Review article

How do abiotic environmental conditions influence shrimp susceptibility to disease? A critical analysis focussed on White Spot Disease

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ABSTRACT

White Spot Syndrome Virus (WSSV) causes White Spot Disease (WSD) and is historically the most devastating disease in the shrimp industry. Global losses from this disease have previously exceeded $3 bn annually, having a major impact on a global industry worth US$19 bn per annum. Shrimp are cultured predominantly in enclosed ponds that are subject to considerable fluctuations in abiotic conditions and WSD outbreaks are increasingly linked to periods of extreme weather, which may cause major fluctuations in pond culture conditions. Combined with the intensity of production in these systems, the resulting suboptimal physicochemical conditions have a major bearing on the susceptibility of shrimp to infection and disease. Current knowledge indicates that pond temperature and salinity are major factors determining outbreak severity. WSSV appears to be most virulent in water temperatures between 25 and 28 °C and salinities far removed from the isoosmotic point of shrimp. Elevated temperatures (> 30 °C) may protect against WSD, depending on the stage of infection, however the mechanisms mediating this effect have not been well established. Other factors relating to water quality that may play key roles in determining outbreak severity include dissolved oxygen concentration, nitrogenous compound concentration, partial pressure of carbon dioxide and pH, but data on their impacts on WSSV susceptibility in cultured shrimps is scarce. This illustrates a major research gap in our understanding of the influence of environmental conditions on disease. For example, it is not clear whether temperature manipulations can be used effectively to prevent or mitigate WSD in cultured shrimp. Therefore, developing our understanding of the impact of environmental conditions on shrimp susceptibility to WSSV may provide insight for WSD mitigation when, even after decades of research, there is no effective practical prophylaxis or treatment.

1. Introduction

Exponential growth in the global human population is placing significant pressure on natural resources and enhancing the need for greater food production. The most recent estimates of population growth predict that by 2050 there will be in excess of 9.7 billion people (United Nations, 2015). In order to meet food needs, production has to increase by at least 70% (FAO, 2009). An expanding middle income sector has resulted in an increased consumption of animal products of 2.5% annually (Garcia and Rosenberg, 2010; Peterson and Fronc, 2007). Aquaculture has the potential to significantly relieve some of these pressures, but is not always included in nutritional and food

security strategies (Fisher et al., 2017).

The majority of global aquaculture sites (~90%) operate on a small scale and are situated in Asia, where there has been an almost eight-fold growth in aquaculture since 1950 (FAO, 2016). In 2015, an estimated 76.6 million tonnes of aquaculture food products were harvested worldwide, 9.6% of which were farmed crustaceans. Euryhaline shrimp are the major output of crustacean farms and fisheries, with their farming dominated by two penaeid species; the Pacific whiteleg shrimp (*Penaeus vannamei*) and giant tiger prawn (*Penaeus monodon*). These penaeids are the two most valuable commodities in the international seafood trade, contributing $19bn and $5bn, respectively, to annual market sales (Food and Agriculture Organization of the United Nations

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Statistics Division (FAOSTAT), 2017). Although most crustacean farming takes place in Asia and Central America, the main consuming regions are the USA, Japan and Europe with exports fuelling the globalisation and success of the industry. Governments of developing countries that are capable of farming shrimp have exploited this opportunity as a means of reducing poverty locally. However, building ponds within tidal zones, which eliminates the cost of pumping water from the sea, has incurred an environmental cost to wetland ecosystems which in turn have suffered degradation impacting adversely on wild fishery nurseries (Barraza-Guardado et al., 2013; Didar-Ul Islam and Bhuiyan, 2016).

Rapid growth of the shrimp industry and intensification of farming methods has been coupled with the emergence of devastating diseases, arising as a result of complex interactions between the host, pathogen and environment. Significant losses in the region of up to 70% of annual marine and euryhaline shrimp harvests have been estimated to occur as a result of disease (Flegel, 2019), providing a clear constraint on current and future yields (Flegel, 2006; Lightner, 2011). Data from the Global Aquaculture Alliance (GAA) shrimp farming survey has revealed that the majority of losses (60%) were due to viral pathogens (Flegel, 2012).

Six viral diseases of Crustacea (including White Spot Disease, Yellow Head Disease and Taura Syndrome) are currently listed by the World Organisation for Animal Health (OIE), which recognise their potential to cause substantial economic loss and spread to trading countries. Of these, the greatest threat to shrimp aquaculture worldwide is White Spot Disease (WSD) caused by White Spot Syndrome Virus (WSSV) (Flegel, 2009). This single disease has caused an estimated 21bn USD in economic damage since its emergence detected in 1992 (Lightner, 2011; Stentiford et al., 2012).

WSSV infection affects both wild and farmed shrimp populations (Cavalli et al., 2010; Lo et al., 1996), but its impacts are most significant within intensive aquaculture settings, where animals are reared at unnaturally high densities. The majority of reviews thus far have focussed on host physiology and molecular responses to infection (Flegel and Srituyalucksana, 2011), nutrition and feed enhancement (Tacon et al., 2013) and the application of probiotics (Kumar et al., 2016) to prevent disease outbreaks. However, WSD outbreaks are increasingly associated with changes in environmental conditions that may lead to physiological stress and a compromised ability of shrimp to resist disease. Changes in water temperature, salinity, oxygenation and pH are particularly important in ensuring good animal health in aquaculture systems and managing water quality remains a major challenge for farms. Furthermore, there is often a lack of understanding amongst shrimp farmers on the importance of good water quality for optimising shrimp health (Kumaran et al., 2015). The high stocking density of aquaculture ponds contributes to many of the physicochemical stressors seen. As an example, high biomass can cause hypoxia and drive acidification due to elevated respiratory oxygen consumption and release of CO_2 (Vinatea et al., 2011). Periodic and synchronous moulting of these calcifying Crustacea also alters the ionic composition of the water across the production cycle (Saksena et al., 2006; Sahu et al., 2013). This process is exacerbated by pond-side management and prophylactic addition of inorganic salts, often based on an incomplete understanding of pond physicochemistry and resultant impacts on shrimp physiology. It is therefore important that the relationship between disease susceptibility and environmental abiotic conditions are determined, as suboptimal conditions within shrimp farms may promote infection, leading to increased losses across farms. Moreover, there may be practical solutions relating to improvements in specific pond conditions that could serve to reduce the rates of shrimp diseases.

This review critically evaluates evidence from the literature on the effects of alterations in abiotic environmental conditions on the occurrence and severity of WSD outbreaks. For each abiotic parameter considered within this review, we summarise the available information on their effects on penaeid shrimp physiology, evaluate evidence for altered WSD outbreak occurrence or severity and discuss the mechanisms that may lead to altered susceptibility (*e.g.* compromised immune response). This review also considers the potential for conditions in aquaculture systems to be optimised for disease prevention given their importance as predictors of outbreak. Opportunities for improvement include the monitoring and management of key water parameters that could otherwise be favourable to WSD outbreaks if left unmanaged. Critical appraisal of the data within this field has highlighted gaps for many of the factors considered important for shrimp aquaculture. The link between these factors and disease outbreak remain speculative due to the sparse available information. Due to the variable available information, it was not possible to conclude which abiotic factors are most important in determining shrimp disease susceptibility. For instance, it is also not known whether the mechanism for increased disease susceptibility is uniform across, or specific to, different abiotic factors. Finally, we identify areas in which further research will facilitate our understanding of disease dynamics and implementation of practical solutions to the problems caused by WSD in an aquaculture setting.

