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REVIEW

White spot disease (WSD), past, present and future: a review

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Abstract The shrimp industry has significantly progressed in recent years, although the White Spot Syndrome Virus (WSSV) caused the W.S. disease (WSD). This destructive viral disease is one of the most important pathogens in this valuable business. It has significantly impacted shrimp aquaculture worldwide, creating economic problems country-wide. Therefore, it can be considered a deterrent factor for shrimp culture and aquatic farm development. Numerous experiences of developing aquaculture show that WSD has been responsible for mortality and excessive economic losses worldwide. This present review prepared an enormous amount of knowledge of WSD for increasing awareness for researchers in this field. The collected data include taxonomic classification, virus structure, transmission routes, geographical distribution, hosts, virus pathogenesis, clinical signs, diagnosis, and prevention methods. Moreover, according to the economic value of shrimp and its crucial role in supplying animal protein, the present review will state the current knowledge of this devastating virus. Consequently, it will provide helpful information for researchers and the aquaculture industry that deals with this serious issue.

Keywords White spot syndrome virus. Shrimp. Aquaculture. Control. Prevention

Introduction

The increasing human population has put significant pressure on natural resources, leading to more food production. Aquaculture is a suitable strategy to reduce these issues significantly but is not always included in nutritional and food security (Fisher et al. 2017). Two benefits of shrimp farming are contributing to economic growth and creating significant job opportunities in developing countries (Geetha et al. 2019). Worldwide, 67% of shrimp production comes from aquaculture and 33% is from wild capture. The whiteleg shrimp, Penaeus vannamei, and the giant tiger prawn, Penaeus monodon, are the most commonly used species in shrimp aquaculture as marine species, and Macrobrachium rosenbergii and Macrobrachium nipponense are the most commonly used species as freshwater prawns. The leading consumer areas for shellfish farming are the USA,

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Japan, and Europe, with exports fuelling the globalization and success of the industry (Didar-Ul Islam and Bhuiyan 2016). The rapid growth of the shrimp industry and intensification of farming methods have been coupled with the emergence of devastating diseases, arising as a result of complex interactions between the host, pathogen, and environment, as well as uncontrolled trade with shrimps which causes significant losses (up to 70%) of annual marine and euryhaline shrimp harvests have been estimated to occur as a result of disease (Flegel 2019). In general, within 3-10 days of infection, the cumulative mortality rate is approximately 90-100% (Wang et al. 1999; Millard et al. 2021). Managing health and disease is one of the most critical issues facing aquaculture, especially in aquaculture activities, so several financial losses are caused to fish and shrimp farmers yearly. According to the worldwide extension of aquaculture activity, in crustaceans and shrimps, there are about twenty known viral diseases, four bacterial diseases, three fungal diseases and a few protozoan diseases. Some devastating diseases in aquaculture include WSD (White Spot Disease), TSV (Taura Syndrome Virus) and EMS (Early Mortality Syndrome) or AHPND (Acute Hepatopancreatic Necrosis Disease) that has been added to the World Organization for Animal Health (WOAH) list of shrimp diseases in recent years (Zorriehzahra and Banaederakhshan 2015). As far as WSD is concerned, it is caused by White Spots Syndrome Virus (WSSV) (Thornber et al. 2020), which is not only one of the most virulent shrimp viruses infecting many species of crustaceans worldwide (WOAH 2019), but it also has been plaguing the global shrimp farming industry and resulting in huge production losses for more than two decades (Stentiford et al. 2012). WSSV was initially recognized in *Penaeid* shrimp in 1992 in Taiwan (Chen 1995), and subsequently in the Fujian province of China in 1991/1992 (Flegel 1997; Jiang et al. 2017). The first report of WSSV infection in crayfish occurred in 1995 at the National Zoo of Washington, D.C., United States (Richman et al. 1997). The virus is a giant, circular double-stranded DNA virus belonging to the genus *Whispovirus* of the *Nimaviridae* family (Wang et al. 2019). Recently, there have been reports of outbreaks of WSD in some EU countries, such as Saudi Arabia, Mozambique, Madagascar, and Australia. Knibb et al. (2018) have affirmed the susceptibility of shrimp farming to WSD regardless of the climate zone. The quarterly report of the Network of Aquaculture Centers in Asia-Pacific (NACA) shows that despite the implementation of biosecurity measures, WSD continues to be a major problem in many shrimp producing countries in the Asia-Pacific region. Virulent to decapod crustaceans in both salt and fresh water, this virus is regulated over a wide range of salinities. Since WSD is an epidemic, it is listed as a notifiable disease by WOAH (Ding et al. 2015; Pace et al. 2016). Lethargic behavior, hepatopancreatic discoloration, and diminished feeding and primping are typical symptoms of this disease that resulting in the loosening of the cuticle (Pradeep et al. 2012). In WSSV-infected animals, the lesions, which appear as white spots, are usually found in the outer skeleton. Shrimp also have spots on their carapace, which are usually white but can vary in color from reddish to pinkish, and shrimp are always discolored. In addition, shrimp usually show abnormal behavior such as lethargy, slow swimming, and swimming at the surface, swimming along the pond edge and reduced feed intake (WOAH 2019). Based on some findings, Millard et al. (2021) demonstrated that pond temperature and salinity are significant factors determining outbreak severity. WSSV appears to be most virulent at water temperatures between 25-28°C and salinities far from the shrimp's isosmotic point. Elevated temperatures (>30°C) may protect against WSD, depending on the stage of infection. Nevertheless, the mechanisms mediating this effect have not been well established. In addition, Islam et al. (2023) studied the molecular detection techniques of the WSSD virus and the problems and solutions associated with it in shrimp farming. Furthermore, (Mohammadidoust et al. 2019) have discovered that experimental immunogenic treatment of the inactivated white spot disease virus with radiation has created a very positive impact in expanding these indicators. So, their amount increased immensely from day 8 to day 21 during the test period. It has been shown that WSSV had colonized the offshore wild crustacean populations in the Bohai Sea, and the potential negative impact of the spread of WSSV on wild crustacean populations, together with the marine ecosystem, deserves close attention and further research (Xu et al. 2021). Given that shrimps have constantly been exposed to viral pathogens, the use of immune system stimulants and waxing to immunize shrimps to control and prevent white spot disease is presented (Namikoshi et al. 2004). The vaccines are classified into three categories: live or weak, killed or inactive, subacute, and toxins. Live vaccines stimulate the host's immune system like natural infections (infection without symptoms and limiting) and cause long-term protection with the lowest amount of vaccine administration in the host. Today, by utilizing recombinant proteins, organisms can be vaccinated with high amounts of specific antigens, which will be tried to increase the resistance of shrimps to white spot disease with new methods of immunization (Mohammadidoust et al. 2019). Advanced genetic studies and biosecurity measures used in

the management of WSSV have been the focus of most reviews on WSSV (Vaseeharan et al. 2016; Bir et al. 2017; Sivasankar et al. 2017). Shrimp farming practices are currently dynamic, and recently, the aquaculture industry has seen the use of some new technologies to improve WSD management. The present review aims to highlight and evaluate the syndrome of WSD in shrimp based on the existing literature on the presence of WSSV in aquatic organisms.

Virus structure (genome and morphology)

WSSV consists of a circular dsDNA genome that is approximately 300 kb in size (shown in Figure 1). Genomic sequences for four WSSV isolates are available: a Chinese isolate (*WSSV-CN*: GenBank Accession AF332093) (Yang et al. 2001), an isolate from Thailand (*WSSV-TH*: GenBank Accession AF369029) (Van et al. 2001a), a Taiwanese isolate (*WSSV-TW*: GenBank Accession AF440570), and a Korean isolate (*WSSV-KR*: GenBank Accession JX515788) (Chai et al. 2013). The size of the WSSV ranges from 210-420 nm in length and from 70-167 nm in diameter (Guoxing et al. 1997). The viral envelope is a lipid bilayer membrane that is 6-7 nm thick, whose envelope-nucleocapsid area varies between 2 and 7.5 nm. The nucleocapsid, which is 180-420 nm long and 54-85 nm in diameter, is tightly packed inside the virion (Durand et al. 1997). Virion contains up to 40 structural proteins (Wang et al. 2019).

Replication/transcription events

The life cycle of a virus can generally be divided into different phases; entering the host cell (through fusion or endocytosis), opening the genome, replication, assembly and maturation of virions, and releasing virus particles through budding or cytolysis (Escobedo-Bonilla et al. 2007). Binding of WSSV to the surface of the host cell membrane initiates the replication cycle of this virus. Once the virus has attached itself, it enters the cell by endocytosis. Fusion of the WSSV envelope with the endosome activates release of the nucleocapsid into the cytosol. The nucleocapsid is released from the cell. It contacts the nucleus and inserts the viral genome into the nucleus through a nuclear pore. Meanwhile, degradation of envelope and capsid proteins occurs in the cytoplasm (Li et al. 2015). The virus particle must express its replication gene once it has entered the host cell nucleus. This is because the transcription machinery is not present in all viruses, including WSSV, they first need to rely on the host cell to ensure that this machinery is set up to start replicating (Sánchez-Paz 2010).

