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REVIEW

REVIEWS IN Aquaculture

White spot syndrome virus host range and impact on transmission

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Abstract

White spot syndrome virus (WSSV), the etiological agent of white spot disease (WSD), is a significant pathogen affecting shrimp farming industry worldwide. White spot syndrome virus is a generalist virus mainly infecting decapod crustaceans. The aims of this review were to: (1) Re-evaluate and update the status of reported WSSV host and vector species based on the methods used when detecting replication and transmission to shrimp and 2) make a critical evaluation of existing literature on the presence of WSSV in aquatic organisms and the potential role these organisms might play in the transmission of WSSV in pond systems and the wild. An evaluation of literature about WSSV reported host and vector species showed an increase from 33 families to 50 families including 11 families of non-crustacean hosts, proved the virus continues to spread beyond farmed shrimp and the shrimp pond environment. White spot syndrome virus transmission in the aquatic environment is complex as depicted in our model. Containment of WSSV in ponds and the natural environment is challenging, mainly because of its generalist nature and a lack of understanding about (1) WSSV transmission in the aquatic setting, (2) the route of WSSV transmission among species exist in the aquatic environment and (3) information on the transmission dynamics between WSSV in farmed crustaceans and non-farmed animals. Information presented in this review provides the research direction on methods to control WSSV.

KEYWORDS
host range, shrimp farming, transmission, WSSV

1 | INTRODUCTION

White spot syndrome virus (WSSV) is a large, circular double-stranded DNA virus belonging to the genus Whispovirus of the Nimaviridae family.[1,2] WSSV is the etiological agent of white spot disease (WSD), which has plagued the global shrimp culture industry for the last 25 years, causing massive production losses.[3–6] The virus is well adapted to a broad salinity range and pathogenic to decapod crustaceans in brackish water[7] and freshwater alike.[8,9] As a result, the disease occurs in all types of crustacean farming systems. Currently, WSD is a pandemic disease and listed by the World Organization for Animal Health (OIE) as a notifiable disease. The disease transmission

at the regional level can be partially controlled by implementing regulations to prevent transboundary disease spreading.[10–12]

WSD was first reported in *Marsupenaeus japonicus* in 1992 in Taiwan[3] and Japan.[4,5] Soon thereafter, WSD spreads to other shrimp-producing countries in Asia[13–15] and developed into an endemic disease.[6,16,17] More recent WSD outbreaks were reported in some EU countries,[18] Saudi Arabia, Mozambique, Madagascar and Australia.[11,12,18,19] Knibb et al confirmed the vulnerability of shrimp farming to WSD regardless of the climate zone.[12] The Quarterly Report from Network of Aquaculture Centres in Asia-Pacific[20] showed that WSD is still causing major problems in many shrimp-producing countries in the Asia-Pacific region despite implementing biosecurity measures. For a multi-host virus, for example a virus that uses multiple species as a host, the knowledge of the host and vector range has epidemiological significance for the design of a proper pathogen control system. There is a broad variation in the definition of a host and vector concerning host-virus interactions. Essentially, viral host(s) is/are organisms in which a virus replicates naturally.[21] The term experimental host is used to show the susceptibility of an animal to certain virus under experimental conditions. Regardless of the infection condition, both natural and experimental hosts are important for biosecurity measures. According to OIE, a vector is any living organism that can transmit a pathogenic agent to a susceptible species. In a vector, the virus does not necessarily replicate, as is required to be categorised as a host. The majority of reported WSSV hosts and vectors consists of crustaceans living in brackish water and, to a lesser extent, in freshwater and sea water. White spot syndrome virus was detected in a broad range of aquatic invertebrates, mainly belonging to 34 families of crustaceans,[22,23] which increased to 39 families in this review. In addition, reports on 13 non-crustacean species (this review) as vectors and hosts of WSSV, show the generalist nature of this virus. In contrast, other shrimp viruses listed by OIE such as infectious myonecrosis virus (IMNV), Taura syndrome virus (TSV) infect mainly Pacific white shrimp (*L. vannamei*), which make the latter diseases more manageable than WSSV.

Fifty per cent of all host species within the scope of this review (Tables 1 and 2) support WSSV replication; however, only 35% result from natural infections. The remaining 15% are WSSV hosts identified under laboratory conditions by pairwise one-to-one species transmission experiments. The two most common WSSV transmission routes used in these experiments were injection and/or feeding WSSV-infected shrimp. The relevance of experimentally observed transmission to farm or natural conditions is still a matter of debate to be discussed later.

Our understanding of WSSV transmission in the aquatic environment is less than that at the level of the host or at cellular levels, which make it difficult to design effective control strategies. In our opinion, there is a lack of knowledge in some critical aspects of WSSV transmission:

1. The route of WSSV transmission among species. Under laboratory conditions, WSSV can spread through water, cohabitation, cannibalism, and via the trophic food chain. The importance of each route might vary according to whether the transmission occurs within a shrimp pond or in the natural environment. Moreover, the degree of transmission depends on the virulence of the pertinent virus strain, density of susceptible hosts, the individual host defence status, initial viral dose and environmental biotic and abiotic factors.[93–97]
2. The transmission of WSSV between farmed crustaceans and non-farmed animals. The fact that WSSV is found in wild animals from different geographic areas shows that WSSV is very prevalent in the wild. The question is whether wild animals get WSSV infection as a spillover from shrimp ponds or is it vice versa.
3. WSSV transmission in the aquatic setting. The aquatic environment is a complex system containing numerous organisms that can act as vectors or host but not all of these species are equally susceptible to or propagate the virus.[47,55,58,98,99]

The objectives of the current review are to critically (1) re-evaluate and update the status of reported WSSV host and vector species based on the methods used when detecting replication and transmission to shrimp and (2) evaluate existing literature on the presence of WSSV in aquatic organisms and the potential role these organisms might play in the transmission of WSSV in ponds and in the wild. This information is essential to assess and evaluate the risk of WSSV transmission in shrimp ponds and to develop or implement effective disease control strategies. Finally, we propose a WSSV transmission model within and outside the shrimp pond environment including biotic and abiotic factors.

We structured this review as follows: first detecting and determining the status and identifying the reservoir host; next, evaluate the relevance of lab results in the field; followed by exploring how human activities, for example farming practices, contribute to the transmission and finally, analysing the interaction between host and vectors to clarify WSSV transmission in the aquatic environment.

2 | DETECTION OF WSSV TO DETERMINE HOST STATUS

The World Organization for Animal Health (OIE) recommended a combination of microscopic, immunological and molecular techniques to detect WSSV.[2] Diagnosis of WSSV in shrimp usually starts with visible, behavioural or clinical signs such as lethargy, loss of appetite and white spots on the carapace, followed by detecting the etiological agent using polymerase chain reaction (PCR) method (conventional 1-step and nested-PCR and real-time PCR or quantitative PCR). A nested PCR can be employed to enhance the detection level and is useful to investigate asymptomatic carrier species or lightly infected animals.

