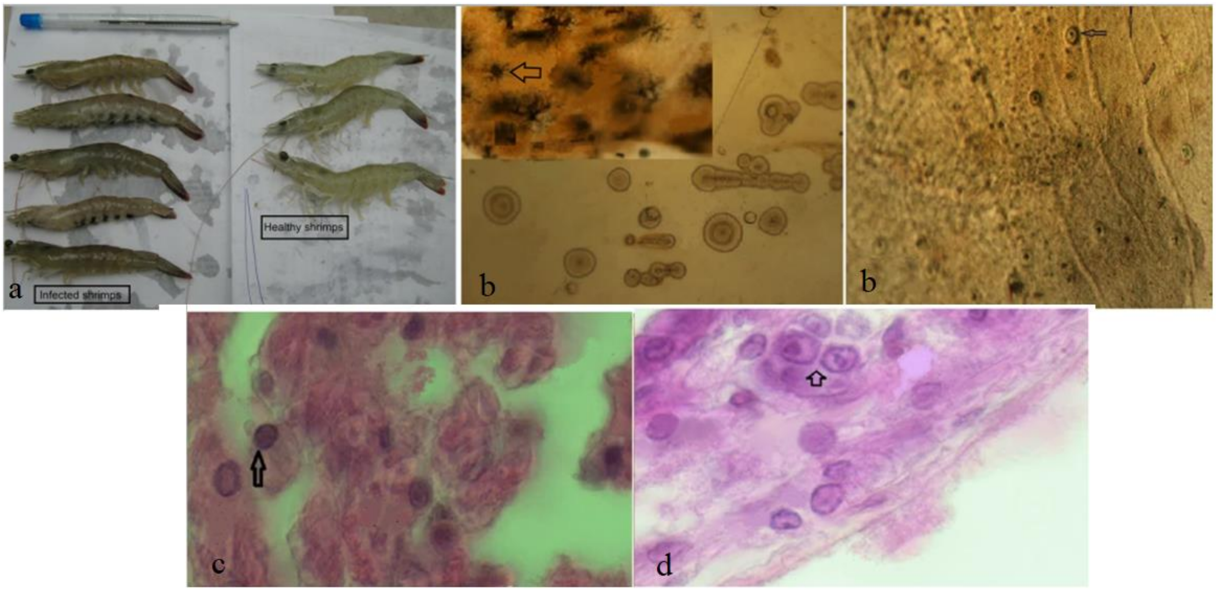

Figure 2: (a) The mortality of acute WSSV infection is occurred SPF- *P. vanemmie* 2-3 days after exposure. (b) In acute conditions of infection, white spots can be seen as concentric circles with the naked eye. (c) Transverse section of WSSV inclusion in heart muscle tissue. (d) Inclusion of WSSV in the interstitial tissue of the hepatopancreas.

When WSSV infects shrimp, it replicates rapidly and causes widespread damage to the host's tissues and organs, including the cuticle. The cuticle serves as a protective barrier against environmental stressors and pathogens, and also plays a role in maintaining the shrimp's osmotic balance. During WSSV infection, the virus causes damage to the underlying tissue of the cuticle, leading to the release of calcium ions. The increased levels of calcium ions in the hemolymph of infected shrimp can lead to the formation of calcium carbonate crystals, which accumulate in the damaged cuticle and become visible as white spots. The white spots are typically found on the carapace, tail fan, and walking legs of infected shrimp. The accumulation of calcium carbonate in the cuticle can have several negative effects on infected shrimp. First, the accumulation of calcium carbonate can weaken the cuticle, making it more susceptible to further damage and infection. Additionally, the white spots can affect the camouflage and visual defenses of the shrimp, making them more vulnerable to predation (Verbruggen *et al.*, 2016; Dey *et al.*, 2020). In addition to the white spots, infected shrimp may exhibit other clinical signs, including lethargy, loss of appetite, and reduced movement. The hepatopancreas, which is the primary digestive organ in shrimp, may also become swollen and discolored, and may contain necrotic foci. Infected shrimp may also display abnormal behavior, such as swimming near the surface or lying on the bottom of the tank (Karthick *et al.*, 2022). As the infection progresses, the clinical signs become more severe, and infected shrimp may exhibit additional symptoms, including opaque or milky hemolymph, which is the shrimp's equivalent of blood. The gills may become pale or discolored, and the shrimp may have difficulty breathing. In severe cases, infected shrimp may die within a few days of infection (Yoganandhan *et al.*, 2003). It is important to note that not all infected shrimp will display all of these clinical signs, and some infected shrimp may not display any clinical signs at all. Additionally, some of these clinical signs may also be present in other shrimp diseases, further highlighting the importance of proper diagnosis (Lee *et al.*, 2022).