The WSSV particle consists of five major proteins and about 14 substructural proteins (Van Hulten et al. 2002; Huang et al. 2002). The five significant proteins have been named according to their sizes found by SDS-PAGE: viral protein (VP) 28, VP26, VP24, VP19, and VP15 (Van Hulten et al. 2000; 2002). VP26, VP24, and VP15 are present in nucleocapsid preparations, while VP28 and VP19 are found in envelope fractions of the virions. As an antiserum against VP28 was able to neutralize WSSV in the shrimp *P. monodon*, this protein is most likely located on the surface of the virus particle that is essential to shrimp systemic

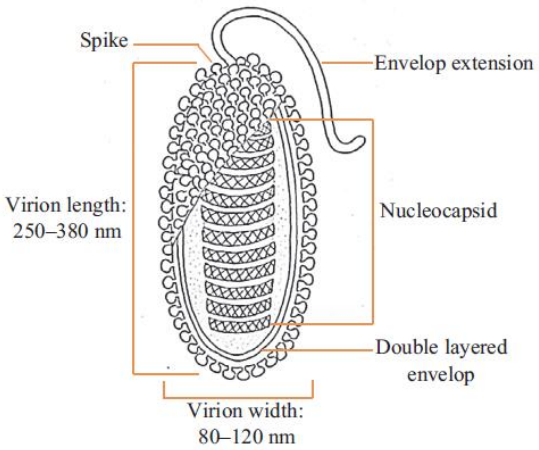

Fig. 1 The structure of the WSSV (Amano et al. 2011)

WSSV infection (Van Hulten et al. 2001b). A putative function for VP15, a fundamental protein with no hydrophobic regions, is that of a histone-like, DNA-binding protein (Zhang et al. 2001; Van Hulten et al. 2002). Genes of most large dsDNA viruses infecting (in) vertebrates are expressed in a cascaded fashion. Immediate early (IE) and early (E) genes are expressed before viral DNA replication, although expression of late (L) genes happens after the viral genome replication for proper late gene expression, the motif containing the transcription initiation site (TIS) often plays an important role in recognition by a virus-encoded RNA polymerase (Davison and Moss 1989; Morris and Miller 1994; Garcia-Escudero and Viñuela 2000; Weir 2001). WSSV genes encoding DNA polymerase (Pol), ribonucleotide reductase (rr) large and small subunits, protein kinase (pk), and chimeric thymidine kinase thymidylate kinase (tk-tmk) all have been used in transcription studies. *P. monodon* had these genes discovered two to four hours after WSSV stench (Tsai et al. 2000; Liu et al. 2001; Chen et al. 2002), what they were suggesting was that these were the early genes. A TATA box 20-28 nucleotides downstream initiates transcription of rr1, rr2, pk and Pol, suggesting a functional role of the TATA box in early transcription. Both rr genes and Pol share a consensus WCABT (W=a /t; B=c/g/t) sequence in which transcription is initiated (Chen et al. 2002). An early promoter element of WSSV may be this somewhat degenerate consensus TIS motif.

Geographical distribution and host range

The WSD was initially detected in Taiwan and Japan, and soon after that spread to other shrimp producing countries in Asia, causing the disease to become endemic in those countries (Stentiford et al. 2012). Some EU countries as well as Saudi Arabia, Mozambique, Madagascar and Australia have recently reported outbreaks of WSD. The susceptibility of shrimp farming to WSD, regardless of climate zone, was established (Knibb et al. 2018). Quarterly reports from the Network of Aquaculture Centers in Asia-Pacific show that WSD continues to be a major problem in many of the shrimp producing countries, in the Asia-Pacific area despite implementing biosecurity measures (WOAH 2020). WSSV has a broad host range. Nearly all *Penaeid* shrimp are vulnerable to WSSV infection. Put another way, WSSV can affect a wide range of potential shrimp species. Many likely shrimp species, including *Penaeid* shrimp, can be infected with white spot syndrome virus. More than 100 arthropod species, either cultured, wild or infected experimentally, have been reported to host or transmit WSSV (Hameed et al. 2003; Musthaq et al. 2006). This wide range of hosts plays a major role in transmitting and causing disease outbreaks in farmed shrimp. Other marine, brackish and freshwater crustaceans can also be infected with the virus that among them are crayfish, crabs and lobsters. WSSV has been detected in a wide diversity of aquatic invertebrates, the majority of which are members of 34 crustacean families (Sánchez-Paz 2010). However, these species can act as reservoirs and carriers of the virus because, unlike *Penaeid* shrimp, infection is often not fatal. There is also at least one other insect, the shore fly (a member of the *Ephyridae* family), as well as copepods collected from farms affected by WSSV, have been diagnosed with WSSV. As WSSV-positive by PCR, suggesting that they are also possible reservoir hosts (Leu et al. 2008) or even carriers or vectors. By PCR dot blot hybridization, WSSV was also detected in resting rotifer eggs from shrimp culture pond sediments. The detection of WSSV in disinfected eggs demonstrates the presence of WSSV in the eggs and indicates the vertical transmission of WSSV (Yan et al. 2004). The various shrimp species and diagnostic methods will be illustrated in Table 1.

Epidemiological aspects

For the occurrence of a disease, the stressful environment provides the conditions as an enabler of the disease process. Aquatic disease is the result of the presence of a sensitive host in an environment full of stress and potential pathogens. The following environmental and management factors appear to play a role in the spread and degradation of the species, and an increase in losses of shrimps infected with white spot virus:

Sudden changes in the quality or temperature of the water (Esparza-Leal et al. 2010; WOAH 2012; Kakoolaki et al. 2014).

High density in post-storage of larvae in breeding ponds (Gunalan et al. 2011).

Research has shown that farms affected by water salinity, next to the coastal areas, in comparison with the fields with lower water salinity, had more problems (adjacent to the sea, apart from salinity, increases the

percentage of presence of wild carriers (Gunalan et al. 2011).

The excessive density of shrimps in breeding ponds and the prolonged breeding period increase the frequency and severity of the disease (Tsai et al. 1999).

Monsoon winds and heavy rains cause the disease to worsen (this factor is observed in the fields around the Gulf of Thailand (Tsai et al. 1999; Gunalan et al. 2011).

White spot disease virus has a wide hosting domain, and so far, all shrimp species have been affected by the disease in laboratory conditions, and all of them have high sensitivity to the virus that causes the disease. The host range of the white spot disease agent is other marine and freshwater crustaceans. It also includes some types of long freshwater crabs (Flegel 2019). Crabs are considered a major reservoir for the disease-causing virus. Since breeding shrimp act as asymptomatic carriers of the virus, they seem to maintain the virus in wild populations for a long time. In addition, evidence shows that the disease can be transmitted vertically (via eggs), making diagnosing the disease more difficult. In contrast, studies show that the virus that causes the disease can survive for two to three days outside the body host in the water column, which helps the transmission of the disease through water (Baldock et al. 1999).

White spot disease can be transmitted by eating infected normal, dying, dead shrimp or other infected crustacean vectors, including copepods (Lo et al. 1996; Flegel 1997). Dead or dying animals can be a source of contamination. Sea birds, aquatic insects, and some microscopic algae (Liu et al. 2007) can transmit the disease. All farmed shrimp from the late post-larval stages to juvenile and mature stages are highly susceptible to disease.