2. White Spot Syndrome Virus

White Spot Syndrome Virus was first detected in 1992 following an outbreak of WSD in shrimp farms of China (Chou et al., 1995) and has since spread throughout the major zones of shrimp farming in Asia, Australia, Central and South America (Bondad Reantaso et al., 2001; Inouye et al., 1994; Karunasagar et al., 1997; Park et al., 1998; Stentiford and Lightner, 2011; Zhan et al., 1998). It is currently listed by the International Committee on Taxonomy of Viruses (ICTV) as the sole member of the genus *Whispovirus* within the family *Nimaviridae* (Mayo, 2002a, 2002b). Several isolates have been sequenced and their differences are reviewed by Verbruggen et al. (2016). Behavioural and physiological symptoms of infection vary in severity between susceptible hosts, and latently infected animals are able to survive in the absence of observable disease symptoms. Diseased animals generally exhibit lethargic behaviour, hepatopancreatic discolouration, reduced feeding and preening, resulting in loosening of the cuticle (Chou et al., 1995; Pradeep et al., 2012). In some species, characteristic white calcified spots also appear on the exoskeleton (Chou et al., 1995). Despite the variation in clinical symptoms, the cumulative mortality of cultured shrimp is consistently high, rapidly reaching 90–100% mortality from 3 to 10 days post infection (Wang et al., 1999; Zhan et al., 1998).

3. Temperature

3.1. Temperature conditions within shrimp ponds

Shrimp are typically reared in enclosed, shallow ponds where low levels of water exchange coupled with tropical weather conditions (Nicholls et al., 2005) allow for significant seasonal and diurnal fluctuations in water temperature to occur. The most commonly farmed penaeid shrimp, *P. vannamei*, is able to tolerate wide variations in temperature, ranging from 7.5 to 42.0 °C, with farming recommended above 12 °C (Kumlu et al., 2010). The optimal temperature for growth of this species is reported to depend on size, with small shrimp (< 5.0 g) growing most rapidly at 30 °C and larger shrimp (> 16.0 g) growing most rapidly at 27 °C (Wyban et al., 1995).

Few studies are available that state the temperature conditions within shrimp ponds and how they fluctuate. Many farmers have the capacity to measure this, however this information is not publically available, and limited published studies link rapid temperature fluctuations in ponds (of 4.2–4.5 °C) following a tropical storm with variation in viral loads and disease outbreak occurrence (Zhang et al., 2016). Of the limited available data on shrimp pond temperature, this is shown to range between 25 and 35 °C (Sahu et al., 2013), whilst in India, water temperatures in semi-intensive shrimp ponds and rice paddy fields have been shown to range between 22 and 37 °C (Gunalan

et al., 2010; Saksena et al., 2006; Selvam et al., 2012), with lowest temperatures being recorded in the morning and highest in the afternoon (Tendencia & Verreth 2011). Due to the limited data in the literature, it is unclear whether these broad temperature ranges are representative of intensive and extensive aquaculture systems on a wider global scale.

Associations between water temperature fluctuations and WSD outbreaks have been inferred within some studies but no causal link proven. Daily fluctuations > 3–4 °C have been weakly correlated with episodes of WSD outbreak (Tendencia & Verreth, 2011) and during the monsoon season, where runoff water from tropical storms led to reductions in pond temperature, outbreaks have been recorded (Esparza-Leal et al., 2010; Peinado-Guevara and López-Meyer, 2006; Tendencia et al., 2010). Modelling of historic data suggests that the incidence of WSD is increased in low ambient temperatures (24.5–27.2 °C) and where daily atmospheric temperature variations are > 10 °C (Piamsomboon et al., 2016). It is unclear to what extent these outbreaks were initiated by changes in water temperature, or by dilution of salinity and increased contaminants originating from runoff water. Seasonal variations in WSD prevalence in broodstock and larvae have also been reported, with increased outbreaks during monsoon season (Withyachumnarnkul et al., 2003), supporting the hypothesis that reduced temperatures may confer an advantage to WSSV infection/virulence. Collectively, these studies illustrate the wide natural variation in pond water temperature and propose a link between unstable temperature conditions and increased WSD outbreaks.

3.2. Disease restrictions at high and low temperatures

WSSV has a wide thermal tolerance that overlaps the entire thermal range of *P. vannamei*, remaining infective following cryopreservation (Momoyama et al., 1998). It is inactivated upon exposure to temperatures above 50 °C for at least 120 min (Nakano et al., 1998). Fig. 1 illustrates the relationship between water temperature and both shrimp growth and WSSV replication. Controlled laboratory experiments have demonstrated that a temperature range between 25 and 28 °C provides optimum conditions for WSSV infection; resulting in higher levels of mortality, with earlier disease onset (Jiang et al., 2019; Raj et al., 2012; You et al., 2010), and higher WSSV copy numbers (You et al., 2010) in WSSV-infected shrimp and crayfish (Jiang et al., 2019) (summarised in Table 1). Protection (*i.e.* reduced mortality and virus replication) from

WSD has consistently been reported at high temperatures (> 30 °C) (Granja et al., 2006, 2003; Jiang et al., 2019; Raj et al., 2012; Vidal et al., 2001; You et al., 2010) regardless of virus exposure route. Very high temperatures (> 50 °C) inactivate WSSV but cannot be applied as a WSD control mechanism as they fall above the maximum thermal tolerance (CTMax) of shrimp.

Laboratory experiments by Rahman et al. (2007a; 2007b) demonstrated that the protective effect of high culture temperatures is dependent on both the duration of the periods of increased temperature and the stage of infection when they occur. In *P. vannamei* juveniles exposed to WSSV during the acute infection stage (12 h post injection), exposure to 33 °C for periods > 6 h per day delayed signs of outbreak and mortality for both high (Thai-1) and low (Viet) virulence WSSV strains. Conversely, periods of increased temperature that lasted only 6 h resulted in accelerated disease progression and increased cumulative mortality (Rahman et al., 2007a). In a second study by these authors, temperature increases from 27 °C to a constant 33 °C during acute infection (prior to clinical signs), reduced and delayed mortality, whereas during chronic infection disease progression was accelerated (Rahman et al., 2007b). During chronic infection, as shrimp succumb to disease, increased stress may prevent the protective effect of high temperature and lead to increased virus replication. However, neither study quantified the viral load (*e.g.* by qPCR) to confirm that this effect was due to reduced viral replication, and thus the mechanism that reduces efficacy of increased temperature during chronic infection was not established.

At temperatures of 32–33 °C, WSSV retains the ability to infect and kill *P. vannamei* (Du et al., 2008; Vidal et al., 2001). The protective effects seen are therefore not due to viral inactivation, and may occur (at least in part) as a result of reduced viral replication (Reyes et al., 2007). A temperature-induced reduction in viral replication has been demonstrated in a range of invertebrate viruses exposed to high environmental temperatures within their host, such as Ross River Virus in *Ochlerotatus vigilax* (Kay and Jennings, 2002), Western Equine Encephalomyelitis Virus in *Culex tarsalis* (Kramer et al., 1983) and Chikungunya Virus in *Aedes albopictus* (Westbrook et al., 2010). These elevated temperatures may be impairing the activity of viral enzymes or enhancing the ability of hosts to respond to infection, with similar mechanisms offering a useful line of investigation in the case of WSSV. In addition, chemically-induced temperature-sensitive mutations in baculovirus enzymes have been shown to have significant implications
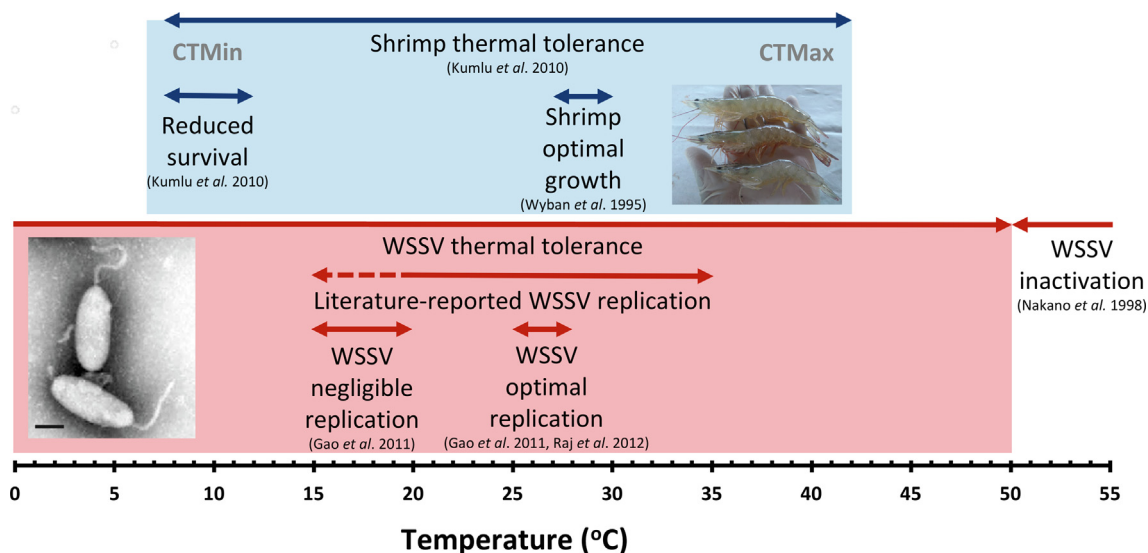

