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## Research Article

# A BRIEF HISTORY OF White spot syndrome virus AND ITS EPIDEMIOLOGY IN **BRAZIL**

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## **ABSTRACT**

White spot syndrome virus (WSSV) is considered the most threatening infectious agent in shrimp aquaculture. Since its first occurrence in 1992, this pathogen has caused economic losses approach one billion US dollars per year. WSSV is a tailed, rod-shaped nucleocapsid, double stranded DNA virus, which belongs to Nimaviridae family. In this report, it is presented a concise overview on WSSV first occurrence and the different features of the virus. Besides, it is reported an update on epidemiology with special attention to its occurrence in Brazil.

Keywords: White spot syndrome virus, Brazil, epidemiology, virus disease Received in August 8, 2013 - Accepted in December 17, 2013 - Published ahead of print in December 20, 2013

# A Brief history

The first record of the disease caused by White spot syndrome virus (WSSV) was made in Japan between march and october 1993, when farms with the kuruma shrimps (Marsupenaeus japonicus) presented 80% of mortality and shrimps displayed clinical signs as abnormal red discolouration and small white spots on the body. This event took place after the importation of juvenile shrimps from China to japanese farming systems (Nakano et al. 1994). After experimental inoculations using filtered extracts of homogenized lymphoid organs from sickened specimens, it was possible to trigger the disease in healthy animals, suggesting that the responsible agent was a virus (Nakano et al. 1994). Furthermore, histopathological comparison of this disease with other well-known diseases affecting penaeid shrimp suggested that this is a new infectious disease, in penaeid shrimp where the aetiological agent might be a virus (Momoyama et al. 1994). Further, electron microscopy revealed the presence of a baciliform, enveloped and large (84 x 226 nm) virus, similar to various baculovirus species. This new virus was temporarily named RV-PJ (Rod-shaped nuclear virus of P. japonicus), although its taxonomical position was ascertained by analyzing the structure of the genomic DNA (Inouye et al. 1994).

There are reports since 1992 demonstrating the

occurrence of outbreaks by this virus in P. japonicus

in Taiwan (Chou et al. 1995). There the disease was

characterized by causing 100% of mortality in shrimp

farming, displaying lethargy and great similarity with

the outbreak in Japan. In 1993, a white spot syndrome

was observed in Penaeus monodon e Fenneropenaeus

penicillatus in Taiwan as well, with negative impacts on

Also there, experiments confirmed that this was a rod-

shaped (baciliform) double-stranded DNA virus with

approximately 330 X 87 nm in diameter (Chou et al.

1995; Wang et al. 1995). Due to the presence of white

spots on the shrimp carapaces and appendage, some

authors have suggested the name "white spot syndrome".

Besides, the main feature on the morphology of this

virus is the presence of tail-like appendix at one end

of the virion (Wang et al. 1995). Based on genetic and

morphological features, the virus was described within

the Nudibaculoviridae family, genus Baculovirus (Non-

occluded Baculovirus - NOB). The name Baculovirus

associated with white spot syndrome (WSBV) was

proposed for the isolate PmNOBIII (Penaeues monodon

non-occluded baculovirus III) to indicate PmNOBIII

the shrimp farming industry (Chou et al. 1995).

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related agents (Wang et al. 1995). During experimental infections of *P. monodon* with *Yellow* head virus (YHV), it was observed that a batch of infected animals with a virus similar to NOB (Wongteerasupaya

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et al. 1995). Transmission electron microscopy analysis revealed that those animals were infected with YHV and another unknown virus which generated basophilic intranuclear inclusions (unlike YHV, which presents eosinophilic inclusions). Isolation and purification of the nucleic acid from the so far new virus yielded double-stranded DNA of approximately 168 kbp. As this virus caused ectodermal and mesodermal infection, it was convenient to name it as Systemic Ectodermal and Mesodermal Baculovirus (SEMBV) (Wongteerasupaya et al. 1995).

A nested-PCR protocol was designed in order to identify this virus in penaeids (Lo et al. 1996a). These authors designated the virus as White spot baculovirus (WSBV). To date, this technique has been recommended by the World Organization for Animal Health (OIE) and widely used for detection of this infectious agent. From 1998, the virus was finally named as White spot syndrome virus (WSSV) (Lightner et al. 1998). However, its previous classification, in the Baculoviridae Family, was no longer accepted due to the lack of molecular data (Murphy et al. 1995).