Table 1 Various species of shrimp and detection methods for WSSV

Species		Detection Method	Reference
	M. brevicornis	PCR	Hossain et al. 2001
Metapenaeus	*M. dobsoni*	Histo, PCR	Hossain et al. 2001; Rajan et al. 2000
	M. ensis	PCR, DNA Probe	Chang et al. 1998
	M. monoceros	Nested PCR, Probe, Histo	Hossain et al. 2001; Rajendran et al. 1999
Latreutes	*L. planirostris*	LAMP, PCR	Xu et al. 2021
	L. anoplonyx	LAMP, PCR	
	F. aztecus	Histo, PCR	Chapman et al. 2004
Farfantepenaeus	*F. duorarum*	Histo	Wang et al. 1999
	F. paulensis	Histo, PCR	Cavalli et al. 2010
	F.brasiliensis	Histo, PCR	
	P. merguiensis	Histo, DNA Probe	Flegel 1997
	P. penicillatus	Nested PCR	Lo et al. 1996
	P. schmitti	Histo, ISH	Unzueta-Bustamante et al. 2004
	P. stylirostris	TEM, PCR, Histo	Galavíz-Silva et al. 2004
	P. japonicus	TEM, Histo, DNA-	Chou et al. 1995; Takahashi et al. 2003; Kawato et al. 2023
Penaeus	*P. monodon*	Sequencing	Chou et al. 1995; Wang et al. 1999; Saravanan et al. 2017
	P. indicus	TEM, Histo	Rajan et al. 2000; Rajendran et al. 1999
	P. chinensis	TEM, Histo	Zhan et al. 1998
	P. semisulcatus	EM, Histo	Wang et al. 1998; Rajendran et al. 1999
	L. setiferus	Nested PCR, Histo	Chapman et al. 2004
	L. vannamei	Histo, PCR	Wang et al. 1999; Galavíz-Silva et al. 2004; Amano et al. 2011;
		TEM, Histo, PCR, Probe	Ma et al. 2022
	A. brevicristatus	Nested PCR	Takahashi et al. 2003
Alpheus	*A. lobidens*	Nested PCR	
	A. japonicus	LAMP, PCR	Xu et al. 2021
	A. distinguendus	LAMP, PCR	
Trachypenaeus curvirostris		LAMP, PCR, EM, DNA Probe	Chang et al. 1998; Xu et al. 2021
Acetes chinensis		LAMP, PCR, EM, ISH, Histo	Xu et al. 2021
Solenocera indica		Nested PCR, Probe	Hossain et al. 2001
Crangon affin		LAMP, PCR	Xu et al. 2021
Squilla mantis		Nested PCR, Probe	Hossain et al. 2001
Austinogebia edulis		PCR, EM	Zhu et al. 2019
Leptochela gracilis		LAMP, PCR	Xu et al. 2021
Parapeneopsis stylifera		Nested PCR, Probe	Hossain et al. 2001
Euphausia pacifica		LAMP, PCR	Xu et al. 2021

Noted PCR: Polymerase Chain Reaction. Histo: Histopathology. LAMP: Loop-mediated isothermal Amplification. ISH: In Situ Hybridization. TEM: Transmission Electron Microscopy. EM: Electron Microscopy.

The virus has survived in seawater outside the host's body in laboratory conditions at 30 degrees Celsius for at least 30 days and has been inactivated for 120 minutes at 50°C. The replication cycle of virus growth in laboratory conditions in the post-larval body of shrimp and cell line was approximately 20 hours at 25°C. Infection with white spot virus is common in a meager amount and undetectable throughout the life of the living organism (WOAH 2009). Transmission of the disease is done vertically through the ovary, and horizontal transmission of the disease is done by consuming infected tissue like homosexuality. Also, transmission can be done through apparently healthy carriers of shrimps and crabs and 40 other types of crustaceans. The exact mechanism of infection has is still unknown, but placing a healthy shrimp next to a sick shrimp can make it sick within 36 to 48 hours through a mechanical vector (Thai Agricultural Standard 2007).

Viral infection in different species

One of the most contagious viral risks that can infect crustaceans such as crabs and shrimps is WSD, and if this disease occurs in farms such as shrimps where the production rate increases drastically, it can lead to the death of shrimps (WOAH 2021). In the first year of its appearance, 1992, this disease caused losses of about 21 billion dollars to the economy. This virus has a wide host range. Since WSD is a highly contagious disease, it can cause a severe viral infection in crustaceans such as shrimp, crabs, and lobsters. If this viral disease penetrates areas with high production, it leads to severe deaths and reduced production (WOAH 2019).

Many aquatic crustaceans, especially decapods, can be infected with the virus, including brackish, marine crabs, freshwater prawns, lobsters, and crayfish (Jiang et al. 2017). This virulent agent is very dangerous and can destroy 100% of farmed panhead shrimps. Most farmed *Penaeid* shrimps, such as *Marsupenaeus japonicus*, *P. monodon*, *Fenneropenaeus indicus,* and *L. vannamei*, are natural hosts for this virus. The researchers have shown that by creating natural challenges, several types of shrimp and several non-penaeid shrimps have been heavily exposed to the virus. It is worth noting that shrimps grown in areas with relatively low-temperature fluctuations and water temperatures above 29°C show more resistance to WSSV (Santosh and Muddana 2020).

In research, three WSSVs of different virulence, including *WSSV-CN01* with high virulence, *WSSV-CN02* with moderate virulence, and *WSSV-CN03* with mild disease (Gao et al. 2014). Recently, in the east coast of India, the Cuddalore region and Tamil Nadu supply, WSSV mortality has not been observed in mud lobsters, but research shows that this transmission has been transmitted to six other lobsters of the *Panulirus* genus (Gunasekaran et al. 2018; Patil et al. 2021). Also, no reports have been of consuming wild spiny lobsters (Ross et al. 2019). Researchers have not yet fully identified the causes of WSSV but it has been shown that wild decapods can act as reservoirs for WSSV, such as *Acetes* sp., *Exopalaemon* sp., *Scylla* sp., *Callianassa* sp., *Helice* sp., *Macrophthalmus* sp., *Alpheus* sp., *Macrophthel* sp., *Metaplax* sp., *Hemigrapsus* sp., *Orithyia* sp., *Palaemonoidea* sp., *Stomatopoda* sp., *Sesarma* sp. (Lei et al. 2002), *Mysis* sp. (Huang et al. 1995). These types can express the disease under the right environmental conditions. Non-decapod crustaceans such as rotifers (Yan et al. 2004), *Balanus* sp. (Lei et al. 2002), Copepods (Huang et al. 1995) carrier animals may be healthy. There is some evidence that *Artemia salina* may also be a carrier, but it has not been conclusively proven (WOAH 2019).

One of the non-indigenous diseases in the European Union is the white spot disease caused by the white spot syndrome virus. Researchers have conducted their research on the spread of this disease in three European Union member countries (Greece, Italy, and Spain) and one European country that is not in the European Union (Turkey) in the years 1995 to 2001 and presented their report. These case reports showed the ability of this virus to cause mortality in *Penaeid* shrimp at ambient temperature in Europe (Stentiford and Lightner 2011).

Bangladeshi researchers have identified white spot disease as an economic factor loss in the shrimp farming professions with surveys conducted in the last two decades and concluded that farm management and environmental and seasonal changes may increase the mortality caused by the disease in shrimp farms. In 2018, a study on WSSV infection by the species-specific gene VP28 was conducted in southwestern Bangladesh using conventional PCR, real-time PCR, and sequencing. It showed that the age of the field, the presence of a nursery pond, post larval reservoir, and weed in the farm area, weed control, stocking density, storage frequency, ammonia, and oxygen concentration can affect the occurrence of the disease. Therefore, the relationship

between the prevalence and severity of the disease, risk factors, and the origin of the strains can role play in the management of WSD (Talukdar et al. 2021) (shown in Figure 2).

Routes of infection and spread

Reservoirs and carriers of the virus are one of the most fundamental agents in the spread of the disease, and include aquatic populations (hatcheries and infected farms), some species of crabs, artemia through water or eggs, and dead aquatics due to shrimp feeding on them (Walker et al. 2011). If the virus is outside the live carrier, it can maintain its virulence for 3-7 days (Sánchez-Paz et al. 2015). Therefore, control, quarantine, care and surveillance measures, extermination, and elimination operations must be done carefully to prevent the disease and its spread. Monitoring is another control factor that includes continuous and systematic programs on a specific (target) aquatic population to track changes in prevalence (Clark et al. 2013) (shown in Figure 3).

Viral transmission

Shrimps acquire white spot infection through vertical transmission (shrimp larvae can be infected through broodstock during spawning) and horizontal (white spot virus by swallowing infected tissue or contaminated water) (Bandeira et al. 2019). WSSV is mainly transmitted via horizontal routes such as exposure to infected water and ingesting moribund/dead carriers or vectors (Lo et al. 1998). The lack of information on the transmission of this disease in the aquatic environment requires more exhaustive research because the data obtained in laboratory conditions differs from that in open-water environments (Huang et al. 2020). In other words, the importance of having any path and the transmission of WSD inside a pool or aquarium and natural environment are very different from each other. Also, the rate of disease transmission depends on several factors, such as the level of defense and the host's defense system, density, the number of susceptible hosts, the dose of the virus, as well as the environment's biotic and abiotic components.