Fig. 1. Thermal ranges for shrimp growth and WSSV replication. Thermal tolerance and optimal growth ranges of Pacific whiteleg shrimp (*Penaeus vannamei*) (blue), and thermal tolerance and optimal replication ranges of White Spot Syndrome Virus (WSSV) (red). The abbreviations on the figure represent critical thermal minima (CTMin) and critical thermal maxima (CTMax). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 1
Laboratory experiments studying the effects of temperature on WSD.

	Species	Temperature	Impact of temperature on WSD outcome	Citation
1	*P. clarkii*	19, 25 and 32 °C	• Reduced mortality and fewer viral copies at 19 °C and 32 °C compared to 25 °C • Impact on immune gene transcription	(Jiang et al., 2019)
2	*P. monodon*	16, 25, 27, 28, 32 and 36 °C	• Significantly higher survival at 32 °C and 36 °C	(Raj et al., 2012)
3	*P. japonicus*	27 and 31 °C	• Mortality reduced at 31 °C compared to 27 °C • WSSV load higher at 27 °C than 31 °C • THC (total haemocyte count) and PO (phenoloxidase) activity significantly higher in shrimp at 31 °C	(You et al., 2010)
4	*P. vannamei*	27 °C-33 °C	• Moralities reduced at 33 °C • Temperature fluctuations to 33 °C for 6 h had both negative (WSSV-Viet) and positive effects (WSSV-Thai-1) on WSD mortalities • Temperature increases of 12 or 18 h per day (WSSV-Thai-1) had positive effects on WSD	(Rahman et al., 2007a)
5	*P. vannamei*	27, 30 and 33 °C	• Shrimp kept at a constant 33 °C showed no signs of disease and low (0–30%) mortality • At constant 27 °C, 30 °C or switch to 27 °C post-challenge shrimp displayed disease symptoms within 24 h	(Rahman, et al., 2007b)
6	*P. clarkii*	10 and 24 °C	• 100% mortality in crayfish transferred from 10 °C to 24 °C following WSSV challenge compared to 0% in those transferred from 24 °C to 10 °C • Lower water temperature reduced viral replication	(Du et al., 2008)
7	*P. vannamei*	25.8 and 32.3 °C	• Survival always above 80% in 32.3 °C tanks compared to 0% at 25.8 °C • Hemolymph PCR negative for WSSV at 32.3 °C	(Vidal et al., 2001)
8	*P. vannamei* subcuticular epithelial cells	26 and 33 °C	• Overexpression of viral genes at 26 °C compared to 33 °C • Hyperthermia reduced WSSV gene expression	(Reyes et al., 2007)
9	*P. chinensis*	15, 23, 28 and 33 °C	• 100% mortality reached by day 6 at 23 °C, delayed mortalities at 15 °C and 33 °C • Greatest viral loads also at 23 and 28 °C • THC lowest at 28 °C	(Guan et al., 2003)
10	*P. vannamei*	25 and 32 °C	• Increased apoptotic index in shrimp at 32 °C	(Granja et al., 2003)
11	*P. chinensis*	15, 20, 25, 30 and 35 °C	• Temperature identified as a crucial factor determining WSSV replication • 25 °C optimum temperature for WSSV replication • Temperatures of 15 and 35 °C significantly reduced WSSV proliferation	(Gao et al., 2011)

for various stages of viral replication and the assembly of dsDNA viruses; including a complete lack of expression of late viral proteins such as envelope proteins (Fan et al., 1996; Shikata et al., 1998). It is plausible therefore that some WSSV genes are only expressed when temperatures remain below 32 °C. To this end, short-term (~12 h) high temperature exposures of aquaculture ponds during the grow out period has been proposed to reduce viral disease outbreaks. In the case of Gill-Associated Virus (GAV) this approach has been shown to effectively reduce chronic infections in *P. monodon* likely due to increased expression of heat shock protein 70 (*Hsp70*) (de la Vega et al., 2006). However, the emergence of Taura Syndrome Virus (TSV) isolates from Belize (TSV-BZ) able to replicate under hyperthermic conditions, where the reference TSV strain (TSV-HI) could not (Côté and Lightner, 2010), indicates that hyperthermic protection can be strain-dependent, and thermal manipulation as a management technique may result in the appearance of temperature-permissible mutants. Moderate pond temperature increases to > 30 °C have also been shown to result in mortalities in uninfected shrimp (Gao et al., 2011; You et al., 2010), questioning the ubiquity of water temperature manipulation as a suitable solution for preventing infection.

3.3. Mechanism of hyperthermic protection

Infections often drive dynamic changes in thermal preference, where aquatic hosts temporarily move towards warmer waters to induce fever and boost immune parameters. Behavioural thermoregulation in response to infection is well-documented in aquatic vertebrates (Boltaña et al., 2013; Reynolds et al., 1976), and has also been described in invertebrates such as the desert locus *Schistocerca gregaria* (Elliot et al., 2002) and freshwater crayfish *Cambarus bartonii* (Casterlin and Reynolds, 1980), and inferred in the Ponto-Caspian amphipod *Dikerogammarus villosus* (Rachalewski et al., 2018). Hyperthermic protection (moving to areas of elevated temperature) is a characteristic feature of several shrimp species to viral infections, such as Infectious

Myonecrosis Virus (IMNV) (da Silva et al., 2015) and Infectious Hypodermal and Haematopoietic Necrosis Virus (IHHNV) (Montgomery-Brock et al., 2007). This suggests that such a strategy may be a ubiquitous response of shrimp to viral infections; however, it is unclear what impact this has on immune function. The presence of such a response has direct implications for enhanced pond design. Traditionally ponds are approximately one metre in depth and uniform. Introducing a varied pond depth, which would enhance temperature stratification, may offer a practical and low-cost strategy to using temperature as a disease prophylaxis, enabling shrimp to display behavioural thermoregulation. This is therefore an important area for future study.

Despite this information, the mechanisms mediating WSD protection at elevated temperatures is not fully understood. Although several studies have proposed that shrimp have increased immunocompetence at elevated temperatures, evidence available to support this hypothesis is somewhat limited. WSSV-infected shrimp reared at > 31 °C had a significantly higher total haemocyte count (THC) (Guan et al., 2003; You et al., 2010) and phenoloxidase (PO) activity (an integral enzyme involved in invertebrate innate immune defences) when compared to infected shrimp reared at 27–28 °C (You et al., 2010). However, an increased apoptotic index associated with hyperthermia in WSSV-infected shrimp has also been proposed as a mechanism for viral clearance (Granja et al., 2003), which would result in contradictory lower THCs in WSSV-infected shrimp at high temperatures. It has been suggested that these effects could occur as a result of temperature-induced changes to the transcription of immune related genes (such as *Hsp70*) (Jiang et al., 2019). In particular, heat shock 70 kDa protein cognate 5 in *P. vannamei* might contribute to WSSV infection tolerance by preventing protein aggregation (Yuan et al., 2017). Temperature increases may therefore enhance the immune system within shrimp potentially delaying mortalities to reach successful harvests, but further evidence is necessary to support such a hypothesis.