Historically, most reports of WSSV infection are based on PCR.[33] However, the mere presence of viral DNA with one-step or two-step (nested) PCR does not necessarily imply that the virus proliferates in a particular host. Application of methods to show WSSV replication or detect WSSV virions is important for confirmation, especially when testing a new potential host for WSSV infection or for surveillance to determine WSSV free zones. To determine whether a species is a natural (replicative) host for the virus or just a vector, bioassay and further testing by a combination of the following assays is necessary:

TABLE 1 Reported crustacean host and vectors of WSSV

Class	Order	Family	Species	Infection method	Detection method	Replication	Transmission to Shrimp	Transmission route	Status	Reference
Brackish water and marine shrimp										
Malacostraca	Decapoda	Penaeidae	*Metapenaeus brevicornis*	Na	PCR	NR	NR	NR	Potential vector	24
Malacostraca	Decapoda	Penaeidae	*M. dobsoni*	Na, F, IN	Histo, PCR	Y	Y	F	Host	25,26
Malacostraca	Decapoda	Penaeidae	*M.ensis*	Na, F	PCR, DNA Probe	NR	NR	NR	Potential vector	27
Malacostraca	Decapoda	Penaeidae	*M. monoceros*	Na, IM, F	Nested PCR, Probe, Histo	Y	Y	F	Host	24,28
Malacostraca	Decapoda	Penaeidae	*Parapeneopsis stylifera*	Na	Nested PCR, Probe	NR	NR	NR	Potential vector	25
Malacostraca	Decapoda	Penaeidae	*Farfantepenaeus aztecus*	Na	PCR, Histo	N	Y	IN	Vector	29
Malacostraca	Decapoda	Penaeidae	*F. duorarum*	F	Histo	Y	NR	NR	Host	30
Malacostraca	Decapoda	Penaeidae	*F. paulensis*	Na	PCR, Histo	NR	NR	NR	Potential vector	31
Malacostraca	Decapoda	Penaeidae	*F. brasiliensis*	Na	PCR, Histo	NR	NR	NR	Potential vector	31
Malacostraca	Decapoda	Penaeidae	*Penaeus merguiensis*	Na	Histo, DNA probe	Y	Y	NR	Host	32
Malacostraca	Decapoda	Penaeidae	*P. penicillatus*	Na	Nested PCR	NR	NR	NR	Potential vector	33
Malacostraca	Decapoda	Penaeidae	*P. schmitti*	IN	Histo, ISH	Y	NR	NR	Host	34
Malacostraca	Decapoda	Penaeidae	*L. setiferus*	Na	PCR, Histo	Y	Y	IN	Host	29
Malacostraca	Decapoda	Penaeidae	*P. stylirostris*	Na,	TEM, PCR, Histo	Y	NR	NR	Host	35
Malacostraca	Decapoda	Penaeidae	*L. vannamei*	Na, F, I	TEM, PCR, Histo	Y	NR	NR	Host	30,35,36
Malacostraca	Decapoda	Penaeidae	*P. japonicus*	Na, IM, F	TEM, Histo	Y	Y	IM	Host	37–39
Malacostraca	Decapoda	Penaeidae	*P. monodon*	Na, IM	TEM, histo	Y	Y	IM	Host	30,37,40
Malacostraca	Decapoda	Penaeidae	*P. indicus*	Na, IN, F	TEM, Histo	Y	Y	F	Host	26,28
Malacostraca	Decapoda	Penaeidae	*P. chinensis*	Na, IN	EM, Histo	Y	Y	I	Host	41
Malacostraca	Decapoda	Penaeidae	*P. semisulcatus*	Na, F, IN	Nested PCR, Histo	Y	Y	F	Host	28,42
Malacostraca	Decapoda	Penaeidae	*Trachypenaeus curvirostris*	Na, F	DNA Probe	NR	NR	NR	Potential vector	43
Malacostraca	Decapoda	Penaeidae	*Trachypenaeus curvirostris*	NA	LAMP, PCR, EM	Y	NR	NR	Host	44
Malacostraca	Decapoda	Sergestidae	*Acetes* sp	IN, F, IM	EM, ISH, Histo	Y	NR	NR	Host	45
Malacostraca	Decapoda	Sergestidae	*Acetes chinensis*	NA	LAMP, PCR	NR	NR	NR	Potential vector	44
Malacostraca	Decapoda	Alpheidae	*Alpheus brevicristatus*	Na	Nested PCR	NR	NR	NR	Potential vector	39
Malacostraca	Decapoda	Alpheidae	*A. lobidens*	Na	Nested PCR	NR	NR	NR	Potential vector	39
Malacostraca	Decapoda	Alpheidae	*Alpheus japonicus*	NA	LAMP, PCR	NR	NR	NR	Potential vector	44
Malacostraca	Decapoda	Alpheidae	*A. distinguendus*	NA	LAMP, PCR	NR	NR	NR	Potential vector	44
Malacostraca	Decapoda	Solenoceridae	*Solenocera indica*	Na	Nested PCR, Probe	NR	NR	NR	Potential vector	25
Malacostraca	Decapoda	Crangonidae	Crangon affinis	NA	LAMP, PCR	NR	NR	NR	Potential vector	44

(Continues)

TABLE 1 (Continued)

Class	Order	Family	Species	Infection method	Detection method	Replication	Transmission to Shrimp	Transmission route	Status	Reference
Malacostraca	Stomatopoda	Squillidae	*Squilla mantis*	Na	Nested PCR, Probe	NR	NR	NR	Potential vector	25
Malacostraca	Decapoda	Upogebiidae	*Austinogebia edulis*	Na	PCR, EM	Y	NR	NR	Host	46
Malacostraca	Decapoda	Pasiphaeidae	*Leptochela gracilis*	NA	LAMP, PCR	NR	NR	NR	Potential vector	44
Malacostraca	Decapoda	Hippolytidae	*Latreutes planirostris*	NA	LAMP, PCR	NR	NR	NR	Potential vector	44
Malacostraca	Decapoda	Hippolytidae	*L. anoplonyx*	NA	LAMP, PCR	NR	NR	NR	Potential vector	44
Malacostraca	Decapoda	Euphausiidae	*Euphausia pacifica*	NA	LAMP, PCR	NR	NR	NR	Potential vector	44
Crabs										
Malacostraca	Decapoda	Xanthidae	*Atergatis integerrimus*	IN, F	PCR, Histo	Y	NR	NR	Host	47
Malacostraca	Decapoda	Xanthidae	*Demania splendida*	IN, F	PCR, Histo	Y	NR	NR	Host	47
Malacostraca	Decapoda	Xanthidae	*Halimede ochtodes*	IN, F	PCR, Histo	Y	NR	NR	Host	47
Malacostraca	Decapoda	Xanthidae	*Liagore rubronaculata*	IN, F	PCR, Histo	Y	NR	NR	Host	47
Malacostraca	Decapoda	Calappidae	*Calappa philargius*	IN, F	PCR, Histo	Y	NR	NR	Host	47
Malacostraca	Decapoda	Calappidae	*C. lophos*	F	PCR	NR	NR	NR	Potential vector	30
Malacostraca	Decapoda	Majidae	*Doclea hybrida*	IN, F	PCR, Histo	Y	NR	NR	Host	47
Malacostraca	Decapoda	Grapsidae	*Grapsus albolineatus*	IN, F	PCR, Histo	Y	NR	NR	Host	47
Malacostraca	Decapoda	Grapsidae	*Metopograpsus messor*	Na	Nested PCR	NR	NR	NR	Potential vector	25
Malacostraca	Decapoda	Grapsidae	*Pseudograpsus intermedius*	Na	Nested PCR	NR	NR	NR	Potential vector	24
Malacostraca	Decapoda	Lithodidae	*Lithodes maja*	IN, F	PCR, Histo	Y	NR	NR	Host	47
Malacostraca	Decapoda	Matutidae	*Matuta miersi*	IN, F	PCR, Histo	Y	NR	NR	Host	47
Malacostraca	Decapoda	Matutidae	*M. Planipes*	Na	Nested PCR	NR	NR	NR	Potential vector	48
Malacostraca	Decapoda	Eriphiidae	*Menippe rumphii*	IN, F	PCR, Histo	Y	NR	NR	Host	47
Malacostraca	Decapoda	Dorippidae	*Paradorippe granulata*	IN, F	PCR, Histo	Y	NR	NR	Host	47
Malacostraca	Decapoda	Parthenopidae	*Parthenope prensor*	IN, F	PCR, Histo	Y	NR	NR	Host	47
Malacostraca	Decapoda	Leucosiidae	*Philyra syndactyla*	IN, F	PCR, Histo	Y	NR	NR	Host	47
Malacostraca	Decapoda	Portunidae	*Podophthalmus vigil*	IN, F	PCR, Histo	Y	NR	NR	Host	47
Malacostraca	Decapoda	Portunidae	*Portunus sanguinolentus*	IN, F	PCR, Histo	Y	NR	NR	Host	27,47
Malacostraca	Decapoda	Portunidae	*P. pelagicus*	IN, F	DNA Probe, Histo, EM	Y	NR	NR	Host	45
Malacostraca	Decapoda	Portunidae	*Thalamita danae*	IN, F	PCR, Histo	Y	NR	NR	Host	47
Malacostraca	Decapoda	Portunidae	*Calinectes arcuatus*	Na	PCR	NR	NR	NR	Potential vector	35
Malacostraca	Decapoda	Portunidae	*C. sapidus*	Na	PCR, ISH, qPCR, immuno-strip	NR	Y	IN	Vector	49,50
Malacostraca	Decapoda	Portunidae	*Carcinus maenas*	IN, F	TEM, Dot Blots, ISH 1-step PCR, Histo	Y	Y	Y	Host	51,52
Malacostraca	Decapoda	Portunidae	*Portunus trituberculatus*	Na, IN, F	Histo, RT PCR	Y	NR	NR	Host	53,54