Because in aquaculture discussions, we sometimes see farmed species and wild aquatic species in the same water column, so they suffer from similar viral challenges. On the other hand, with the ever-increasing ex-

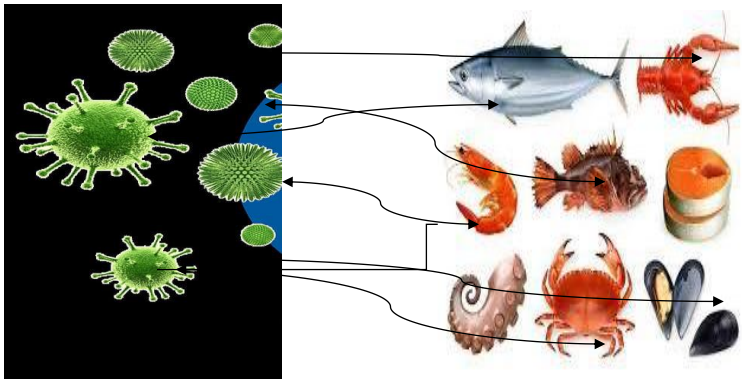

Fig. 2 Viral infection in different species

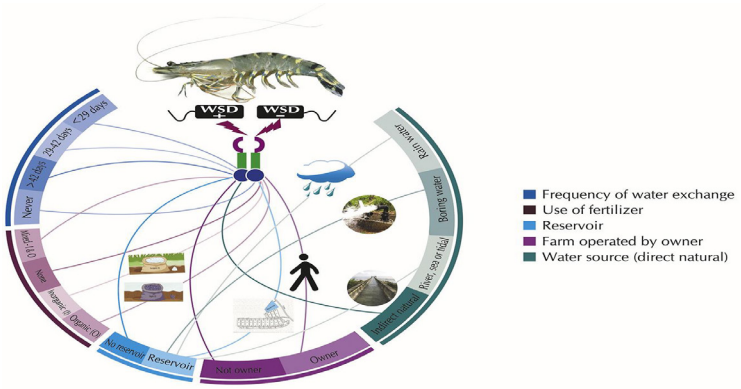

Fig. 3 Factors affecting the occurrence of WSD (Neaz et al. 2020)

pansion of international aquaculture and global trade issues in live fish and the products they produce, viruses are also easily distributed. The continuous emergence of viral diseases in aquaculture can also be caused by animal hosts, environmental factors, and human factors (Kibenge 2019).

Under laboratory conditions, virus transmission can occur through water, food and food chains, cannibalism, and cohabitation. Observing this disease in non-cultivated aquatic animals indicates that virus transmission is widespread. The aquatic environment has many organisms and biological factors that can act as a host or carrier. Since the level of sensitivity in organisms differs, all of them are not equally sensitive to the virus. In open water, mollusca collect viruses in their bodies while feeding by filtering. Research also shows that WSSV replication is not done in mollusca. This indicates that mollusca play the role of carriers (Corre et al. 2012). Research shows that the transmission of the virus through the feeding of dead shrimp is more likely than through water. Also, the results of transmission studies showed that crabs may be the most important and main host and vector of WSD in natural conditions. The researchers showed that healthy shrimp consumption of virus-infected white shrimp tissue resulted in rapid mortality (Oowannayan and Phanthura 2011).

The researchers also stated that the virus has the potential to be transported through the movement of live crustaceans and their products, both from outside the E.U. and between E.U. and non-EU countries (Stentiford and Lightner 2011).

Immunostimulants

Immune stimulators can be defined as molecules that subtly enhance the host's non-specific defense machinery to combat invading microorganisms. They do not have problems using chemotherapy/vaccines and provide a suitable solution for immunity of shrimp. Hence, immunostimulants may be a suitable option for the future and be considered a future perspective for shrimp health management. A concept of "immune priming" regarding the pathogen is given in researchers' studies and is regarded as an optimal solution for the vaccine's effectiveness against WSD (Yang et al. 2021). Immunostimulants are a group of natural substances that cause the host immune system to be stimulated against different pathogens (Barman and Nen 2013).

Effective methods used in shrimp farming to prevent diseases generally include vaccination, chemicals, antibiotics, and immune stimulants. Antiviral/immune stimulants were used as an alternative to antibiotics (shown in Figure 1). They were found to boost the immune system of the shrimp in an environmentally friendly way. If it is maintained with appropriate methods, the use of safety stimuli can be a suitable event for protecting shrimp aquaculture worldwide (Apines-Amar and Amar 2015). Vaccines and immune stimulants are preventive and are used to induce host immunity (Bachère 2000). Musthaq et al. (2009) comprehensively reviewed the WSD vaccination landscape (Musthaq et al. 2009). Depending on their source, immune stimuli are divided into several groups: algae, bacteria, animal-derived, hormones/cytokines, and nutritional factors (Sakai 1999). Researchers have also tested seaweed polysaccharides as immune stimulants for shrimp (Declarador et al. 2014). They have a wide range in terms of efficiency and depict many functions. Research on five different herbal medicinal plants such as *Aegle marmelos*, *Eclipta Alba, Picrorhiza kurooa*, *Tinospora cordifolia,* and *Cyanodon dactylon* with effect on immune stimulations, a significant reduction of viral loads with an increased survival rate (74%) of shrimps (Citarasu et al. 2006). Another immune stimulant can be live bacteria. Research has shown that when the shrimp diet is enriched with probiotic bacteria, they stimulate the cellular and humoral components of the shrimp's innate immune system. Functions of immunostimulants include increasing macrophage activity, increasing lysozyme levels, increasing cytokine activity and interferon levels, increasing bactericidal activities, inducing antiviral activity, stimulating natural killer cells, stimulating free radical production, stimulating complement system, stimulating antibody responses, etc. Also, in the research conducted on food supplements, it was shown that with the injection of vitamin A, C, and E supplements, a significant increase in the resistance of shrimps against pathogenic agents was observed (Lee et al. 2020).

Finally, it is concluded that creating a balance between all the components, especially the triple components, such as ensuring a pathogen-free reserve and increasing the host's defense by giving nutrients and immune stimulants, can strengthen immunity (shown in Figure 4). It is noteworthy that water and feed free from pathogens and good water quality and its maintenance can promote the development and promotion of sustainable shrimp aquaculture.

Pathogenesis

WSSV can affect tissues with ectodermal and mesodermal origins (Lightner 1996). Some studies have found WSSV infections in various tissues, including the testes, ovaries, gills, stomach, body's outer layer (cuticular epithelium), lymphoid organs, antennal glands, and hematopoietic tissues in naturally and artificially infected shrimp (Yoganandhan et al. 2003; Escobedo-Bonilla et al. 2007; Desrina et al. 2022). Additionally, researchers have noted that the primary tissues for WSSV replication are the gills, stomach, cuticular epithelium, hematopoietic tissues, lymphoid organs, and antennal glands (Tan et al. 2001; Durand and Lightner 2002; Escobedo-Bonilla et al. 2007).

As per studies, the foregut, gills, antennal gland, and integument are crucial for maintaining shrimp's balance. Due to WSSV infection, these organs may malfunction, leading to shrimp deaths (Escobedo-Bonilla et al. 2007). In the later stages of WSSV infection, the epithelial cells, hematopoietic tissues, and antennal gland tubules degenerate. After just six hours of disease, WSSV can disrupt the host's defense mechanisms against oxidative stress (Chen et al. 2011).

There are varying results from experiments on WSSV infection in shrimp growing water (Kanchanaphum et al. 1998). Some studies show a high infection rate when shrimp are exposed to virus particles in the water. In contrast, other injection experiments did not lead to infection, even with high virus doses (Prior et al. 2003). Additionally, there are discrepancies in the effects of experimental WSSV infection through the consumption of infected tissues or contaminated feed. While some studies suggest shrimp can get infected orally, others disagree (Lightner and Redman 1998; Vidal et al. 2001; Escobedo-Bonilla et al. 2006).

Moreover, some researchers found that WSSV-contaminated feed has a low oral transmission route but is highly contagious when injected. They also concluded that the peritrophic membrane does not effectively protect shrimp from WSSV infection inside the body. These conflicting findings may result from variations in WSSV strain virulence, delivery methods, viral dosages, test subjects, and other experimental conditions (Van Thuong et al. 2016).

For experimental shrimp inoculation, the oral route challenge is commonly used to test the infectivity of a WSSV stock solution. A standardized oral inoculation method has been developed to deliver virus titers precisely to all inoculated shrimp. Using this method, immunohistochemistry (IHC) detected the main viral replication sites, including the foregut epithelial cells, gills, and, at a high dose, the antennal gland (Escobedo-Bonilla et al. 2006).

The question of how WSSV spreads from the primary replication sites to other target organs remains highly debated. Some studies suggest it can affect crayfish hemoglobin cells to travel from the primary replication sites to distant organs (Wang et al. 2002). However, other research indicates that circulating hemoglobin in freshwater prawns and shrimp is resistant to WSSV infection. These differences may be due to variations in host species.

The occurrence and severity of WSD epidemics in shrimp are known to be affected by environmental conditions such as salinity, pH, and temperature (Tendencia et al. 2010; Dey et al. 2020). For example, in one

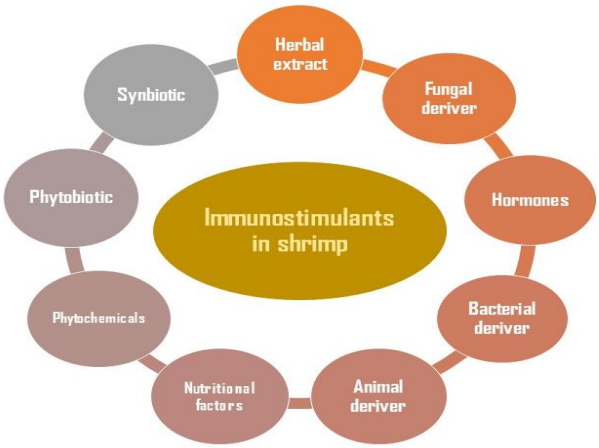

Fig. 4 Sources of immunostimulants

laboratory study, results showed that dropping temperatures below 32°C consistently resulted in high shrimp mortality with the second step of WSSV infection noted in those that survived at higher temperatures. Salinity did not significantly influence shrimp mortality in the same experiment (Raj et al. 2012).

