



# A critical review of susceptibility of crustaceans to Taura syndrome, Yellowhead disease and White Spot Disease and implications of inclusion of these diseases in European legislation

G.D. Stentiford <sup>a,\*</sup>, J.-R. Bonami <sup>b</sup>, V. Alday-Sanz <sup>c</sup>

<sup>a</sup> EC Community Reference Laboratory for Crustacean Diseases, Centre for Environment, Fisheries and Aquaculture Science (Cefas), Barrack Road, Weymouth, Dorset DT4 8UB, United Kingdom

<sup>b</sup> Centre National de la Recherche Scientifique (CNRS), EcoLag UMR 5119, UM2 Place, E. Bataillon, 34095 Montpellier, France

<sup>c</sup> Gran Via 658, 4<sup>a</sup>-1<sup>a</sup>, Barcelona, Spain

## ARTICLE INFO

### Article history:

Received 20 January 2009  
Received in revised form 10 February 2009  
Accepted 28 February 2009

### Keywords:

White Spot Syndrome Virus, WSSV  
Taura Syndrome Virus, TSV  
Yellowhead Virus, YHV  
EC Directive 2006/88/EC  
Crustacean disease  
Susceptible species  
Vector species

## ABSTRACT

The EC Council Directive 2006/88/EC adopted during 2008 has listed three crustacean disease: White Spot Disease (WSD) caused by the White Spot Syndrome Virus (WSSV), Yellowhead disease (YHD) caused by Yellowhead Virus (YHV) and Taura syndrome (TS) caused by Taura Syndrome Virus (TSV). Their inclusion within the Directive acknowledges a lack of protection (regarding biosecurity) to aquaculture and wild stocks of crustaceans in European waters in previous aquatic animal health legislation. In the context of the Directive, it is important to consider the range of host species deemed to be susceptible to these pathogens in order to assess the risk that these species may inadvertently introduce the pathogens to European waters via animal and commodity movements. This review has provided a brief synopsis of available literature for WSD, TS and YHD and has systematically assessed this literature against four objective susceptibility criteria laid down by the European Food Safety Authority (EFSA): (A) Evidence of replication or growth of the organism; (B) Presence of a viable organism; (C) Presence of specific clinico-pathological changes; and (D) Specific location of the pathogen within the host. Importantly these criteria enable discrimination of infected hosts from mechanical carriers (vector status). Hosts are assigned to one of two criteria: Group I hosts for which the literature provides evidence for susceptibility and Group II for which the literature provides limited evidence for susceptibility. The susceptibility of crustacean hosts is discussed in terms of the taxonomic range of these hosts to the specific pathogens and to the use of this information in informing risk assessments for the potential release, exposure and impact of their introduction on the European aquatic environment.

Crown Copyright © 2009 Published by Elsevier B.V. All rights reserved.

## Contents

1.	Background and context . . . . .	2
1.1.	The crustacean industry in Europe . . . . .	2
1.2.	Crustacean diseases in European law . . . . .	2
1.3.	Potential biosecurity threats to Europe and within Europe . . . . .	2
2.	Listed diseases . . . . .	3
2.1.	White Spot Disease (WSD) . . . . .	3
2.2.	Taura syndrome (TS) . . . . .	4
2.3.	Yellowhead disease (YHD) . . . . .	5
3.	Host susceptibility to WSD, TS and YHD . . . . .	10
3.1.	Susceptibility to WSD . . . . .	11
3.2.	Susceptibility to TS . . . . .	11
3.3.	Susceptibility to YHD . . . . .	11
3.4.	Taxonomic range of susceptibility for the three diseases . . . . .	12
3.5.	Focus on susceptibility of European species . . . . .	12

\* Corresponding author.  
E-mail address: [grant.stentiford@cefass.co.uk](mailto:grant.stentiford@cefass.co.uk) (G.D. Stentiford).

4. Future directions for legislation and research in Europe . . . . .	14
Acknowledgements . . . . .	15
References . . . . .	15

## 1. Background and context

### 1.1. The crustacean industry in Europe

In 2005, the European Union (EU) imported around 600,000 Mt of shrimp with a value of \$2.3 billion. Of this, approximately 140,000 Mt (\$500 m) comprised cultured commodity shrimp from several global production regions. The 2005 figure represents an increase in quantity of 45% since 1999 (source <http://ec.europa.eu>). Capture fisheries, mainly for cold-water prawns constitute the major portion of the current market, with tropical marine shrimp forming the majority of imports from aforementioned aquaculture production regions (the main imported product falling under CN code 0306 1350—frozen shrimps of the genus *Penaeus*). The three major buyers within the EU are Spain, Italy and the UK. In value terms, the main exporters of penaeid prawns to the EU are Argentina, Ecuador, India and Brazil, with several other Asian and South American nations also contributing significantly.

In contrast to finfish and shellfish, aquaculture production of crustaceans is currently limited within Europe, only accounting for around 200 Mt/annum, with a total value of c. \$3m. In terms of penaeid shrimp, the FAO lists production areas for the 'kuruma' prawn (*Penaeus japonicus*) in France (40 Mt/annum), Italy (19 Mt/annum) and Spain (44 Mt/annum) with a total value of c. \$2 m in 2004. A small culture of palaemonid prawns occurs in Spain (63 Mt/annum, c. \$200k) while the remainder of crustacean aquaculture production concerns the farming of freshwater crayfish of the family Astacidae (47 Mt/annum, c. \$660k) (Source: <http://www.fao.org/figis>). In terms of value, the top producers of crustacean aquaculture products in Europe are France (\$1.5m), Spain (\$860k) and Italy (\$425k). Smaller producers include Sweden, Ukraine, Estonia and Russian Federation countries.

In contrast to this, the total fishery production of crustaceans from European waters totalled almost 400,000 Mt in 2004, with a large majority comprising marine prawns (c. 200,000 Mt), lobsters (c. 60,000 Mt) and crabs (c. 85,000 Mt). In terms of freshwaters, capture fisheries are solely comprised of crayfish (c. 6000 Mt). Wild fisheries for marine crustaceans are considered key resources in the European area and in many countries (such as the UK) they are amongst the most valuable marine fisheries resources, ranking above several important finfish species in terms of production quantity and value. It is envisaged that the increasing demand for fish products and the documented reduction in supplies of natural fisheries will further stimulate the development of the aquaculture sector within Europe. In terms of crustacean production however, it is debatable (and perhaps unlikely) that production units within Europe could efficiently compete with global markets for these products, particularly for warm water marine prawns. Production units for *P. japonicus* in the Mediterranean are currently small compared with tropical markets and may be hampered by temperature-derived reductions in the length of the production season and labour costs within the EU. However, production of premium products (e.g. ethical, organic) could provide some competitive edge to ensure local sustainability. Potential also exists for the specific culture of freshwater crustaceans within central and eastern European countries particularly via a move towards more intensive farming methods and through the production of premium products such as freshwater crayfish.

In several countries (particularly the UK), following capture, wild marine crustaceans (e.g. *Nephrops norvegicus*, *Cancer pagurus*, *Homarus gammarus*) are transported live to continental Europe (particularly France, Spain and Portugal) and to 3rd countries (non-EU) for resale and

consumption. With the exception of *H. gammarus* (which are subject to certain movement restrictions), the movement of live crustaceans in this way is relatively uncontrolled with losses in transport remaining unrecorded and morbid or dead animals potentially finding their way back in to the aquatic environment at the distant site. Furthermore, water used for transporting animals may be released accidentally or purposefully to local waterways or drains. The significant dearth in knowledge of pathogens of our major commercially exploited species and their potential for transmission to other commercially exploited and reservoir species identify these as high risk practices. Live transport of animals to distant markets when coupled with the apparent high potential for transmission of pathogens to new hosts is cause for concern (Stentiford and Shields, 2005).

In addition to exploited stocks, crustaceans are also considered as keystone elements in most aquatic ecosystems. They form a fundamental component of food chains, and therefore comprise a significant element of the diet of many fish species. In some cases, they are afforded protected status under internationally recognised legislation. In UK freshwaters, the white claw crayfish (*Austropotomobius pallipes*) is one such species considered endangered and is therefore protected under UK and European legislation (including the IUCN Red Data list, the Wildlife and Countryside Act 1981 and the EC Habitats Directive 1992). The listing of crustaceans in such acts acknowledges a requirement for improved understanding of threats to remaining populations and in addition, highlights the necessity for national governments within the European Union to protect not only commercially exploited and farmed animals but also the wildlife species that populate their natural aquatic systems.

### 1.2. Crustacean diseases in European law

The EC Council Directive 2006/88/EC adopted during 2008 lists three crustacean disease: White Spot Disease (WSD) caused by the White Spot Syndrome Virus (WSSV), Yellowhead disease (YHD) caused by Yellowhead Virus (YHV) and Taura syndrome (TS) caused by Taura Syndrome Virus (TSV). WSD is currently listed as a 'non-exotic' pathogen to the EU based upon its reported occurrence in penaeid shrimp farms in Southern Europe (see below) while YHD and TS are listed as exotic due to their apparent absence from the EU. Their inclusion within the new Directive acknowledges the lack of protection (regarding biosecurity) to aquaculture and wild stocks of crustaceans in European waters in previous EC aquatic animal health legislation. In this context, it recognises the global importance of diseases such as WSD, TS and YHD in causing significant economic losses in farming regions, the lack of control measures available to deal with disease outbreaks should they occur and the potential for their international transfer via trade in live and commodity products.

### 1.3. Potential biosecurity threats to Europe and within Europe

The potential for transfer of disease agents around the globe, either via movement of live animals for farming (e.g. broodstock and larvae) or as contaminating agents in commodity products (e.g. frozen shrimps) is amply demonstrated by the pandemic nature of several important diseases of marine shrimp, including WSD, TS and YHD (Flegel, 1997; Lotz, 1997). While acknowledged that live movements, particularly of early life stage shrimp offered the most efficient means for global distribution of crustacean pathogens, several studies have also demonstrated the potential and actual threat of disease

introduction to novel hosts in new geographic regions via commodity products, particularly where climatic regimens in receiving countries are suitable for pathogen survival and replication (Durand et al., 2000, 2003; Reville et al., 2005; Hasson et al., 2006). Despite major markets for tropical commodity shrimp in temperate regions (e.g. Europe) and the potential for establishment of infection in new hosts, relatively little research has been directed towards susceptibility of European species to such pathogens. Furthermore, little information is available on the environmental tolerance of these disease agents or their ability to establish infection and disease in non-target hosts should they be introduced. Available data is especially lacking for European crustaceans, particularly those that exist at temperatures that may be considered outside the normal range experienced by these viruses in endemic zones in Asia and South America. Nevertheless, studies by Corbel et al. (2001) have demonstrated susceptibility to WSSV in a range of marine and freshwater decapods from Europe while other studies have provided evidence that WSSV is able to infect and evoke disease in susceptible species of freshwater crayfish at temperatures conducive to European aquatic habitats (Jiravanichpaisal et al., 2001, 2004; Du et al., 2008). In this context, a review of susceptibility of aquatic crustaceans to pathogens newly listed in EC Directive 2006/88 is timely and provides a context to carefully assess the potential for such disease agents to become established in European waters. Furthermore, knowledge of natural and experimental host range, improved understanding of environmental tolerance of pathogens and an appreciation of actual threat from commodities imported primarily for human consumption will lead to well-informed risk assessment measures to prevent exposure of farmed and wild animals to exotic pathogens while encouraging trade between net producers and net importers of commodity shrimp.

Another much-neglected potential threat to biosecurity of European crustacean populations is represented by the relatively free movement of live animals *within* and *between* Member States of the EU. Losses in transport remain largely unrecorded and morbid or dead animals potentially find their way back to the aquatic environment either at the distant site, or elsewhere *en route*. Furthermore, water used for transporting animals may be released to local waterways or drains, either accidentally or purposefully. The significant dearth in knowledge of potential pathogens of our major commercially exploited species and their potential for transmission to other commercially exploited and reservoir species identify these as high risk practices (Stentiford, 2008). To address issues of biosecurity and to improve diagnostic capacity for crustacean diseases in Europe, the European Commission recently designated a Community Reference Laboratory (CRL) for crustacean diseases while separate Member States are required under EC Directive 2006/88 to designate a National Reference Laboratory (NRL) to fulfil diagnostic requirements for crustacean diseases as laid down in the Directive. These laboratories, overseen by the CRL, will be responsible for carrying out specific diagnostics for the listed exotic and non-exotic crustacean diseases in the Directive within Member States and for the official reporting of their occurrence. Since all European Member States will be required to define their status for the non-exotic WSD, free movement of live animals from Member States designated as 'unknown' or 'infected' to those designate as 'disease free' may be affected.

## 2. Listed diseases

### 2.1. White Spot Disease (WSD)

White Spot Disease (WSD) is listed as a non-exotic disease in EC Directive 2006/88. The name of the disease refers to the clinical sign that has been reported in some susceptible penaeid shrimp hosts; the presence of white spots associated with calcium deposition on the inner surface of cuticle. WSD was first described in China and Taipei in 1991, subsequently spreading throughout Asia and associated with a widespread pandemic by 1994. Occasional reports of WSD caused by

White Spot Syndrome Virus (WSSV) in North America preceded a second pandemic wave that implicated North, South and Central America by 1999. It is also present in the Middle East (Nakano et al., 1994; Flegel, 1997; Mohan et al., 1998; Zhan et al., 1998; Wang et al., 2000). Although there are no published reports, outbreaks of WSD have been observed in shrimp farms in Southern Europe (Lightner, pers. comm.), this providing a basis for its classification as a non-exotic disease in EC Directive 2006/88. WSD is regarded as perhaps the most serious threat facing the global penaeid shrimp farming industry (Sánchez-Martínez et al., 2007) with cumulative losses exceeding \$10bn since 1993 (OIE, 2006).

WSSV is a dsDNA virus recently assigned to its own new genus, *Whispovirus*, in the family *Nimaviridae* (Mayo, 2002a, 2002b). Virions are large (80–120 × 250–380 nm), rod-shaped to elliptical, and are bound by a trilaminar envelop (Inouye et al., 1994; Wang et al., 1995; Durand et al., 1997; Kanchanaphum et al., 1998; Van Hulten et al., 2001). Negatively stained virions purified from shrimp haemolymph show unique, tail-like appendages (Wang et al., 1995). The virus received different names during the first years after it appeared, these including hypodermal and haematopoietic necrosis baculovirus (HHNBV), rod-shaped nuclear virus of *P. japonicus* (RV-PJ) (Inouye et al., 1994; Nakano et al., 1994), systemic ectodermal and mesodermal baculovirus (SEMBV) (Wongteerasupaya et al., 1995b), white spot baculovirus (WSBV) (Chou et al., 1995; Lo et al., 1996a), and Chinese baculovirus (CBV) (Lu et al., 1997). All of these isolates are now recognised as one virus: WSSV, with the three isolates fully sequenced revealing only minor differences, related to a single deletion (GenBank Accession No AF332093, GenBank Accession No AF369029 and GenBank Accession No AF440570). This deletion however may have relevance when assessing the virulence of these isolates (Lan et al., 2002). It has been reported that WSSV can be inactivated in less than 120 min at 50 °C (Nakano et al., 1998) and in less than 1 min at 60 °C (Momoyama et al., 1998). It may however remain viable for at least 30 days in seawater at 30 °C under laboratory conditions, and in ponds for at least 3–4 days (Chang et al., 1998b; Maeda et al., 1998b; Nakano et al., 1998; Jory and Dixon, 1999).