Afterwards, WSSV genomic segments containing ribonucleotide redutase (RR) genes and repeated regions were analyzed in order to investigate its taxonomic status (van Hulten et al. 2000a). Thus, it was further established that the RRs from baculovirus and WSSV did not share a common ancestor, showing that this virus belongs to a new family. Later on, two major proteins of WSSV were identified: VP28 and VP26 associated to the envelope and nucleocapsid, respectively. The protein sequences were deposited in Genbank under the accession numbers: AF173993 (VP28) e AF173992 (VP26) (van Hulten et al. 2000b). Usually, viral proteins are well conserved among members from the same family. However, neither VP28 nor VP26 shares significant homology with other known structural proteins from Baculovirus available on databases. These results indicated the possibility that WSSV might belong to a new viral family, Whispoviridae (van Hulten et al. 2000b; van Hulten et al. 2000c).

The complete sequence of the double-stranded, circular DNA genome of WSSV was determined in 2001 (van Hulten et al. 2001; Yang et al. 2001). Both authors described a genome size ranging from 292 to 305 kb and containing 181 to 184 major open reading frames (ORF) besides, a low similarity with available sequences in database. Only a few genes have shown some degree of homology with herpesvirus genes (Yang et al. 2001). Together with phylogenetic analysis of the DNA polymerase, these informations have confirmed previous reports of a new viral family (van Hulten et al. 2001). Further phyogenetic studies based on WSSV codifying genes of polymerase DNA, major ribonucleotide redutase (RR1), ribonucleotide redutase R2, protein kinase and endonuclease revealed that WSSV is not related to other viral families (van Hulten et al. 2001).

Thus, based on phylogenetic analysis, the International Committee on Taxonomy of Viruses (ICTV) included WSSV as the type species of the genus *Whispovirus* within the newly recognized family *Nimaviridae* ("nima" is the Latin name for "thread") due to the physical feature of the virus, which is a tail-like polar projection (Mayo 2002).

# Morphology

WSSV virions have an ovoid to bacillar morphology with a long envelope extension at one extremity (Chou et al. 1995; Wang et al. 1995; Wongteerasupaya et al. 1995). Enveloped particles have about 350 x 130 nm with size variations ranging from 300 to 400 nm length and 110 to 140 nm in diameter. The appendage at the extremity measures 270 to 310 nm in length and about 30 nm in diameter (Durand et al. 1996). The virion is surrounded by a 6-7 nm thick loose-lifting outer lipid layer, with a trilaminar envelope (Durand et al. 1997; Nadala et al. 1998; Wongteerasupaya et al. 1995). The nucleocapsid is slightly striated and its dimensions are 180–420 in length and 54–85 nm in diameter, indicating that it is tightly packed within the virion (Durand et al. 1997).

# **Major viral proteins**

Over the past decade, several studies have been carried in order to identify viral proteins from WSSV. Major structural proteins on the envelope and capsid, as well as non-structural proteins have been successfully identified. The structural proteins compose the viral particle, besides having an important role on viral assembly and virus entry. On the other hand, non-structural proteins are involved in the process of viral replication and inhibition of host cell function (Liu et al. 2006).

The major structural proteins present on the envelope are: VP28, VP19 (van Hulten et al. 2000b), VP466 (Huang et al. 2002a), VP76 (Huang et al. 2005), VP124 (Zhu et al. 2005), VP281 (Huang et al. 2002b), VP110 (Li et al. 2006), VP22 (Zhang et al. 2002), VP31 (Li et al. 2006), VP76 (Huang et al. 2005), VP36B, VP38A, VP51B, VP53A (Tsai et al. 2006), VP150, VP52A, VP52B, VP41A, VP41B (Xie et al. 2006). Proteins located on the viral envelope are mainly involved in the attachment to the host cell and entry. Several other proteins were identified in the nucleocapsid, such as VP26, VP24 (van Hulten et al. 2000b), VP15 (van Hulten et al. 2002), VP35 (Chen et al. 2002), VP51, VP76 (Wu & Yang 2006), VP136A (Tsai et al. 2006). Non-structural proteins like VP9 (Liu et al. 2006) WSV021 (Zhu et al. 2007) e WSV477 (Han et al. 2007) are involved in the transcription, regulation of viral replication and viral DNA replication, respectively.

### Genome

Two complete genome sequences were established for isolates from Tailand (van Hulten et al.

2001) and China (Yang et al. 2001). A third sequence, from Taiwan, is available in the GenBank under the accession number AF440570. Genome size was reported differently for each isolate: 292,967 nucleotides for WSSV-TH (van Hulten et al. 2001), 305,107 nucleotides for WSSV-CH (Yang et al. 2001) and 307,287 for WSSV-TW (AF440570). Notwithstanding, these three sequences are very similar among them, and the biggest difference is a gene deletion of approximately 13 kb (WSSV-TH) and 1 kb (WSSV-CH) in the same genomic region, in relation to WSSV-TW (position 31134-31135) (Marks et al. 2003; Marks et al. 2004). The second biggest difference among the three isolates is genetic variation located at the 22961-23619 genomic region of WSSV-TH (genomic segment responsible for codifying ORF14 and 15) (Marks et al. 2004).