In another study, catastrophic mortality was associated with salinity levels that were either lower or higher than average when WSD conditions were present. Additionally, a study found that low temperature and high pH influenced WSSV infection in cultivated shrimp (Kakoolaki et al. 2011).

The infection process

Mechanisms of virus entry

WSSV enters host cells to start the infection process. This involves interactions between several host cell surface receptors and structural proteins of the virus. Several endocytic routes, such as clathrin-mediated endocytosis, caveola-mediated endocytosis, and macropinocytosis, are possible for WSSV to enter host cells (Huang and Zhang 2013; Huang et al. 2015; Chen et al. 2016). The virus entrance process needs to be started by these contacts. The virus enters the cell more easily thanks to host cell surface receptors like vascular endothelial growth factor receptors and the shrimp polymeric immunoglobulin receptor-like protein (Niu et al. 2019). Nevertheless, there are still questions about the precise molecular mechanisms behind WSSV entry and the relative contributions of several endocytic routes to the effectiveness of WSSV internalization (Millard 2020).

Exiting the endosome

Once inside the host cell, WSSV virions become encapsulated within early endosomes (Lozach et al. 2011). The enormous size of the encapsulated virions usually directs early endosomes toward destruction. During their maturation process, these endosomes experience a gradual acidification of the vesicle lumen, which permits internalized receptor ligands to dissociate and return to the cell membrane (Hu et al. 2015). To initiate infection, WSSV must, however, escape from endosomes that are headed for lysosomes. Endosome escape is specifically mediated by lowering pH, alternating between intracellular and cell surface receptors, and endosomal protease processing. There are a few known possibilities for this escape mechanism, however there are still numerous questions about how to leave without being detected by a host (Staring et al. 2018).

Nucleus targeting and invasion

WSSV must target the host cell nucleus and penetrate the nuclear envelope after emerging from the endosome. The precise processes by which WSSV targets the nucleus remain unclear, and research is still being done on the functions of several viral proteins, including VP35 and the nucleocapsid protein VP15 (Sangsuriya et al. 2011). For WSSV to go through the dense cellular environment with efficiency, host molecular motors could be required. It is essential to comprehend the mechanisms underlying nucleus targeting because they dictate whether or not the virus can infiltrate the nucleus and start reproducing. Interrupting this process can potentially lessen the impact of WSD (Hennig and O'Hare 2015).

WSSV replication

Immediate early genes play an important role in initiating viral gene transcription (Durand et al. 1997). Host transcription factors regulate these genes and can be grouped into categories such as transcription factors, kinases, or E3 ubiquitin ligases. Among the immediate early genes, ie1 is extensively studied and functions as a transcription factor for other WSSV genes. Host transcription factors, including STAT, Dorsal, Relish, high mobility group box genes, prohibitin2 protein homolog, Yin Yang 1, and Krüppel-like factor, activate immediate early gene promoters. These promoters and associated transcription factors are critical in enhancing WSSV replication. However, many aspects of the promoters and functions of immediate early genes remain poorly understood (Sánchez-Paz 2010).

Early genes

During the early stages of WSSV replication, which typically occurs between 2 to 6 hours post-infection, the expression of early genes is crucial (Sánchez-Paz 2015). These early genes are dependent on the prior transcription of immediate early genes. Their primary function is to support DNA replication and nucleotide metabolism to produce the necessary genomes for new viral progeny. Essential early genes include DNA polymerase, dUTPase, DNA helicase, ribonucleotide reductase, thymidylate synthase, thymidine kinase/thymidylate kinase, and homologous-region binding proteins (Samal et al. 2007). These genes facilitate DNA replication and the generation of new viral genomes independently of the host cell's division status. Interestingly, WSSV early genes have no roles in transcription, indicating their dependence on host machinery for mRNA biogenesis (Van Hulten et al. 2001b).

Late genes

The final stage of WSSV replication, occurring around 12 hours after infection, results in the transcription of a substantial number of WSSV genes, with up to 65.6% of predicted WSSV ORFs expressed (Van Hulten et al. 2001b). Most of these late genes encode major structural components of the nucleocapsid and the viral envelope, encasing newly formed genomes. However, late genes are also the ones whose endonucleases enable WSSV propagation and proteins that mediate movement to a nuclear membrane for its assembly (Apitanyasai et al. 2018). Several late genes play roles in nucleosome assembly disruption. These late genes rely on the host RNA polymerase II, similar to the strategy employed by baculoviruses to transcribe structural proteins. Notable late structural proteins include VP19, VP31, VP52B, VP28, VP36B, VP39A, VP95, VP26, VP36A, VP399, VP664, VP51C, and VP60B. VP28, in particular, is a major envelope protein crucial for attachment and entry (Tsai et al. 2006).

Small RNAs

Focusing on microRNAs (miRNAs), researchers have identified short RNAs (sRNAs) produced during WSSV infection. Nonetheless, the majority of sRNAs reveal considerable sequence variety and the features of small interfering RNAs (siRNAs), which are produced from ORFs (Liu et al. 2016). On the other hand, miRNAs typically originate from non-coding areas and have unique distribution patterns. During WSSV replication, RNA interference machinery, such as Dicer, is synthesized by siRNA and miRNAs to control the translation of target genes through precise and cooperative binding (Geiss et al. 2005). Although it hasn't been confirmed, the host's capacity to create miRNAs may be impacted by the generation of viral sRNAs during fast WSSV replication. Interestingly, viruses with double-stranded DNA genomes appear to be the only ones capable of producing miRNAs. It has been determined that WSSV miRNAs are involved in the initiation of viral propagation, regulation of viral gene expression, and assessment of virus viability in response to cellular stress. Although the whole impact of viral miRNAs on host gene function is still unknown, they may also affect host gene expression (Bruscella et al. 2017).

Host response

The interactions between hosts and pathogens in WSSV infection have been studied extensively and have given us much information. WSSV uses various methods to block or control processes inside host cells. For example, it changes the body's balance to its advantage by using NF-B-associated signaling pathways. It also changes the host's metabolism similarly to the Warburg effect to support its genome replication. WSSV prevents apoptosis proteins from triggering antiviral reactions and can stop myelinization (Apitanyasai et al. 2018). However, most of this research has only shown the physical traits, which isn't enough to understand how viral genes affect the shrimp's immune response (shown in Figure 5). We need more research to determine how WSSV avoids or takes over the host's immune system. We also don't know much about the exact molecular mechanisms of the shrimp's innate immunity. More research is being done to understand

the relationship between the host and WSSV, which will help us understand how WSSV causes disease and develop new ways to control it. We can look forward to a more detailed explanation of this host-pathogen interaction soon, and this will be important for creating effective WSSV control methods (Li et al. 2019).

Clinical signs

Some scientists have reported that although it may take some time for WSSV symptoms to appear, infected animals typically die within 3 to 8 days, resulting in a high mortality rate (Corbel et al. 2001). A few days before their death, infected shrimp congregate at the pond's edge and exhibit clinical symptoms. Lethargy, decreased food intake, reddish staining of the body and appendages, a decrease in preening activities, cuticle loosening, discoloration of the hepatopancreas, decreased appetite, decreased response to stimuli, and swelling of branchiostegites as a result of fluid buildup are some of these signs. Along with clinical symptoms, animals affected by the disease may also show gross pathology, including calcified white patches on the exoskeleton and white to reddish-brown staining on the heads and carapaces. The cephalothorax and tail cuticles of infected shrimp have circular white spots or patches on them (Van Hulten et al. 2001a; Rout et al. 2005). A potential field diagnostic technique for the disease is the appearance of calcified patches on the exoskeleton of an affected animal. However, this clinical symptom is not universally seen in all host species, as white spots were not observed in experiments with acute WSSV infection in P. indicus and P. monodon; instead, tiredness and an appetite deficit were the only symptoms noted. Additionally, in P. indicus, the carapace had to be removed to confirm WSSV infection because the body had become reddish (Desrina et al. 2022). WSD results in rapid death in farmed shrimp, with a typical cumulative mortality rate between 90% and 100% (SiouNing et al. 2023). The exact mechanisms of white spot development and deposition are still unknown. However, other research suggests that WSSV infection may disrupt the respiratory and integument systems, leading to the accumulation of calcium salts in the cuticle, which causes the formation of white spots (Wang et al. 1999). Histologically, eosinophilic inclusion bodies distinguish WSSV infection in the early stages of infected cells. In advanced stages of infection, inclusion bodies with a stronger basophilic stain can be found in the hypertrophied nucleus of infected cells (Lo et al. 1996). Additionally, infected nuclei gradually enlarge and become more basophilic (Hameed et al. 2003). A distinctive diagnostic feature of WSSV is the cross-hatched appearance of the nucleocapsid. Karyorrhexis and cell disintegration may occur during the final stages of infection, leading to necrotic sites with vacuolization (Karunasagar et al. 1997). Due to the high virulence of