Egg-associated transmission mechanisms have been confirmed, while true vertical transmission is suspected. Horizontal transmission by consumption of infected tissue (e.g. cannibalism, predation, etc.), and by water-borne routes has also been demonstrated (Lo et al., 1997; Chou et al., 1998; Lo and Kou, 1998). While transmission can occur among apparently healthy animals, dead and moribund animals are considered dominant sources of disease transmission (Lo et al., 1997; Chou et al., 1998; Lo and Kou, 1998). Rotifers (Yan et al., 2004), bivalves, polychaete worms (Vijayan et al., 2005) and non-decapod crustaceans including *Artemia salina* and the copepods (all of which are common feedstock for penaeid larvae and broodstock) have been identified as mechanical vectors as have various aquatic arthropods, such as sea slaters (Isopoda) and Euphydradae insect larvae. All of these groups are able to accumulate high concentrations of viable WSSV, although there is no evidence of virus replication within these hosts (Lo et al., 1996a; Chang et al., 2002; Li et al., 2003; Yan et al., 2004). WSSV infected shrimp have also been found in products sampled in US markets (Reville et al., 2005). As with the other crustacean viruses, infectious dose is not documented.

WSD generally results in high mortality in susceptible hosts with clinical signs appearing in farmed penaeid shrimp 14–40 days following stocking and mortalities often reaching 100%. The characteristic white spots are not always present. Survivors may carry the virus for life and may pass the virus to their progeny by vertical transmission (Lo et al., 1996a, 1997). Mortality among crabs, crayfish, freshwater prawns, spiny lobster and clawed lobsters is highly variable (Momoyama et al., 1994; Nakano et al., 1994; Takahashi et al., 1994; Cai et al., 1995; Chen et al., 2000; Sahul-Hameed et al., 2000; Jiravanichpaisal et al., 2001; Hossain et al., 2001; Rodríguez et al., 2003; Yoganandhan et al., 2003), suggesting a non-uniform

response, particularly in non-penaeid susceptible hosts. The prevalence is highly variable and seasonal, from less than 1% in infected wild populations to up to 100% in captive populations. During cold and/or rainy seasons in tropical regions, prevalence may increase rapidly in captive and wild populations (Lo et al., 1996a; Maeda et al., 1998a; Hossain et al., 2001; Peng et al., 2001; Vaseeharan et al., 2003). Disease outbreaks may be induced by stressors, such as rapid change in salinity and drop in temperature (Vidal et al., 2001; Granja et al., 2003; Guan et al., 2003). Detailed diagnostic protocols utilized to investigate for presence of WSSV, including the use of histopathology, transmission electron microscopy, immuno-histochemical techniques and nucleic acid detection are provided by the OIE (2006). A summary of WSSV agent characteristics is provided in Table 1.

## 2.2. Taura syndrome (TS)

Taura syndrome (TS) is listed as an exotic disease in EC Directive 2006/88. The name of the disease derives from the Taura River in Ecuador where the disease and mortalities were first reported in *Penaeus vannamei* in 1992 (Jimenez, 1992). Initially interpreted as a toxicological problem with mortalities due to fungicides used in the treatment of banana trees in the region, a viral aetiology was demonstrated a few years later (Hasson et al., 1995); the causative agent named Taura Syndrome Virus (TSV). It is suspected by farmers that the disease was already present in this area by the mid-1980s. Originally limited to the Americas, more recently the disease has been reported in Asia following its introduction with infected imported *P. vannamei* from Central and South America (Tu et al., 1999; Yu and Song, 2000; Chang et al., 2004; Nielsen et al., 2005). To date, TSV virus has not been described in cold-water species. The agent is a small non-enveloped ssRNA icosahedral virus, 32 nm in diameter, developing in the cytoplasm of tissues of ectodermic and mesodermic origin. It is classified in the Dicistroviridae family (Fauquet et al., 2005). Virions have a buoyant density of  $1.338 \text{ g ml}^{-1}$  in CsCl gradients. Three major (55, 40 and 24 kDa) and one minor (58 kDa) polypeptide constitute its

capsid (Bonami et al., 1997). The genome consists of a single piece of a linear, positive sense molecule of ssRNA, 10,205 nt long (excluding a poly-A tail) divided into two open reading frames (ORF) (Mari et al., 2002) separated by an intergenic region of 207 nt. The ORFs are flanked by two UTRs, 377 nt long at 5' and 266 nt at 3' extremities. In ORF1, the sequence motifs of helicase, protease and RNA-dependant RNA-polymerase are located, whereas capsid proteins are coded in ORF2 but in a different reading frame. Strain variation may cause difficulties in performing an accurate diagnosis (Côté et al., 2008). At least three genotypic variants have been identified based on the sequence of VP1 (=CP2) structural protein. They are the American group, the South-East Asian group and the Belize group (Chang et al., 2004; Nielsen et al., 2005; Tang and Lightner, 2005). Using the MAb 1A1 produced to an isolate of the reference strain USA-H194 (Poulos et al., 1999), two distinct variants were demonstrated: type A reacting to MAb 1A1 and those that did not react, which are subdivided into type B (TSV 98 Sinaloa, Mexico) and type C (TSV 02 Belize), based on the host and virulence (OIE, 2006).

While no real data are available concerning survival and resistance of TSV, it is generally considered as extremely resistant, particularly in seawater. There are no available scientific data of TSV survival in fresh water. It was shown that virions found in the faeces of sea birds after feeding on diseased shrimp were still infectious for up to 48 h (Garza et al., 1997; Vanpatten et al., 2004). Although not documented, vertical transmission may be important since TS is best known as a disease of nursery phase shrimp, occurring within 14 to 40 days of stocking into grow out ponds (Lightner, 1996). Oral transmission, particularly due to cannibalism or by contaminated water also occurs (Hasson et al., 1995; White et al., 2002). Wound transmission is theoretically possible (experimentation) but is perhaps not an efficient means of transmission (J.R. Bonami, pers. observation). An aquatic insect, the water boatman (*Trichocorixa reticulata*) feeding on shrimp carcasses in ponds was demonstrated to serve as a mechanical vector (Brock, 1997). TSV infected shrimp have also been found in products sampled in US markets (Nunan et al.,

**Table 1**  
Summary features of crustacean diseases listed in EC Directive 2006/88.

	Taura Syndrome	White Spot Disease	Yellowhead disease
Abbreviation	TS	WSD	YHD
Agent	Taura Syndrome Virus (TSV) unassigned sp. from Family Dicistroviridae	White spot syndrome virus (WSSV). Family Nimaviridae, genus <i>Whispovirus</i>	Yellowhead Virus (YHV). One of six known genotypes in yellowhead complex. Family Roniviridae, genus <i>Okavirus</i>
Agent features	32 nm non-enveloped virion, ssRNA, 3 genotypes (Americas, SE Asia and Belize)	300 nm rod-shaped, enveloped virion, dsDNA, 293 kb genome	200 nm rod-shaped virion with prominent projections at surface
Target hosts	Cultured Penaeids and other genera in wild	Cultured Penaeids and potentially all other decapod and non-decapod crustaceans	Cultured Penaeids. Wild and cultured Palemonids and other species
Mortalities	Up to 100% in affected farm ponds	Up to 100% in affected farm ponds	Up to 100% in affected farm ponds
Vectors and biosecurity	Infected broodstock and larvae, aquatic insect, seabirds. Horizontal and vertical transmission likely	Viable for at least 30 days in laboratory seawater. Rotifers, polychaetes, bivalve, insect and non-decapod reservoirs. Horizontal and vertical transmission likely	No vectors reported in literature
Gross symptoms	Moribund shrimp, expansion of chromatophores, moult mortalities, empty gut, high bird numbers around ponds, melanised shell lesions	Moribund shrimp near pond surface, reduced feeding, lethargy, high colour variation, white spots under cuticle, high bird numbers around ponds	Very high feeding rates followed by sudden cessation. Moribund shrimp at pond edge, bleached or yellow appearance of cephalothorax
Histopathology	Necrosis of cuticular epithelium, haemopoietic tissues, antennal gland. Spheroids in lymphoid organ and ectopically	Ectodermal and mesodermal tissues, especially cuticular epithelium and sub-cuticular connective tissues	Ectodermal and mesodermal tissues incl. lymphoid organ, haemocytes, haemopoietic tissue, gills and connective tissues
Immune and molecular diagnostics	Antibodies and ISH/PCR probes available	Antibodies and ISH/PCR probes available	Antibodies and ISH/PCR probes available
Control measures	Screening of broodstock and larvae, use of SPF stock, some resistant animal lines. No vaccines, chemotherapy or immunostimulants	Screening of broodstock and larvae, use of SPF stock. No resistant animal lines reported. No vaccines or chemotherapy. Potential for immunostimulants.	Screening of broodstock and larvae, use of SPF stock. No resistant animal lines reported. No vaccines, chemotherapy or immunostimulants
Affected countries <sup>a</sup>	China, Peru, Belize, Ecuador, Costa Rica, Honduras, Thailand, Taiwan, Mexico, Nicaragua, USA	Costa Rica, China, Panama, Peru, Honduras, Iran, India, Bangladesh, Taiwan, Japan, El Salvador, Ecuador, Nicaragua, Singapore, Thailand, USA	China, India, Indonesia, Malaysia, Philippines, Sri Lanka, Thailand, Vietnam, Australia, Mozambique

TS and YHD are listed as exotic to the European Union while WSD is listed as non-exotic.

<sup>a</sup> Affected countries list is not exhaustive. Please refer to [www.oie.com](http://www.oie.com) for up to date information on international status.

2004). As for all other crustacean viruses, the infectious dose is not documented due to the lack of available crustacean cell lines or other types of cell that support the replication of shrimp viruses. *In vivo* titration has not been performed for TSV.

In addition to effects in nursery or post larval stages, larger juveniles and adults can also be affected (Lightner, 1996; Hasson, 1998). The disease is characterized by two phases; acute and chronic (Lightner, 1996; Hasson, 1998; Hasson et al., 1999a). The acute phase involves expansion of red chromatophores leading to a red colouration of the telson and pleopods. These animals exhibit a soft shell and an empty gut. Diseased animals die during moulting and cumulative mortality can reach 80 to 95%. A chronic phase (or 'recovery phase'), involves shrimp surviving the acute episode and which return to normal feeding and behaviour patterns. Animals show multifocal melanized cuticular lesions looking like typical bacterial shell disease and still carry active TSV at this stage. In regions where the virus is enzootic in farmed stocks, the prevalence has been found to range from 0 to 100%. While Taura syndrome epizootics may result in 80 to 95% cumulative losses in infected ponds or tank-cultured populations, survivors of epizootics display survival rates of 60% or higher (Lightner, 1996; OIE, 2006). Detailed diagnostic protocols utilized to investigate for presence of TSV, including the use of histopathology, immuno-histochemical techniques and nucleic acid detection are provided by the OIE (2006). A summary of TSV agent characteristics is provided in Table 1.

### 2.3. Yellowhead disease (YHD)

Yellowhead disease (YHD) is listed as an exotic disease in EC Directive 2006/88. The name 'yellowhead' refers to yellow discolouration of the dorsal cephalothorax and bleached appearance of affected shrimp (Chantanachookin et al., 1993). First recorded in mortality events in black tiger prawn (*Penaeus monodon*) in Thailand in 1990 (Limsuwan, 1991), the causative agent was named Yellowhead Virus (YHV) (Boonyaratpalin et al., 1993; Chantanachookin et al., 1993). YHV has since been reported widely in Asia, while other genotypes in the Yellowhead disease complex (including Gill Associated Virus—GAV) have been reported from healthy *P. monodon* from Australia, Asia and Africa (Wijegoonawardane et al., in press). At least one incident of YHD has been reported in farmed penaeids from the USA. Effluent from nearby shrimp packing plants importing and reprocessing raw, frozen shrimp the presumed source of the virus (Lightner, 1996). Such incidents indicate that agents causing YHD can be transported to local stocks of shrimp not known to be natural hosts for YHV. Data from the OIE confirms outbreaks of Yellowhead disease in Australia and Thailand during 2005, with a suspected (but not confirmed) outbreak in Sri Lanka in the same year (<http://www.oie.int>; accessed on 20/9/07). YHV virus has not been described in cold-water species.

Although the causative agent of YHD was named Yellowhead Virus (YHV) (Boonyaratpalin et al., 1993; Chantanachookin et al., 1993) the taxonomy of the agent has been the subject of some controversy. Originally reported as baculovirus-like (Boonyaratpalin et al., 1993; Chantanachookin et al., 1993), pathological and molecular evidence showed that in contrast to the DNA-containing baculoviruses, YHV primarily resided in the cytoplasm of infected host cells (Lu et al., 1994; Wongteerasupaya et al., 1995b) and was therefore likely an RNA virus (Wongteerasupaya et al., 1995a). Later studies by Nadala et al. (1997) provisionally classified YHV as a rhabdovirus-like agent. More recent work has shown YHV to be a positive sense ssRNA virus in the genus *Okavirus* in a new family (Roniviridae) of the order Nidovirales (Cowley et al., 2000; Cowley and Walker, 2002; Mayo, 2002a,b; Sittidilokratna et al., 2002; Jitrapakdee et al., 2003). It exists in at least three different genotypic clades (Walker et al., 2001), the original clade from Thailand differing from a Gill Associated Virus (GAV) clade from Australia by approximately 15% of its nucleic acid sequence (Cowley et al., 1999), and a third clade has also been described from Thailand and Vietnam, which collectively comprise the YHV-complex (Walker et al., 2001; Soowannayan et al., 2003). There is evidence of genetic recombination between the genotypes (Wijegoonawardane et al., 2004). YHV virions are enveloped, rod-shaped particles measuring c. 40 × 170 nm. Virions have prominent surface projections (11 nm) and a helical nucleocapsid showing parallel cross-striations (Wongteerasupaya et al., 1995b). The nucleic acid is 32 kb positive sense ssRNA (Cowley et al., 1999). Purified YHV virions contain three structural proteins; gp116 (110–135 kDa), gp64 (63–67 kDa) and p20 (20–22 kDa). The gp116 and gp64 glycoproteins likely form the envelope projections while the p20 is the viral nucleocapsid protein (Jitrapakdee et al., 2003; Cowley et al., 2004). Sequencing of the open reading frame (ORF) genes ORF1a and ORF1b have aided the discrimination of YHV from GAV and the other viruses within this complex (Cowley et al., 2000; Sittidilokratna et al., 2002; Wijegoonawardane et al., in press).

YHV remains viable outside the host, in aerated seawater, for up to 72 h and the agent can be inactivated by heating to 60 °C for 15 min (Flegel et al., 1995a,b), by exposure to 30 ppm chlorine (Flegel, 1997) and possibly by 3% formalin for 10 min, 2% NaOH for 10 min, calcium hypochlorite (30 ppm) or iodine compounds (250 ppm for 30 min). No other chemical survival conditions are reported but YHV is likely to be sensitive to oxidising agents, SDS, non-ionic detergents and lipid solvents (Source: Schering-Plough Animal Health, [www.spaquaculture.com](http://www.spaquaculture.com); accessed on 10/6/07). Experimental studies have shown that YHV can be reproduced by direct injection or ingestion of infected tissue or tissue extracts and by co-habitation of naïve shrimp with infected conspecifics (Flegel et al., 1995a,b; Lightner, 1996). Flegel et al. (1995a,b) have also demonstrated that injection of extracts from shrimp paste (*Asctes*

**Table 2**

Specific techniques and characteristics applicable to support criteria A – D for crustacean diseases listed in EC Directive 2006/88.