Diagnosis

Clinical signs of WSSV can vary depending on the severity of the infection, the species of crustacean affected, and the stage of the disease. The most common clinical sign of WSSV is the presence of white spots on the exoskeleton of the crustacean. These spots are caused by the accumulation of viral particles in the cuticle, and they appear as small white or opaque spots that are about 0.5 to 2 mm in diameter. As the disease progresses, these spots will become more numerous and larger, and the crustacean may exhibit other symptoms such as lethargy, loss of appetite, and discoloration of the exoskeleton (Amarakoon *et al.*, 2016; Cheng *et al.*, 2021).

In addition to the visible white spots, crustaceans affected by WSSV may also exhibit behavioral changes such as reduced activity and hiding in the corners of the tank. Infected crustaceans may also show signs of respiratory distress, such as rapid breathing and gill discoloration. In severe cases, crustaceans may exhibit hemorrhages in the exoskeleton, and may show signs of paralysis or death (Jithendran *et al.*, 2009; Ananda Raja and Jithendran, 2015). According to a study by de Souza Valente *et al.* (2020), infected shrimp may also exhibit "empty gut syndrome", where the digestive tract of the shrimp appears empty or devoid of any food. Additionally, infected shrimp may have a milky white appearance due to the accumulation of excess fluid in the body cavity (Wang *et al.*, 1999). In some cases, WSSV may also cause the gills of infected shrimp to turn pale or translucent, which can lead to respiratory distress and ultimately death (Yoganandhan *et al.*, 2003).

Consequently, there is still numerous discussions on the main portal of pathogen entry. The intestine and other tissues are exactly sheltered by a non-penetrable coating (Fig. 2) of cuticle, a peritrophic matrix (PM) (Van Thuong *et al.*, 2016). PM is an acellular chitin and glycoprotein layer that lies the invertebrate midgut (Erlandson *et al.*, 2019). Recent studies indicated that the cuticle and peritrophic layers completely serve as firm wall against WSSV (Corteel *et al.*, 2009). The shrimp antennal gland is a basic gate for entry of pathogens such as WSSV.This tissue lacks an impermeable cuticle and looks like a kidney, linked to a bladder with a nephropore and an opening (Fig. 3) without protection (De Gryse *et al.*, 2020). Therefore, a sudden change in water salinity, which is generally performed after raining or water replacement with remarkable different salinity, osmoregulation enforces the kidney like organ to absorb water accompanied with pathogen (If any) into the shrimp body (Van Thuong *et al.*, 2016) to adjust the osmolality of hemolymph (Prayitno *et al.*, 2022). They showed that, the antennal gland is the first organ to become infected. It is suggested that the time and volume of water replacement are critical points for WSSV infection.