Along this segment, WSSV-TH and WSSV-TW possess different sequences of 657 and 834 bp, respectively, without homology with any available nucleotide sequence in the database (Marks et al. 2004). The third difference is an insert of 1337 bp in the TW isolate, at the region 254028-254029, which codifies ORF (Marks et al. 2004). Furthermore, there is a small variation related to the number of ORFs 184 (WSSV-TH) an 181 (WSSV-CH), which codify more than 50 proteins (van Hulten et al. 2001; Yang et al. 2001).

# **Pathogenicity**

The vírus infects cells in tissues of ectodermal and mesodermal origins, including: exoskeleton, appendages and inside the epidermis. Signs of WSSV include lethargy, reduction in food consumption, red discoloration of body and appendages and a decrease in hemolymph circulation (Durand et al. 1996; Durand et al. 1997). WSSV-infected shrimp develop white spots ranging from 0,5 – 3,0 mm in diameter, associated to subcuticular epithelial cells dysfunction and abnormal deposits of calcium (Durand et al. 1997). The white spots are not considered a reliable sign for preliminary diagnosis of this disease, since these spots are not always present and similar spots could be produced after bacterial infections, high alkalinity and stress (Sánchez-Paz 2010). On the cellular level the virus causes margination of chromatin and nuclear hipertrophy (Durand et al. 1997).

# **Host range and vectors**

WSSV can infect a very broad host range amongst decapod crustaceans (Escobedo-Bonilla et al. 2008). In addition, there are reports demonstrating the occurrence of the virus in freshwater species like *Macrobrachium rosenbergii* (Chakraborty et al. 2002). Up to date, more than 93 species of arthopods have been reported as hosts or carriers of WSSV, besides rotifers (Yan et al. 2004) and polychaetes (Vijayan et al. 2005). Table 1 shows some reports on crustacean species infected by WSSV.

Table 1: Reports on different crustacean species infected by

#### WSSV

WSSV	
Species	Report
shrimp	
M. japonicus	Inouye et al. 1994; Nakano et al. 1994; Momoyama et al. 1994
P. monodon, F. penicillatus	Chou et al. 1995
Macrobrachium rosenbergii,	Lo et al. 1996b; Chakraborty et al. 2002
P. semisulcatus, Palaemon sp	Lo et al. 1996b
L. setiferus	Lightner 1996; Lightner et al. 1998
F. aztecus, F. duorarum, L. vannamei	Lightner et al. 1998
Metapenaeus monoceros, M. brevicornis, Exopalaemon styliferus	Hossain et al. 2000
Metapenaeus dobsoni, Para- penaeopsis stylifera, Solenoce- ra crassicornis	Hossain et al. 2001
Heterocarpus sp., Aristeus sp., Metapenaeus elegans	Chakraborty et al. 2002
crabs	
Charybdis feriatus, Portunus pelagicus, P. sanguinolentus, Helice tridens	Lo et al. 1996b
Pseudograpsus intermedius	Hossain et al. 2000
Charybdis annulata, C. cruciata, Macrophthalmus sulcatus, Gelasimus marionis nitidus e Metopograpsus messor	Hossain et al. 2001
Cancer pagurus	Corbel et al. 2001
Charybdis hoplites	Chakraborty et al. 2002
Chasmagnathus granulata	Marques et al. 2011, Cavalli et al. 2013

## **Transmission**

WSSV transmission can occur through vertical or horizontal pathways. The presence of viral inclusions in reproductive organs of *P. monodon* broodstock indicates the vertical transmission of the virus (Lo et al. 1997). However, no virus infection was found in mature females, which may imply that infected eggs died by the virus before maturation (Lo et al. 1997). The horizontal transmission can occur among individuals by direct contact, or indirectly, by ingestion of infected organisms.

# **Epidemiology**

Since its first ocurrence in 1992 (Chou et al. 1995), WSSV has been spread worldwide. In 1993, it was confirmed that the virus was disseminated throughout Asia (Inouye et al. 1994; Nakano et al. 1994; Momoyama et al. 1994). In november 1995, the first case of infection by WSSV was described in the New World, affecting a shrimp farming in Texas, USA (Lightner 1996). In Latin

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America, the presence of the virus was reported in 1999 in Mexico, Panama, Peru, Costa Rica, El Salvador, Colombia, Nicaragua, Honduras (*Annual animal health status* - http://www.oie.int/hs2/report.asp) and Ecuador (Rodriguez et al. 2003). The first notification of WSSV in shrimp farms in Brazil occurred in 2005, in the states of Santa Catarina (South) (Seiffert et al. 2006) and Ceará (Northeast) (OIE 2005).