TABLE 1 (Continued)

Class	Order	Family	Species	Infection method	Detection method	Replication	Transmission to Shrimp	Transmission route	Status	Reference
Malacostraca	Decapoda	Portunidae	*Charybdis granulata*	F	DNA Probe	NR	NR	NR	Potential vector	27
Malacostraca	Decapoda	Portunidae	*Ch. annulata*	Na, IN, F	PCR, Histo	Y	NR	NR	Host	25,47
Malacostraca	Decapoda	Portunidae	*Ch. lucifera*	Na, IN, F	Nested PCR, Histo	Y	NR	NR	Host	47
Malacostraca	Decapoda	Portunidae	*Ch. natator*	IN, F	PCR, Histo	Y	NR	NR	Host	47
Malacostraca	Decapoda	Portunidae	*Ch. cruciata*	Na	Nested PCR,	NR	NR	NR	Potential vector	25,42
Malacostraca	Decapoda	Portunidae	*Ch. feriata*	F	Nested- PCR	NR	NR	NR	Potential vector	42
Malacostraca	Decapoda	Portunidae	*Ch. japonica*	Na	Nested PCR	NR	NR	NR	Potential vector	39
Malacostraca	Decapoda	Portunidae	*Ch. callinassa*	Na	Nested PCR	NR	NR	NR	Potential vector	25
Malacostraca	Decapoda	Portunidae	*Scylla serrata*	IN, F	DNA Probe, PCR, Histo	Y	Y	F, C	Host	28,55
Malacostraca	Decapoda	Portunidae	*S. tranquebarica*	Na, IN, F	PCR, SEM, Histo	Y	Y	F, IM	Host	55–57
Malacostraca	Decapoda	Portunidae	*S. olivacea*	IN	qPCR Histo, IHC	Y	NR	NR	Host	58
Malacostraca	Decapoda	Portunidae	*S. paramamosain*	IN	qPCR, Histo, IHC	Y	NR	NR	Host	58
Malacostraca	Decapoda	Portunidae	*Liocarcinus depurator*	IN, F	TEM, Dot Blots, ISH, 1-step PCR	Y	NR	NR	Host	52
Malacostraca	Decapoda	Portunidae	*L. puber*	IN, F	TEM, Dot Blots, ISH, 1-step PCR	Y	NR	NR	Host	52
Malacostraca	Decapoda	Sesarmidae	*Sesarma* sp	IN, F	DNA Probe, PCR, Histo	Y	Y	C	Host	28,55
Malacostraca	Decapoda	Sesarmidae	*Sesarma oceanica*	Na	Nested PCR, Probe	NR	NR	NR	Potential vector	25
Malacostraca	Decapoda	Ocypodidae	*Uca pugilator*	IN	DNA Probe, PCR, Histo	Y	Y	C	Host	55
Malacostraca	Decapoda	Ocypodidae	*Gelasimus marionis nitidu*	Na	Nested PCR,	NR	NR	NR	Potential vector	25
Malacostraca	Decapoda	Ocypodidae	*Macropthalmus sulcatus*	Na	Nested PCR,	NR	NR	NR	Potential vector	25
Malacostraca	Decapoda	Grapsidae	*Metapograpus* sp.	F	Histo	Y	Y	F	Host	28
Malacostraca	Decapoda	Grapsidae	*Metapograpus messor*	Na	Nested PCR	NR	NR	NR	Potential vector	25
Malacostraca	Decapoda	Cancridae	*Cancer pagurus*	IN, F	TEM, ISH, Histo, 1-step PCR	Y	Y	IN	Host	51,52
Malacostraca	Decapoda	Varunidae	*Helice tridens*	Na	Nested PCR	NR	NR	NR	Potential vector	33
Malacostraca	Decapoda	Varunidae	*Chasmagnathus granulata*	Na	Nested PCR	NR	NR	NR	Potential vector	59
Malacostraca	Decapoda	Varunidae	*Eriocheir sinensis*	IN, Na	Nested PCR, TEM, Histo	Y	Y	IN	Host	9,51
Malacostraca	Decapoda	Paguridae	*Pagurus minutus*	IN	Nested PCR, TEM	Y	NR	NR	Host	60
Malacostraca	Decapoda	Paguridae	*P. angustus*	IN	Nested PCR	NR	NR	NR	Potential vector	60
Malacostraca	Decapoda	Diogenidae	*Diogenes aff. nitidimanus*	IN	Nested PCR	NR	NR	NR	Potential vector	60
Malacostraca	*Decapoda*	Parathelphusidae	*Paratelphusa hydrodomus*	IN, F	PCR, Histo, RT PCR, ELISA	Y	Y	IN	Host	61,62
Malacostraca	Decapoda	Parathelphusidae	*P. pulvinata*	IN, F	PCR, Histo	Y	NR	NR	Host	61

(Continues)

TABLE 1 (Continued)