A recent study in freshwater crayfish *Pacifastacus leniusculus* has hypothesised that WSSV entry into cells could occur only in replicating

cells at an optimum water temperature (Korkut et al., 2018). In addition, there is now strong evidence for the involvement of heat shock proteins in WSSV tolerance at elevated temperatures. Knockdown of NAD-dependent aldehyde dehydrogenase *(aldh),* proteasome alpha 4 subunit (*proteasome α4*) and *Hsp70* by RNA interference in *P. monodon* resulted in the disappearance of hyperthermic protection when challenged with WSSV at 32 °C, indicating the involvement of these factors in the host protection mechanism (Lin et al., 2011). Furthermore, study of heat shock proteins (particularly heat shock 70 kDa protein cognate 5) has confirmed their involvement in WSSV tolerance (Yuan et al., 2017). However, further research is required to fully elucidate the functionality of this response, and the impact of temperature on virus entry, replication, assembly and release.

3.4. Temperature management and future directions

Taken together, the literature indicates that the optimum temperature range for virus replication is within the optimal growth range of its penaeid host. This is to be expected as viruses depend almost entirely on their hosts for their replication. Hyperthermic protection depends both on the duration of hyperthermia and on the stage of infection, and occurs by mechanisms that are not yet fully understood but may involve the increased immune responses of the host and/or upregulation of heat shock proteins. Without a clear understanding of the physiological consequences of culturing penaeids at high-temperatures it would be ill-advised to promote this costly strategy to manage WSD among farmers. In addition, due to WSSV having a wider thermal tolerance window than shrimp (Fig. 1), alterations in temperature have the potential to contribute to the mitigation of WSD but not to completely prevent or treat this disease.

4. Salinity

4.1. Osmolarity within shrimp ponds

Penaeid shrimp are euryhaline, generally exhibiting a type 3 osmoregulation pattern during their development (Charmantier et al., 1988); they begin life as osmoconformers and transition to osmoregulators once metamorphosed into their adult form (Chong-Robles et al., 2014). The majority of ion and water exchange in penaeids takes place in the gill, gut and hypodermal tissues (Charmantier et al., 1988), with *P. vannamei* able to tolerate extreme salinities of 0.5 to beyond 45 practical salinity units (psu) (equivalent to 0.5–45 ppt) (Wyban and Sweeney, 1991).

Salinity has been extensively studied in relation to WSSV infection as it affects many aspects of shrimp physiology, including: metabolic rate, susceptibility to toxic metabolites, feeding rate, moulting, growth and development (Brito et al., 2000; McCoid et al., 1984; McNamara et al., 1986; O'Brien, 1994; Pequeux, 1995; Ponce-Palafox et al., 1997). Salinity is shown to vary greatly in shrimp ponds, ranging from $0-40$ psu depending on pond locality, which is determined by the site-specific degree of water evaporation and rainfall (John et al., 1990; Saksena et al., 2006; Selvam et al., 2012; Zhang et al., 2016). *P. vannamei* inhabits a wide range of salinities from 1 to 40 psu (Menz and Blake, 1980), with an optimum salinity that is close to its isoosmotic point (24.7 psu). Direct comparison of pond salinity data across sites is difficult as measurements are not standardised. Nonetheless, pond salinity predominantly depends on the source of water each farm uses, which dictates whether high (seawater) or low (freshwater) salinity culture is employed. In each condition, shrimp may be under osmotic stress during periods when salinity deviates from its optimum potentially increasing their susceptibility to other stressors and/or disease. Salinity is measured regularly by farmers, and adjusted by the addition of salts, especially following periods of heavy rainfall. These rapid changes in salinity are likely to result in physiological stress to culture animals and therefore alterations in their susceptibility to disease.

Outbreaks in ponds are frequently recorded following periods of heavy rainfall where salinity drops to below 15 psu (Tendencia & Verreth 2011) and following heavy surface runoff into ponds (Oseko, 2006; Tendencia et al., 2010). As well as reducing salinity and temperature, such runoff can also carry contaminants that modify the biotic and abiotic conditions within the ponds. There is no field data currently available that links elevated pond salinity (such as can result from evaporation) with a greater risk of disease outbreak, although this is likely to cause significant stress to cultured animals.

4.2. High and low salinities are linked to disease outbreak

Following WSSV infection, the ability of *P. vannamei* to osmoregulate decreases significantly. Studies have shown that penaeid shrimp maintained at suboptimal salinities were more susceptible to WSD, succumbing to disease earlier, exhibiting increased mortality (Lin et al., 2012; Liu et al., 2006; Ramos-Carreño et al., 2014; Vaseeharan et al., 2013) and displaying increased copy numbers of viral major structural protein VP664 transcripts (Liu et al., 2006; Ramos-Carreño et al., 2014). These effects were most severe when there was a rapid rate of salinity change (Liu et al., 2006; Van Thuong et al., 2016). The ability to successfully farm shrimp at stable, low salinities (< 5 psu) supports the theory that it is the rate of change, rather than the absolute salinity, that may play a pertinent role in determining disease susceptibility. This is particularly important in the face of climate change, which is projected to result in increased occurrence of extreme weather events that result in rapid alterations to abiotic factors (Fischer and Knutti, 2015). At high salinities (well above 35 psu), shrimp have been shown to undergo weight loss and exhibit abnormally low locomotive activity in both infected and uninfected states; possibly due to the elevated energetic demand of osmoregulation, as well as the water loss experienced during acclimation to high salinities (Bray et al., 1994; Perez-Velazquez et al., 2007; Ramos-Carreño et al., 2014).

There is growing evidence that increased susceptibility to WSD is due to an inability of osmotically-stressed shrimp to mount a regular immune response. These responses have been characterised by changes in haematological and biochemical variables including: THC, total haemolymph protein level, PO activity and alkaline phosphatase activity (Joseph and Philip, 2007). THC was shown to decrease in shrimp following exposure to osmotic stress combined with WSSV infection (Liu et al., 2006; Vaseeharan et al., 2013; Yu et al., 2003). Haemocytes are responsible for clotting and the elimination of foreign materials from the haemolymph, and reductions in levels of haemocytes are strongly correlated with increased susceptibility to pathogens (Le Moullac et al., 1998; Persson et al., 1987). Coagulation at WSSV injection sites, phagocytosis and cell lysis during osmoregulation are the hypothesised causes of reduced THC (Vaseeharan et al., 2013), with the additional reduction due to salinity stress likely playing an important role in modifying shrimp immunocompetence.

Following long-term (24-week) low salinity (2.5 and 5 psu) exposure, *P. vannamei* is shown to have significantly lower immune parameter measures such as PO activity, respiratory bursts, superoxide dismutase (SOD) activity and lysozyme activity than those reared at 25 psu (Lin et al., 2012). Despite decreased haemocyte counts, the longevity and expression of pathogen recognition proteins that initiate the proPO cascade (including lipopolysaccharide and β-glucan binding protein and peroxinectin) were increased (Lin et al., 2012). However, these results must be interpreted with care, as the water temperature varied greatly during this experiment (20–32 °C), making the impact of salinity as a single factor impossible to assess.