The presence of WSSV in wild shrimps was reported by Lo et al. (1996b) in four species of shrimp in Taiwan. Nunan et al. (2001) reported a viral prevalence of 2% in L. vannamei caught in the Pacific Ocean, at the offshore of Panama, using dot blot hybridization technique. Different prevalences were reported for Fenneropenaeus indicus, P. monodon, Metapenaeus spp e Scylla serrata infected in the east coast of India (Vaseeharan et al. 2003). Chapman et al. (2004) described the presence of WSSV in shrimps of South Carolina, USA, in the North Atlantic Ocean. Uma et al. (2005) revealed the presence ranging from 25-50% of WSSV in Penaeus monodon breeders from Southeastern India. In Brazil wild shrimp species Farfantepenaeus brasiliensis and F. paulensis were found to be infected by this virus (Cavalli et al. 2010 and 2011). However, the most austral occurrence of the virus in the South America was registered for wild crustaceans of Bahia Blanca, Argentina (Martorelli et al. 2010).

# **WSSV** in Brazil

In november 2004, *Litopenaeus vannamei* cultivated in ponds (1400 ha.) in Lagoa de Imaruí, Laguna, Southern Brazil, were infected by WSSV. Mortality rates reached 90%, causing economic losses of approximately US\$ 3 million at Laguna, Southern Brazil (Seiffert et al. 2006). The disease led to a decrease in shrimp production from 4.189t in 2004 to 480t in 2006 (Seiffert et al. 2006). This was the first report of WSSV in Brazil and notified to World Organization for Animal Health (OIE) in january 2005. In December 2010, OIE brought out another occurrence of the disease in Santa Catarina state. In North coast of Santa Catarina, a great number of *White spot syndrome virus particles*, were visualized by the negative staining technique (Hipolito et al. 2012).

WSSV detection was also reported in Ceará, Pernambuco and Rio Grande do Norte states (Guerrelhas & Teixeira 2012). Viral co-infection with *Infectious myonecrosis* virus (IMNV) and WSSV was also report in Ceara (Feijó et al. 2013). Rio Grande do Norte and Ceará are the major shrimp producers in Brazil, responsible for about 80% of total shrimp production. Therefore, it is necessary special attention concerning management and vírus control in these areas in order to prevent further impacts.

In wild animals, the virus has already been detected in Farfantepenaeus paulensis and F. brasiliensis

in the Atlantic Ocean (Cavalli et al. 2010). Likewise, the presence of viral DNA was confirmed in *F. paulensis* in the Laguna estuarine system (Cavalli et al. 2010) and *Litopenaeus vannamei* from farms in Santa Catarina state (Cavalli et al. 2010; Costa et al. 2010). Moreover, in the southern region, the virus has been detected in wild *F. paulensis* and *L. vannamei* produced in ponds in the Lagoa dos Patos, Rio Grande do Sul state (Cavalli et al. 2011).

The arrival of the virus into the brazilian shrimp cultivation remains not well known. However, an epidemiological study suggests that the entry of the virus in Santa Catarina occurred upon nauplius and postlarvae import from Northeastern Brazil (Costa 2010). The entry of pathogens in shrimp farming occurs mainly due to contaminated food and objects, infected breeders and animals which act as vectors (Fegan & Clifford 2001; Lightner 2005).

In addition, environmental factors such as sudden changes in temperature(Rahman et al. 2006, Rahman et al. 2007), salinity (Liu et al. 2006) an increase in the number of predators and population density, as well as other potentially stressful factors in animal production can trigger the development of diseases. Stress factors may affect appreciably the physiological balance of the aquatic organisms, consequently changing their imune system, thus decreasing their ability to respond to pathogens (Pavanelli et al. 1998).

# **CONCLUSIONS**

For the control of WSSV disease, it is important the use of prophylactic measures in order to prevent the virus transmission. Fish industries must be focused on biosecurity and programs that include the reduction of water exchange as this is a risky management option for shrimp farmers unless both influent and effluent stream are disinfected (Lotz 1997). More strict controls are important on the entry of live animals (tested or not), as they present a potential risk to introduce the infection (Lightner 2005). Import procedures must include a rigorous quarantine and screening for diseases for breeding stocks before their transfer to aquaculture (Flegel & Fegan 2002). In addition to breeders and larvae (Flegel, 2006), the spread of shrimp viruses can include frozen shrimps (Durand et al. 2000, Flegel & Fegan 2002) and ballast water (Flegel & Fegan 2002). Moreover, considering that only few epidemiological researches have been conducted and these indicated the presence of WSSV in Brazil, surveillance studies on the Brazilian coast are necessary in order to better determine the presence of WSSV in wild shrimps and the spreading of the disease in our coast in order to identify the hotspots, or regions relatively free of the virus.