Class	Order	Family	Species	Infection method	Detection method	Replication	Transmission to Shrimp	Transmission route	Status	Reference
Lobster										
Malacostraca	Decapoda	Scyllaridae	*Scyllarus arctus*	IN, F	TEM, Dot Blots, ISH, 1-step PCR	Y	NR	NR	Host	27,63
Malacostraca	Decapoda	Palinuridae	*Panulirus homarus*	F	Histo	Y	Y	F	Host	28
Malacostraca	Decapoda	Palinuridae	*P. ornatus*	F	Nested PCR, Histo	Y	Y	F	Host	28,63
Malacostraca	Decapoda	Palinuridae	*P. polyphagus*	F	Histo	Y	Y	F	Host	28
Malacostraca	Decapoda	Palinuridae	*P. versicolor*	F	Nested PCR, DNA Probe	NR	NR	NR	Potential vector	27,42
Malacostraca	Decapoda	Palinuridae	*P. penicillatus*	F	Nested PCR, DNA Probe	NR	NR	NR	Potential vector	27,42
Malacostraca	Decapoda	Palinuridae	*P. longipes*	F	Nested PCR	NR	NR	NR	Potential vector	42
Malacostraca	Decapoda	Panuliridae	*P. argus*	IN	qPCR	NR	NR	NR	Potential vector	64
Malacostraca	Decapoda	Nephropidae	*Nephrops norvegicus*	F	Nested PCR, TEM, Histo	Y	Y	IN	Host	51
Malacostraca	Decapoda	Nephropidae	*Homarus gammarus*	F	Nested PCR, TEM, Histo	Y	Y	IN	Host	51
Malacostraca	Decapoda	Nephropidae	*Homarus americanus*	IN	RT-qPCR, histo, TEM	Y	NR	NR	Host	65
Freshwater shrimp, crayfish										
Malacostraca	Decapoda	Palaemonidae	*Exopalaemon orientalis*	Na, F	Nested PCR, DNA Probe	NR	NR	NR	Potential vector	27,42
Malacostraca	Decapoda	Palaemonidae	*Palaemon adspersus*	IN, F	TEM, Dot Blots, ISH, 1-step PCR	Y	NR	NR	Host	52
Malacostraca	Decapoda	Palaemonidae	*P. ritteri*	F	RT-PCR	Y	NR	NR	Host	66
Malacostraca	Decapoda	Palaemonidae	*P. pandaliformis*	Na	LAMP	NR	NR	NR	Potential vector	67
Malacostraca	Decapoda	Palaemonidae.	*P. gravieri*	NA	LAMP, PCR	NR	NR	NR	Potential vector	44
Malacostraca	Decapoda	Palaemonidae	*Macrobrachium* sp.	F	DNA Probe	Y	NR	NR	Potential vector	27
Malacostraca	Decapoda	Palaemonidae	*M. rosenbergii*	Na, IM, F, IN	Nested PCR, Southern blot, Histo	Y	Y	F	Host	24,28,68
Malacostraca	Decapoda	Palaemonidae	*M. idella*	F, IM, IN	Western blot, Histo	Y	NR	NR	Host	69
Malacostraca	Decapoda	Palaemonidae	*M.lamarrae*	F, IM, IN	Western blot, Histo	Y	NR	NR	Host	69
Malacostraca	Decapoda	Palaemonidae	*M.nipponense*	IN, F	qPCR, histo	Y	NR	NR	Potential vector	70,71
Malacostraca	Decapoda	Cambaridae	*Procambarus clarkii*	Na, F, IN	Histo, Nested PCR, qPCR, TEM	Y	NR	NR	Host	8,42,72–75
Malacostraca	Decapoda	Cambaridae	*Orconectes limosus*	IN, F	TEM, Dot Blots, ISH, 1-step PCR	Y	NR	NR	Host	52
Malacostraca	Decapoda	Cambaridae	*O. punctimanus*	Na	DNA probe	NR	NR	NR	Potential vector	33
Malacostraca	Decapoda	Astacidae	*Astacus leptodactylus*	IN, F	TEM, Dot Blots, ISH, 1-step PCR	Y	NR	NR	Host	52
Malacostraca	Decapoda	Astacidae	*A. astacus*	IN, F	PCR	NR	NR	NR	Potential vector	76
Malacostraca	Decapoda	Astacidae	*Pacifastacus leniusculus*	IN, F	Nested PCR, TEM, Histo	Y	Y	Y	Host	51,76
Malacostraca	Decapoda	Parastacidae	*Cherax destructor albidus*	F, IN	DNA Probe, Histo	Y	NR	NR	Host	77
Malacostraca	Decapoda	Parastacidae	*C. quadricarinatus*	IN, F, C	TEM, ISH, IHC, Nested PCR	Y	Y	C	Host	78,79

TABLE 1 (Continued)

Class	Order	Family	Species	Infection method	Detection method	Replication	Transmission to Shrimp	Transmission route	Status	Reference
Malacostraca	Decapoda	Astacidae	*Austropotamobius pallipes*	F	Nested PCR, TEM, Histo	Y	Y	IN	Host	51
Brine shrimp and copepods										
Branchiopoda	Anostraca	Artemiidae	*Artemia franciscana*	IM	Nested PCR	N	N	F	Vector	80
Branchiopoda	Anostraca	Artemiidae	*Artemia*	F	Nested PCR	NR	Y	F	Vector	81
Maxillopoda	Harpacticoida	Ameiridae	*Nitocra* sp	F	Nested PCR	NR	Y	F, IN	Vector	82
Arthropoda	Hexanauplia	Cyclopodae	*Apocyclops royi*	IM	Nested PCR, RT-PCR, qPCR	Y	NR	NR	Host	83

Note: Host = WSSV replication in this animal has been shown based on a detection method besides PCR or DNA Probe. Vector = WSSV was detected with PCR or DNA probe and the virus was transmitted to shrimp or crabs. Potential vector = WSSV detected in this animal based on PCR or DNA probe and no transmission to shrimp or crab was reported.

Abbreviations: C, experimental infection/transmission by cohabitation; Histo, histopathology; IM, experimental infection/transmission by immersion; IN, experimental infection/transmission by injection; ISH, in situ hybridisation; LAMP, loop-mediated isothermal amplification; N, no; Na, natural infection; NA, not applicable; NR, not reported in the reference; O, experimental infection/transmission through feeding; TEM, transmission electron microscope; Y = yes.

(1) immunohistochemistry to detect infected tissue using virus-specific antibodies; (2) electron microscopy (EM) to view virions in infected cells; (3) reverse transcriptase PCR (RT-PCR) to detect viral mRNA and (4) sequencing to compare the DNA sequence to known sequence in the public database like NCBI. Currently, quantitative PCR (qPCR), which can show the approximate number of DNA copies/μl in a specimen – thus the potential viral DNA load – is the preferred approach.

3 | THE ROLE OF WSSV HOSTS AND VECTORS IN THE TRANSMISSION

For a virus, infection is the only way to proliferate and maintain its existence in the host and the environment. Successful infection is influenced by the availability and density of susceptible hosts, exposure of the host to the virus, and the viral dose. At the time of the WSSV emergence, the term host was erroneously used when WSSV was detected with the 1-step or nested PCR in wild animals without evidence of replication[25,33] while the term vector was used according to OIE. For the purpose of this review, we defined 'host' as an organism in which WSSV has been shown to replicate by RT-PCR, histology and/ or EM. The host may not necessarily show mortality or may be asymptomatic, but produces infectious virus, and transmit the virus to shrimp. A vector is as an organism in which WSSV was detected, but no WSSV replication was reported, yet the virus was transmitted to shrimp. We define an organism in which the virus was detected, but neither replication nor transmission to shrimp was reported as a potential vector.

The principal phyla of macro-benthic organisms found in brackish water environments are arthropods (*Arthropoda*), molluscs (*Mollusca*), annelids (*Annelida*) and nematodes (*Nematoda*), which are also important natural food for shrimp.[100–102] By far, arthropods are the most frequently reported hosts of WSSV (Table 1), mainly consisting of penaeid shrimp and crab. However, there is a growing number of studies that identified non-crustacean hosts and vectors of WSSV such as molluscs,[67,90] annelids[88] and zooplankton,[103] both in brackish water and freshwater environments (Table 2). The number of reported hosts or vectors increased from 31 in 1997[32] to 46 in 2006,[16] then to 94 in 2010[22,104] (reaching 137 species in this review (Tables 1 and 2). The susceptibility to WSSV varies among hosts and is difficult to rank because of variation in WSSV isolates, doses, batches of experimental animals and experimental conditions. Due to the importance of the shrimp farming industry, most studies of WSSV transmission focused on farmed shrimp, for example *P. monodon*, *P. indicus*, *P. japonicus*, *P. penicilllatus*, *L. vannamei*. In this section, we review what constitutes being a WSSV host or vector and how a particular host or vector contributes to the WSSV transmission both inside and outside the shrimp pond.