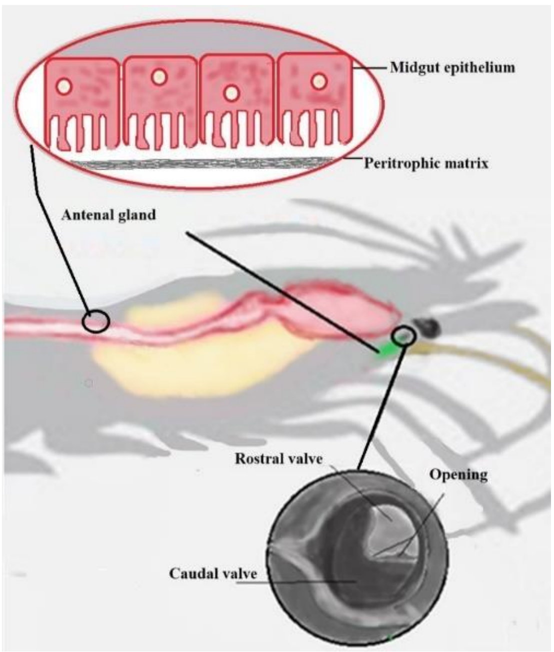

Figure 3: Intestine tissue with cuticle and opening in antennal gland-base shows no cuticle.

Prevention of WSSV involves maintaining good water quality and minimizing stressors on the crustaceans, as stressed crustaceans are more susceptible to infections (Alapide-Tendencia, 2012). Quarantining new crustaceans before introducing them into an established tank can also help prevent the spread of the disease. Biosecurity measures such as disinfection of tanks, equipment, and water sources can also be effective in preventing the introduction and spread of the virus (Hasan *et al.*, 2020).

Tissue tropism

White Spot Syndrome Virus (WSSV) is known to display a specific tissue tropism in shrimp, which means that the virus tends to infect certain types of tissues more readily than others. WSSV has a particular affinity for certain types of cells within the shrimp, including hemocytes (cells that play a role in the shrimp's immune response), lymphoid organ cells, and cuticular epithelial cells (cells that make up the exoskeleton) (Ling *et al.*, 2000). The virus can also infect other tissues, including the hepatopancreas (a digestive organ in the shrimp), muscle, and nerve tissue, although the severity of infection in these tissues can vary depending on a number of factors, including the shrimp's age and size, and the virulence of the virus (Pan *et al.*, 2005). Tissue tropism can play an important role in the pathogenesis and transmission of the virus. By targeting specific tissues, the virus can more easily establish an infection and spread throughout the shrimp's body. Also, it is important to note that the virus has been found to target specific types of cells within these tissues. For example, in the hemocytes, WSSV has been shown to target granular cells, which are a type of hemocyte that play a role in the shrimp's immune response (Jiravanichpaisal *et al.*, 2006; Desrina *et al.*, 2022). In the lymphoid organ cells, WSSV primarily infects the cells that make up the lymphoid organ sinus, which is a network of channels that help to filter and remove foreign particles from the shrimp's body (Owens, 2010). In the cuticular epithelial cells, WSSV infects the cells that are responsible for producing and maintaining the exoskeleton. This can lead to the characteristic white spots that are seen on the shrimp's exoskeleton during a WSSV infection (Rodríguez *et al.*, 2003). The tissue tropism of WSSV can also help to explain some of the clinical signs that are seen in infected shrimp. For example, the infection of the hepatopancreas can lead to a reduction in digestive function, which can cause the shrimp to stop eating and lose weight. Similarly, the infection of nerve tissue can lead to abnormal swimming behavior and lethargy (Sun *et al.*, 2013).

Understanding the tissue tropism of WSSV is an important step in developing effective treatments and prevention strategies for the disease. By targeting the tissues and cells that are most susceptible to infection, researchers can develop targeted therapies and vaccines that can help to mitigate the impact of WSSV on the shrimp farming industry (Ninawe *et al.*, 2017; Premanand *et al.*, 2018; Amar *et al.*, 2021).