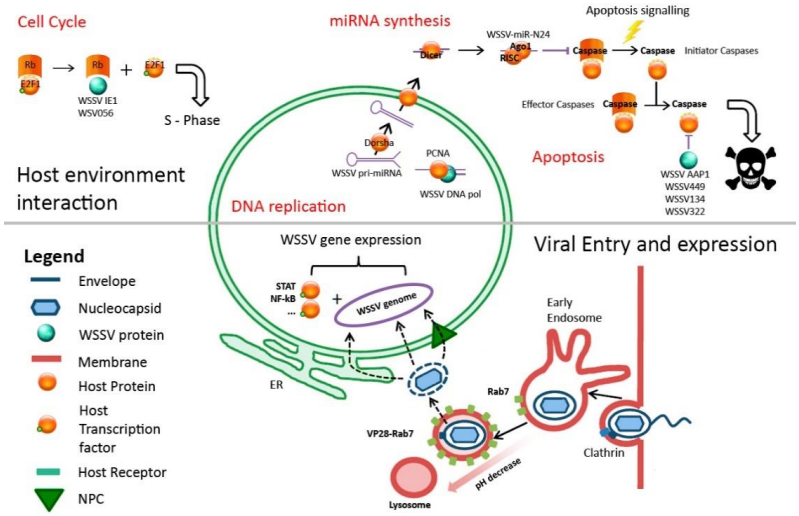

Fig. 5 A summary of the interactions between WSSV entries and their surroundings. Access of viruses into host cells. By interacting with host receptors, WSSV proteins trigger endocytosis mediated by clathrin. After then, WSSV moves through endosomes. The pH decreases as the virus matures, indicating that it is ready to exit the endosome. At this point, interactions between VP28 and Rab7 might be implicated. How WSSV penetrates the nuclear membrane is a mystery. Intracellular interactions between WSSV and host cell occur when host transcription factors attach to her WSSV genome and start viral gene expression when they enter the nucleus. In order to obtain the host machinery needed for WSSV DNA replication, E2F1 allows WSSV to capture the cell cycle in the S phase. Apoptosis signaling can be affected by WSSD by miRNA-mediated inhabitation of the initiator or by a viral protein that inhibits effector caspase activity (Verbruggen et al. 2016).

acute WSSV infection, an effective and speedy diagnosis method is essential to stop the disease from spreading. Based on the diagnostic validity at various levels of severity, the diagnostic strategy of confirmatory diagnosis using real-time PCR assay after presumptive diagnosis using one-step PCR and rapid diagnostic kits at different seasonal periods could help in preventing the outbreak and spread of WSD with speed, accuracy, and cost-effectiveness (Kim et al. 2023a).

Diagnostic methods

Among plenty of diagnostic methods, electron microscopy is mainly considered the first option, especially transmission electron microscope (TEM) using ×1000 resolution, which allows the detection of viruses directly (Dey et al. 2020). On the other hand, detecting WSSV by antibody-based techniques such as dot blotting, western blotting, immunohistochemistry, etc., has been demonstrated as another valuable way that has been recommended due to high sensitivity (Vaniksampanna et al. 2017; Wiradana et al. 2019). Lateral flow immunoassay (LFIA) has been illustrated as an effective and fast assay in the aquaculture industry (Kulabhusan et al. 2017). The ELISA-based method was designed in a performed study, and the ICP11 protein of WSSV was identified as a target in ELISA. This cost-effective method has been found to detect antigens in shrimp tissues and has several advantages (Murugan and Sankaran 2018). Apart from all the methods mentioned by WOAH, molecular detection of the virus is genuinely recommended because of its sensitivity and specificity. It is often determined that molecular methods, including one-step PCR, Nested-PCR, Taq man PCR, LAMP, etc., are used to detect viruses all around the world, and they are more popular among other well-known methods (Dey et al. 2020; Desrina et al. 2022) (Figure 6).

Prevention and control

WSSV has been known as an agent responsible for economic loss in the shrimp industry worldwide for ages. In the meantime, prevention and control of this devastating disease decrease monetary damages in involved countries. Some deterrent mechanisms were introduced by different researchers, even though none of them can deter shrimp after challenges. However, there is no treatment available to interfere with the uninhibited occurrence and spread of the disease. Numerous strategies have provided shrimp against this infection (shown in Figure7). They consist of vaccination, immunostimulation, disinfection of eggs and larvae, breeding shrimp using resistance progress, and use of Specific Pathogen Free (SPF) and RNA interference (RNAi) (Robalino et al. 2005; WOAH 2019; Muliani et al. 2021) and probiotics (Lakshmi et al. 2013; Pham et al. 2017). Furthermore, due to the increase in shrimp aquaculture, the use of some drugs was rising. However, it developed shrimp resistance and created environmental pollution that can seriously threaten the health of both humans and shrimp. According to numerous resources, natural compounds play an integral role in improving the performance of animals and preventing diseases (Zhang et al. 2023). Raw materials like mangroves and herbal plants have started the experiment even though it has been limited to the scale of the laboratory (Babuselvam

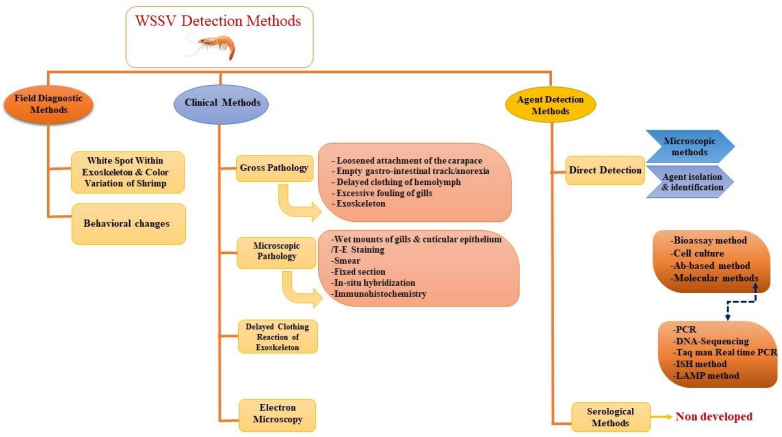

Fig. 6 Summarized diagnosis methods

et al. 2012; Velmurugan et al. 2012; Chakraborty et al. 2014; Zhang et al. 2023). Immune stimulation using stimulants such as beta-glucan, vitamin C, seaweed extract (fucoidan), etc., are other methods that improve WSD resistance (Chang et al. 2003; Chotigeat et al. 2004). Oocyte sterilization for oocyte transfer is probably effective (Lo and Kou 1998), but has not yet been validated in formal scientific trials.

It should not be forgotten, although WSSV has a wide range of tolerance in variable situations, it is influenced by environmental factors like temperature, salinity, dissolved oxygen (DO), pH, and nitrogen compounds. Therefore, considering the importance of these factors can help avoid developing WSSV. For example, shrimp can tolerate high temperatures, and 25- 28 °C can provide the optimum temperature for them. Consequently, keeping the balance of the growth situation should be considered the first way to protect shrimp from WSSV (Millard et al. 2021). General husbandry practices that have been successfully used to manage WSD include avoiding stocking in the cold season, using specific pathogen-free (SPF) or polymerase chain reaction (PCR)-negative seed stocks, use of bio-secure water and culture systems and polyculture of shrimp and fish (WOAH 2019). On the other hand, it is worth mentioning that the crucial motivation for producing SPF animals in the aquatic industry was created by the emergence and spread of WSD when *P. monodon* was the major cultivated shrimp in Asian countries. It was revealed that the main source of WSSV in shrimp was infected post-larvae (Withyachumnarnkul 1999) and monitoring was not effective to minimize it. Therefore, the availability of SPF stocks of *P. vannamei* with pathogen exclusion strategy led to becoming the dominant cultivated shrimp species in Asia. Because of the advantages of using improved SPF stocks of *P. vannamei* to make healthy post larval, the term SPF in Asia formed stocks with more increased disease resistance or tolerance. Nowadays, there are two ways to provide SPF shrimp: firstly, finding a geographical area with low prevalence or a long-term absence of specific pathogens, and secondly, consistent screening of shrimps for major pathogens during a determined period (Alday-Sanz et al. 2018). The following paragraphs will explain the main preventive and control methods of WSD in the shrimp industry.