Haemocytes are responsible for the production of PO, which is often increased following reductions in THC as a compensatory mechanism to maintain pathogen resistance (Le Moullac et al., 1998). However, conflicting results have been published with respect to salinity impacts on PO production. Some support a projected increase associated with osmotic stress (Liu et al., 2006; Yu et al., 2003), whilst others report a

decrease (Vaseeharan et al., 2013) or no significant change (Joseph and Philip, 2007). In the latter study, *P. monodon* were maintained at 15 psu before acute changes to 0 psu and 35 psu, but all of these experimental salinities are far from the isoosmotic point of this species (24.7 psu), which may explain the lack of any PO response. Salinity increases can lead to an acidosis in the haemolymph of decapod crustaceans, whilst decreases can lead to alkylosis (Whiteley et al., 2001), which may drive the observed changes to shrimp immune function.

Damage to the epithelial tissues, that includes the gills, which are key players in osmotic and ionic regulation (Henry et al., 2012) and also the primary target for WSSV infection, may also result in increased WSD susceptibility. Carbajal-Sánchez et al. (2008) showed that susceptibility to WSD was constant at a range of salinities from 2 to 35 psu, except at 15 psu where infections in the gills and gastric epithelia were more severe. This study did not address specifically whether different salinities affected tissue structure in the absence of WSSV infection as a control, and instead focussed on counting hypertrophied nuclei to gauge severity. In addition, whilst per-oral exposure to virions provides a more accurate reflection of natural exposure routes, this method can result in uneven virus dose delivery to animals that is biased by larger, more voracious, individuals consuming greater viral loads (Gitterle et al., 2006).

The combined effects of possible cellular damage, increased osmoregulation requirements, and reduced immune parameters are likely to explain the increased susceptibility of shrimp to WSD at non iso-osmotic salinities and is supported by evidence that susceptibility to Yellow Head Virus (YHV) (Navarro-Nava et al., 2011), TSV (Lightner, 2011), *Photobacterium samselae* subsp. *damselae* (Wang and Chen, 2006) and *Vibrio alginolyticus* (Lin et al., 2012; Wang and Chen, 2005) infections also increased in penaeids reared under those conditions.

4.3. Implications for salinity management on farms

At a range of salinities from 0 to 40 psu, severe infection levels are rapidly reached indicating that modifying salinity alone will not be sufficient to deter WSSV outbreaks. At salinities of 25 psu (isoosmotic), shrimp demonstrate a greater resilience to infection, with enhanced immune parameters and greater energy availability due to the diminished need for continuous osmoregulation and stress responses. However, the results of immune function studies must be interpreted carefully, taking into account the experimental design adopted, as at the time of the WSSV challenge shrimp immune systems may have been fatigued following periods of acclimation to suboptimal salinities (and salinity stress).

5. Dissolved oxygen concentrations

5.1. Oxygenation within aquatic environments

Within aquatic systems, dissolved oxygen (DO) concentrations are heterogeneous, fluctuate depending on physical, chemical and biological factors of the surrounding area, and undergo strong diurnal variations, plummeting overnight due to the continued respiration of aquatic life in the absence of photosynthesis. Oxygen becomes depleted when demand outweighs autochthonous production and can be driven by anthropogenic factors including the over-enrichment of the water with nutrients (*e.g.* phosphorous compounds); usually via surface water runoff from nearby agricultural sites and subsequent eutrophication. The resulting hypoxic conditions can result in areas unable to support the majority of aquatic life, giving rise to patches of habitat loss and local degradation of water quality (Altieri and Gedan, 2015; Jenny et al., 2016). *In situ* pond measurements of DO concentration are limited with pond-scale studies reporting DO levels ranging from 2.9 to 5.0 mg/L (Gunalan et al., 2010; Zhang et al., 2016). However, despite this knowledge gap, evidence suggests that DO concentrations are significantly reduced following heavy rainfall (Zhang et al., 2016).

5.2. Oxygen regulation in penaeids

Penaeid shrimp are oxyregulators, meaning they are able to actively maintain their internal O_2 concentration independently of environmental O_2 partial pressure, up to a critical threshold (Herreid, 1980). At or below this threshold, their critical oxygen tension (P_{CRIT}; which is dependent on temperature and life stage), O_2 consumption becomes the limiting factor for metabolic rate. During short-term exposure to hypoxia, shrimp exhibit erratic behaviour and increase swimming to avoid unfavourable conditions (Renaud, 1986). Conversely, during prolonged exposure to reduced environmental oxygen (below P_{CRIT}), penaeid shrimp reduce their movement and lower their metabolic rate and O_2 consumption (MacKay, 1974). Prolonged absence of sufficient DO also leads to an increase in anaerobic metabolism, in order to maintain survival (Kulkarni and Joshi, 1980).

During short-term exposures to hypoxia, shrimp can also display avoidance behaviour, characterised by an increase in swimming and erratic movement, aimed at moving away from areas with unfavourable conditions (Renaud, 1986). Oxygen-sensitive transcription factors (including hypoxia inducible factors (HIF)) are responsible for inducing a wide range of gene expression changes when the cellular concentrations of O_2 are reduced in order to enhance survival in hypoxic conditions. To date, HIF-1 has been characterised in *P. vannamei* (Sonanez-Organis et al., 2009) and its expression is associated with induction of glycolytic genes (Godoy-Lugo et al., 2019) and increased viral load in shrimp (Miranda-Cruz et al., 2018) during WSSV infection.

5.3. DO concentrations and disease outbreaks

Generally, it is advised that DO concentrations are maintained above 3.0 mg/L within aquaculture systems to sustain shrimp cultures, and should be at least 5.0 mg/L within intensive systems (Cheng et al., 2003b). However, these values are less than or equal to the P_{CRIT} (the O_2 partial pressure below which an animal's oxygen consumption rate becomes dependent on O_2 partial pressure) of *P. vannamei* which is 5.0 mg/L (at 28 °C) (Martínez-Palacios et al. 1996). DO concentrations for shrimp culture are not generally reported within the literature, but oxygen concentrations at which mortalities were reported were as low as 1.2 mg/L in some instances (MacKay, 1974). To increase our understanding of pond conditions, accurate measurements of DO are required alongside temperature. These should be made throughout 24 h periods, at different pond depths, and accounting for the impact of respiring microbes present within the water and sediments on the pond DO budget. A single laboratory study investigating the impacts of hypoxia on WSSV infection demonstrated that at 2.06 mg/L DO (at 23 °C) *P. vannamei* susceptibility to infection increased causing significantly higher cumulative mortalities (Lehmann et al., 2016). However, as DO was experimentally maintained in part by respiratory O_2 consumption by animals, CO_2 may have risen concomitantly throughout the study period due to respiration. Therefore within this experimental setting it is not possible to determine the relative contribution of reduced DO and increased CO_2 on the susceptibility of shrimp to WSSV.

There is a significant lack of information on the impacts of DO concentrations on WSD. Although modelling of pond data from infected farms in Mexico has inferred that DO plays an important role in determining the severity of mortality events (with higher aeration earlier in the culture period resulting in reduced shrimp mortalities in small ponds (Ruiz-Velazco et al., 2010)), experimental data is required to support this hypothesis. Hypoxia has been shown to increase susceptibility of shrimp to bacterial infections including *Vibrio alginolyticus, Enterococcus* (KM002) and *Vibrio parahaemolyticus* (Cheng et al., 2002a; Le Moullac et al., 1998; Mikulski et al., 2000). However, it is not yet clear from the available data whether hypoxia increases susceptibility to WSD, and, importantly, the relative impact of low oxygen in ponds compared to high CO_2, as both stressors are often linked.