Crabs comprise the largest group (36 species) of reported WSSV hosts as opposed to 15 shrimp species (Table 3). Crab ubiquity, roaming habits in aquatic and terrestrial environments and foraging behaviour increase their opportunity to acquire the virus and shed it

TABLE 2 Non-crustacean host and vectors of WSSV

Phylum	Class	Order	Family	Species	Detection method	Infection method	Replication	Transmission to Shrimp	Transmission route	Status	Reference
Plankton											
Chlorophyta	Trebuxiophyceae	Chlorellales	Chlorellaceae	*Chlorella* sp	Nested PCR	C	NR	N	Y	Vector	84
Dinophyta	Dinophyceae	Gonyaulacales	Gonionomataceae	*Alexandrium tamarense*	Probe	IM	NR	Yes	F	Vector	85
Dinophyta	Dinophyceae	Gonyaulacales	Gonionomataceae	*A. minutum*	Probe	IM	NR	Yes	F	Vector	85
Rotifera	Eurotatoria	Ploima	Brachionidae	*Brachionus urceus*	Nested PCR, Dot Blot hybridisation	F	NR	Yes	F	Vector	56,85
Rotifera	Eurotatoria	Ploima	Brachionidae	*B. plicatilis*	Nested PCR	IM	NR	Yes	F, C	Vector	86
Polychaetes											
Annelida	Polychaeta	Eunicida	Eunicidae	*Marphysa* spp.	Nested and 1-step PCR	Na, F	NR	Y	F	Vector	87
Annelida	Polychaeta	Phyllodocida	Nereididae	*Dendronereis* spp.	Nested PCR, IHC, RT-PCR	Na	Y	Y	F	Host	88,89
Oyster, Clam, snail											
Mollusca	Bivalvia	Ostreoidea	Ostreidae	*Crassostrea gigas*	Nested PCR	Na	NR	NR	NR	Potential vector	90
Mollusca	Bivalvia	Veneroida	Veneridae	*Meretrix lusoria*	Nested PCR, qPCR, RT-PCR	IM	N	Y	F	Vector	83
Mollusca	Gastropoda	Lepetellida	Haliotidae	*Haliotis diversicolor*	MDA	Na	N	N	N	Vector	91
Mollusca	Gastropoda	Architaenioglossa	Ampullaridae	*Pomacea lineata*	LAMP	Na	N	N	N	Vector	67
Mollusca	Gastropoda	Caenogastropoda	Thiaridae	*Melanoides tuberculatus*	LAMP	Na	N	N	N	Vector	67
Insects											
Arthropoda	Hexapoda	Diptera	Ephydridae		Nested PCR	Na	NR	NR	NR	Vector	92

Note: Host = WSSV replication in this animal has been shown based on a detection method besides PCR or DNA Probe. Vector = WSSV was detected with PCR or DNA probe and the virus was transmitted to shrimp or crabs. Potential vector = WSSV detected in this animal based on PCR or DNA probe and no transmission to shrimp or crab was reported.

Abbreviations: C, experimental infection/transmission by cohabitation; Histo, histopathology; IM, experimental infection/transmission by immersion; IN, experimental infection/transmission by injection; ISH, in situ hybridisation; LAMP, loop-mediated isothermal amplification; N, no; Na, natural infection; NA, not applicable; NR, not reported in the reference; O, experimental infection/transmission through feeding; TEM, transmission electron microscope; Y, yes.

TABLE 3 Summary of WSSV host and vectors

No	Animal group	Total number of reported host and vector species	host and vectors with natural WSSV occurrence	Host	Vector and potential vector
	Crustacean				
1.	Shrimp	36	33	15	21
2.	Crab	55	19	36	19
3.	Lobster	11	0	7	4
4.	Freshwater shrimp and crayfish	19	6	13	5
5.	Brine shrimp and copepods	4	0	1	3
	Non-crustacean				
6.	Plankton	5	0	0	4
7.	Polychaetes	2	2	1	1
8	Oyster, clam and snail	5	4	0	5

into the environment. Susceptibility to WSSV differs between crab species and between cultured or wild animals. Some crab species show asymptomatic WSSV infection as the infection persisted up to 45 dpi without visible signs of disease and showing no mortality.[47,55] For example, the crab species *Scylla serrata*,[58] *Uca pugilator*,[55] *Atergatis integerrimus*, *Demania splendida*, *Charybdis natator*, *Menippe rumphii*,[47] *Sesarma* spp. and *Portunus pelagicus*[98] all showed some degree of resistance to WSSV. While other crabs, such as *Scylla oliviaceae*, *Paratelphusa hydrodomous* and *P. pulvinata*, *Charybdis annulate*, *Grapsus albolineatus* and *Eriocheir sinensis* are highly susceptible, showing clinical signs of the disease upon infection.[9,47,58,61]

Being phylogenetically close to shrimp, crabs exhibit similar tissue tropism to WSSV infection as shrimp.[105] Although the number of hypertrophied nuclei was high, less tissue damage was observed in severely infected non-penaeid shrimp and crabs than in penaeid shrimp,[32] indicating that some species can sustain the infection. While farmed and infected shrimps are confined to the pond, thus transmitting the virus inside the pond during the production period, crabs roam freely and may disseminate the virus to neighbouring shrimp ponds or to the natural environment. Taken together, in the fields and ponds crabs can be a more important WSSV source of infection than infected cultured shrimp.

Unlike crabs, molluscs and polychaetes are permanently living inside the pond and constantly exposed to any change and condition including the WSSV load in the water and sediment. As filter feeders, molluscs can accumulate the virus in their bodies. White spot syndrome virus was detected in the gills and gut of Pacific oyster *Crassostrea gigas*,[90] freshwater gastropods *Pomacea lineata* and *Melanoides tuberculatus*[67] and common oriental clam *Meretrix lusoria*,[83] confirming that macro-benthic invertebrates living in the pond sediment could acquire WSSV, causing these animals being listed as potential vectors for WSSV (Table 2) due to the niche they occupy and their foraging habits. Up to now, only the mollusc *Meretrix lusoria* showed virus transmission to shrimp, however, no WSSV replication has been reported in molluscs so far, hence, molluscs are vectors. Polychaetes are dominant invertebrates in soft bottom estuaries,[106,107] representing 13% of the benthic animal biomass in extensive shrimp ponds with zero water exchange.[108] Polychaetes are preferred and highly nutritious prey for shrimp.[100,109,110] They are an important component of the maturation diets of shrimp broodstock because of their nutritional properties. While some authors considered the polychaete *Marphyssa* spp. a passive WSSV vector,[87] others reported that WSSV replicates in the naturally infected polychaete *Dendronereis* spp.[88] and can be transmitted by the polychaete to naïve shrimp[111]; thus, some polychaete species can be a host of WSSV. Mobility and feeding habits of polychaetes certainly bring this animal in close contact with WSSV in 'infected' soil. The viral load in polychaetes can be as high as in the infected shrimp.[112] Their niche, burrowing behaviour, mobility, scavenging activity, detritus feeding habit, and being a prey of shrimp make polychaetes more prone to acquire WSSV. They may transmit the virus more easily to shrimp through feeding than sedentary molluscs.

Plankton exists in the aquatic ecosystem as suspended solid, which make them available for long contact with WSSV in the water. White spot syndrome virus was attached to and detected in zooplankton[113] and phytoplankton[84,85] in shrimp ponds and adjacent environments. However, only the rotifers *Brachionus urceus*[85] and *B. plicatilis*[86] could experimentally be infected with WSSV and transmit the virus to shrimp (Table 2), suggesting that plankton is a vector.