Vaccination

Groups and educational institutions conducted various investigations and trials to develop effective viral vaccines; nonetheless, only some vaccines are certified (Mousavi and Zorriehzahra 2021). The shrimp immune system relies solely on innate immune mechanisms, encompassing cellular and humoral immunological responses. This lack of memory-type immunity has posed significant challenges in developing vaccines against shrimp infections. Nonetheless, Venegas et al. demonstrated a quasi-immune response in *P. japonicus* naturally or experimentally infected with WSSV in 2000. When survivors of a spontaneous WSSV epidemic were re-challenged after four months, they showed a relative survival rate of 94%. This suggested that exposure to WSSV enhanced a quasi-immune response, which offered the best chance of survival. In subsequent experiments, survivors of experimental WSSV infections displayed resistance to re-challenge with WSSV at weeks 3 or 4, and this resistance lasted up to 2 months. Wu et al. concluded that the survivor's plasma contained neutralizing components responsible for this resistance (Wu et al. 2002). These findings prompted scientists to explore the possibility of immunizing shrimp against WSSV. Over recent years, various studies have inves-

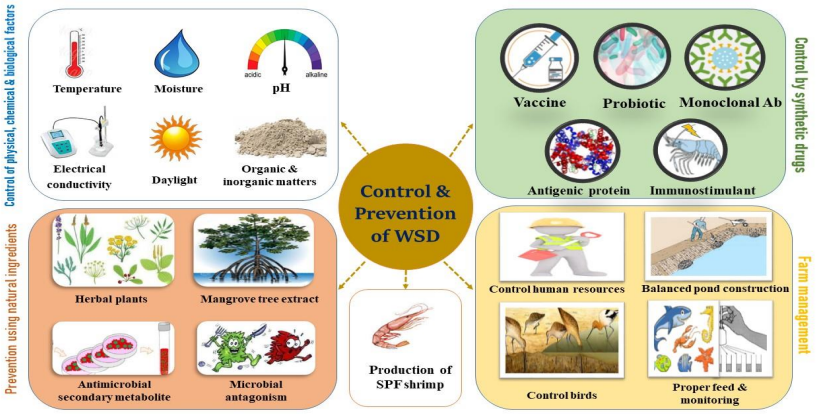

Fig. 7 Experimented ways to control and prevention of white spot diseases

tigated anti-WSSV defense mechanisms for shrimp, including inactivated vaccines (Namikoshi et al. 2004; Singh et al. 2005), recombinant protein vaccines, and DNA vaccines (Fu et al. 2010).

While numerous anti-WSSV techniques have been explored, the initial focus in WSSV vaccine development has been on envelope proteins. These proteins are crucial because viral infections often rely on them for entry, assembly, and budding processes. VP28, an essential envelope protein of WSSV, is partly responsible for systemic shrimp infection (Musthaq et al. 2006; Van Thuong et al. 2016). VP28 interacts with host cellular proteins, such as PmRab7, heat shock cognate protein 70, and signal transducer and activator of transcription (STAT) during infection. It also acts as a viral attachment protein to shrimp cells (Liu et al. 2007; Tasakka et al. 2022). Several studies have shown that VP28-based vaccinations provided protection or enhanced the survival rate of WSSV-challenged shrimp compared to untreated shrimp (Namikoshi et al. 2004; Jha et al. 2006). However, this protection is insignificant and wanes notably after ten days following the test. To address this challenge, one potential approach is to express envelope proteins in eukaryotic expression systems, which can also serve as a delivery method or vector for the vaccine (Musthaq and Kwang 2014). In addition, shrimp-fed food pellets coated with inactivated bacteria overexpressed VP28 showed a better survival rate after the WSSV challenge (Witteveldt et al. 2004). Moreover, according to new research in 2023, VP28-expressing *C. vulgaris* PKVL7422 had a potent protective effect against WSSV infection when given as an oral feed additive vaccination. Additionally, the genes proPO, ALF, and CTL, important for shrimp resistance against WSSV infection, were expressed at higher levels in the vaccinated shrimp. *C. vulgaris* has a lot of potential for use in industrial shrimp vaccine production because it produced large amounts of the vaccine protein VP28 and is linked to low production costs, simplicity of use, and high protective efficacy, which may be an essential tool for disease prevention in the shrimp aquaculture industry (Kim et al. 2023b).

Antibody therapy

Shrimp can be passively immunized against WSSV using antibodies, such as egg yolk immunoglobulin (IgY) from hens and antibodies from mammals, once the animals have been immunized with the target antigens (Cui et al. 2022). By giving shrimp that have just been exposed to the virus pre-made anti-WSSV antibodies, this method offers instant but transient protection. In contrast to active vaccines, this approach does not elicit an immune response from the shrimp; instead, the antibodies specifically target and neutralize the virus (Chang et al. 2018). The virus can be completely coated by one antibody, or it can be neutralized by binding just one antibody to the virus's envelope proteins (Parren and Burton 2001). The procedures outlined in the section on biologically active compounds should be followed to evaluate the efficacy of anti-WSSV antibodies against free virions (Cui et al. 2022). It is noteworthy that the concentration of antibodies required to inhibit free virus infections may be lower than that needed to prevent cell-to-cell propagation (Shulgin et al. 2021). Shrimp should be exposed to WSSV in a way that replicates natural infection to assess the correlation between in vitro neutralization and in vivo protection during WSSV infection. In the meantime, protective antibodies can be given via injection, immersion, or feeding (Chen et al. 2010). As demonstrated in a study where losses in antibody-treated shrimp may have resulted from cannibalism rather than treatment failure, individual housing of shrimp is advised to minimize data variability caused by cannibalism or reinfection. The potential of anti-WSSV antibodies could be investigated in a group challenge paradigm after in vivo evaluation (Safriani et al. 2019).

RNAi-based therapy

Double-stranded RNA (dsRNA) in shrimp triggers RNA interference (RNAi), a conserved immunological response that results in gene silence to protect cells against viruses and transposons. The first step in this process is the digestion of dsRNA into 21–23 nucleotide small interfering RNA (siRNA) by the enzyme Dicer. Thus, homologous viral mRNA is selectively degraded by these siRNAs, rendering RNA interference (RNAi) one of the few focused antiviral defenses in shrimp (Hammond et al. 2001; Obbard et al. 2009).

In shrimp aquaculture, RNAi offers a viable method of fighting viral diseases such as the White Spot Syndrome Virus (WSSV). Research has demonstrated that in shrimp species such as *M. japonicus*, injecting VP28-siRNAs in conjunction with WSSV suppresses viral multiplication (Zhu and Zhang 2012).

Furthermore, VP28 and VP37-dsRNA have been successful in getting rid of WSSV from *P. vannamei* and *M. japonicas* (Rámos-Carreño et al. 2021). Another study showed that oral administration of bacterially expressed VP28 dsRNA protected shrimp against WSSV (Sarathi et al. 2008). Large-scale shrimp farming is not feasible due to the intramuscular injection used in the majority of RNA interference research. Rapid disintegration during feed processing and digestion, along with shrimp feeding behavior that results in RNA loss in water, provide problems for oral delivery of RNA (Cox et al. 2024). To overcome these challenges, effective oral delivery strategies have been developed, including using virus-like nanocarriers (Rámos-Carreño et al. 2014), dsRNA-enriched bacteria (Thammasorn et al. 2015), transgenic microalgae expressing dsRNA (Charoonnart et al. 2023), and viable brine shrimp zygotes (Alam et al. 2023). By providing dsRNAs or siRNAs that encode WSSV-specific sequences, RNAi-based therapeutics precisely target viral reproduction without neutralizing free virions. It is advised that these treatments be tested in vivo, with individual housing of shrimp being used for early testing and group housing for later phases. To guarantee that particular immune responses are triggered, it is preferable to use WSSV injection techniques that imitate genuine infections (Cox et al. 2024).

Immunostimulation

The use of immunostimulants as an alternative to the drugs, chemicals, and antibiotics currently being used to control diseases in shrimp culture is attracting the attention of many researchers (Bairwa et al. 2012). An immunostimulant is a naturally occurring substance that stimulates the immune system of the host against pathogens (Barman and Nen 2013). Immunostimulants can be divided into several groups depending on their sources: bacterial, algae-derived, animal-derived, nutritional factors, and hormones/cytokines (Sakai 1999). It is possible to use immune stimulants to increase shrimp resistance to disease. Immune stimulants such as peptidoglycan, alpha-1 and 3-glucan, and lipopolysaccharides in food increase the non-specific defense of shrimps against pathogenic agents. Several reports have shown that beta-glucan, vitamin C, seaweed extracts (fucoidan), and other immunostimulants may improve resistance to WSD. Although crustaceans do not have a humoral immune response through the production of immunoglobulins, a semi-immune response by producing immunoglobulin-like substances against viral diseases in shrimp has been proven through the immune cells in the hemolymph, including hyalonocytes, semi-yranoter, and yranoter cells (Rámos-Carreño et al. 2014). Mechanisms of immune responses in shrimp include phagocytosis, ehandol, cytotoxicity (cell poisoning), encapsulation, and prophenol oxide system (Bachère 2000).