5.4. Implications for DO management on farms

Evidence suggests that maintaining DO is important to reduce the occurrence and/or minimise the impacts of disease outbreaks. Monitoring of pond DO concentrations is of interest to farmers as under hypoxic conditions feed consumption and growth rate is decreased and penaeid shrimp are thought to exhibit increased susceptibility to disease due to depression in the phagocytic activity of haemocytes (Direkbusarakom and Danayadol, 1998). The minimum required aeration within ponds will depend on the P_{CRIT}, density, biomass and age of the species being cultured and the phytoplankton/microbe community within the pond (such as in biofloc systems (Lara et al., 2017)). DO concentrations are commonly maintained either by pumping air in from the base of ponds or by surface agitation using paddlewheel aerators, which have been shown to increase pond yield (Wyban et al., 1989). However, in order to maximise economic return from aerator use, diurnal patterns in DO concentrations must be monitored. For example, it has been proposed that in ponds containing photosynthetic organisms, aeration may not be required during daylight hours when peak photosynthetic activity provides supersaturation of ponds (McGraw et al., 2001). The relationship between DO concentrations, paddlewheel aeration and shrimp feeding rates have been determined and provide a powerful tool to allow aquaculturists to determine aeration requirements based on maximum daily feed amounts and stocking densities (Hopkins et al., 1991).

6. Hypercapnia and pH

6.1. pH of aquatic environments

Hypercapnia, which is the elevation of carbon dioxide (CO_2) concentrations in aquatic systems, occurs as a result of biological activity, via the build-up of respiratory derived CO_2. Peak CO_2 concentrations therefore usually occur overnight in aquaculture ponds when photosynthetic organisms cease carbon fixation due to lack of light, or following feeding when respiratory activity is very high. Hypercapnia results in acidification of pond water and directly impacts the physiology of the organisms in the pond (Burnett, 1997; Metzger et al., 2007). pH is monitored extensively in shrimp aquaculture, and manipulated artificially via the addition of alkali compounds (*e.g.* NaOH, CaO, CaOH), which aims to maintain ponds within an ideal pH range from 7.8 to 8.3 to support high growth and calcification in euryhaline shrimp (ASEAN, 1978). Nonetheless, despite a narrow proposed ideal range, typical pH conditions in ponds across India and Bangladesh have been shown to range from 5.24 to 8.25 (Sahu et al., 2013; Saksena et al., 2006), suggesting that conditions are not always maintained within this ideal boundary. Moreover, despite active pH manipulation, alkali addition does not solve the underlying causal increase in pCO_2, an issue that remains largely overlooked due to the difficulty of measuring CO_2 directly in aquatic systems. Further data is required to determine typical pCO_2 ranges in shrimp ponds, but the limited available data from aquaculture settings that employ minimal water exchange indicate that pCO_2 may be extremely high (up to 17,000 µatm or 35x current atmospheric levels) (Ellis et al., 2017).

6.2. pH regulation in penaeids

Decapod crustaceans buffer their body fluids against pH changes in the environment by altering the exchange of ions at the gills (Henry et al., 1981), altering bicarbonate concentration in their haemolymph (Defur, 1988) and by mobilising mineral carbonates of their exoskeleton (Adelung, 1971; Henry et al., 1981; Morgan and McMahon, 1982). Each of these mechanisms is however energetically expensive, with costs traded off against growth and other biological processes. In accordance with this, shrimp mortality is increased at both high (> 8.5) and low (< 6.0) pH stress (Chen and Chen, 2003; Han et al., 2018;

Wang et al., 2002; Zhou et al., 2009). *P. vannamei* exhibit a strong adaptive ability during gradual pH decrease (6.65) defined by a stabilising cumulative mortality (6.67%), length and weight gain percentage. In contrast, gradual pH increase (9.81) resulted in steadily increasing mortalities (up to 39.9%) and continual length and weight gain percentage decreases (Han et al., 2018). However, rapid decreases in pH may negatively impact the ability of shrimp to regulate haemolymph pH effectively (Pan et al., 2007). In sediment dwelling organisms like penaeid shrimp, haemolymph osmotic pressure is significantly reduced when sediment pH is lowered from 7.0 to 6.5 (Lemonnier et al., 2004) and results in slowed penaeid growth either through decreased moulting frequency, a reduced size increment during moulting, or a combination of the two. Under reduced pH conditions ions required for carapace formation are depleted, altering carapace thickness, hardness and structure in decapod crustaceans (Wickins, 1984). In densely stocked conditions, the shore crab, *Carcinus maenas,* invests resources in producing a thicker carapace to defend against nearby neighbours (Souza et al., 2011). Reduced carapace calcification at low pH or reduced environment bicarbonate may therefore impede the ability of crustaceans to produce this protective layer in certain culture conditions and increase the probability of crop loss by cannibalism.

6.3. pH and disease outbreak

Within the wider literature, there are few environmental studies addressing the effects of hypercapnia on shrimp physiology, and fewer that consider hypercapnia together with disease outbreaks. Current knowledge for WSD is limited to pond-scale studies, which are unable to link single environmental conditions as causal to disease outbreak. Laboratory studies that have tested this suggest that variations in CO_2 and pH increase the risk of infection in shrimp by opportunistic pathogens such as *V. parahaemolyticus* (Han et al., 2018; Mikulski et al., 2000), *V. alginolyticus* (Chen et al., 2015; Li and Chen, 2008) and *Lactococcus garvieae* (Cheng et al., 2003a). Gao et al. (2011) reported that pH had a lower impact on WSSV proliferation in Chinese shrimp compared to temperature and salinity. Optimum virus replication occurred at pH 8.0 and was restrained at both high (8.5 and 9.0) and low (6.5 and 7.5) pH. This is in contrast with data generated by monitoring pond conditions which inferred that high pH may be associated with WSSV outbreaks when in combination with low temperatures (Gunalan et al., 2010), consistent with earlier predictions that high pH may be associated with mass mortalities (Corsin et al., 2001). The discrepancy between these results is most likely due to the variation in methods, with one study altering pH alongside temperature and salinity within tanks and the other using field data to infer correlations between conditions and outbreak events in ponds. Hydrochloric acid addition was used to manipulate pH within laboratory experiment, which does not replicate pond conditions as it has no impact on pCO_2 concentrations, the driver of pH changes in intensive production settings. Recently, Kathyayani et al. (2019) demonstrated increased cumulative mortality in WSSV-injected *P. vannamei* following exposure to basic pH (pH 8 and pH 10) stress. In order to determine the individual impacts of pH and of pCO_2 on WSD status of ponds, further studies that examine the impact of pH and pCO_2 each in isolation, before considering their interaction and impacts in combination with other factors in environmentally realistic scenarios are required.

6.4. Implications for pH management in farms

Throughout the culture period of shrimp, increasing biomass drives CO_2 production, and subsequent pond acidification. Maintenance of optimal pH (target 7.8–8.3) in shrimp ponds is achieved by the addition of alkali compounds; some of which replenish ions required for carapace formation following moults (*e.g.* CaO), and others that may enhance their depletion via calcium carbonate precipitation (*e.g.* NaOH). Current evidence suggests that whilst considered alongside other

factors, deviations in pH from an optimal range results in increased occurrence of WSD outbreaks (Gao et al., 2011). Elevated pH increases ammonia toxicity (Randall and Tsui, 2002) and prolonged exposure can result in excessive calcium deposition in pockets beneath the exoskeleton leading to misdiagnosis of WSD in shrimp farms (Sahoo et al., 2005). Therefore, pH should be managed to minimise ammonia toxicity, prevent unnecessary emergency harvests and ensure fast and efficient carapace formation to minimise losses by cannibalism. Critically farmers must also consider the wider implications of elevated pCO_2, as well as the impacts of changes in other minerals within the water, which are presently not considered and therefore may be overlooked with respect to WSD outbreaks.