	A: Replication	B: Viability	C: Pathology	D: Location
YHD	Presence of characteristic inclusion bodies and positive labelling of inclusion bodies by ISH or IFAT Presence of virions in inclusions bodies by TEM Serial passage from individual to SPF individual	Passage bioassay to a SPF susceptible host	Characteristic inclusion bodies, with picknosis and karyorrhectic nuclei in target tissues and no haemocytic infiltration	Haemocytes, heart, peripheral nerves, eye, lymphoid organ and sinuses, connective tissue
WSD	Presence of characteristic intranuclear inclusion bodies Presence of virions in inclusions bodies by TEM Positive labelling of inclusion bodies by ISH or IFAT Serial passage from individual to SPF individual	Passage bioassay to a SPF susceptible host	Eosinophilic inclusions within nuclei of target organs and tissues	Cells of tissues of ectodermic and endodermic origin
TS	Presence of characteristic inclusion bodies and positive labelling of inclusion bodies by ISH or IFAT Serial passage from individual to SPF individual	Passage bioassay to a SPF susceptible host	Characteristic inclusion bodies, with picknosis and karyorrhectic nuclei in target tissues and no haemocytic infiltration	Cells of tissues of ectodermic and endodermic origin

Scientific literature pertinent to particular hosts was assessed in accordance to these criteria and outcomes of the review are given in Tables 3, 4 and 5 for WSD, TS and YHD respectively.

**Table 3**  
Evidence for susceptibility of hosts to WSD according to fulfilment of categories A–D as stated in Table 2.

Host species	Natural (N) or experimental (E) Invasive (I) or Non-invasive (NI)	A	B	C	D	Assessment	Pathogen ID	Group
<i>Penaeus aztecus</i>	E NI	X	nd	X	X	A. Lightner et al. (1998) B. No scientific data available C. Lightner et al. (1998) D. Lightner et al. (1998)	Molecular confirmation	I
<i>Penaeus duorarum</i>	E NI	X	nd	X	X	A. Lightner et al. (1998) B. No scientific data available C. Lightner et al. (1998) D. Lightner et al. (1998)	Molecular confirmation	I
<i>Penaeus chinensis</i>	N, E I	X	X	X	X	A. Lu et al. (1997); Zhan et al. (1998) B. Huang et al. (2001); Zhan et al. (1998) C. Lu et al. (1997); Zhan et al. (1998) D. Lu et al. (1997); Zhan et al. (1998)	Molecular confirmation	I
<i>Penaeus indicus</i>	N, E I	X	X	X	X	A. Rajendran et al. (1999); Sahul Hameed et al. (2000); Rajan et al. (2000). B: Rajendran et al. (1999) C. Rajendran et al. (1999); Sahul Hameed et al. (2000) D. Rajendran et al. (1999); Sahul Hameed et al. (2000); Rajan et al. (2000)	Molecular confirmation	I
<i>Penaeus merguensis</i>	N	X	X	X	X	A: Partial demonstration (Lo, pers. com. in Flegel, 1997) B: Partial demonstration (Lo, pers. com. in Flegel, 1997) C. Partial demonstration (Lo, pers. com. in Flegel, 1997) D. Barnett et al. (pers. com.)	Molecular confirmation	I
<i>Penaeus setiferus</i>	E NI	X	nd	X	X	A. Lightner et al. (1998) B. No scientific data available C. Lightner et al. (1998) D. Lightner et al. (1998)	Molecular confirmation	I
<i>Penaeus stylirostris</i>	N, E I	X	nd	X	X	A. Lightner et al. (1998); Lu et al. (1997) B. No scientific data available C. Lightner et al. (1998); Lu et al. (1997) D. Lightner et al. (1998); Lu et al. (1997)	Molecular confirmation	I
<i>Penaeus vannamei</i>	N, E NI	X	nd	X	X	A. Lightner et al. (1998); Lu et al. (1997) B. No scientific data available C. Lightner et al. (1998); Lu et al. (1997) D. Lightner et al. (1998); Lu et al. (1997)	Molecular confirmation	I
<i>Penaeus japonicus</i>	N, E I, NI	X	nd	X	X	A. Lu et al. (1997); Wang et al. (1998b); Chou et al. (1998); Zhan et al. (1998) B. No scientific data available C. Lu et al. (1997); Wang et al. (1998b); Chou et al. (1998) D. Lu et al. (1997); Wang et al. (1998b); Chou et al. (1998)	Molecular confirmation	I
<i>Metapenaeus brevicornis</i>	N	nd	nd	nd	x	D. Partial demonstration (Hossain et al., 2001)	Molecular confirmation	II
<i>Metapenaeus dobsonii</i>	N, E I, NI	X	X	X	X	A. Rajendran et al. (1999) B. Rajendran et al. (1999) C. Rajendran et al. (1999) D. Rajendran et al. (1999); Rajan et al. (2008); Hossain et al. (2001)	Molecular confirmation	I
<i>Metapenaeus ensis</i>	N, E NI	X	nd	X	X	A. Wang et al. (1998b); Chang et al. (1998a,b) B. No scientific data available C. Wang et al. (1998b) D. Chang et al. (1998a,b); Wang et al. (1998a,b)	Molecular confirmation	I
<i>Metapenaeus monoceros</i>	N, E I, NI	nd	X	nd	X	A. No scientific data available B: Rajendran et al. (1999) C. No scientific data available D. Partial demonstration (Hossain et al., 2001)	Molecular confirmation	I
<i>Penaeus monodon</i>	N, E I, NI	X	X	X	X	A. Sahul Hameed et al. (2000); Wang et al. (1998b); Rajendran et al. (1999); Zhan et al. (1998); Rajan et al. (2008) B: Lightner et al. (1999) C. Sahul Hameed et al. (2000); Wang et al. (1998b); Rajendran et al. (1999) D. Wang et al. (1998b); Wang et al. (1998a; Lo et al. (1996a)	Molecular confirmation	I
<i>Penaeus penicillatus</i>	N, E I, NI	X	nd	X	X	A. Chou et al. (1998) B. No scientific data available C. Chou et al. (1998) D. Chou et al. (1998); Wang et al. (1998a); Lo et al. (1996a)	Molecular confirmation	I
<i>Penaeus semisulcatus</i>	N, E NI	X	X	X	X	A. Rajendran et al. (1999) B. Rajendran et al. (1999) C. Rajendran et al. (1999) D. Rajendran et al. (1999); Wang et al. (1998a); Lo et al. (1996a)	Molecular confirmation	I
<i>Parapenaeopsis styliifera</i>	N	nd	nd	nd	X	A, B, C. No scientific data available D. Partial demonstration (Hossain et al., 2001)	Detection by PCR in target tissues and organs (Hossain et al., 2001)	II
<i>Solenocera indica</i>	N	nd	nd	Nd	X	A, B, C. No scientific data available D. Partial demonstration (Hossain et al., 2001)	Detection by PCR in target tissues and organs (Hossain et al., 2001)	II

Table 3 (continued)

Host species	Natural (N) or experimental (E) Invasive (I) or Non-invasive (NI)	A	B	C	D	Assessment	Pathogen ID	Group
<i>Trachypenaeus curvirostris</i>	N, E NI	X	nd	nd	X	A. Chang et al. (1998a,b) B. No scientific data available C. No scientific data available D. Partial demonstration (Chang et al. 1998a,b; Wang et al., 1998a,b)	Detection by PCR in target tissues and organs (Wang et al. 1998a,b)	I
<i>Crangon crangon</i>	E I	X	nd	nd	X	A. (V. Alday personal observation) B. No scientific data available C. No scientific data available D. (V. Alday pers. com.)	Molecular confirmation	I
<i>Alpheus lobidens</i>	N	nd	nd	nd	nd	A–D No scientific information available but positive for WSSV by PCR (Takahashi et al., 2003)	Molecular confirmation	II
<i>Alpheus brevicristatus</i>	N	nd	nd	nd	nd	A–D No scientific information available but positive for WSSV by PCR (Takahashi et al., 2003)	Molecular confirmation	II
<i>Callinassa</i> sp.	N	nd	nd	nd	nd	A–D No scientific information available but positive for WSSV by PCR (Lo et al., 1996a)	Molecular confirmation	II
<i>Exopalaemon orientalis</i>	E NI	X	nd	nd	X	A. Partial demonstration (Chang et al. 1998a,b; Wang et al. 1998a) B. No scientific information available C. No scientific information available D. Partial demonstration (Chang et al. 1998a,b; Wang et al., 1998a)	Detection by PCR in target tissues and organs Wang et al. (1998a)	I
<i>Palaemon</i> sp.	N	nd	nd	nd	X	A, B, C. No scientific data available D. Partial demonstration (Lo et al., 1996a)	Detection by PCR in target tissues and organs (Lo et al., 1996a,b)	II
<i>Palaemon adspersus</i>	E I	X	nd	nd	X	A. Corbel et al. (2001) B, C. No scientific data available D. Partial demonstration Corbel et al. (2001)	Molecular confirmation	I
<i>Macrobrachium idella</i>	E I, NI	X	nd	X	X	A. Rajendran et al. (1999) B. No scientific data available C. Rajendran et al. (1999) D. Rajendran et al. (1999)	Molecular confirmation	I
<i>Macrobrachium lamerrae</i>	E I, NI	X	nd	X	X	A. Sahul-Hameed et al. (2000) B. No scientific data available C. Sahul-Hameed et al. (2000) D. Sahul-Hameed et al. (2000)	Molecular confirmation	I
<i>Macrobrachium rosenbergii</i>	N, E I, NI	X	X	X	X	A. Sahul Hameed et al. (2000); Rajendran et al. (1999); Hossain et al. (2001); Lo et al. (1996a) B. Rajendran et al. (1999) C. Sahul Hameed et al. (2000); Rajendran et al. (1999) D. Sahul Hameed et al. (2000); Hossain et al., (2001), Lo et al. (1996a,b)	Molecular confirmation	I
<i>Panulirus homarus</i>	E NI	X	X	X	X	A–D. Rajendran et al. (1999)	Molecular confirmation	I
<i>Panulirus longipes</i>	N, E I, NI	X	X	X	X	A–C. Rajendran et al. (1999) D. Rajendran et al. (1999); Wang et al. (1998a)	Molecular confirmation	I
<i>Panulirus ornatus</i>	N, E I, NI	X	X	X	X	A–C. Rajendran et al. (1999) D. Rajendran et al. (1999); Wang et al. (1998a)	Molecular confirmation	I
<i>Panulirus penicillatus</i>	E NI	X	nd	nd	X	A. Chang et al. (1998a,b) B. No scientific data available C. No scientific data available D. Chang et al. (1998a,b); Wang et al. (1998a,b)	Molecular confirmation	I
<i>Panulirus polyphagus</i>	N, E I, NI	X	X	X	X	A–D. Rajendran et al. (1999)	Molecular confirmation	I
<i>Panulirus versicolor</i>	E NI	X	nd	nd	X	A. Partial demonstration (Chang et al. 1998a,b) B, C. No scientific data available D. Partial demonstration (Chang et al. 1998a,b; Wang et al., 1998a)	Detection by PCR in target tissues and organs Wang et al., 1998a	I
<i>Homarus gammarus</i>	E NI	X	nd	X	X	A. (G.D. Stentiford pers. com.) C. No scientific data available C. G.D. Stentiford pers. com.) D. (G.D. Stentiford pers. com.)	Molecular confirmation	I
<i>Scyllarus arctus</i>	E I	X	nd	nd	X	A. Corbel et al. (2001) B, C. No scientific data available D. Target organs involved	Detection by PCR in target tissues and organs Corbel et al. (2001)	I
<i>Astacus astacus</i>	E I, NI	nd	nd	nd	X	A, B, C. No scientific data available D. Partial demonstration (Jiravanichpaisal et al., 2004)	Molecular confirmation	II
<i>Astacus leptodactylus</i>	E I	X	nd	nd	X	A. Corbel et al. (2001) B, C. No scientific data available D. Corbel et al. (2001)	Molecular confirmation	I
<i>Cherax destructor</i>	E I	X	nd	X	X	A. Edgerton (2004) B. No scientific data available C. Edgerton (2004) D. Edgerton (2004)	Molecular confirmation	I
<i>Cherax quadricarinatus</i>	E I	X	nd	X	X	A. Shi et al. (2000) B. No scientific data available	Molecular confirmation	I

(continued on next page)

Table 3 (continued)