Prevalent stressors

White Spot Syndrome Virus (WSSV) is a highly contagious and devastating virus that affects shrimp farming globally. It causes high mortality rates, resulting in significant economic losses to the shrimp industry. The prevalence of WSSV in shrimp is influenced by several stressors. One of the stressors is water quality, which has been shown to play a crucial role in the prevalence of WSSV in shrimp. Poor water quality, including high levels of ammonia, nitrite, and nitrate, can increase the susceptibility of shrimp to WSSV infection. On the other hand, maintaining good water quality, including proper pH, dissolved oxygen, and temperature levels, can reduce the prevalence of WSSV in shrimp (Cavalli *et al.*, 2008). Another critical stressor for WSSV in shrimp is stocking density. High stocking densities can lead to increased stress levels in shrimp, making them more susceptible to WSSV infection. In addition, high stocking densities can also result in poor water quality, which can further exacerbate the problem. On the other hand, lower stocking densities can reduce stress levels in shrimp, making them less susceptible to WSSV infection. Therefore, maintaining optimal stocking densities is crucial to reducing the prevalence of WSSV in shrimp (Apún-Molina *et al.*, 2017). Feed quality and nutrition are also critical stressors for WSSV in shrimp. Poor feed quality and inadequate nutrition can lead to weakened immune systems in shrimp, making them more susceptible to WSSV infection. On the other hand, providing high-quality feed and proper nutrition can strengthen the immune systems of shrimp, reducing the prevalence of WSSV. Therefore, it is essential to maintain proper nutrition and feed quality to reduce the prevalence of WSSV in shrimp (Emerenciano *et al.*, 2022).

Other stressors that can affect the prevalence of WSSV in shrimp include water temperature, salinity, and pH. Extreme temperatures and salinity levels can stress shrimp, making them more susceptible to WSSV infection. Similarly, high or low pH levels can also stress shrimp and increase their susceptibility to WSSV infection. Therefore, maintaining optimal water temperature, salinity, and pH levels is crucial to reducing the prevalence of WSSV in shrimp (Joseph and Philip, 2007; Tendencia *et al.*, 2010).

DO depletion

Dissolved oxygen (DO) depletion is one of the most critical stressors for the susceptibility of shrimp to White Spot Syndrome Virus (WSSV) infection. DO is an essential factor for aquatic organisms, and the depletion of DO can cause significant stress and mortality in shrimp. DO depletion can occur due to various factors, including high stocking densities, poor water quality, and environmental stressors, such as high temperatures. Under DO-depleted conditions, shrimp are more susceptible to WSSV infection, resulting in high mortality rates. The susceptibility of shrimp to WSSV infection under DO-depleted conditions is due to the negative impact of DO depletion on the immune system of shrimp. DO plays a crucial role in the immune response of shrimp, and its depletion can lead to a weakened immune system, making shrimp more vulnerable to WSSV infection. Under DO-depleted conditions, the immune response of shrimp to WSSV infection is compromised, resulting in higher mortality rates. Therefore, maintaining optimal DO levels is essential to reduce the prevalence of WSSV in shrimp (Direkbusarakom and Danayadol, 1998; Chen and He, 2019).

Several strategies have been proposed to mitigate the negative effects of DO depletion on the susceptibility of shrimp to WSSV infection. One such strategy is the use of aeration systems to increase DO levels in shrimp ponds. Aeration systems can increase DO levels and improve water quality, reducing the susceptibility of shrimp to WSSV infection. Proper pond management, including regular monitoring of DO levels and stocking densities, can also help mitigate the negative effects of DO depletion on shrimp health and reduce the prevalence of WSSV in shrimp (Ruiz-Velazco *et al.*, 2010; Rahayani and Gunawan, 2018).

In addition to aeration systems, the use of probiotics has also been proposed as a strategy to mitigate the negative effects of DO depletion on the susceptibility of shrimp to WSSV infection. Probiotics are beneficial microorganisms that can improve the health and immune response of shrimp. Studies have shown that the use of probiotics can improve the survival rate of shrimp under DO-depleted conditions and reduce the prevalence of WSSV infection (Martínez Cruz *et al.*, 2012; Chattaraj *et al.*, 2022).