7. Nitrogenous compounds

7.1. Nitrogenous compounds in the aquatic environment

Within pond ecosystems (particularly those that are fully enclosed), ammonia (NH_3), nitrite (NO_2^-) and nitrate (NO_3^-) concentrations often exceed naturally occurring levels (Camargo et al., 2005; Ferreira et al., 2011) due to the degradation of excess feed and metabolic wastes excreted by culture animals (Millamena, 1990; Nhan et al., 2006). In general, the toxicity of NH_3, NO_2^- and NO_3^- in crustaceans varies depending on developmental stage, with greater potency and often the largest differences in tolerance reported during larval and juvenile stages (Furtado et al., 2014; Jensen, 1990; Kuhn et al., 2010; Mallasen and Valenti, 2006; Romano and Zeng, 2007; Zhao et al., 1997). Elevated concentrations of these compounds have similar physiological impacts on penaeid shrimp, including reduced feed intake, slowed development, significantly reduced growth rates despite increased moult frequency (Chen and Chen, 1992; Kuhn et al., 2010), and damage to the gills including fouling, loss of structure and loss of function (De Freitas Rebelo et al., 2000; Furtado et al., 2014; Kuhn et al., 2010; Romano and Zeng, 2007). Increases in temperature and pH are also critically linked to increasing NH_3 toxicity in aquatic systems (Wurts, 1992) and oxygen consumption in NH_3-exposed penaeids is significantly higher than controls (Chen and Lai, 1992; Chen and Lin, 1995; Racotta and Hernández-Herrera, 2000; Wang et al., 2003). Exposure to nitrogenous stress results in immunological responses in some crustaceans including reductions in THC due to oxidative damage and apoptosis (Xian et al., 2011), and significant changes in the expression of many genes that are thought to play a role in apoptosis and immune function (Guo et al., 2013; Lu et al., 2016). These alterations indicate a compromised immune response (Jiang et al., 2004; Rodríguez-Ramos et al., 2008) which may in turn infer an increased susceptibility to infections.

7.2. Nitrogenous compounds and disease outbreak

Few studies have explored the relationship between WSSV and NH_3 stress, and those available have produced conflicting results, seemingly due to differences in experimental design. Within studies that expose penaeids to NH_3 stress at the point of WSSV challenge, total ammonia nitrogen (TAN) concentrations of 0.34–14 mgL^{-1} resulted in no significant differences in cumulative mortality or viral replication (Xue et al., 2017). In contrast, acclimation of *P. monodon* to 1.1–8.1 mgL^{-1} TAN for 10 days prior to WSSV challenge resulted in significantly higher viral loads in the haemolymph, gills and pereopods of infected shrimp, which were maximum at the highest NH_3 concentration (8.1 mg^{-1}) (Fouzi et al., 2010).

These results suggest that prolonged exposure to nitrogenous compounds that might occur in shrimp ponds increases susceptibility to WSSV infection, and was recently confirmed experimentally by Kathyayani et al. (2019). However, the hypothesis that 5 mg L^{-1} NH_3 concentrations may reduce the virulence of WSSV (Jiang et al., 2004) requires further study. The severity of bacterial infections has been shown to increase in the presence of high NH_3 concentrations. For

example, at increased NH_3 concentrations *M. rosenbergii* susceptibility to *L. garvieae* infection increased due to decreased phagocytic activity and bacterial clearance (Cheng et al., 2003a), and *P. vannamei* mortality increased following *V. alginolyticus* infection due to decreases in phagocytic activity (Liu and Chen, 2004). Similarly in the presence of nitrites there is an increased susceptibility to bacterial infection (Chand and Sahoo, 2006; Cheng et al., 2002b; Tseng and Chen, 2004).

The effects of chronic exposure to sublethal nitrogen concentrations and to elevated NO_2^- and NO_3^- concentrations on WSD in shrimp are yet to be studied. However, as they have been shown to impact the immune responses of euryhaline crustaceans they have the potential to cause significant losses if not managed appropriately. Nitrogen accumulation can be limited by stocking ponds at carrying capacity, supplying only the required amount of feed, and by the periodic removal of excess settleable solids from pond bottoms (Burford and Longmore, 2001). The latter is aided by incorporation of a central sloped well at the pond bottom known as a "shrimp toilet" (Khan, 2018) to collect excess waste. Rapid waste removal has been beneficial in the reduction of Acute Hepatopancreatic Necrosis Disease (AHPND)-causing *V. parahaemolyticus* in ponds (Kawahigashi, 2017) and so may also be applicable in the management of other diseases of shrimp.

8. Conclusion

Evidence from the reviewed literature supports the suggestion that environmental factors influence the susceptibility of shrimp to WSD. The available data is biased towards studies focused on temperature and salinity and for these factors evidence suggests that the rate of change, shrimp age and infection stage during exposure (*e.g.* to increased temperatures) may dictate differences in susceptibility. Due to the sparse information available many critical research questions remain and are summarised in Fig. 2. They include the need for further research on the less studied abiotic factors such as salinity, hypoxia, hypercapnia and nitrogenous compounds, and crucially, the effects of combined changes in abiotic and biotic environmental conditions on disease outbreak. This is particularly important when considering that environmental stressors rarely occur in isolation and organisms in farm settings are likely to be exposed to multiple biotic and abiotic stressors simultaneously and in a fluctuating manner over time. However, published measurements of abiotic conditions from across a wide range of production settings that could inform our understanding of farm dynamics are not currently available, and when data are available, its utility is hindered due to a lack of standardised measurements. Until these knowledge gaps have been addressed, guidelines for the management of culture conditions at farms to improve resistance to disease remain undefined.

Movement towards fully enclosed systems will offer the undeniable benefit of stricter regulation of environmental conditions, however, their implementation will be expensive and present specific challenges for the management of water chemistry. In addition, the findings of this review are of increasing importance in the face of climate change, as the occurrence of extreme weather events that result in rapid changes in environmental conditions are predicted to increase in frequency. Resulting changes to environmental factors such as salinity and temperature have the ability to alter the severity of disease outbreaks in shrimp ponds if not carefully managed. These effects will be greatest for (vulnerable) small-scale farmers in developing regions who are less able to control pond conditions.