Host species	Natural (N) or experimental (E) Invasive (I) or Non-invasive (NI)	A	B	C	D	Assessment	Pathogen ID	Group
<i>Pacifastacus leniusculus</i>	E I	X	nd	X	X	C. Shi et al. (2000) D. Shi et al. (2000) A. Jiravanichpaisal et al. (2001) B. No scientific data available C. Jiravanichpaisal et al. (2001) D. Jiravanichpaisal et al. (2001)	Molecular confirmation	I
<i>Squilla mantis</i>	N	nd	nd	nd	X	A, B, C. No scientific data available D. Partial demonstration (Hossain et al., 2001b)	Detection by PCR in target tissues and organs (Hossain et al., 2001b)	II
<i>Procambarus clarkii</i>	E I, NI	X	nd	nd	X	A. Chang et al. (1998a,b); Huang et al. (2001) B, C. No scientific data available D. Chang et al. (1998a,b), Huang et al. (2001), Wang et al. (1998a), Du et al. (2008)	Detection by PCR in target tissues and organs (Wang et al., 1998a; Huang et al., 2001; Du et al., 2008)	I
<i>Orconectes punctimanus</i>	N	nd	nd	nd	X	A, B, C. No scientific data available D. Partial demonstration (Lo et al., 1999)	Viral DNA extracted and analyzed by PCR with II specific primers and restriction fragmental length polymorphism (Lo et al., 1999)	II
<i>Orconectes limosus</i>	E I	X	nd	nd	X	A. Corbel et al. (2001) B, C. No scientific data available D. Partial demonstration (Corbel et al., 2001)	Molecular confirmation	I
<i>Atergatis integerrimus</i>	E I, NI	X	nd	X	x	A. Sahul-Hameed et al. (2003) B. No scientific data available C. Sahul-Hameed et al. (2003) D. Sahul-Hameed et al. (2003)	Molecular confirmation	I
<i>Calappa philarigus</i>	N, E I, NI	X	nd	X	X	A. Sahul-Hameed et al. (2003) B. No scientific data available C. Sahul-Hameed et al. (2003) D. Sahul-Hameed et al. (2003)	Molecular confirmation	I
<i>Calappa lophos</i>	E NI	nd	nd	nd	X	A, B, C. No scientific data available D. Partial demonstration Wang et al. (1998a)	Detection by PCR in target tissues and organs (Wang et al., 1998a)	II
<i>Cancer pagurus</i>	E I	X	nd	nd	X	A. Corbel et al. (2001) B, C. No scientific data available D. Partial demonstration Corbel et al. (2001)	Molecular confirmation	I
<i>Carcinus maenas</i>	E I	X	nd	nd	X	A. Corbel et al. (2001) B, C. No scientific data available D. Partial demonstration Corbel et al. (2001)	Molecular confirmation	I
<i>Charybdis annulata</i>	N, E I, NI	X	nd	X	X	A. Sahul-Hameed et al. (2003) B. No scientific data available C. Sahul-Hameed et al. (2003) D. Sahul-Hameed et al. (2003)	Molecular confirmation	I
<i>Charybdis cruciata</i>	N	nd	nd	nd	X	A, B, C. No scientific data available D. Partial demonstration (Hossain et al., 2001)	Detection by PCR in target tissues and organs (Hossain et al., 2001)	II
<i>Charybdis feriatus</i>	N, E NI	X	nd	nd	X	A. Kou et al. (1998) B, C. No scientific data available D. Kou et al. (1998); Lo et al. (1996b); Wang et al. (1998a)	Molecular confirmation	I
<i>Charybdis granulata</i>	E NI	X	nd	nd	X	A. Chang et al. (1998a,b) B, C. No scientific data available D. Chang et al. (1998a,b); Wang et al. (1998a)	Molecular confirmation	I
<i>Charybdis japonicus</i>	N	nd	nd	nd	?	A, B, C. No scientific data available but positive for WSSV by PCR (Takahashi et al., 2003)	Molecular confirmation	II
<i>Charybdis lucifera</i>	N, E I, NI	X	nd	X	X	A. Sahul-Hameed et al. (2003) B. No scientific data available C. Sahul-Hameed et al. (2003) D. Sahul-Hameed et al. (2003); Lo et al. (1999)	Molecular confirmation	I
<i>Charybdis natator</i>	N, E I, NI	X	nd	X	X	A. Sahul-Hameed et al. (2003); Kou et al. (1998) B. No scientific data available C. Sahul-Hameed et al. (2003) D. Sahul-Hameed et al. (2003); Kou et al. (1998)	Molecular confirmation	I
<i>Demania splendida</i>	E I, NI	X	nd	X	X	A. Sahul-Hameed et al. (2003); Kou et al. (1998) B. No scientific data available C. Sahul-Hameed et al. (2003) D. Sahul-Hameed et al. (2003)	Molecular confirmation	I
<i>Doclea hybrida</i>	E I, NI	X	nd	X	X	A. Sahul-Hameed et al. (2003); Kou et al. (1998) B. No scientific data available C. Sahul-Hameed et al. (2003) D. Sahul-Hameed et al. (2003)	Molecular confirmation	I
<i>Gelasimus marionis nitidus</i>	N	nd	nd	nd	X	A, B, C. No scientific data available D. Partial demonstration (Hossain et al., 2001)	Detection by PCR in target tissues and organs (Hossain et al., 2001b)	II
<i>Grapsus albolineatus</i>	E I, NI	X	nd	X	X	A. Sahul-Hameed et al. (2003) B. No scientific data available C. Sahul-Hameed et al. (2003) D. Sahul-Hameed et al. (2003)	Molecular confirmation	I
<i>Halimede ochtodes</i>	E I, NI	X	nd	X	X	A. Sahul-Hameed et al. (2003) B. No scientific data available	Molecular confirmation	I

Table 3 (continued)

Host species	Natural (N) or experimental (E) Invasive (I) or Non-invasive (NI)	A	B	C	D	Assessment	Pathogen ID	Group
<i>Helice tridens</i>	N	nd	nd	nd	X	C. Sahul-Hameed et al. (2003) D. Sahul-Hameed et al. (2003) A, B, C. No scientific data available D. Partial demonstration (Lo et al., 1996b; Kou et al., 1998)	Detection by PCR in target tissues and organs (Lo et al., 1996a,b; Kou et al., 1998)	II
<i>Liagore rubronaculata</i>	E I, NI	X	nd	X	X	A. Sahul-Hameed et al. (2003) B. No scientific data available C. Sahul-Hameed et al. (2003) D. Sahul-Hameed et al. (2003)	Molecular confirmation	I
<i>Liocarcinus depurator</i>	E I	X	nd	nd	X	A. Corbel et al. (2001) B, C. No scientific data available D. Partial demonstration Corbel et al. (2001)	Molecular confirmation	I
<i>Liocarcinus puber</i>	E I	X	nd	nd	X	A. Corbel et al. (2001) B, C. No scientific data available D. Partial demonstration Corbel et al. (2001)	Molecular confirmation	I
<i>Lithodes maja</i>	E I, NI	X	nd	X	X	A. Sahul-Hameed et al. (2003) B. No scientific data available C. Sahul-Hameed et al. (2003) D. Sahul-Hameed et al. (2003)	Molecular confirmation	I
<i>Macrophthalmus sulcatus</i>	N	nd	nd	nd	X	A, B, C. No scientific data available D. Partial demonstration (Hossain et al., 2001)	Detection by PCR in target tissues and organs (Hossain et al., 2001b)	II
<i>Matuta miersi</i>	E I, NI	X	nd	X	X	A. Sahul-Hameed et al. (2003) B. No scientific data available C. Sahul-Hameed et al. (2003) D. Sahul-Hameed et al. (2003)	Molecular confirmation	I
<i>Matuta planipes</i>	N	nd	nd	nd	X	A, B, C. No scientific data available D. Partial demonstration (Otta et al., 1999)	Detection by PCR in target tissues and organs (Otta et al., 1999)	II
<i>Menippe rumphii</i>	E I, NI	X	nd	X	X	A. Sahul-Hameed et al. (2003) B. No scientific data available C. Sahul-Hameed et al. (2003) D. Sahul-Hameed et al. (2003)	Molecular confirmation	I
<i>Metapograpsus</i> sp.	E I, NI	X	X	X	X	A–D. Rajendran et al. (1999)	Molecular confirmation	I
<i>Metapograpsus messor</i>	N	nd	nd	nd	X	A, B, C. No scientific data available D. Partial demonstration (Hossain et al., 2001)	Detection by PCR in target tissues and organs (Hossain et al. 2001b)	II
<i>Paradorippe granulata</i>	E I, NI	X	nd	X	X	A. Sahul-Hameed et al. (2003) B. No scientific data available C. Sahul-Hameed et al. (2003) D. Sahul-Hameed et al. (2003)	Molecular confirmation	I
<i>Paratelphusa hydrodomous</i>	E I, NI	X	nd	X	X	A. Sahul-Hameed et al. (2001) B. No scientific data available C. Sahul-Hameed et al. (2001) D. Sahul-Hameed et al. (2001)	Molecular confirmation	I
<i>Paratelphusa pulvinata</i>	E I, NI	X	nd	X	X	A. Sahul-Hameed et al. (2001) B. No scientific data available C. Sahul-Hameed et al. (2001) D. Sahul-Hameed et al. (2001)	Molecular confirmation	I
<i>Parthenope pensior</i>	E I, NI	X	nd	X	X	A. Sahul-Hameed et al. (2003) B. No scientific data available C. Sahul-Hameed et al. (2003) D. Sahul-Hameed et al. (2003)	Molecular confirmation	I
<i>Phyllira syndactyla</i>	E I, NI	X	nd	X	X	A. Sahul-Hameed et al. (2003) B. No scientific data available C. Sahul-Hameed et al. (2003) D. Sahul-Hameed et al. (2003)	Molecular confirmation	I
<i>Podophthalmus vigil</i>	E I, NI	X	nd	X	X	A. Sahul-Hameed et al. (2003) B. No scientific data available C. Sahul-Hameed et al. (2003) D. Sahul-Hameed et al. (2003)	Molecular confirmation	I
<i>Portunus pelagicus</i>	N, E I, NI	X	nd	X	X	A. Supamattaya et al. (1998); Kou et al. (1998) B. No scientific data available C. Supamattaya et al. (1998) D. Kou et al. (1998); Supamattaya et al. (1998)	Molecular confirmation	I
<i>Portunus sanguinolentus</i>	N, E I, NI	X	nd	X	X	A. Sahul-Hameed et al. (2003); Chang et al. (1998a,b); Kou et al. (1998) C. Sahul-Hameed et al. (2003) D. Lo et al. (1996a,b); Sahul-Hameed et al. (2003); Wang et al. (1998b)	Molecular confirmation	I
<i>Pseudograpsus intermedius</i>	N	nd	nd	nd	X	A, B, C. No scientific data available D. Partial demonstration (Hossain et al., 2001)	Detection by PCR in target tissues and organs (Hossain et al., 2001b)	II
<i>Sesarma</i> sp.	E I, NI	X	X	X	X	A. Rajendran et al. (1999); Kanchanaphum et al. (1998); Kanchanaphum et al. (1998) B: Kanchanaphum et al. (1998); Rajendran et al. (1999)	Molecular confirmation	I

(continued on next page)

Table 3 (continued)

Host species	Natural (N) or experimental (E) Invasive (I) or Non-invasive (NI)	A	B	C	D	Assessment	Pathogen ID	Group
<i>Sesarma oceanica</i>	N	nd	nd	nd	X	C. Rajendran et al. (1999); Kanchanaphum et al. (1998) D. Kanchanaphum et al. (1998) A, B, C. No scientific data available D. Partial demonstration Otta et al. (1999)	Detection by PCR in target tissues and organs Otta et al. (1999)	II
<i>Scylla serrata</i>	N, E I, NI	X	X	X	X	A. Rajendran et al. (1999); Sahul-Hameed et al. (2003); Kanchanaphum et al. (1998); Supamattaya et al. (1998) B: Kanchanaphum et al. (1998); Rajendran et al. (1999) C. Rajendran et al. (1999); Kanchanaphum et al. (1998) D. Lo et al. (1996a,b); Kanchanaphum et al. (1998); Sahul-Hameed et al. (2003)	Molecular confirmation	I
<i>Scylla tranquebarica</i>	E I, NI	X	X	X	X	A–D. Rajendran et al. (1999)	Molecular confirmation	I
<i>Thalmita danae</i>	E I, NI	X	nd	X	X	A. Sahul-Hameed et al. (2003) B: No scientific data available C. Sahul-Hameed et al. (2003) D. Sahul-Hameed et al. (2003)	Molecular confirmation	I
<i>Uca pugilator</i>	E I	X	X	X	X	A–D. Kanchanaphum et al. (1998)	Molecular confirmation	I
Sergestoidea ( <i>Acetes</i> sp.)	E I, NI	X	nd	X	X	A. Supamattaya et al. (1998) B. No scientific data available C. Supamattaya et al. (1998) D. Supamattaya et al. (1998)	Molecular confirmation	I
Cirripedia ( <i>Balanus</i> sp.)	N, E	nd	nd	nd	nd	A–D. No scientific data available Detection by PCR (Ramirez-Douriet et al., 2005)	Molecular confirmation	II
Branchiopoda Cladocera	N	nd	nd	nd	nd	A–D. No scientific data available Detection by PCR (Ramirez-Douriet et al., 2005)	Molecular confirmation	II
<i>Artemia salina</i>	N	nd	nd	nd	nd	A–D. No scientific data available Detection by PCR Otta et al. (1999)	Molecular confirmation	II
Copepoda	N	nd	nd	nd	nd	A–D. No scientific data available Detection by PCR (Lo et al., 1996b; Ramirez-Douriet et al., 2005)	Molecular confirmation	II
Chaetognata	N	nd	nd	nd	nd	A–D. No scientific data available Detection by PCR Ramirez-Douriet et al. (2005)	Molecular confirmation	II
Rotifera	N	nd	nd	nd	nd	A–D. No scientific data available Positive PCR and dot blot hybridization Yan et al. (2004). Rotifers were washed and disinfected prior testing. Washing water was negative	Molecular confirmation	II
Polychaeta ( <i>Marphysa</i> sp.)	N, E NI	nd	nd	nd	nd	A–D. No scientific data available Detection by PCR Vijayan et al. (2005).	Molecular confirmation	II
Coleoptera (Ephydriidae)	N	nd	nd	nd	nd	A–D. No scientific data available Detection by PCR Lo et al. (1996b)	Molecular confirmation	II

Key: X (fulfilment of category by reports in scientific literature), nd (no data available), Group I (Host species for which scientific evidence supports susceptibility to listed diseases), Group II (Host species for which scientific data partially supports susceptibility to listed diseases).

sp.) collected from YHV-affected shrimp ponds can cause disease in naïve shrimp. Viruses in the complex (e.g. GAV) have been shown to transmit from the infected male and female parents, although this likely occurs via contamination of the surface of the fertilised egg (Cowley et al., 2002). Contaminated pond water is the major abiotic vector with rapid transmission through the water from infected shrimp and by cannibalism of weak or moribund shrimp. Transmission can occur by introduction of infected but apparently healthy carrier crustaceans into rearing ponds in intake water. Infected transport water, intake water, nets and other equipment are likely sources of YHV introduction to a naïve system. As for other viral pathogens of crustaceans, an infectious dose is not documented due to the lack of available crustacean cell lines.

In field conditions, mortality associated with YHD can occur in late postlarval stages but mass mortalities are more common in early to late juveniles of 5–15 g (Limsuwan, 1991). When the disease was initially described, complete crop loss occurred within 24 h of the appearance of the initial clinical signs (Chantanachookin et al., 1993). Early studies on YHD affected shrimp also demonstrated frequent co-infections with bacterial pathogens, hepatopancreatic parvovirus (HPV), and with monodon baculovirus (MBV). Secondary

opportunistic pathogens (particularly bacteria) may play a role in eventual mortality of YHD (and other virus) infected shrimp (Chantanachookin et al., 1993). The overall prevalence of Yellowhead complex viruses in healthy *P. monodon* from most wild and cultured populations in Australia, Asia and east Africa is high (50–100% by nested PCR). However, the prevalence of the individual genotypes is known to vary by location and situation. Genotype 1 (YHV) prevalence may be less than 1% in healthy wild or farmed *P. monodon* but its prevalence would approach 100% in ponds undergoing Yellowhead disease outbreaks (OIE, 2006). Detailed diagnostic protocols utilized to investigate for presence of viruses within the Yellowhead disease complex, including the use of histopathology, immuno-histochemical techniques and nucleic acid detection are provided by the OIE (2006). A summary of YHV agent characteristics is provided in Table 1.

### 3. Host susceptibility to WSD, TS and YHD

In terms of supporting international trade whilst protecting farmed and wild crustacean species within European aquatic habitats, it is important to define which host species, particularly

those that are traded, are susceptible to the listed diseases (WSD, TS, YHD) and therefore, which may pose a risk of transporting the pathogen into the EU via normal trade routes. Separate analyses are required to address the risk that these pathogens will make contact with the aquatic environment and the hosts therein (exposure assessment), and further the likelihood that disease may establish and that effect may occur (consequence assessment). These latter issues are not dealt with here.

Annex IV of EC Directive 2006/88 contains a list of susceptible species to the diseases listed in the Directive. In the context of European legislation, the definition of a 'susceptible species' (along with definitions of 'infection' and 'disease') related to a listed disease are also provided within this Directive. Accordingly, susceptible species are primarily susceptible to infection with or without disease manifestation. A susceptible species is a species that can support replication of an agent or an infestation, which may lead to the development of disease. Whilst it is recognised that definitions of susceptibility are inherently subjective and prone to differential interpretation, utilising principles laid down by the European Food Safety Authority (EFSA) and to avoid possible misinterpretation of the working definition, the scientific information reviewed in the current study was assessed with consideration of: i) reflection of 'natural pathways' provided by the experimental design utilised in reported studies, ii) compliance with four objective criteria pertaining to host susceptibility, and iii) thorough identification of the causative agent.