The susceptibility of cultured freshwater crayfish (*Cherax quadricarinatus*)[78] and giant freshwater shrimp (*Macrobrachium rosenbergii*)[114] to WSSV may facilitate the spread of the virus beyond the brackish water environment. Horizontal WSSV transmission from red claw crayfish (*Cherax quadricarinatus*) to tiger shrimp (*P. monodon*) can pose problems for shrimp farming in fresh water and brackish water. White spot syndrome virus occurrence in wild gastropods and wild crayfish showed that the virus is already established in the natural freshwater environment outside aquaculture facilities but showed different vulnerability to infection. For example, the freshwater giant prawn *Macrobrachium nipponensis*[70] and spiny lobster (*Palinurus argus*)[64] showed resistance to WSSV. The latter was resistant because of avoidance behaviour to predate on diseased animals, a strategy to prevent the disease spreading under natural conditions.

WSSV transmission between farmed shrimp and other crustacean and non-crustacean host species in the environment shows a high degree of spatio-temporal variation that in turn supports genetic

variation. The distribution of WSSV genotypes is high in extensive ponds because of the nature of this farming system. For example, improved extensive systems in Vietnam and India tend to harbour more diverse WSSV genotypes than semi-intensive farms,[97,115] possibly because the frequency of in-pond transmission is higher. Twenty five WSSV genotypes were detected in infected wild crabs and crustaceans, plankton and cultured shrimp during a WSD outbreak in a traditional pond cluster in India.[116] The plankton contained the highest number of genotypes, with fewer genotypes found in farmed shrimps than in wild crustaceans and planktonic species. Moreover, the dominant genotypes in farmed shrimps differed from the dominant genotypes present in non-cultured species. These findings accentuate the complexity of WSSV interaction with various hosts and vectors in pond settings. Repeated virus transfer between closely related hosts could also lead to host switching.[117] Hence, a high genetic variability might be the result of cross-species transmission in a cascaded way. Nevertheless, maintaining a high genetic variability could also be a survival strategy of WSSV. Both high genetic variation and repeated cross-species transmission may foster the survival of WSSV over time and space.

OIE regulations (Code of conduct for aquatic animals) for transport of live animals are meant to limit WSSV transmission at the international level. The role of WSSV transmission by frozen shrimp for human consumption and occurrence in indigenous shrimp remains an open question. Information on WSSV transmission between wild animals and farmed crustaceans vice versa is still unclear and needs more detailed investigation.

4 | THE RESERVOIR HOST

In epidemiology, the reservoir is the natural habitat of a disease agent that can be both an animal or the environment. The term reservoir host(s) is broadly used to indicate a species or species community that supports the persistence of a pathogen in the population and transmits it directly or indirectly to the target species.[118] For several important viruses causing severe disease in humans and livestock, the reservoir host are wild animals such as bats that are phylogenetically very distant to humans and harbour high concentrations of the virus but are rarely killed by the virus.[119–121] For WSSV to persist in the aquatic environment, it requires a reservoir that can be either living organism(s) or non-living matter (water and sediment, see Section 6). The reservoir host of WSSV in the environment might be different from that in the ponds, but, as shrimp ponds are often semi-open systems, this difference is not a clear-cut distinction. The method to identify reservoir hosts in shrimp differs from the known approach in higher animals. In vertebrates, reservoir hosts can be traced, among others, by testing for antibodies against specific pathogens. However, this method does not work for WSSV because invertebrates do not have antibodies. Therefore, in this review the reservoir host is predicted based on the reported occurrence of WSSV.

Earlier the assumption was that a WSSV reservoir consisted of wild animals that live inside and in the vicinity of the pond,[122] but this opinion was erroneous, because infected farmed shrimp (as the target population) can also be the reservoir of infection.[123] In search of the reservoir host, we discuss here-under the occurrence of WSSV in different environments.

WSSV occurs in wild invertebrates over a broad geographical range, although the prevalence is generally low. When infected under culture conditions, WSSV prevalence in *L. vannamei* ranged from 40 to 71%[124] and was 100% during a WSD outbreak.[124] In contrast, several authors showed that the prevalence of WSSV infection in *P. monodon* broodstock collected at sea, varied between seasons.[125–127] In the Philippines, WSSV prevalence was higher during the dry season (10%) than during the wet season (0.3%),[126] while it was the opposite in Thailand[125] and India.[127] In the latter country, WSSV prevalence in wild *P. monodon* ranged from 0.6% to as high as 56.2%, but at the same time WSSV-resistant *P. monodon* was also found. White spot syndrome virus prevalence in the mud crab *Scylla serrata* ranged from 18% in India,[128] 35% in China,[129] to 60% in Taiwan.[105] On the other hand, in certain areas wild shrimp were not infected with WSSV, for example, in Brunei[130] and Argentina.[131] A more recent study in Bohai Sea, China, showed that WSSV was detected in 11 species of wild shrimp with a prevalence ranging from 6.8% to 21.9%.[44] Hence, WSSV prevalence in wild crustaceans (non-farmed shrimp) is highly variable, site-dependent, and largely related to the extent of shrimp farming in the area.

WSSV transmission through wild crustaceans and plankton has not received much attention. While the infection in wild animals might not be as detrimental as in farmed crustaceans, wild animals facilitate WSSV to maintain its survival in the aquatic environment. In addition, they spread the virus across a broad salinity range because most crustaceans are migratory breeders that require different salinities for different stages of their life history. For example, juvenile penaeids live in the same brackish water area where shrimp farming is practiced. They may acquire the virus by ingesting infected animals, plankton, soil and water before migrating to the sea when reaching maturity and act as carrier. The reverse process occurs on the Chinese mitten crab that reach adulthood in freshwater.

Pond management and biosecurity measures may be the reason that the reservoir of WSSV infection is different in intensive and extensive systems. White spot syndrome virus infection in intensive ponds comes presumably from WSSV infected larvae only,[132] while in extensive systems, it may come from infected larvae, neighbouring ponds, WSSV circulating inside the ponds,[115] from wild crabs (*Scylla serrata*) or plankton.[99,133] Further, infected farmed shrimp may constitute the reservoir of WSSV for other animals and environment (sediment, water) within the pond, which can spill the virus to the outside environment.[132,134] For example, WSSV prevalence in wild shrimp decreased when the farms surrounding the sampling area employed biosecurity measures, thus decreasing the WSSV released to the environment.[44] This report confirmed that farmed shrimp can also be the reservoir of infection for wild crustaceans. Therefore, future studies should focus more on modelling transmission in the aquatic environment among natural hosts and farmed shrimp as the target host.

In a pond setting, the role of plankton as WSSV vectors has not gained much attention. Being suspended solid, plankton can drift and spread over a large area and transmit the virus through the food chain (Figure 1). White spot syndrome virus was present in brine shrimp obtained from shrimp ponds.[48] Walker and co-authors[99] showed that high WSSV prevalence in plankton preceded WSD outbreaks in extensive farms. In summary, the phytoplankton-zooplankton route for WSSV transmission in ponds might play a more important role than currently assumed and requires further research. From the above, we infer that infected farmed crustacean constitute the most important reservoir host. Indeed, the farming conditions, especially the density, favour WSSV proliferation and thus also the subsequent spill to the environment.