Herbal intervention

Plants are the storehouses and rich sources of safer and cheaper chemical compounds. These natural plant products have been reported to have various activities like antistress, growth promoters, appetiser, tonic, immunostimulants and antimicrobials (Citarasu et al. 2002). Moreover, the substances are obtained from natural sources, besides possessing other interesting properties like non-toxic, biodegradable and biocompatible (Citarasu et al. 2003). Natural plant products promote various activities such as antistress, growth promotion, appetite stimulation, immunostimulation, aphrodisiac, and antimicrobial properties. Due to the active principles such as alkaloids, flavonoids pigments, phenolics, terpenoids, steroids, and essential oils (Kumar Bairwa et al. 2012). Plants serve as a repository of secure and economic chemical compounds that depict various properties such as growth promoters, immunostimulants, and antimicrobials (Citarasu et al. 2002). Immunostimulants from various herbs oral administration of immunostimulants like lipopolysaccharides, etc., have shown an increase in defensive effectiveness in WSD (Citarasu et al. 2003). Recently, a variety of herbal geniposide. It is a natural cross-linker that has low toxicity and excellent biocompatibility. Therefore, it is used to synthesize diverse biological polymers for drug delivery purposes (Sung et al. 2001; Mahgoub et al. 2017). It depicts-inflammatory, neuroprotective, antidiabetic, antiproliferative, antioxidative, and antiviral activities (Wang et al. 2017). Lately, the antiviral activity of Genipin (GN) against WSSV has been illustrated in crayfish *Procambarus clarkii* and in shrimp *L. vannamei* (Huang et al. 2019).

Several different forms of immunostimulants and plant-derived chemicals that have been reported to be

antiviral against WSSV include:

Antiviral activity of bis(2methylheptyl) phthalate from Pongamia pinnata leaves.

Antimicrobials from Argemone Mexicana.

Immunomodulatory effect of polysaccharide gel extracted from Durio zibethinus.

Antiviral extract from Cyanodon dactylon.

Antivirals from algae.

Antiviral activity of Genipin.

Also, certain plants, such as seaweed and duckweed, are known to contain bioactive compounds, and numerous studies have been conducted on them (Yadav et al. 2024; Debbarma et al. 2024; Thanigaivel et al. 2019). Duckweed is particularly abundant in various bioactive metabolites, including flavonoids, antioxidants, polyunsaturated fatty acids, vitamins, and minerals, which have diverse industrial uses in human food, animal and fish feed, nutraceuticals, cosmetics, and pharmaceuticals (Ifie et al. 2021). The research has indicated that duckweed positively influences fish growth and feed conversion ratios without adversely affecting survival rates. It has been effectively utilized as a complete feed for fish and shrimp (Flores-Miranda et al. 2015). Additionally, duckweed shows linear increases in biomass yield and crude protein content when fertilized with biodigester effluent (Dang et al. 2011).

Similarly, seaweed is rich in a variety of bioactive substances, including polyphenols, pigments, essential fatty acids, vitamins, and amino acids. Seaweed polyphenols have been shown to boost immune responses and disease resistance in fish (Tabarsa et al. 2022). Seaweeds and their extracts are increasingly being utilized as preventive and therapeutic agents in aquaculture for managing aquatic health (Thanigaivel et al. 2019). Debbarma et al. (2024) discovered that seaweeds serve as a valuable source of antiviral agents for developing innovative vaccines and treatments against the Tilapia lake virus. Seaweeds are recognized as promising sources for the identification of biologically active compounds, attributable to their extensive biodiversity and safety profile. They are capable of synthesizing a variety of valuable antioxidants, including carotenoids, tocopherol, ascorbic acid, chlorophyll derivatives, terpenoids, polysaccharides, phlorotannins, polyphenols, and mycosporine-like amino acids (Ghafarizadeh and Niroomand 2021). Furthermore, seaweeds present potential as sources of bioactive compounds and feed ingredients for aquaculture, owing to their favorable nutritional composition, environmental sustainability, and potential health benefits for farmed fish (Wan et al. 2019). An increasing body of research has demonstrated that the incorporation of seaweed and seaweed-derived functional metabolites into aquafeed enhances serum immune and antioxidant status (Akbary et al. 2018) and improves disease resistance (Thepot et al. 2021) in fish.

Thanigaivel et al. (2019) reported that the dietary inclusion of total phenolic compounds (TPC) derived from *Gracilaria foliifera* (Rhodophyta) and *Sargassum longifolium* (Phaeophyceae) at levels ranging from 14.71 mg/g GAE to 18.42 mg/g GAE (gallic acid equivalent) in *Mozambique tilapia* (*Oreochromis mossambicus*) resulted in increased survival rates against *Aeromonas salmonicida* infections, highlighting the nutritional value of these seaweeds as sources of minerals, vitamins, proteins, fibers, and polyunsaturated fatty acids. They have suggested the potential of utilizing seaweed extracts for disease management in both shrimp and fish, thereby opening avenues for the application of seaweed extracts as immune stimulants (Thanigaivel et al. 2019). Recent research has rekindled interest in the use of seaweed as a safe alternative to conventional preventive and therapeutic drugs in aquaculture, aimed at mitigating economic losses associated with infectious diseases (Thepot et al. 2021). Seaweed and its extracts are noted for their exceptional antioxidant and immunomodulatory properties (Narasimhan et al. 2013). The application of seaweed extracts, such as sodium alginate and carrageenan from Macrocystis pyrifera and Chondrus crispus, in grouper (*Epinephelus coicoides*) has led to significant enhancements in respiratory burst, superoxide dismutase activity, and phagocytic functions, which are critical indicators of antioxidant status.

Reducing environmental manipulations

Manipulating using human activities has local, regional, and global environmental effects on aquaculture. These impacts cause natural habitat alteration, biodiversity reduction, and water changes, contributing

mainly to global warming, eutrophication, and eco-toxicity (Millard et al. 2021). In addition, current production systems demand more energy because of aerators, water interchangers (Gao et al. 2011) and other agricultural activities, causing climate change. Besides, not only does the use of breeders in some aquaculture systems lead to overfishing and depletion of wild shrimp populations, but Pair-trawling also causes habitat destruction, changes in the benthic community, trophic displacement, and the loss of biodiversity. In the meantime, changes in temperature and salinity are considered as two main factors determining the outbreak of WSSV. Other factors related to water quality may play a vital role in outbreak severity involve DO, pH, carbon dioxide, and concentration of nitrogenous compounds. Hence, any human-associated manipulation influencing the mentioned cases results in a WSSV outbreak (Millard et al. 2021).

Conclusion

In recent years, WSSV infection has resulted in extended mortality within a short-term period. Hence, the widespread of WSSV is propounded as the most important disease inhibiting the development and growth of shrimp. According to its profound impacts, the intention of this threatening agent is increasing. The threat agent's importance is growing due to its severe impact. This research aims to understand better the interaction between the virus and the host, disease control, prevention, or treatment. Also, using some compounds such as immunostimulants, lipopolysaccharides (LPS), and probiotics can improve the shrimp's immune system and increase their protection against this hazardous and destructive pathogen in the shrimp farming industry. To conclude, despite many strategies for controlling and preventing it that were experienced, no entirely determined method or influence happened to remedy it. Consequently, developing commercial vaccines or SPF shrimp against this devastating virus will assist the shrimp industry and economic growth worldwide.

Competing interests the authors confirm that there is no conflict of interest.

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List of abbreviations

AHPND	Acute Hepatopancreatic Necrosis Disease
dsRNA	Double-stranded RNA
DNA	Deoxyribonucleic acid
DO	Dissolves Oxygen
E	Early
EM	Electron Microscopy
EMS	Early Mortality Syndrome
GN	Genipin
Histo	Histopathology
IE	Immediate early
IHC	Immunohistochemistry
ISH	In Situ Hybridization
L	Late
LFIA	Lateral flow immunoassay
LAMP	Loop-mediated isothermal Amplification
NACA	Network of Aquaculture Centers in Asia-Pacific
Pk	Protein kinase
Pol	Polymerase
PCR	Polymerase Chain Reaction
rr	Ribonucleotide reductase
miRNAs	microRNAs
sRNAs	short RNAs
RNA	Ribonucleic acid
RNAi	RNA interference
SPF	Specific pathogen free
STAT	Signal transducer and activator of transcription
TEM	Transmission Electron Microscopy
TIS	Transcription initiation site
tk-tmk	Thymidine kinase thymidylate kinase
TSV	Taura Syndrome Virus
VP	Viral protein
WSSV	White Spot Syndrome Virus
WSD	White Spot Disease
WOAH	World Organization for Animal Health

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