Whilst very little knowledge exists on the natural pathways of infectious diseases of aquatic animals, biology of the host species may provide valuable indications on possible routes of transmission. Specific characteristics and traits, such as frequent aggression and fights, cannibalism, etc., may assist in the way experimental data based on oral dosing or injection may be interpreted. Here, experimental data supporting susceptibility of a particular host were classified as "invasive" or "non-invasive" with natural (wild or farm) cases constituting a third category. Cohabitation, bath, and oral dosing are three modes of exposure that would generally be accepted as a basis for non-invasive exposure that likely mimic real-life pathways. Direct injection is an invasive treatment that nevertheless demonstrates the potential susceptibility of a species. In this context, and particularly with regard to crustacean hosts, experimental data based solely on injection of the pathogenic agent has not been ignored and may in some cases be considered to mimic real-life pathways of pathogen introduction associated with wounding and limb loss caused by conflict and moulting.

Following pathogen introduction, four criteria were used to assess susceptibility of host species to WSD, TS and YHD: (A) evidence of replication or growth of the organism, (B) presence of a viable organism, (C) presence of specific clinico-pathological changes, and (D) specific location of the pathogen within the host. Importantly these criteria enable discrimination of actual infection from mechanical carriage (vector status). The type of scientific data supporting criteria A–D varies according to the pathogen under consideration and these features are illustrated in Table 2. All available scientific literature pertaining to WSD, TS and YHD was screened in relation to these key criteria.

For example, in relation to the viral pathogens causing WSD, TS and YHD, evidence of replication (criterion A) can be provided by the presence of characteristic inclusion bodies, RNA [for the DNA virus causing WSD], and TEM demonstration of virus arrays. In the absence of crustacean cell lines, the presence of a viable organism (criterion B) may be inferred from successful transmission from the species of interest to specific pathogen free (SPF) susceptible hosts. Detection of characteristic clinico-pathological changes (criterion C) and the anatomic location of the pathogen (criterion D) are important features when excluding potential passive contamination of the host. These criteria can be addressed by techniques such as histology, immunohistochemistry (IHC), or in situ hybridisation (ISH) or alternatively, target organ dissection and specific detection using techniques such as

quantitative PCR (QPCR). In the case of WSD, TS and YHD, a species would be regarded as infected and therefore susceptible by interpretation of combinations of A, B, C, and D. Criterion B alone (presence of viable organism) would not be enough to identify a species as susceptible because it does not exclude mechanical contamination. In these cases, 'hosts' may be assigned vector status. Following assessment of the available literature pertinent to a potential species, hosts are assigned to one of two criteria: Group I (for which the literature provides evidence for susceptibility), and Group II (for which the literature provides limited evidence for susceptibility).

### 3.1. Susceptibility to WSD

Currently, all decapods are listed as susceptible to WSD virus in the Directive 2006/88/EC. A total of 98 potential host species or genera were identified from the scientific literature. A detailed review is presented in Table 3. Scientific data are available to support susceptibility of 67 species. However, for 20 species information was considered insufficient to scientifically assess susceptibility with regards to criteria A to D. Numerous aquatic organisms, including rotifers (Yan et al., 2004), bivalves, polychaete worms (Vijayan et al., 2005) and non-decapod crustaceans, such as *Artemia* sp. and copepods were reported as potential mechanical vectors for WSSV, as well as aquatic arthropods, such as Isopoda and Euphydradae insect larvae (EFSA, 2007). In fact, any insect or living organism present in a WSSV infected pond may become a mechanical vector of the disease by surface or gut contamination with the viral particles. Most of these species are here regarded as potential susceptible species. In the context of assessing susceptibility of novel hosts to WSSV, it is important to consider recent evidence that suggests potential for cross-reactivity between the predominantly utilized PCR primers recommended by the OIE (OIE, 2006) and elements of the crustacean genome (Claydon et al., 2004). In the context of this evidence, since some of the studies listed in Table 3 may not have sequenced the PCR amplification product from surveys of new hosts, at least some of these listings may be due to false positive reactions, particularly where supporting susceptibility data is not presented (see OIE, 2006).

### 3.2. Susceptibility to TS

Gulf white shrimp (*Penaeus setiferus*), Pacific blue shrimp (*P. stylirostris*), and Pacific white shrimp (*P. vannamei*) are currently listed as species susceptible to TS virus in the Directive 2006/88/EC. Ten potential host species were identified from the scientific literature. A detail review is presented in Table 4. Scientific data are available to support susceptibility of *P. vannamei*, *P. duorarum*, *P. monodon*, *P. setiferus*, *P. chinensis*, *P. stylirostris*, *P. aztecus*, and *Metapenaeus ensis*. There are scientific data suggesting susceptibility of *Penaeus schmitti* with some uncertainty however on pathogen identification. Information on *P. schmitti*, and *P. japonicus* was considered insufficient to scientifically assess susceptibility with regards to criteria A to D. Scientific data suggesting susceptibility of *P. japonicus* are essentially experimental and invasive.

### 3.3. Susceptibility to YHD

Gulf brown shrimp (*Penaeus aztecus*), Gulf pink shrimp (*P. duorarum*), Kuruma prawn (*P. japonicus*), black tiger shrimp (*P. monodon*), Gulf white shrimp (*P. setiferus*), Pacific blue shrimp (*P. stylirostris*), and Pacific white shrimp (*P. vannamei*) are currently listed as species susceptible to YH virus in the Directive 2006/88/EC. Eighteen potential host species were identified from the scientific literature. A detailed review is presented in Table 5. Scientific data are available to support susceptibility of *P. monodon*, *P. merguensis*, *P. vannamei*, *P. setiferus*, *P. aztecus*, *P. duorarum*, *Metapenaeus brevicornis*, *M. affinis*, *Palaemon styliiferus*. There are scientific data suggesting

**Table 4**  
Evidence for susceptibility of hosts to TS according to fulfilment of categories A–D as stated in Table 2.

Species	Natural (N) experimental (E) Invasive (I) or Non-invasive (NI)	A	B	C	D	Assessment	Pathogen ID	Group
<i>Penaeus vannamei</i>	N, E  I, NI	X	X	X	X	A. Brock et al. (1995); Lightner et al. (1995); Hasson et al. (1995, 1999); Poulos et al. (1999). B. Brock et al. (1995); Hasson et al. (1995) C. Lightner et al. (1995); Hasson et al. (1995, 1999a,b). D. Lightner et al. (1995); Hasson et al. (1995, 1999a,b)	Pathogen characterised by sequencing of VP1 (structural protein) gene	I
<i>Penaeus duorarum</i>	E I, NI	X	X	X	X	A–D. Overstreet et al. (1997)	Sucrose-gradient purified Ecuadorian isolate of TSV	I
<i>Penaeus schmitti</i>	N	nd	nd	nd	nd	Note: Personal communication stating this species as 'highly prone' to TS (in Brock et al., 1997)	No scientific data available	II
<i>Penaeus monodon</i>	N, E I	X	X	X	X	A–D. Srisuvan et al. (2005)	Pathogen characterised by sequencing of VP1 (structural protein) gene.	I
<i>Penaeus setiferus</i>	N, E I, NI	X	X	X	X	A–D. Overstreet et al. (1997)	Sucrose-gradient purified Ecuadorian isolate	I
<i>Penaeus chinensis</i>	E I	X	nd	X	X	A. Overstreet et al. (1997) B. No scientific data available C. Overstreet et al. (1997) D. Overstreet et al. (1997)	Sucrose-gradient purified Ecuadorian isolate	I
<i>Penaeus japonicus</i>	E I	X	nd	nd	nd	A. Partial demonstration (Chang et al., 2004)	Pathogen characterised by sequencing of VP1 (structural protein) gene Taiwanese isolate	II
<i>Metapenaeus ensis</i>	N	X	X	X	X	A. Partial demonstration (Chang et al., 2004). B. Chang et al. (2004) C. Partial demonstration (Chang et al., 2004) D. Partial demonstration (Chang et al., 2004).	Pathogen characterised by sequencing of VP1 (structural protein) gene. Taiwanese isolates	I
<i>Penaeus stylirostris</i>	N, E I, NI	X	X	X	X	A. Robles-Sikisaka et al. (2002) B. Erickson et al. (2002) C. Robles-Sikisaka et al. (2002) D. Robles-Sikisaka et al. (2002)	Pathogen characterised by sequencing of VP1 and VP2 (structural protein) genes Mexican isolate	I
<i>Penaeus aztecus</i>	E I, NI	X	X	X	X	A–D. Overstreet et al. (1997)	Pathogen characterization not reported	I

Key: X (fulfilment of category by reports in scientific literature), nd (no data available), Group I (Host species for which scientific evidence supports susceptibility to listed diseases), Group II (Host species for which scientific data partially supports susceptibility to listed diseases).

susceptibility of *Penaeus esculentus*, *P. japonicus*, *P. stylirostris*, *M. ensis*, and *M. bennettiae* with uncertainty on virus identification. Information on *P. esculentus*, *M. ensis*, *M. bennettiae*, and *Macrobrachium lancesteri* was considered insufficient to scientifically assess susceptibility with regards to criteria A to D. Scientific data suggesting susceptibility of *M. lancesteri*, *M. sintangense*, and *Palaemon serrifer* are essentially experimental and invasive. Since evidence exists for differential virulence and geographic presence of genotypes within the YHD complex, future research will be required to assess whether individual genotypes pose specific threats to naïve hosts via international trade in live shrimp and commodity and particularly, whether these genotypes display a specific host range and environmental tolerance.

### 3.4. Taxonomic range of susceptibility for the three diseases

In reviewing susceptibility of aquatic hosts to pathogens, it may be useful to consider the taxonomic range over which susceptible hosts exist. Such an approach may be used to better inform risk assessors and risk managers for the importation of potentially susceptible hosts compared to a fixed list of susceptible species for which exclusion is often based on lack of evidence rather than true resistance. Susceptibility of crustacean hosts to TS, YHD and WSD illustrates this point. In contrast to the apparently rather limited susceptible host ranges for TS and YHD, Directive 2006/88/EC lists susceptibility to WSD (WSSV) in 'all decapods'. The Decapoda comprise over 20,000 species across 2 suborders (Dendrobranchiata and Pleocyemata). Members of both suborders have been shown to be susceptible. This higher-level taxonomic diversity in WSD susceptibility demonstrated by representation across these two suborders is likely the basis for the statement that 'all decapods' are susceptible to WSSV but it should be taken into account that most of the Families within the two suborders have not been tested.

To illustrate this point, only three families (Penaeidae, Solenoceridae, Sergestidae) of the seven families in the Suborder Dendrobranchiata have been studied in this context. Similarly, of the approximately 94 families that comprise the various Infraorders and Superfamilies of the Suborder Pleocyemata, only 24 have been demonstrated to be naturally or experimentally susceptible (or to act as carrier/vector). Furthermore, within the Suborder Pleocyemata, of the 8 Infraorders (Anomura, Astacidea, Brachyura, Caridea, Palinura, Palinuridea, Stenopodidea and Thalassinidea), only 5 have been demonstrated to contain susceptible or vector species (exceptions being the Infraorders Palinuridea, Stenopodidea and Thalassinidea).

Nevertheless, WSD appears to have a wide host range compared to TS and YHD. In addition, all decapod crustaceans from marine and brackish or freshwater sources that have been subjected to experimental infection trials have been successfully infected. An understanding of taxonomic spread in host range is therefore a new concept in addressing susceptibility and will undoubtedly highlight the variation in virulence strategies for the pathogens (including those of fish and mollusks) listed in Directive 2006/88/EC. As stated above, a risk assessment based upon taxonomic range may also by-pass the potential for rapid outdated of lists of susceptible species (as new literature becomes available) and would allow a precautionary principle to be applied to those species within a potentially susceptible taxonomic group that for various reasons have never been rigorously tested for susceptibility.

### 3.5. Focus on susceptibility of European species

Tables 3 (WSD), 4 (TS) and 5 (YHD) include several species that are present in European marine, brackish and freshwater habitats.

**Table 5**  
Evidence for susceptibility of hosts to YHD according to fulfilment of categories A–D as stated in Table 2.

Species	Natural (N) or Experimental (E) Invasive (I) or Non-invasive (NI)	A	B	C	D	Assessment	Pathogen ID	Group
<i>Penaeus monodon</i>	N, E I, NI	X	X	X	X	A. Boonyaratpalin et al. (1993); Chantanachookin et al. (1993); Sithigorngul et al. (2000) B. Boonyaratpalin et al. (1993); Flegel et al. (1995a,b); Longyant et al. (2006); Walker et al. (2001); Kiatpathomchai et al. (2004) C. Boonyaratpalin et al. (1993); Chantanachookin et al. (1993) D. Boonyaratpalin et al. (1993); Chantanachookin et al. (1993)	Pathogen characterised by sequence comparisons of structural protein genes (ORF2 and ORF3), intergenic regions (IGRs) and the long 3'-UTR (Walker et al. submitted)	I
<i>Penaeus esculentus</i>	N, E I*	nd	nd	nd	nd	A. No scientific data available though external signs observed (in Munro and Owens, 2007) and high mortalities following injection with GAV (Spann et al., 2000)*.	Pathogen not characterised *Note: Natural infections with YHV reported from <i>P. esculentus</i> co-cultivated with <i>P. monodon</i> (Munro and Owens, 2007) while Spann et al. (2000) report mortality of <i>P. esculentus</i> following injection with a pathogenic strain of GAV	II
<i>Penaeus japonicus</i>	N, E I*	X	nd	X	X	A. Wang et al. (1996). B. No scientific data available* C. Wang et al. (1996) D. Wang et al. (1996)	Pathogen not characterised *Note: Spann et al. (2000) report mortality of <i>P. japonicus</i> following injection with a pathogenic GAV isolate	II
<i>Penaeus merguensis</i>	N (YHV), E (GAV) I (GAV)	X	nd	X	X	A. Partial demonstration (Chantanachookin et al., 1993) B. No scientific data available C. Withyachumnarnkul and Boonsaeng, pers.com. in Flegel (1997) (YHV) and Spann et al. (2000) (GAV) D. Spann et al. (2000) (GAV)	Pathogen characterised. Pathogenic GAV isolate (Spann et al., 2000)	I
<i>Penaeus vannamei</i>	N, E I, NI	X	X	X	X	A. Lightner et al. (1998); Pantoja and Lightner (2003); Tang and Lightner (1999). B. Lightner et al. (1998) C. Lightner et al. (1998); Pantoja and Lightner (2003) D. Lightner et al. (1998); Pantoja and Lightner (2003)	Pathogen characterised. Thai isolate from <i>P. monodon</i> . (Lightner et al., 1998)	I
<i>Penaeus stylirostris</i>	N, E I	X	nd	X	X	A. Lu et al. (1994) B. No scientific data available C. Lu et al. (1994) D. Lu et al., 1994	Pathogen not characterised	II
<i>Penaeus setiferus</i>	N, E NI	X	nd	X	X	A. Lightner et al. (1998) B. No scientific data available C. Lightner et al. (1998) D. Lightner et al. (1998)	Pathogen characterised. Thai isolate from <i>P. monodon</i> (Lightner et al., 1998)	I
<i>Penaeus aztecus</i>	E NI	X	nd	X	X	A. Lightner et al. (1998) B. No scientific data available C. Lightner et al. (1998) D. Lightner et al. (1998)	Pathogen characterised. Thai isolate from <i>P. monodon</i> (Lightner et al., 1998)	I
<i>Penaeus duorarum</i>	E NI	X	nd	X	X	A. Partial demonstration (Lightner et al., 1998) B. No scientific data available C. Lightner et al. (1998) D. Lightner et al. (1998)	Pathogen characterised Thai isolate from <i>P. monodon</i> (Lightner et al., 1998)	I
<i>Metapenaeus ensis</i>	E I	X	nd	nd	nd	A. Partial demonstration (reported anecdotally in Chantanachookin et al., 1993). B. No scientific data available C. No scientific data available D. No scientific data available	Pathogen not characterised. Descriptions of mortalities and pathology though not presented as data.	II
<i>Metapenaeus bennettiae</i>	E* I	nd	nd	nd	nd	A–D No scientific data available	Pathogen not characterised Listed by Munro and Owens (2007) and OIE (2006) and Walker et al. (2001) for ability to infect experimentally with GAV though data not reported	II
<i>Metapenaeus brevicornis</i>	E I*	X	nd	X	X	A. Longyant et al. (2006) B. No scientific data available C. Longyant et al. (2006) D. Longyant et al. (2006)	Pathogen not characterised Virus isolate from infected <i>P. monodon</i> (Longyant et al., 2006). *Transmission not successful via feeding (Longyant et al., 2006).	I
<i>Metapenaeus affinis</i>	E I, NI	X	nd	X	X	A. Longyant et al. (2006) B. No scientific data available C. Longyant et al. (2006) D. Longyant et al. (2006)	Pathogen not characterised Virus isolate from infected <i>P. monodon</i> (Longyant et al., 2006).	I
<i>Macrobrachium lanchesteri</i>	E I	X	nd	nd	nd	A. Partial demonstration (Longyant et al., 2005) B–D No scientific data available.	Pathogen not characterised Virus isolate from infected <i>P. monodon</i> (Longyant et al., 2005).	II