5 | WSSV TRANSMISSION TRIALS AND THEIR PRACTICAL RELEVANCE IN THE FIELD

WSSV can be transmitted experimentally by injection, feeding, immersion, or cohabitation. In the published records, each method served the purpose depending on the objective of the experiment. The question is how applicable findings from laboratory experiments are in the field. An injection is not a natural way for the virus to enter the animal. However, this method ensures that the virus enters the experimental animal at a predetermined dose. The response may not reflect the natural susceptibility to WSSV because of the likelihood that the immune system is overwhelmed by the high number of viruses injected. Therefore, studies on transmission through feeding, immersion or cohabitation might provide a better insight into the natural infection routes.

WSSV transmission through rearing water[3] was less effective in transmission than through ingestion of (parts of) infected animals,[37,135] while dead shrimp with WSD are the most crucial source for WSSV transmission once a WSD outbreak occurs.[136] WSSV transmission through immersion has also been reported for mud crab.[3,105] Farmed shrimp, Australian red claw crayfish, *Cherax quadricarinatus*,[78] and different crab species[55] were also infected by cohabitation with infected animals. In contrast, cohabitation with infected *P. monodon* did not induce infection in Australian red claw crayfish. These results should be interpreted with care because, in cohabitation experiments in which the infection source and healthy animals are housed in the same aquarium, the possibility that transmission resulted from eating infected tissue cannot be excluded.

A major problem in comparing WSSV transmission studies is that there is no viral concentration or dose standard, especially for transmission studies through feeding. The high virulence and pathogenic traits observed in the laboratory may be caused by a high initial dose, which in many cases was not predetermined prior to the experiment. Further, most studies focus on transmission between WSSV-suspected hosts to farmed shrimp on a one-to-one species basis and in a qualitative or semi-quantitative way. It makes the extrapolation of laboratory findings to the field difficult and sometimes even irrelevant because cross-species transmission of

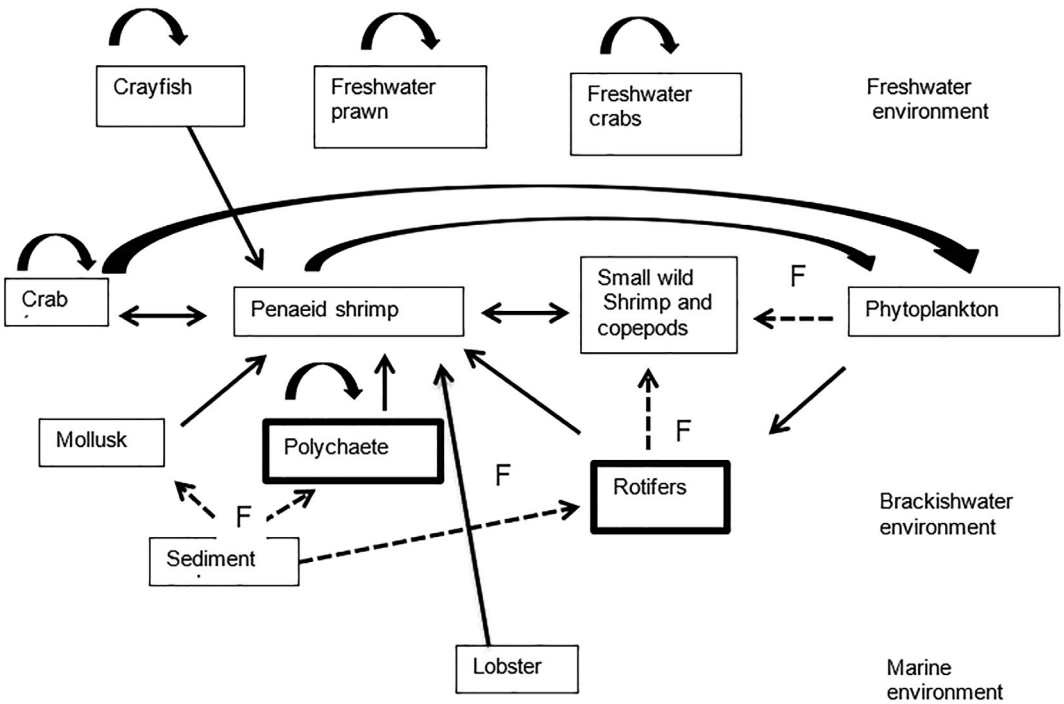

FIGURE 1 Model of routes of WSSV transmission among reported host and vector groups in the aquatic environment showing the complex pathway through the food chain. Penaeid shrimp are the most susceptible host in this model. White spot syndrome virus is transmitted within and among hosts, consisting mainly of wild species cohabiting in and outside the shrimp pond environment. The importance of each host and vector is dynamic and determined by the shrimp farming system

WSSV among animals inside and outside the pond environment complicates the picture.[137]

Studies indicate that WSSV can be transmitted through the food chain, which is a rare route of transmission for a virus. Results of studies with polychaetes,[87,89] with the brine shrimp *Artemia*,[81] and with crabs[47] showed the importance of the oral route in WSSV transmission across trophic levels (Figure 1). White spot syndrome virus binds in vitro to the *Artemia* cell membrane, which might have a WSSV receptor similar to receptors described for shrimp gill cells.[138] However, WSSV infection through *Artemia* was only possible in the hatchery where it can be easily detected and managed. Experimentally, WSSV was transmitted from infected phytoplankton to brine shrimp, the rotifer *B. urceu* and the copepod *Apocyclops royi*[81,83,85] before being consumed by the shrimp. Further, Dinoflagellates of the genus *Alexandrium* became WSSV-positive after 24 h of co-culture with WSSV-infected shrimp. White spot syndrome virus attachment to phytoplankton, however, is temporal[84] and could be related to the high virus concentration in the water.

Based on the results of transmission studies, crabs may be the most important host and vectors of WSSV in nature. Data in Table 1 showed that 51 crab species carry the infection by oral and cohabitation transmission with or without clinical signs. However, they showed higher resistance to infection than penaeid shrimp. Mortality of crabs is relatively low and occurs over a long period from 1 week to 1 month and the infection could be reversed or cleared.[45,47] White spot syndrome virus was transmitted to the mud crab *S. serrata* and the blue swimmer crab *P. pelagicus* by consuming WSSV-infected shrimp without causing mortality or clinical signs, which may represent the actual condition in nature.

In quantitative terms, the transmission rate is an essential parameter in the dynamics of WSSV transmission and the emergence and progress of an epidemic. The transmission rate of a virus (e.g. WSSV) depends on the reproduction ratio (R_0) of the virus, host density and environmental factors.[139] Very little information is available in the literature on the dynamics of WSSV transmission. One study[140] reported that cohabitation resulted in a lower transmission rate (β) than by ingestion of an infected animal, emphasizing the importance of the transmission through the oral route at the onset of a WSSV epidemic. In a later study,[141] using pair cohabitation conditions, the reproduction ratio (R_0) of WSSV was found to be 3.19 for *P. monodon* and 1.97 for *L. vannamei*. These values are well in a range of an outbreak that would quickly occur in ponds once infected shrimp become present.

6 | WSSV TRANSMISSION AT THE POND, THE LEVEL AND INTERRELATEDNESS WITH CULTURE CONDITIONS

The emergence of new pathogens in domesticated animals is often associated with farming systems that hold cultured animals in a setting very different from their natural environment.[142,143] Farming practices are linked to WSSV transmission within and between ponds and between cultured shrimp and wild hosts and vectors. Under experimental conditions in the laboratory, WSD develops very fast (in a matter of days) and causes 100% mortality in 7 days. However, it took longer for the outbreak and severe mortality to occur in a pond in intensive farming conditions, even when the pond was stocked with WSSV-positive larvae.[132] It shows that the pond condition is crucial for the emergence and establishment of WSD. The impact of shrimp density on the WSD outbreak may vary between shrimp species. For *P. monodon*, density is more critical for the onset of WSD than for *L. vannamei*,[141] explaining the severity of WSSV outbreaks on *P. monodon* farming during the emergence of WSSV in the 1990s.