#### REFERENCES

Cavalli LS, Nornberg BFS, Netto SA, Poersch L, Romano LA, Marins LF, Abreu PC 2010. White spot syndrome

- virus in wild penaeid shrimp caught in coastal and offshore Waters in the Southern Atlantic Ocean. *J. Fish Dis.* 33:533-536.
- Cavalli LS, Romano LA, Marins LF, Abreu PC 2011. First report of *White spot syndrome* virus in farmed and wild penaeid shrimp from Lagoa dos Patos estuary, southern Brazil. *Braz. J. Microbiol.* 42:1176-1179.
- Cavalli LS, Batista CR, Nornberg BF, Mayer FQ, Seixas FK, Romano LA, Marins LF, Abreu PC 2013. Natural occurrence of White spot syndrome virus and Infectious hypodermal and hematopoietic necrosis virus in Neohelice granulata crab. J. Invertebr Pathol. 114(1):86-88.
- Chakraborty A, Otta SK, Joseph B, Kumar S, Hossain Md S, Karunasagar I, Venugopal MN 2002. Prevalence of white spot syndrome virus in wild crustaceans along the coast of India. *Curr.Sci.* 82(11):1392-1397.
- Chapman RW, Browdy CL, Savin S, Prior S, Wenner E 2004. Sampling and evaluation of white spot syndrome virus in commercially important Atlantic penaeid shrimp stocks. *Dis. Aquat. Org.* 59:179-185.
- Chen LL, Leu JH, CJ Huang, Chou CM, Chen SM, Wang CH, Lo CF, Kou GH 2002. Identification of a nucleocapsid protein (VP35) gene of shrimp *White spot syndrome virus* and characterization of the motif important targeting VP35 to the nuclei of transfected insect cells. *Virology* 293:44-53.
- Chou HY, Huang CY, Wang CH, Chiang HC, Lo CF 1995. Pathogenicity of a baculovirus infection causing *White spot syndrome virus* in cultured penaeid shrimp in Taiwan. *Dis. Aquat. Org.* 23:165-173.
- Corbel V, Zuprisal Z, Shi C, Huang, Sumartono, Arcier JM, Bonami JR 2001. Experimental Infection of european crustaceans with white spot syndrome vírus (WSSV). *J. Fish Dis.* 24:377-382.
- Costa SW 2010. Prospecção de fatores associados à manifestação e dispersão da enfermidade do vírus da síndrome da mancha branca em Santa Catarina. *Tese de doutorado* Universidade Federal de Santa Catarina, Centro de Ciências Agrárias. Programa de Pós-Graduação em Aquicultura, Florianópolis, SC, 145 p.
- Costa SW, Vicente LRM, Souza, TM, Andreatta ER, Marques MRF 2010. Parâmetros de cultivo e a enfermidade da mancha-branca em fazendas de camarões de Santa Catarina. *Pesqui. Agropecu.Bras.* 45(12):1521-1530.
- Durand S, Lightner DV, Nunan LM, Redman RM, Mari J, Bonami JR 1996. Application of gene probes as diagnostic tools for White spot baculovirus (WSBV) of penaeid shrimp. *Dis. Aquat. Org.* 27:59-66
- Durand S, Lightner DV, Redman RM, Bonami JR 1997. Ultrastuture and morphogenesis of White spot syndrome baculovirus (WSSV). *Dis. Aquat. Org.* 29:205-211.
- Durand S, Tang KFJ, Lightner DV. 2000. Frozen