(continued on next page)

Table 5 (continued)

Species	Natural (N) or Experimental (E) Invasive (I) or Non-invasive (NI)	A	B	C	D	Assessment	Pathogen ID	Group
<i>Macrobrachium sintangense</i>	E I	X	nd	X	X	A. Partial demonstration (Longyant et al., 2005) B. No scientific data available C. Partial demonstration (Longyant et al., 2005) D. Partial demonstration (Longyant et al., 2005)	Pathogen not characterised Virus isolate from infected <i>P. monodon</i> (Longyant et al., 2005).	II
<i>Palaemon styliferus</i>	N, E I	X	X	X	X	A. Flegel (1997); Longyant et al. (2005) B. Flegel et al. (1995a,b) C. Flegel (1997); Longyant et al. (2005) D. Flegel (1997)	Pathogen not characterised Virus isolate from infected <i>P. monodon</i> (Longyant et al., 2005).	I
<i>Palaemon serrifer</i>	E I	X	nd	X	X	Partial demonstration (Longyant et al., 2005) No scientific data available C. Partial demonstration (Longyant et al., 2005) D. Partial demonstration (Longyant et al., 2005)	Pathogen not characterised Virus isolate from infected <i>P. monodon</i> (Longyant et al., 2005)	II
<i>Acetes</i> sp.	E*	nd	X	nd	nd	A, C, D. No scientific data available B. *Anecdotal reports that farmers using frozen krill ( <i>Acetes</i> sp.) as shrimp feed experienced YHV mortalities 10 days after feeding and that injection of extracts of krill ( <i>Acetes</i> sp.) collected from YHV-affected shrimp ponds into laboratory held <i>P. monodon</i> caused disease (In: Flegel et al., 1995a,b).	Pathogen not characterised	II

Note that all viruses comprising Yellowhead complex (Walker et al., 2008) were included in analysis. Key: X (fulfilment of category by reports in scientific literature), nd (no data available), Group I (Host species for which scientific evidence supports susceptibility to listed diseases), Group II (Host species for which scientific data partially supports susceptibility to listed diseases).

Additionally, each table contains species that may be considered as economically important (farmed or fished), ecologically important (e.g. protected under international legislation), or incidental (no current economic value and not protected by legislation). In the context of global trade, it is perhaps common sense to consider that movements of economically important susceptible species pose the greatest risk of pathogen transfer. Conversely, species considered as incidental are unlikely to pose a significant threat since they are less likely to be moved with intention between regions. This assumption may however be challenged if incidental species movements occur unintentionally (e.g. via ship ballast water). In terms of importing regions, those with stocks of ecologically and economically important species are likely to be at highest direct risk of effect from imported pathogens, while those containing only incidental species may still undergo indirect effects of introduction (e.g. by alterations in food chain structure by the disease). These effects may only be observed at different levels in the food chain (e.g. loss of predators) and may not be easily attributable to any obvious cause.

Taken together, individual European Member States may be broadly categorised into 3 regional types. Type 1 states possess cold-water marine borders, estuaries and freshwaters (e.g. Northern Europe); Type 2 states possess warmer water marine borders, estuaries and rivers (e.g. Mediterranean); and Type 3 states are landlocked and only contain freshwaters (e.g. Central and Eastern Europe). Each of the three types may or may not support commercially significant susceptible species (e.g. lobsters, crabs, crayfish) and ecologically significant susceptible species (e.g. crayfish), while all types are likely to contain susceptible incidental species (at least to WSSV). For Type 1 states, known susceptible marine species include shore crab (*Carcinus maenas*), edible crab (*C. pagurus*), swimming crab (*Liocarcinus depurator*), velvet crab (*Liocarcinus puber*), brown shrimp (*Crangon crangon*) and lobster (*H. gammarus*) while susceptible freshwater species include several crayfish species (*Pacifastacus leniusculus*, *Astacus leptodactylus*, *Orconectes limosus*). Given the apparent relatively low susceptibility range of TS and YHD, Type 1 states may be at greatest risk from the introduction of broader range pathogens such as WSD. For Type 2 states, additional susceptible marine species include farmed and wild penaeid shrimp species (e.g.

*P. japonicus*, *P. kerathurus*, *P. semisulcatus*, *Metapenaeus* spp.) (Can et al., 2004; Aktas et al., 2006; Türkmen 2007). In these states, farmed and wild stocks may be potentially at risk from introduction of the penaeid-oriented pathogens YHD and TS, in addition to the broader range pathogen causing WSD. Type 3 states (containing only freshwaters) will only support crayfish species and other susceptible incidental hosts and as such, introduction of WSD poses the greatest risk in these cases. As stated previously, the potential for release, exposure and consequence of such introductions, particularly with regard to environmental constraints of the listed pathogens, is not covered in this review.

#### 4. Future directions for legislation and research in Europe

The recent listing of TS, YHD and WSD in EC Directive 2006/88 is in direct recognition of the important negative contribution of crustacean pathogens to global aquaculture and also, to the potential for these (and other) diseases to transfer to new hosts in new geographic regions. Europe has a very important marine, brackish and freshwater crustacean fauna, significant proportions of which are increasingly exploited commercially for food. In addition, crustaceans occupy key positions in aquatic food chains and therefore play an important ecological role in the functioning of aquatic systems. The co-existence of crustacean diseases with listed fish and mollusc diseases in EC Directive 2006/88 provides a legislative tool for Member States to protect important aquatic resources while ensuring that trade routes into and out of the European Union for live aquatic products and commodity remain open. This is achieved via a certification system for imported live aquaculture products and commodity and a requirement for individual Member States to assess and document their status for those diseases known to occur at least in some regions of the Community (i.e. non-exotic pathogens). Understanding potential threats from incoming products is an important tool for maintaining biosecurity across the Community whilst formation of competent laboratory networks throughout the Member States assist with rapid response to breaches in biosecurity. The listing of crustacean diseases in EC Directive 2006/88 aligns this approach with that already in place for fish and mollusc diseases and is likely to lead to a better

understanding of not only threats from exotic pathogens but also, from those pathogens that are endemic within economically and ecologically important populations.

This review has highlighted a diverse literature associated with TS, YHD and WSD. However, it has also revealed a relative dearth in knowledge of the potential effect of transfer of these pathogens to new hosts species in temperate regions. Since the global aquaculture industry for shrimp products is largely associated with transfer of products from tropical net producing nations to temperate net importing nations it is important to consider whether this poses a special threat to the biosecurity of receiving countries. This issue has recently been the topic of an import risk assessment (IRA) for commodity shrimp products to Australia (Biosecurity Australia, 2006). In this context, biosecurity must be considered both from the point of view of producer and consumer, with measures to encourage low pathogen prevalence and safe packaging of products occurring at source and additional measures to ensure secure processing, distribution and usage occurring once imported. Certification associated with EC Directive 2006/88 (and associated Commission Regulation 1250/2008) considers these angles and should help to encourage a shared responsibility while continuing to ensure free trade of safe products from producer nations to the EU.

## Acknowledgements

The authors acknowledge the anonymous members of the European Food Safety Authority (EFSA) Working Groups for Vector Species and Susceptible Species for valuable discussion during the preparation of data included in this review and particularly the respective chairs of those groups, Drs Ana Afonso and Franck Berthe. GDS acknowledges funding under Cefas contract C3108 for completion of this review.

## References

- Aktas, M., Turan, C., Bozkurt, A., 2006. Taxonomic description of three shrimp species (*Melicertus kerathurus*, *Metapenaeus monoceros*, *Penaeus semisulcatus*) using multivariate morphometric analyses. *J. Anim. Vet. Adv.* 5, 172–175.
- Biosecurity Australia 2006. Revised Draft Generic Import Risk Analysis Report for Prawns and Prawn Products, Part B. Biosecurity Australia, Canberra, Australia. 284 pp.
- Bonami, J.R., Hasson, K.W., Mari, J., Poulos, B.T., Lightner, D.V., 1997. Taura syndrome of marine Penaeid shrimp: characterization of the viral agent. *J. Gen. Virol.* 78, 313–319.
- Boonyaratpalin, S., Supamataya, K., Kasornchandra, J., Direkbusarakom, S., Ekpanithanpong, U., Chantanachookin, C., 1993. Non-occluded baculo-like virus the causative agent of yellow-head disease in the black tiger shrimp *Penaeus monodon*. *Fish Pathol.* 28, 103–109.
- Brock, J.A., 1997. Special topic review: Taura syndrome, a disease important to shrimp farms in the Americas. *World J. Microbiol. Technol.* 13, 415–418.
- Brock, J.A., Gose, R., Lightner, D.V., Hasson, K.W., 1995. An overview on Taura Syndrome, an important disease of farmed *Penaeus vannamei*. In: Browdy, C.L., Hopkins, J.S. (Eds.), *Swimming Through Troubled Water, Proceedings of the Special Session on Shrimp Farming, Aquaculture '95*. World Aquaculture Society, Baton Rouge, LA, USA, pp. 84–94.
- Brock, J.A., Gose, R.B., Lightner, D.V., Hasson, K.W., 1997. Recent developments and an overview of Taura syndrome of farmed penaeid shrimp in the Americas. In: Flegel, T.W., MacRae, I.H. (Eds.), *Diseases in Asian Aquaculture III*. Fish Health Section, Asian Fisheries Society, Manila.
- Cai, S., Huang, J., Wang, C., Song, X., Sun, X., Yu, J., Zhang, Y., Yang, C., 1995. Epidemiological studies on the explosive epidemic disease of prawn in 1993–1994. *J. Fish. China* 19, 112–117.
- Can, M.F., Mazlum, Y., Demirci, A., Aktas, M., 2004. The catch composition and catch per unit effort of swept area (CPUE) of penaeid shrimps in the bottom trawls of Iskenderun Bay, Turkey. *Turk. J. Fish. Aquat. Sci.* 4, 87–91.
- Chang, P.S., Chen, H.C., Wang, Y.C., 1998a. Detection of white spot syndrome associated baculovirus in experimentally infected wild shrimp, crabs and lobsters by in situ hybridization. *Aquaculture* 164, 233–242.
- Chang, P.S., Chen, L.J., Wang, Y.C., 1998b. The effect of ultraviolet irradiation, heat, pH, ozone, salinity and chemical disinfectants on the infectivity of white spot syndrome baculovirus. *Aquaculture* 166, 1–17.
- Chang, Y.S., Lo, C.F., Peng, S.E., Liu, K.F., Wang, C.H., Kou, G.H., 2002. White spot syndrome virus (WSSV) PCR-positive *Artemia* cysts yield PCR-negative nauplii that fail to transmit WSSV when fed to shrimp postlarvae. *Dis. Aquat. Org.* 49, 1–10.
- Chang, Y.-S., Peng, S.-E., Yu, H.-T., Liu, F.-C., Wang, C.-H., Lo, C.-F., Kou, G.-H., 2004. Genetic and phenotypic variations of isolates of shrimp Taura syndrome virus found in *Penaeus monodon* and *Metapenaeus ensis* in Taiwan. *J. Gen. Virol.* 85, 2963–2968.
- Chantanachookin, C., Boonyaratpalin, S., Kasornchandra, J., Direkbusarakom, S., Aekpanithanpong, U., Supamataya, K., Sriuraitana, S., Flegel, T.W., 1993. Histology and ultrastructure reveal a new granulosis-like virus in *Penaeus monodon* affected by yellow-head disease. *Dis. Aquat. Org.* 17, 145–157.
- Chen, L.L., Lo, C.F., Chiu, Y.L., Chang, C.F., Kou, G.H., 2000. Natural and experimental infection of white spot syndrome virus (WSSV) in benthic larvae of mud crab *Scylla serrata*. *Dis. Aquat. Org.* 40, 157–161.
- Chou, H.Y., Huang, C.Y., Wang, C.H., Chiang, H.C., Lo, C.F., 1995. Pathogenicity of a baculovirus infection causing White Spot Syndrome in cultured penaeid shrimp in Taiwan. *Dis. Aquat. Org.* 23, 165–173.
- Chou, H.Y., Huang, C.Y., Lo, C.F., Kou, G.H., 1998. Studies on transmission of white spot syndrome associated baculovirus (WSBV) in *Penaeus monodon* and *P. japonicus* via waterborne contact and oral ingestion. *Aquaculture* 164, 263–276.
- Claydon, K., Cullen, B., Owens, L., 2004. OIE white spot syndrome virus PCR gives false positive results in *Cherax quadricarinatus*. *Dis. Aquat. Org.* 62, 265–268.
- Corbel, V., Zuprisal, Z., Shi, C., Huang, L., Sumartono, C., Arcier, J.M., Bonami, J.R., 2001. Experimental infection of European crustaceans with white spot syndrome virus (WSSV). *J. Fish. Dis.* 24, 377–382.
- Côté, I., Navarro, S., Tang, K.F.J., Noble, B., Lightner, D.V., 2008. Taura syndrome virus from Venezuela is a new genetic variant. *Aquaculture* 284, 62–67.
- Cowley, J.A., Walker, P.J., 2002. The complete genome sequence of gill associated virus of *Penaeus monodon* prawns indicates a gene organisation unique among nidoviruses. *Arch. Virol.* 147, 1977–1987.
- Cowley, J.A., Dimmock, C.M., Wongteerasupaya, C., Boonsaeng, V., Panyim, S., Walker, P.J., 1999. Yellow head virus from Thailand and gill-associated virus from Australia are closely related but distinct prawn viruses. *Dis. Aquat. Org.* 36, 153–157.
- Cowley, J.A., Dimmock, C.M., Spann, K.M., Walker, P.J., 2000. Gill-associated virus of *Penaeus monodon* prawns: an invertebrate virus with ORF1a and ORF1b genes related to arteri- and coronaviruses. *J. Gen. Virol.* 81, 1473–1484.
- Cowley, J.A., Hall, M.R., Cadogan, L.C., Spann, K.M., Walker, P.J., 2002. Vertical transmission of gill-associated virus (GAV) in the black tiger prawn *Penaeus monodon*. *Dis. Aquat. Org.* 50, 95–104.
- Cowley, J.A., Cadogan, L.C., Spann, K.M., Sittidilokratna, N., Walker, P.J., 2004. The gene encoding the nucleocapsid protein of gill-associated nidovirus of *Penaeus monodon* prawns is located upstream of the glycoprotein gene. *J. Virol.* 78, 8935–8941.
- Du, H., Dai, W., Han, X., Li, W., Xu, Y., Xu, Z., 2008. Effect of low water temperature on viral replication of white spot syndrome virus in *Procambarus clarkii*. *Aquaculture* 277, 149–151.
- Durand, S., Lightner, D.V., Redman, R.M., Bonami, J.R., 1997. Ultrastructure and morphogenesis of White Spot Syndrome Baculovirus (WSSV). *Dis. Aquat. Org.* 29, 205–211.
- Durand, S.V., Tang, K.F.J., Lightner, D.V., 2000. Frozen commodity shrimp: potential avenue for introduction of white spot syndrome virus and yellow head virus. *J. Aquat. Anim. Health* 12, 128–135.
- Durand, S.V., Redman, R.M., Mohney, L.L., Tang-Nelson, K., Bonami, J.R., Lightner, D.V., 2003. Qualitative and quantitative studies on the relative virus loads of tails and heads of shrimp acutely infected with WSSV. *Aquaculture* 216, 9–18.
- Edgerton, B.F., 2004. Susceptibility of the Australian freshwater crayfish *Cherax destructor albidus* to white spot syndrome virus (WSSV). *Dis. Aquat. Org.* 59, 187–193.
- Erickson, H.S., Zarain-Herzberg, M., Lightner, D.V., 2002. Detection of Taura syndrome virus (TSV) strain differences using selected diagnostic methods: diagnostic implications in penaeid shrimp. *Dis. Aquat. Org.* 52, 1–10.
- Fauquet, C.M., Mayo, M.A., Maniloff, J., Desselberger, U., Ball, L.A., 2005. Virus taxonomy. Classification and nomenclature of viruses. Eighth Report of the International Committee on Taxonomy of Viruses. Elsevier, Academic Press, 1259 pp.
- Flegel, T.W., 1997. Special topic review: major viral diseases of the black tiger prawn (*Penaeus monodon*) in Thailand. *World J. Microb. Biol.* 13, 433–442.
- Flegel, T.W., Fegan, D.F., Sriurairatana, S., 1995a. Environmental control of infectious diseases in Thailand. In: Shariff, M., Subasinghe, R.P., Arthur, J.R. (Eds.), *Diseases in Asian Aquaculture II*. Asian Fisheries Society, Manila, The Philippines, pp. 65–79.
- Flegel, T.W., Sriurairatana, S., Wongteerasupaya, C., Boonsaeng, V., Panyim, S., Withyachumnarnkul, B., 1995b. Progress in characterization and control of yellow-head virus of *Penaeus monodon*. In: Browdy, C.L., Hopkins, J.S. (Eds.), *Swimming Through Troubled Water, Proceedings of the Special Session on Shrimp Farming, Aquaculture '95*. World Aquaculture Society, Baton Rouge, USA, pp. 76–83.
- Garza, J.R., Hasson, K.W., Poulos, B.T., Redman, R.M., White, B.L., Lightner, D.V., 1997. Demonstration of infectious Taura syndrome virus in the feces of sea gulls collected during an epizootic in Texas. *J. Aquat. Anim. Health* 9, 156–159.
- Granja, C.B., Aranguren, L.F., Vidal, O.M., Aragon, L., Salazar, M., 2003. Does hyperthermia increase apoptosis in white spot syndrome virus (WSSV) infected *Litopenaeus vannamei*? *Dis. Aquat. Org.* 54, 73–78.
- Guan, Y., Yu, Z., Li, C., 2003. The effects of temperature on white spot syndrome infections in *Marsupenaeus japonicus*. *J. Invertebr. Pathol.* 83, 257–260.
- Hasson, K.W., 1998. Taura syndrome of marine penaeid shrimp: discovery of the viral agent and diseases characterization studies. Ph.D. Thesis, The University of Arizona, 365 pp.
- Hasson, K.W., Lightner, D.V., Poulos, B.T., Redman, R.M., White, B.L., Brock, J.A., Bonami, J.R., 1995. Taura syndrome in *Penaeus vannamei*: demonstration of a viral etiology. *Dis. Aquat. Org.* 23, 115–126.
- Hasson, K.W., Lightner, D.V., Mohney, L.L., Redman, R.M., Poulos, B.T., White, B.M., 1999a. Taura syndrome virus (TSV) lesion development and the disease cycle in the Pacific white shrimp *Penaeus vannamei*. *Dis. Aquat. Org.* 36, 81–93.
- Hasson, K.W., Lightner, D.V., Mari, J.M., Bonami, J.R., Poulos, B.T., Mohney, L.L., Redman, R.M., Brock, J.A., 1999b. The geographic distribution of Taura syndrome virus (TSV)