DO depletion is a prevalent stressor for the susceptibility of shrimp to WSSV infection. Under DO-depleted conditions, the immune response of shrimp to WSSV infection is compromised, resulting in higher mortality rates. Mitigating the negative effects of DO depletion on the susceptibility of shrimp to WSSV infection requires maintaining optimal DO levels through the use of aeration systems, proper pond management, and the use of probiotics. Further research is needed to better understand the interactions between DO depletion and WSSV infection in shrimp and to develop more effective strategies to reduce the prevalence of WSSV in shrimp farming (Lehmann *et al.*, 2016).

Nitrogen compounds

Nitrogen compounds are prevalent stressors for the susceptibility of shrimp to White Spot Syndrome Virus (WSSV) infection. Nitrogen compounds, including ammonia, nitrite, and nitrate, are byproducts of shrimp metabolism and are commonly found in aquaculture systems. High levels of nitrogen compounds can cause stress and mortality in shrimp and increase their susceptibility to WSSV infection. Therefore, maintaining optimal levels of nitrogen compounds is crucial to reducing the prevalence of WSSV in shrimp (Kathyayani *et al.*, 2019).

Ammonia is one of the most toxic nitrogen compounds for shrimp and can cause significant stress and mortality at high levels. Ammonia toxicity can lead to gill damage, respiratory distress, and weakened immune systems, making shrimp more susceptible to WSSV infection. Therefore, maintaining low levels of ammonia in shrimp ponds is essential to reducing the prevalence of WSSV in shrimp. Several strategies, including proper feed management, water exchange, and biofiltration, can be employed to maintain low levels of ammonia in shrimp ponds (Fang *et al.*, 2017; Xue *et al.*, 2017). Nitrite is another toxic nitrogen compound that can cause stress and mortality in shrimp. Nitrite toxicity can lead to methemoglobinemia, a condition where the blood of shrimp cannot transport oxygen efficiently. This can cause respiratory distress and weakened immune systems, making shrimp more susceptible to WSSV infection. Therefore, maintaining low levels of nitrite in shrimp ponds is crucial to reducing the prevalence of WSSV in shrimp. Strategies such as proper feed management, water exchange, and biofiltration can also be employed to maintain low levels of nitrite in shrimp ponds. Nitrate is a less toxic nitrogen compound than ammonia and nitrite, but high levels of nitrate can still cause stress and mortality in shrimp. Nitrate toxicity can lead to reduced growth rates, reduced reproductive performance, and weakened immune systems, making shrimp more susceptible to WSSV infection. Therefore, maintaining low levels of nitrate in shrimp ponds is also essential to reducing the prevalence of WSSV in shrimp. Strategies such as proper feed management, water exchange, and biofiltration can also be employed to maintain low levels of nitrate in shrimp ponds (Yusoff *et al.*, 2011; Romano and Zeng, 2013). In addition to the direct toxic effects of nitrogen compounds, they can also indirectly increase the susceptibility of shrimp to WSSV infection by causing stress and weakening the immune system of shrimp. High levels of nitrogen compounds can cause stress in shrimp, making them more susceptible to WSSV infection. In addition, high levels of nitrogen compounds can also lead to the proliferation of harmful microorganisms, which can further weaken the immune system of shrimp. Therefore, maintaining optimal levels of nitrogen compounds is crucial to reducing the prevalence of WSSV in shrimp (Zhao *et al.*, 2020).

Several strategies have been proposed to mitigate the negative effects of nitrogen compounds on the susceptibility of shrimp to WSSV infection. One such strategy is the use of biofiltration systems, which can remove nitrogen compounds from shrimp ponds and improve water quality. Proper feed management and water exchange can also help maintain optimal levels of nitrogen compounds in shrimp ponds. In addition, the use of probiotics has also been proposed as a strategy to improve the immune response of shrimp and reduce their susceptibility to WSSV infection under high nitrogen compound conditions. Probiotics can improve the gut microbiota of shrimp, leading to strengthened immune systems and reduced susceptibility to WSSV infection. Therefore, the use of probiotics can be an effective strategy to reduce the negative impact of nitrogen compounds on the susceptibility of shrimp to WSSV infection (Kasan *et al.*, 2018).