- commodity shrimp: potencial avenue for introduction of *White spot syndrome virus and Yellow head virus. J. Aquat. Anim. Health* 12:128-135.
- Escobedo-Bonilla CM, Alday-sanza V, Ville M, Sorgeloos P, Pensaert MB, Nauwynck HJ 2008. A review on the morphology, molecular characterization, mophogenesis and pathogenesis of *White spot syndrome virus*. *J. Fish Dis.* 31:1-18.
- Fegan DF, Clifford HC 2001. Health management for viral diseases in shrimp farms. *In:* Browdy, C.L. and Jory, D.E. editors. The new Wave, Proceedings of the special session on sustainable shrimp culture, Aquaculture. *The World Aquaculture society*, Baton Rouge, LA, USA. p.105-135.
- Feijó RG, Kamimura MT, Oliveira-Neto JM, Vila-Nova CMVM, Gomes ACS, Coelho MGL, Vasconcelos RF, Gesteira TCV, Marins LF, Rodrigo Maggioni R 2013. Infectious myonecrosis virus and white spot syndrome virus co-infection in Pacific white shrimp (Litopenaeus vannamei) farmed in Brazil. *Aquaculture* 380-383:1-5.
- Flegel TW 2006. The special danger of viral pathogens in shrimp translocated for aquaculture. *Science Asia* 32:215-221.
- Flegel TW, Fegan DF 2002. Strategies for preventing the spread of fish and shellfish diseases. *Fisheries Sci.* 68(1):776-788.
- Guerrelhas AC, Teixeira APG 2012. O panorama da situação da mancha branca no Nordeste. *Panorama da Aquicultura* 22(129):38-41.
- Han F, J Xu, X Zhang 2007. Characterization of an early gene (wsv477) from white spot syndrome virus (WSSV). *Virus Genes* 37:193-198.
- Hipolito M, Catroxo MHB, Martins AMCRPF, Melo NA, Pituco EM, Galleti NTC, Ranzani-Paiva MJT, Mouriño JLP, Ferreira CM 2012. Detection of white spot syndrome virus in Brazil using negative staining, immunoelectron microscopy and immunocytochemistry techniques. *Int. J. Morphol.* 30(2):761-768.
- Hossain MS, Chakraborty A, Otta SK, Karunasagar I, Karunasagar I 2000. Detection of white spot syndrome vírus (WSSV) in wild captured shrimp and in non-cultured crustaceans from shrimp ponds in Bangladesh by polymerase chain reaction. *Fish Pathol.* 36(2):93-95.
- Hossain MS, Chakraborty A, Joseph B, Otta SK, Karunasagar I, Karunasagar I 2001. Detection of new hosts for white spot syndrome vírus of shrimp using nested polymerase chain reaction. *Aquaculture* 198:1-11.
- Huang C, Zhang X, Lin Q, Xu X, Hu Z, Hew CL 2002a. Proteomic analysis of shimpr White spot syndrome viral proteins and characterization of a novel envelope protein VP466. *Mol. Cell. Proteomics* 1(3):223-231.
- Huang C, Zhang XB, Lin QS, Xu X, Hew CL 2002b.

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Characterization of a novel envelope protein (VP281) of shrimp white spot syndrome virus by mass espectometry. *J. Gen. Virol.* 83: 2385-2392.

- Huang R, Xie Y, Zhang J, Shi Z 2005. A novel envelope protein involved in *White spot syndrome virus infection. J. Gen. Virol.* 86:1357-1361.
- Inouye K, Miwa S, Oseko N, Nakano H, Kimura T, Momoyama K, Hiraoka M 1994. Mass mortalities of cultured kuruma shrimp, *Penaeus japonicus*, in Japan in 1993: electron microscopic evidence of the causative vírus. *Fish Pathol.* 29:149-158.
- Li L, Shumei L, Yang F 2006 Characterization of an envelope protein (VP110) of *White spot syndrome virus. J. Gen. Virol.* 87:1909-1915.
- Lightner DV 1996. A Handbook of shrimp pathology and diagnostic procedures for diseases of cultured penaeid shrimp. World Aquaculture Society, Baton Rouge, Lousiana.
- Lightner DV 2005. Biosecurity in shrimp farming: pathogen exclusion through use of SPF stock and routine surveillance. *J. World Aquac. Soc.* 36(3):229-248.
- Lightner DV, Hasson KW, White BL, Redman RM 1998. Experimental Infection of western hemisphere penaeid shrimp with Asian White spot syndrome virus and Asian Yellow head virus. *J. Aquat. Anim. Health* 10:271-281.
- Liu B, Yu Z, Song X, Guan Y, Jian X, He J 2006. The effect of acute salinity change on white spot syndrome (WSS) outbreaks in *Fenneropenaeus chinensis*. *Aquaculture* 253:163-170.
- Lo CF, Leu JH, Ho CH, Chen CH, Peng SE, Chen YT, Chou CM, Yeh PY, Huang CJ, Chou HY, Wang CH, Kou GH 1996a. Detection of baculovirus associated with white spot syndrome (WSBV) in penaeid shrimps using polymerase chain reaction. *Dis. Aquat. Org.* 25:133-141.
- Lo CF, Ho CH, Peng SE, Chen CH, Hsu HC, Chiu YL, Chang CF, Liu KF, Su MS, Wang CH, Kou GH 1996b. White spot syndrome baculovirus (WSBV) detected in cultured and captured shrimp, crabs and other arthropods. *Dis. Aquat. Org.* 27:215-225.
- Lo CF, CH Ho, Chen CH, Liu KF, Chiu YL, Yeh PY, Peng SE, Hsu HC, Liu HC, Chang CF, Su MS, Wang CH, Kou GH 1997. Detection and tissue tropism of white spot syndrome baculovirus (WSBV) in captured brooders of Penaeus monodon with a special emphasis on reproductive organs. *Dis. Aquat. Org.* 30:53-72.
- Lotz JM 1997. Viruses, biosecurity and specific pathogenfree stocks in shrimp aquaculture. *World J. Microb. Biot.* 13(4):405-413.
- Mayo MA 2002. A summary of taxonomic changes recently approved by ICTV. *Arch. Virol.* 147(8):1655-1656.
- Marks H, Mennens M, Vlak JM, van Hulten MCW 2003. Transcriptional analysis of the white spot syndrome