- in the Americas: determination by histopathology and in situ hybridization using TSV-specific cDNA probes. *Aquaculture* 171, 13–26.
- Hasson, K.W., Fan, Y., Reisinger, T., Venuti, J., Varner, P.W., 2006. White-spot syndrome virus (WSSV) introduction into the Gulf of Mexico and Texas freshwater systems through imported, frozen bait-shrimp. *Dis. Aquat. Org.* 71, 91–100.
- Hossain, S., Chakraborty, A., Joseph, B., Otta, S.K., Karunasagar, I., Karunasagar, I., 2001. Detection of new hosts for white spot syndrome virus of shrimp using nested polymerase chain reaction. *Aquaculture* 198, 1–11.
- Huang, C.H., Zhang, L.R., Zhang, J.H., Xiao, L.C., Wu, Q.J., Chen, D.H., Li, J.K.K., 2001. Purification and characterization of White Spot Syndrome Virus (WSSV) produced in an alternate host: crayfish, *Procambarus clarkii*. *Virus Res.* 76, 115–125.
- Inouye, K., Miwa, S., Oseko, N., Nakano, H., Kimura, T., Momoyama, K., Hiraoka, M., 1994. Mass mortality of cultured kuruma shrimp *Penaeus japonicus* in Japan in 1993: Electron microscopic evidence of the causative virus. *Fish Pathol.* 29, 149–158.
- Jimenez, R., 1992. Síndrome de Taura (Resumen). *Acuicultura del Ecuador. Camara Nacional de Acuicultura, Guayaquil, Ecuador*, pp. 1–16.
- Jiravanichpaisal, P., Bangyeekhun, E., Söderhäll, K., Söderhäll, I., 2001. Experimental infection of white spot syndrome virus in freshwater crayfish *Pacifastacus leniusculus*. *Dis. Aquat. Org.* 47, 151–157.
- Jiravanichpaisal, P., Söderhäll, K., Söderhäll, I., 2004. Effect of water temperature on the immune response and infectivity pattern of white spot syndrome virus (WSSV) in freshwater crayfish. *Fish Shell. Immunol.* 17, 265–275.
- Jitrapakdee, S., Unajak, S., Sittidilokratna, N., Hodgson, R.A.J., Cowley, J.A., Walker, P.J., Panyim, S., Boonsaeng, V., 2003. Identification and analysis of gp116 and gp64 structural glycoproteins of yellow head nidovirus of *Penaeus monodon* shrimp. *J. Gen. Virol.* 84, 863–873.
- Jory, D.E., Dixon, H.M., 1999. Shrimp whitespot in the western hemisphere. *Aquaculture* 25, 83–91.
- Kanchanaphum, P., Wongteerasupaya, C., Sittidilokratana, N., Boonsaeng, V., Panyim, S., Tassanakajon, A., Withayachumarnkul, B., Flegel, T.W., 1998. Experimental transmission of white spot syndrome virus (WSSV) from crabs to shrimp *Penaeus monodon*. *Dis. Aquat. Org.* 34, 1–7.
- Kiatpathomchai, W., Jitrapakdee, S., Panyim, S., Boonsaeng, V., 2004. RT-PCR detection of yellow head virus (YHV) infection in *Penaeus monodon* using dried haemolymph spots. *J. Virol. Methods* 119, 1–5.
- Kou, G.H., Peng, S.E., Chiu, Y.L., Lo, C.F., 1998. Tissue distribution of white spot syndrome virus (WSSV) in shrimp and crabs. In: Flegel, T.W. (Ed.), *Advances in Shrimp Biotechnology*. National Center for Genetic Engineering and Biotechnology, Bangkok, pp. 267–271.
- Lan, Y., Lu, W., Xu, X., 2002. Genomic instability of prawn white spot bacilliform virus (WSBV) and its association to virus virulence. *Virus Res.* 9, 269–274.
- Li, Q., Zhang, J., Chen, Y., Yang, F., 2003. White spot syndrome virus (WSSV) infectivity for *Artemia* at different developmental stages. *Dis. Aquat. Org.* 57, 261–264.
- Lightner, D.V. (Ed.), 1996. *A Handbook of Shrimp Pathology and Diagnostic Procedures for Diseases of Cultured Penaeid Shrimp*. World Aquaculture Society, Baton Rouge, Louisiana, USA. 304 pp.
- Lightner, D.V., Redman, R.M., Hasson, K.W., Pantoja, C.R., 1995. Taura syndrome in *Penaeus vannamei* (Crustacea: Decapoda): gross signs, histopathology and ultrastructure. *Dis. Aquat. Org.* 21, 53–59.
- Lightner, D.V., Hasson, K.W., White, B.L., Redman, R.M., 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.
- Lightner, D.V., et al., 1999. The penaeid shrimp viruses TSV, IHNV, WSSV and YHV: current status in the Americas, available diagnostic methods and management strategies. *J. Appl. Aquac.*
- Limsuwan, C., 1991. *Handbook for Cultivation of Black Tiger Prawns*. Tansetakit Co. Ltd., Bangkok, Thailand. (in Thai) 202 pp.
- Lo, C.F., Kou, G.H., 1998. Virus-associated white spot syndrome of shrimp in Taiwan: a review. *Fish Pathol.* 33, 365–371.
- Lo, C.F., Ho, C.H., Peng, S.E., Chen, C.H., Hsu, H.C., Chiu, Y.L., Chang, C.F., Liu, K.F., Su, M.S., Wang, C.H., Kou, G.H., 1996a. White spot syndrome baculovirus (WSBV) detected in cultured and captured shrimp, crabs and other arthropods. *Dis. Aquat. Org.* 27, 215–225.
- Lo, C.F., Leu, J.H., Chen, C.H., Peng, S.E., Chen, Y.T., Chou, C.M., Yeh, P.Y., Huang, C.J., Chou, H.Y., Wang, C.H., Kou, G.H., 1996b. Detection of baculovirus associated with White Spot Syndrome (WSBV) in penaeid shrimps using polymerase chain reaction. *Dis. Aquat. Org.* 25, 133–141.
- Lo, C.F., Ho, C.H., Chen, C.H., Liu, K.F., Chiu, Y.L., Yeh, P.Y., Peng, S.E., Hsu, H.C., Liu, H.C., Chang, C.F., Su, M.S., Wang, C.H., Kou, G.H., 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.
- Lo, C.F., Hsu, H.C., Tsai, M.F., Ho, C.H., Peng, S.E., Kou, G.H., Lightner, D.V., 1999. Specific genomic DNA fragment analysis of different geographical clinical samples of shrimp white spot syndrome virus. *Dis. Aquat. Org.* 35, 175–185.
- Longyant, S., Sithigorngul, P., Chaivisuthangkura, P., Rukpratanporn, S., Sithigorngul, W., Menasveta, P., 2005. Differences in the susceptibility of palaemonid shrimp species to yellow head virus (YHV) infection. *Dis. Aquat. Org.* 64, 5–12.
- Longyant, S., Sattaman, S., Chaivisuthangkura, P., Rukpratanporn, S., Sithigorngul, W., Sithigorngul, P., 2006. Experimental infection of some penaeid shrimps and crabs by yellow head virus (YHV). *Aquaculture* 257, 83–91.
- Lotz, J.M., 1997. Special topic review: viruses, biosecurity and specific pathogen-free stocks in shrimp aquaculture. *World J. Microbiol. Biotechnol.* 13, 405–413.
- Lu, Y., Tapay, L.M., Brock, J.A., Loh, P.C., 1994. Infection of the yellow head baculo-like virus (YBV) in two species of penaeid shrimp *Penaeus stylirostris* (Stimpson) and *Penaeus vannamei* (Boone). *J. Fish Dis.* 17, 649–656.
- Lu, Y., Tapay, L.M., Gose, R.B., Brock, J.A., Loh, P.C., 1997. Infectivity of Yellow Head Virus (YHV) and the Chinese baculo-like virus (CBV) in two species of penaeid shrimp *Penaeus stylirostris* (Stimpson) and *Penaeus vannamei* (Boone). In: Flegel, T.W., MacRae, I.H. (Eds.), *Diseases in Asian Aquaculture III*. Asian Fisheries Society, Manila, The Philippines, pp. 297–304.
- Maeda, M., Itami, T., Furumoto, A., Henning, O., Imamura, T., Kondo, M., Hirono, I., Takashi, A., Takahashi, Y., 1998a. Detection of penaeid rod-shaped DNA virus (PRDV) in wild-caught shrimp and other crustaceans. *Fish Pathol.* 33, 373–380.
- Maeda, M., Kasornchandra, J., Itami, T., Suzuki, N., Henning, O., Kondo, M., Albaladejo, J.D., Takahashi, Y., 1998b. Effect of various treatments on white spot syndrome virus (WSSV) from *Penaeus japonicus* (Japan) and *P. monodon* (Thailand). *Fish Pathol.* 33, 381–387.
- Mari, J., Poulos, B.T., Lightner, D.V., Bonami, J.R., 2002. Shrimp Taura syndrome virus: genomic characterization and similarity with members of the genus Cricket paralysis-like viruses. *J. Gen. Virol.* 83, 915–926.
- Mayo, M.A., 2002a. A summary of taxonomic changes recently approved by the ICTV. *Arch. Virol.* 147, 1655–1656.
- Mayo, M.A., 2002b. Virus taxonomy – Houston 2002. *Arch. Virol.* 147, 1071–1076.
- Mohan, C.V., Shankar, K.M., Kulkarni, S., Sudha, P.M., 1998. Histopathology of cultured shrimp showing gross signs of yellow head syndrome and white spot syndrome during 1994 Indian epizootics. *Dis. Aquat. Org.* 34, 9–12.
- 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: histopathological study. *Fish Pathol.* 29, 141–148.
- Momoyama, K., Hiraoka, M., Nakano, H., Sameshima, M., 1998. Cryopreservation of penaeid rod-shaped DNA virus (PRDV) and its survival in sea water at different temperatures. *Fish Pathol.* 33, 95–96.
- Munro, J., Owens, L., 2007. Yellow head-like viruses affecting the penaeid aquaculture industry: a review. *Aquacult. Res.* 38, 893–908.
- Nadala, E.C.B., Tapay, L.M., Loh, P.C., 1997. Yellow-head virus: a rhabdovirus-like pathogen of penaeid shrimp. *Dis. Aquat. Org.* 31, 141–146.
- 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 trails. *Fish Pathol.* 29, 135–139.
- Nakano, H., Hiraoka, M., Sameshima, M., Kimura, T., Momoyama, K., 1998. Inactivation of penaeid rod-shaped DNA virus (PRDV), the causative agent of penaeid acute viraemia (PAV), by chemical and physical treatments. *Fish Pathol.* 33, 65–71.
- Nielsen, L., Sang-Oum, W., Cheevadhanarak, S., Flegel, T.W., 2005. Taura syndrome virus (TSV) in Thailand and its relationship to TSV in China and the Americas. *Dis. Aquat. Org.* 63, 101–106.
- Nunan, L.M., Tang-Nelson, K., Lightner, D.V., 2004. Real-time RT-PCR determination of viral copy number in *Penaeus vannamei* experimentally infected with Taura syndrome virus. *Aquaculture* 229, 1–10.
- OIE, 2006. *Manual of Diagnostic Tests for Aquatic Animals 2006*. OIE, Paris. 469 pp.
- Otta, K., Shubha, G., Joseph, B., Chakraborty, A., Karunasagar, I., Karunasagar, I., 1999. Polymerase Chain Reaction (PCR) Detection of White Spot Syndrome Virus (WSSV) in Cultured and Wild Crustaceans in India. *Dis. Aquat. Org.* vol. 38 67–70.
- Overstreet, R.M., Lightner, D.V., Hasson, K.W., McIlwain, S., Lotz, J.M., 1997. Susceptibility to Taura syndrome virus of some penaeid shrimp species native to the Gulf of Mexico and the southeastern United States. *J. Invertebr. Pathol.* 69, 165–176.
- Pantoja, C.R., Lightner, D.V., 2003. Similarity between the histopathology of white spot syndrome virus and yellow head syndrome virus and its relevance to diagnosis of YHV disease in the Americas. *Aquaculture* 218, 47–54.
- Peng, S.E., Lo, C.F., Lin, S.C., Chen, L.L., Chang, Y.S., Liu, K.F., Su, M.S., Kou, G.H., 2001. Performance of WSSV-infected and WSSV-negative *Penaeus monodon* postlarvae in culture ponds. *Dis. Aquat. Org.* 46, 165–172.
- Poulos, B.T., Kibler, R., Bradley-Dunlop, D., Mohney, L.L., Lightner, D.V., 1999. Production and use of antibodies for the detection of the Taura syndrome virus in penaeid shrimp. *Dis. Aquat. Org.* 37, 99–106.
- Rajan, P.R., Ramasamy, P., Purushothaman, V., Brennan, G.P., 2000. White spot baculovirus syndrome in the Indian shrimp *Penaeus monodon* and *P. indicus*. *Aquaculture* 184, 31–44.
- Rajendran, K.V., Vijayan, K.K., Santiago, T.C., Krol, R.M., 1999. Experimental host range and histopathology of white spot syndrome virus (WSSV) infection in shrimp, prawns, crayfish and lobsters from India. *J. Fish Dis.* 22, 183–191.
- Ramirez-Douriet, C., De Silva-Davila, R., Mendez-Lozana, J., Escobedo-Urias, D., Leyva-Arana, I., Lopez-Meyer, M., 2005. White spot syndrome virus detection in zooplankton of coastal lagoons and shrimp commercial ponds in Sinaloa, Mexico 135th Annual Meeting of the American Fisheries Society, Anchorage, Alaska.
- Reville, C., Al-Beik, J., Meehan-Meola, D., Xu, Z., Goldsmith, M.L., Rand, W., Alcivar-Warren, A., 2005. White spot syndrome virus in frozen shrimp sold at Massachusetts supermarkets. *J. Shellfish Res.* 24, 285–290.
- Robles-Sikisaka, R., Hasson, K.W., Garcia, D.K., Brovont, K.E., Cleveland, K.D., Klimpel, K.R., Dhar, A.K., 2002. Genetic variation and immunohistochemical differences among geographic isolates of Taura syndrome virus of penaeid shrimp. *J. Gen. Virol.* 83, 3123–3130.
- Rodríguez, J., Bayot, B., Amino, Y., Panchana, F., De 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.
- Sahul-Hameed, A.S., Charles, M.X., Anilkumar, M., 2000. Tolerance of *Macrobrachium rosenbergii* to white spot syndrome virus. *Aquaculture* 183, 207–213.
- Sahul-Hameed, A.S., Yoganandhan, K., Sathish, S., Rasheed, M., Murugan, V., Jayaraman, K., 2001. White spot syndrome virus (WSSV) in two species of freshwater crabs (*Paratellus hydrodomus* and *P. pulvinata*). *Aquaculture* 201, 179–186.
- Sahul-Hameed, A.S., Balasubramanian, G., Syed Musthaq, S., Yoganandhan, K., 2003. Experimental infection of twenty species of Indian marine crabs with white spot syndrome virus (WSSV). *Dis. Aquat. Org.* 57, 157–161.
- Sánchez-Martínez, J.G., Aguirre-Guzmán, G., Mejía-Ruiz, H., 2007. White spot syndrome virus in cultured shrimp: a review. *Aquac. Res.* 38, 1339–1354.