Shrimp mortality caused by WSSV varies, even among ponds practicing the same farming system. This is mainly caused by environmental conditions, site, and farming management. Applying Best Management Practices (BMP) and biosecurity does not always result in a successful harvest,[97] because pond conditions affect the physiology and shrimp responses to the invading pathogen, hence, the transmission. Based on our observation, a WSD outbreak can occur even after employing biosecurity measures indicating that the methods may not cover all transmission routes. Nevertheless, stocking WSSV-free larvae increases the chance for a successful crop. Although stocking WSSV-infected larvae increases the risk of a WSD outbreak, harvest can be successful under good culture conditions because shrimp tolerate a light WSSV infection without developing WSD.[125,132,144] Poor water quality influences shrimp health and aggravates WSSV infection in shrimp, such as a sudden change (= drop) in salinity and water temperature due to heavy rain.[145] Acute salinity changes, such as after heavy rain, increased the susceptibility to WSSV infection[146] because both reduced hemolymph osmotic pressure during infection,[147] reduced hemocytes count and lowered phenoloxidase activity,[148] increased WSSV load in infected shrimp.[149] A recent study[150] elucidated that the nephropore in the antennal gland is also a port of entry for WSSV. Shrimp produce more urine at low salinity to maintain osmolality of its hemolymph, causing the nephropore to open more frequently and increase shrimp' susceptibility to WSSV infection. Experiments to determine a temperature effect on the WSSV-infection outcomes yielded different results in different hosts. Prolonged exposures of *L. vannamei* at high water temperature (33°C) delayed mortality due to WSSV infection,[151] while daily temperature fluctuations of 5°C above the optimum shrimp culture temperature had either a positive or negative effect.[152] Warm water culture conditions (29 ± 0.5°C) increased WSSV load in *L. vannamei*.[153] In contrast, cold water culture conditions (4–12°C) reduced WSSV pathogenicity in the temperate crustacean species *P. leniusculus* and *A. astacus* because of lower WSSV replication.[76] On the other hand, low temperature increased WSSV load in the mud crab *S. serrata*.[154] Although all these reports were based on laboratory experiments and focused mainly on shrimp, the findings give insight into how salinity and temperature may affect WSD outbreaks in ponds.

A mixture of living or dead infected animals releases viruses and maintains the survival of WSSV in the water and the soil. White spot syndrome virus persisted for 1 year after a WSD outbreak in Vietnamese ponds[134] and for 10 months in pond soil stored at room temperature.[155] Moreover, WSSV remained viable for nearly 40 days

in 30°C seawater in the absence of a host species,[156] for 19 days in sun-dried sediment and for 35 days in waterlogged sediment[157] in which the viability of WSSV in the soil was affected by the type of soil.[158] In both latter studies, the decayed shrimp tissue in the sediment may have sustained the virus to persist for a reasonable time length in the pond sediment, despite the absence of known living vectors. Hence, the water and soil are a crucial repository of the virus and contribute to WSSV transmission.

The pond environment may create conditions favouring contact between WSSV and different resident host species, many of which are ubiquitous in ponds[101,159,160] and which could be new to the virus. High genetic variation might be advantageous to a generalist virus, which allows it to infect a broad range of host species, enhancing its survival options.[161] For example, extensive shrimp ponds provide more opportunities for cross-species transmission because (1) macrobenthic invertebrate species enter and leave easily, either settling or moving between ponds, (2) stocking with non-WSSV specific pathogen free (SPF) post-larvae, (3) practicing partial cropping and stocking, allowing transmission between successive cohorts and (4) the ponds are rarely drained, totally dried or disinfected. Based on studies on human pathogens, cross-host exposure is a crucial factor in cross-species virus transmission and is affected by the potential hosts' ecological and geographical distribution.[117] During a WSD outbreak, high numbers of viruses were released into the water and sediment. The presence of different macrobenthic invertebrate species in ponds provides favourable conditions for WSSV host jumping. A virus primarily infects phylogenetically closely related host species. Nevertheless, the intensity of contact between the virus and potential host is equally important.[117] Although WSSV transmission from most hosts to the cultured shrimp is possible, the dynamics of WSSV transmission between and within each host species in the field remains largely unknown.

Pond management and WSSV mitigation require more stringent connections to pond biosecurity than currently employed and it should be applied to all types of farming system. Many methods used to cut the transmission, including using biosecurity measures, limiting contact with soil by covering the pond bottom using plastic lining or using circular plastic ponds, closed system with limited water exchange and using chemicals to kill the virus, its host and vector, are not always effective to control the outbreak. In addition, local wisdom to ensure sustainable shrimp farming and reduce the WSSV transmission rate by using lower stocking densities could constitute an alternative strategy. Those methods including crop rotation or polyculture with fish[162] and sea weeds can provide favourable pond conditions for shrimp and reduce the WSSV load in the water and sediment, and thus also subsequent transmission to susceptible hosts. Mitigation is crucial to control the WSSV transmission within the farmed system and beyond.

7 | CONCLUSION AND THE WAY FORWARD

This review has brought to light that WSSV is present in a plethora of crustacean and non-crustacean invertebrates in aquatic and benthic environments (Tables 1 and 2). It also explained the complexity and the multiple interactions between WSSV and its aquatic/benthic hosts and vectors in pond environments (Figure 1).

Detection of WSSV is critical in our understanding of WSSV-host interactions both in the laboratory and in the field. It is highly relevant when testing a suspected host for WSSV presence to verify whether the virus replicates and whether a sylvatic transmission cycle exists or not. Revisiting the current literature in the light of this review calls for the importance of viral dose and standard protocols to determine whether WSSV replicates and is transmitted.

Studies on the spread of WSD in pond environments have received less attention so far, because of its complexity compared to laboratory studies (aquaria). It is recommended to continue screening other resident organisms in pond systems for the presence of WSSV and to check if the virus is resident or replicates in these organisms. The relative importance of hosts versus vectors in the transmission of WSSV is enigmatic, but the high reproduction rate of WSSV in shrimp explains in part the speed of WSD outbreaks in ponds. In the transmission of WSSV, a high virus load in a vector can be offset by a low virus load in a replicative carrier/host, but the latter may have more impact in the long term because the virus may persist in this host. A confounding factor in all of this is the presence of hosts that do not show symptoms, as was documented for crabs and polychaetes. Considering shrimp are cultured primarily in ponds, which are semi-open ecosystems with a cornucopia of natural species present, field studies targeting to elucidate the ecology of WSSV in respect to non-shrimp host and vectors in ponds are needed.

In summary, the number of reported crustacean and non-crustacean WSSV hosts is ever-increasing, with many species continuously present in pond systems even after shrimp farming stopped and outside the system. Some of these hosts are present in high numbers and hence may be important reservoirs for WSSV. It would be highly relevant to determine the relative importance of each of these host species in the development of WSSV in shrimps in pond systems.

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CONFLICT OF INTEREST

The authors declare there is no conflict of interest.

AUTHOR CONTRIBUTIONS

Desrina: Conceptualization; data curation; formal analysis; funding acquisition; investigation; methodology; writing – original draft; writing – review and editing. **S.B. Prayitno:** Writing – review and editing. **Marc Verdegem:** Conceptualization; formal analysis; investigation; methodology; supervision; writing – review and editing. **Johan Verreth:** Conceptualization; funding acquisition; project administration; supervision; writing – review and editing. **Just Vlak:** Investigation; methodology; supervision; writing – review and editing.

DATA AVAILABILITY STATEMENT

Data available on request from the authors

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