- virus major virion protein genes. *J. Gen. Virol.* 84:1517-1523.
- Marks H, Goldbach RW, Vlak JM, van Hulten MCW 2004. Genetic variation among isolates of White spot syndrome virus. *Arch. Virol.* 149:673-697.
- Marques JS, Müller IC, Moser JR, Sincero TC, Marques MRF 2011. Wild captured crab, *Chasmagnathus granulata* (Dana, 1851), a new host for white spot syndrome vírus (WSSV). *Aquaculture* 318(1-2):20-24.
- Martorelli SR, Overstreet RM, Jovonovich JA, 2010 First report of viral pathogens WSSV and IHHNV in Argentine crustaceans. *Bull. Mar. Sci.* 86 (1):117-131.
- Momoyama K, Hiraoka M, Nakano H, Koube H, Inouye K, Oseko N 1994. Mass mortalities of cultured kuruma shrimp, *Penaeus japonicus*, in Japan in 1993: Histopatological study. *Fish Pathol.* 29: 141-148.
- Murphy FA, Fauquet CM, Bishop DHL, Ghabrial SA, Jarvis AW, Martelli GP, Mayo MA, Summers MD 1995. Virus taxonomy: Classification and nomenclature of viruses. VI report of the ICTV. Springer, Wien New York, Arch. Virol. 10.
- Nadala EC, Jr Tapay LM, Loh PC 1998. Characterization of a non-occluded baculovirus-like agent pathogenic to penaeid shrimp. *Dis Aquat. Org.* 33:221–229.
- Nakano H, Koube H, Umezawa S, Momoyama K, Hiraoka M, Inouye K, Oseko N 1994. Mass mortalities of cultured kuruma shrimp, *Penaeus japonicus*, in Japan in 1993: Epizootiological survey and infection trials. *Fish Pathol.* 29:135-139.
- Nunan LM, Arce SM, Staha RJ, Lightner DV 2001. Prevalence of Infectious Hypodermal and Hematopoietic Necrosis Virus (IHHNV) and White Spot Syndrome Virus (WSSV) in *Litopenaeus vannamei* in the Pacific Ocean off the Coast of Panama. *J. World Aquac. Soc.* 32:330-334.
- OIE (World Organisation for Animal Health) 2005. White spot disease in Brazil. *Follow-up report No. 1* (04/08/2005).
- Pavanelli GC, Eiras JC, Takemoto RM 1998. Doenças de Peixes profilaxia, diagnóstico e tratamento. Maringá, *EDUEM*, 311p.
- Rahman MM, Escobedo-Bonilla CM, Corteel M, Dantas-Lima JJ, Wille M, Alday-Sanz V, Pensaert MB, Sorgeloos P, Nauwynck HJ 2006. Effect of high water temperature (33 °C) on the clinical and virological outcome of experimental infections with with spot syndrome virus (WSSV) in specific pathogen-free (SPF) *Litopenaeus vannamei. Aquaculture* 261:842-849.
- Rahman MM, Corteel M, Wille M, Alday-sanz V, Pensaert MB, Sorgeloos P, Nauwynck HJ 2007. The effect of raising water temperature to 33 °C in *Penaeus vannamei* juveniles at different stages of infection with white spot syndrome virus (WSSV). *Aquacultre* 272:240-245.
- Rodriguez J, Bayot B, Amano Y, Panchana F, Blas I,