Salinity changes

Salinity is an important abiotic factor that affects the growth and survival of aquatic organisms, including shrimp. Changes in salinity can occur naturally or as a result of human activities, and can have significant impacts on the health and susceptibility of shrimp to diseases such as White Spot Syndrome Virus (WSSV). Several studies have shown that changes in salinity can increase the susceptibility of shrimp to WSSV. For example, a study by Ramos-Carreño *et al.* (2014) found that WSSV-infected shrimp exposed to low salinity levels had higher mortality rates compared to those exposed to higher salinity levels. Also Tendencia and Verreth (2011) found that the virus replicated more rapidly in the tissues of shrimps exposed to low salinity levels, suggesting that low salinity may enhance the pathogenicity of the virus. The mechanism by which low salinity increases the virulence of WSSV is not fully understood. However, it is hypothesized that exposure to low salinity may impair the immune system of the shrimp, making them more susceptible to viral infections. Pang *et al.* (2019) found that exposure to low salinity led to a decrease in the activity of various immune-related enzymes in shrimp, which may have contributed to the higher mortality rates observed in infected shrimp.

Furthermore, changes in salinity can also affect the physiological condition of shrimps, making them more vulnerable to WSSV. The exposure to low salinity levels led to a decrease in the activity of antioxidant enzymes in shrimp, which can increase the production of reactive oxygen species (ROS) and oxidative stress. This can damage the cells and tissues of the shrimp and compromise their immune function, making them more susceptible to WSSV infection (Mathew *et al.*, 2007; Parrilla-Taylor *et al.*, 2013).

In addition to low salinity, high salinity levels can also be a stressor for shrimp and can increase their susceptibility to WSSV. WSSV-infected shrimp exposed to high salinity levels had higher mortality rates compared to those exposed to lower salinity levels which suggested that exposure to high salinity may lead to physiological stress in the shrimp, which can impair their immune function and make them more susceptible to WSSV infection (Raj *et al.*, 2012).

Temperature fluctuation

Temperature is an important abiotic factor that affects the growth, reproduction, and survival of aquatic organisms, including shrimp. Fluctuations in temperature, particularly rapid changes or extremes, can cause stress in shrimp and increase their susceptibility to diseases such as White Spot Syndrome Virus (Ren *et al.*, 2021). Several studies have shown that temperature fluctuations can increase the susceptibility of shrimp to WSSV. For example, a study by Zhang *et al*. (2019) found that WSSV-infected shrimp exposed to rapid temperature fluctuations had higher mortality rates compared to those exposed to stable temperatures. The study also found that the virus replicated more rapidly in the tissues of shrimps exposed to rapid temperature fluctuations, suggesting that temperature fluctuations may enhance the pathogenicity of the virus (Jiravanichpaisal *et al.*, 2004). The mechanism by which temperature fluctuations increase the virulence of WSSV is not fully understood. However, it is hypothesized that exposure to temperature fluctuations may impair the immune system of the shrimp, making them more susceptible to viral infections (Wang *et al.*, 2020). A study by Li *et al*. (2021) found that exposure to rapid temperature fluctuations led to a decrease in the activity of various immune-related enzymes in shrimp, which may have contributed to the higher mortality rates observed in infected shrimp (Fajardo *et al.*, 2022).

Furthermore, temperature fluctuations can also affect the physiological condition of the shrimp, making them more vulnerable to WSSV. A study by Estrada-Cárdenas *et al.* (2021) found that exposure to high temperatures led to a decrease in the activity of antioxidant enzymes in shrimp, which can increase the production of reactive oxygen species (ROS) and oxidative stress. This can damage the cells and tissues of the shrimp and compromise their immune function, making them more susceptible to WSSV infection. Additionally, temperature fluctuations can affect the replication and transmission of WSSV. Moser *et al.* (2012) found that rapid temperature fluctuations increased the shedding of WSSV in infected shrimp, which can lead to the spread of the virus in the environment and increase the risk of infection in other shrimps.

Confilicts of interest

The authors declare that this research was conducted without any conflict of interest with any party.

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