- Shi, Z., Huang, C., Zhang, J., Chen, D., Bonami, J.R., 2000. White spot syndrome virus (WSSV) experimental infection of the freshwater crayfish *Cherax quadricarinatus*. *J. Fish Dis.* 23, 285–288.
- Sithigorngul, P., Chauyuchuwong, P., Sithigorngul, W., Longyant, S., Chaivisuthangkura, P., Menasveta, P., 2000. Development of a monoclonal antibody specific to yellow head virus (YHV) from *Penaeus monodon*. *Dis. Aquat. Org.* 42, 27–34.
- Sittidilokratna, N., Hodgson, R.A.J., Cowley, J.A., Jitrapakdee, S., Boonsaeng, V., Panyim, S., Walker, P.J., 2002. Complete ORF1b-gene sequence indicates yellow head virus is an invertebrate nidovirus. *Dis. Aquat. Org.* 50, 87–93.
- Soowannayan, C., Flegel, T.W., Sithigorngul, P., Slater, J., Hyatt, A., Cramerri, S., Wise, T., Crane, M.S.J., Cowley, J.A., McCulloch, R.J., Walker, P.J., 2003. Detection and differentiation of yellow head complex viruses using monoclonal antibodies. *Dis. Aquat. Org.* 57, 193–200.
- Spann, K.M., Donaldson, R.A., Cowley, J.A., Walker, P.J., 2000. Differences in susceptibility of some penaeid prawn species to gill-associated virus (GAV) infection. *Dis. Aquat. Org.* 42, 221–225.
- Srisuvan, T., Tang, K.F.J., Lightner, D.V., 2005. Experimental infection of *Penaeus monodon* with Taura syndrome virus (TSV). *Dis. Aquat. Org.* 67, 1–8.
- Stentiford, G.D., 2008. Diseases of the European edible crab (*Cancer pagurus*): a review. *ICES J. Mar. Sci.* 65, 1578–1592.
- Stentiford, G.D., Shields, J.D., 2005. A review of the parasitic dinoflagellates *Hematodinium* species and *Hematodinium*-like infections in marine crustaceans. *Dis. Aquat. Org.* 66, 47–70.
- Supamattaya, K., Hoffman, R.W., Boonyaratpalin, S., Kanchanaphum, P., 1998. Experimental transmission of white spot syndrome virus (WSSV) from black tiger shrimp *Penaeus monodon* to the sand crab *Portunus pelagicus*, mud crab *Scylla serrata* and krill *Acartia* sp. *Dis. Aquat. Org.* 32, 79–85.
- Takahashi, Y., Itami, T., Kondom, M., Maeda, M., Fuji, R., Tomonaga, S., Supamattaya, K., Boonyaratpalin, S., 1994. Electron microscopic evidence of baciliform virus infection in Kuruma shrimp (*Penaeus japonicus*). *Fish Pathol.* 29, 121–125.
- Takahashi, Y., Fukuda, K., Kondo, M., Chongthaleong, A., Nishi, K., Nishimura, M., Ogata, K., Shinya, I., Takise, K., Fujishima, Y., Matsumura, M., 2003. Detection and prevention of WSSV infection in cultured shrimp. *Asian Aquaculture Magazine* November 2003, pp. 25–27.
- Tang, K.F.J., Lightner, D.V., 1999. A yellow head virus gene probe: nucleotide sequence and application for in situ hybridization. *Dis. Aquat. Org.* 35, 165–173.
- Tang, K.F.J., Lightner, D.V., 2005. Phylogenetic analysis of Taura syndrome virus isolates collected between 1993 and 2004 and virulence comparison between two isolates representing different genetic variants. *Virus Res.* 112, 69–76.
- Tu, C., Huang, H.T., Chuang, S.H., Hsu, J.P., Kuo, S.T., Li, N.J., Hus, T.L., Li, M.C., Lin, S.Y., 1999. Taura syndrome in Pacific white shrimp *Penaeus vannamei* cultured in Taiwan. *Dis. Aquat. Org.* 38, 159–161.
- Türkmen, G., 2007. Pond culture of *Penaeus semisulcatus* and *Marsupenaeus japonicus* (Decapoda, Penaeidae) on the west coast of Turkey. *Turk. J. Fish. Aquat. Sci.* 7, 7–11.
- Van Hulten, M.C.W., Witteveldt, J., Peters, S., Kloosterboer, N., Tarchini, R., Fiers, M., Sandbrink, H., Lankhorst, R.K., Vlask, J.M., 2001. The White Spot Syndrome Virus DNA genome sequence. *Virology* 286, 7–22.
- Vanpatten, K.A., Nunan, L.M., Lightner, D.V., 2004. Seabirds as potential vectors of penaeid shrimp viruses and the development of a surrogate laboratory model utilizing domestic chickens. *Aquaculture* 241, 31–46.
- 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.
- Vidal, O.M., Granja, C.B., Aranguren, F., Brock, J.A., Salazar, M., 2001. A profound effect of hyperthermia on survival of *Litopenaeus vannamei* juveniles infected with White Spot Syndrome Virus. *J. World Aquacult. Soc.* 32, 364–372.
- Vijayan, K.K., Stalin Raj, V., Balasubramanian, C.P., Alavandi, S.V., Thillai Sekhar, V., Santiago, T.C., 2005. Polychaete worms—a vector for white spot syndrome virus (WSSV). *Dis. Aquat. Org.* 63, 107–111.
- Walker, P.J., Cowley, J.A., Spann, K.M., Hodgson, R.A.J., Hall, M.R., Withyachumnarnkul, B., 2001. Yellow head complex viruses: transmission cycles and topographical distribution in the Asia-Pacific Region. In: Browdy, C.L., Jory, D.E. (Eds.), *The New Wave, Proceedings of the Special Session on Sustainable Shrimp Culture, Aquaculture 2001*. The World Aquaculture Society, Baton Rouge, LA, USA, pp. 292–302.
- Wang, C.H., Lo, C.F., Leu, J.H., Chou, C.M., Yeh, P.Y., Chou, H.Y., Tung, M.C., Chang, C.F., Su, M.S., Kou, G.H., 1995. Purification and genomic analysis of baculovirus associated with White Spot Syndrome (WSBV) of *Penaeus monodon*. *Dis. Aquat. Org.* 23, 239–242.
- Wang, C.S., Tang, K.F.J., Chen, S.N., 1996. Yellow head disease-like infection in the Kuruma shrimp *Penaeus japonicus* cultured in Taiwan. *Fish Pathol.* 31, 177–182.
- Wang, Y.C., Lo, C.F., Chang, P.S., Kou, G.H., 1998a. Experimental infection of white spot baculovirus in some cultured and wild decapods in Taiwan. *Aquaculture* 164, 221–231.
- Wang, C.S., Tsai, Y.J., Chen, S.N., 1998b. Detection of white spot disease virus (WSDV) infection in shrimp using in situ hybridization. *J. Invertebr. Pathol.* 72, 170–173.
- Wang, Q., Poulos, B.T., Lightner, D.V., 2000. Protein analysis of geographic isolates of shrimp white spot syndrome virus. *Arch. Virol.* 145, 263–274.
- White, B.L., Schofield, P.J., Poulos, B.T., Lightner, D.V., 2002. A laboratory challenge method for estimating Taura syndrome virus resistance in selected lines of Pacific white shrimp *Penaeus vannamei*. *J. World Aquac. Soc.* 33, 341–348.
- Wijegoonawardane, P., Cowley, J.A., Kiatpathomchai, W., Meilsen, L., Walker, P.J., 2004. Phylogenetic analysis and evidence of genetic recombination among six genotypes of yellow head complex viruses from *Penaeus monodon*. *Book of Abstracts, 7th Asian Fisheries Forum, Penang, Malaysia, 2004*, p. 210.
- Wijegoonawardane, P.K., Cowley, J.A., Phan, T., Hodgson, R.A., Nielsen, L., Kiatpathomchai, W., Walker, P.J., 2004. Genetic diversity in the yellow head nidovirus complex. *Virology* (in press).
- Wongteerasupaya, C., Sriurairatana, S., Vickers, J.E., Akarajomorn, A., Boonsaeng, V., Panyim, S., Tassanakajon, A., Withyachumnarnkul, B., Flegel, T.W., 1995a. Yellow-head virus of *Penaeus monodon* is an RNA virus. *Dis. Aquat. Org.* 22, 45–50.
- Wongteerasupaya, C., Vickers, J.E., Sriurairatana, S., Nash, G.L., Akarajomorn, A., Boonsaeng, V., Panyim, S., Tassanakajon, A., Withyachumnarnkul, B., Flegel, T.W., 1995b. 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.
- Yan, D.C., Dong, S.L., Huang, J., Yu, X.M., Feng, M.Y., 2004. White spot syndrome virus (WSSV) detected by PCR in rotifers and rotifer resting eggs from shrimp pond sediments. *Dis. Aquat. Org.* 59, 69–73.
- Yoganandhan, K., Thirupathi, S., Hameed, A.S., 2003. Biochemical, physiological and hematological changes in white spot syndrome virus-infected shrimp, *Penaeus indicus*. *Aquaculture* 221, 1–11.
- Yu, C.I., Song, Y.L., 2000. Outbreaks of Taura syndrome in Pacific white shrimp *Penaeus vannamei* cultured in Taiwan. *Fish Pathol.* 32, 21–24.
- Zhan, W.B., Wang, Y.H., Fryer, J.L., Yu, K.K., Fukuda, H., Meng, Q.X., 1998. White spot syndrome virus infection of cultured shrimp in China. *J. Aquat. Anim. Health* 10, 405–410.