- Alday V, Calderon J 2003. White spot syndrome virus infection in cultured *Penaeus vannamei* (Boone) in Ecuador with emphasis on histopathology and ultrastructure. *J. Fish Dis.* 26:439-450.
- Sanchez-Paz A 2010. White spot syndrome virus: an overview on an emergent concern. *Vet. Res.* 41(43):1-31.
- Seiffert WQ, Beltrame E, Andreatta ER, Maggioni DS 2006. Enfermidades, uma oportunidade para repensar o cultivo de camarões marinhos. *Panaroma da Aqüicultura* 97:32-38.
- Tsai JM, Wang HC, Leu JH, Wang A HJ, Zhuang Y, Walker PJ, Kou GH, Lo CF 2006. Identification of the Nucleocapsid, Tegument, and Envelope Proteins of the Shrimp White Spot Syndrome Virus Virion. *J. Virol.* 80(6):3021-3029.
- Uma A, Koteeswaran A, Karunasagar I 2005. Prevalence of white spot syndrome virus and monodon baculovirus in *Penaeus monodon* broodstock and postlarvae from hatcheries in southeast coast of India. *Curr. Sci.* 89:1619-1622.
- van Hulten MCW, Tsai MF, Schipper CA, Lo CF, Kou GH, Vlak JM 2000a. Analysis of a genoic segmento f white spot syndrome virus of shrimp robonucleotide redutase genes and repeat regions. *J. Gen. Virol.* 81:307-316.
- van Hulten MCW, Westenberg M, Goodall SD, Vlak JM 2000b. Identificaction of two major virion protein genes of white spot syndrome virus of shrimp. *Virology* 266:227-236.
- van Hulten MCW, Goldbach RW, Vlak JM 2000c. Tree funcitionally diverged major structural proteins of white spot syndrome virus evolved by gene duplication. *J. Gen. Virol.* 81:2525-2529.
- van Hulten MCW, Witteveld J, Peters S, Kloosterboer N, Tarchini R, Fiers M, Sandbrink H, Lankhorst RK, Vlak JM 2001. The White spot syndrome virus DNA genome sequence. *Virology* 286:7-22.
- van Hulten MCW, Rejins MA, Vermeesch MG, Zandbergen F, VLAK JM 2002. Identification of VP19 and VP15 of white spot syndrome virus 123 (WSSV) and glysosylation status of the WSSV major structural proteins. *J. Gen. Virol.*, 83: 257-265.
- Vaseeharan B, Jayakumar R, Ramasamy P 2003. PCR-based detection of white spot syndrome virus in cultured and captured crustaceans in India. *Lett. Appl. Microbiol.* 37:443-447.
- Vijayan KK, Stalin VRAJ, Balasubramanian CP, Alavandi SV, Thillai SV, Santiago TC 2005. Polychaete worms a vector for white spot syndrome virus (WSSV). *Dis. Aquat.*
- Wang CH, Lo CF, Leu JH, Chou CM, Yeh PY, Chou HY, Tung MC, Chang CF, Su MS, Kou GH 1995. Purification and genomic analysis of baculovirus associated with white spot syndrome (WSBV) of Penaeus monodon. *Dis. Aquat. Org.* 23:239-242.

- Wongteerasupaya C, Vickers JE, Sriurairatana S, Nash GL, Akarajamorn A, Boosaeng, V, Panyim S, Tassanakajon A, Withyachumnarnkul B, Flegel TW 1995. A non-occluded, systemic baculovirus that occurs in cells of ectodermal and mesodermal origin and causes high mortality in the black tiger prawn *Penaeus monodon*. *Dis. Aquat. Org.* 21:69-77.
- Wu C, Yang F 2006. Localization studies of two white spot syndrome virus structural proteins VP51 and VP76. *Virol. J.* 3:76-83.
- Xie X, Xu L, Yang F 2006. Proteomic Analysis of the major envelope and nucleocapsid proteins of White spot syndrome virus. *J. Virol.* 80(21):10615-10623.
- Yan DC, Dong SL, Huang J, Yu XM, Feng MY, Liu XY 2004. White spot syndrome virus (WSSV) detected by PCR in rotifers and rotifer resting eggs from shrimp ponds sediments. *Dis. Aquat. Org.* 59:69-73.
- Yang F, He J, Lin X, Li Q, Pan D, Zhang X, Xu X 2001. Complete genome sequence of the shrimp White spot syndrome baciliform virus. *J. Virol.* 75(23):11811-11820.
- Zhang X, Huang C, Xu X, Hew CL 2002. Transcriptional and identification of an envelope protein gene (p22) from shrimp white spot syndrome virus. *J. Gen. Virol.* 83:471-477.
- Zhu Y, Xie X, Yang F 2005. Transcription and identification of a novel envelope protein (VP124) gene of shrimp white spot syndrome virus. *Virus Res.* 113:100-106.
- Zhu Y, Ding Q, Yang F 2007. Characterization of a homologous-region-binding protein from white spot syndrome virus by phage display. *Virus Res.* 125:145-152.