Continued research toward effective disease treatments for WSD, together with improving disease resistance of shrimp stocks by genetic selection, should remain a priority. However, this needs to occur in parallel with improved understanding and management of combined environmental conditions to relieve WSD and other disease-related losses and to promote sustainable shrimp aquaculture.
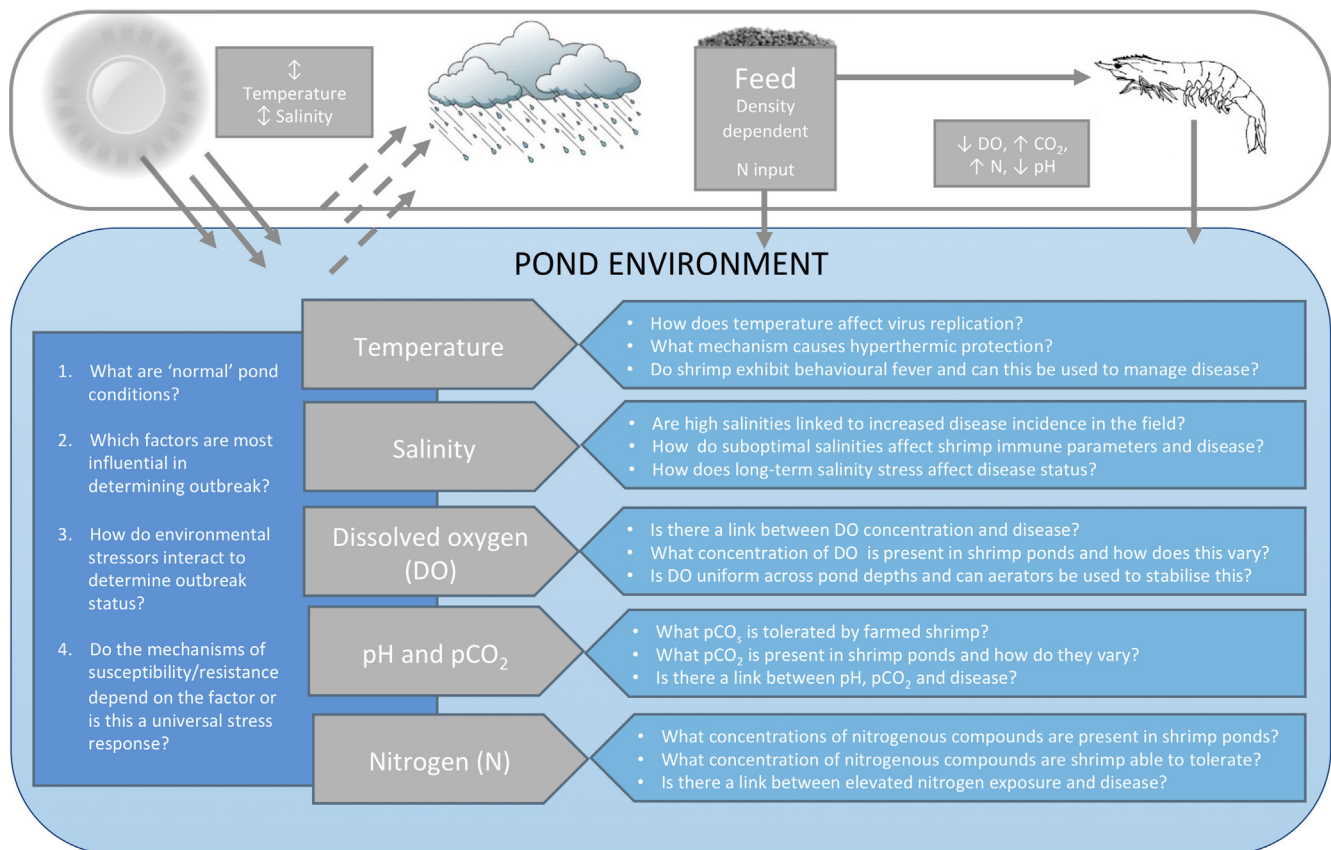
Fig. 2. Critical knowledge gaps in the influence of abiotic environmental factors on penaeid shrimp physiology and White Spot Disease susceptibility. The top panel presents factors that contribute to the variation of abiotic conditions within ponds. Knowledge gaps relating to how exposure to changes in environmental factors affects WSD are identified on the left panel. In the right panel we present three critical research questions for each environmental factor discussed within this review, which we consider to be priorities in future research.

Declaration of Competing Interest

The authors declared that there is no conflict of interest.

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Appendix A. Supplementary material

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References

Adelung, D., 1971. Studies on moulting physiology of decapod crustaceans as exemplified by shore crab *Carcinus* maenas. Helgoländer Wissenschaftliche Meeresuntersuchungen 22, 66–119. https://doi.org/10.1007/BF01611365.

Altieri, A., Gedan, K., 2015. Climate change and dead zones. Glob. Chang. Biol. 21, 1395–1406. https://doi.org/10.1111/gcb.12754.

ASEAN, 1978. Manual on pond culture of penaeid shrimp. ASEAN National Coordinating Agency of the Philippines, Ministry of Foreign Affairs.

Barraza-Guardado, R.H., Arreola-Lizárraga, J.A., López-Torres, M.A., Casillas-Hernández, R., Miranda-Baeza, A., Magallón-Barrajas, F., Ibarra-Gámez, C., 2013. Effluents of shrimp farms and its influence on the coastal ecosystems of bahía de Kino. Mexico. Sci. World J. 2013, 8. https://doi.org/10.1155/2013/306370.

Boltaña, S., Rey, S., Roher, N., Vargas, R., Huerta, M., Huntingford, F.A., Goetz, F.W., Moore, J., Garcia-Valtanen, P., Estepa, A., MacKenzie, S., 2013. Behavioural fever is a synergic signal amplifying the innate immune response. Proc. R. Soc. B Biol. Sci. 280 (1766), 201313811. https://doi.org/10.1098/rspb.2013.1381.

Bondad Reantaso, M.G., McGladdery, S.E., East, I., Subasinghe, R.P., 2001. Asia diagnostic guide to aquatic animal diseases, FAO. Fisheries Technical Paper.

Bray, W.A., Lawrence, A.L., Leung-Trujillo, J.R., 1994. The effect of salinity on growth and survival of *Penaeus vannamei*, with observations on the interaction of IHHN virus and salinity. Aquaculture 122, 133–146. https://doi.org/10.1016/0044-8486(94)90505-3.

Brito, R., Chimal, M.E., Rosas, C., 2000. Effect of salinity in survival, growth, and osmotic capacity of early juveniles of *Farfantepenaeus brasiliensis* (Decapoda: Penaeidae). J. Exp. Mar. Bio. Ecol. 244, 253–263. https://doi.org/10.1016/S0022-0981(99)00142-2.

Burford, M.A., Longmore, A.R., 2001. High ammonium production from sediments in hypereutrophic shrimp ponds. Mar. Ecol. Prog. Ser. 224, 187–195. https://doi.org/10.3354/meps224187.

Burnett, L.E., 1997. The challenges of living in hypoxic and hypercapnic aquatic environments. Am. Zool. 37, 633–640. https://doi.org/10.1093/icb/37.6.633.

Camargo, J.A., Alonso, A., Salamanca, A., 2005. Nitrate toxicity to aquatic animals: a review with new data for freshwater invertebrates. Chemosphere 58 (9), 1255–1267. https://doi.org/10.1016/j.chemosphere.2004.10.044.

Carbajal-Sanchez, I.S., Castro-Longoria, R., Grijalva-Chon, J.M., 2008. Experimental white spot syndrome virus challenge of juvenile *Litopenaeus vannamei* (Boone) at different salinities. Aquac. Res. 39, 1588–1596. https://doi.org/10.1111/j.1365-2109.2008.02030.x.

Casterlin, M.E., Reynolds, W.W., 1980. Fever and antipyresis in the crayfish *Cambarus bartoni*. J. Physiol. 303, 417–421. https://doi.org/10.1113/jphysiol.1980.sp013296.

Cavalli, L.S., Nornberg, B.F.S., Netto, S.A., Poersch, L., Romano, L.A., Marins, L.F., Abreu, P.C., 2010. White spot syndrome virus in wild penaeid shrimp caught in coastal and offshore waters in the southern Atlantic Ocean. J. Fish Dis. 33, 533–536. https://doi.org/10.1111/j.1365-2761.2010.01141.x.

Chand, R.K., Sahoo, P.K., 2006. Effect of nitrite on the immune response of freshwater prawn *Macrobrachium malcolmsonii* and its susceptibility to *Aeromonas hydrophila*. Aquaculture 258, 150–156. https://doi.org/10.1016/j.aquaculture.2006.05.001.

Charmantier, G., Charmantier-Daures, M., Bouaricha, N., Thuet, P., Aiken, D.E., Trilles, J.P., 1988. Ontogeny of osmoregulation and salinity tolerance in two decapod crustaceans: *Homarus americanus* and *Penaeus japonicus*. Biol. Bull. 175, 102–110. https://doi.org/10.2307/1541897.

Chen, J.C., Chen, S.F., 1992. Effects of nitrite on growth and molting of *Penaeus monodon* juveniles. Comp. Biochem. Physiol. Part C Comp. Pharmacol. 101, 102–110. https://doi.org/10.1016/0742-8413(92)90069-J.

Chen, J.C., Lai, S.H., 1992. Oxygen consumption and ammonia nitrogen excretion of *Penaeus japonicus* adolescents exposed to ambient ammonia. Comp. Biochem. Physiol., C: Comp. Pharmacol. Toxicol. 102, 129–133. https://doi.org/10.1016/0742-8413(92)90054-B.

Chen, J.C., Lin, C.Y., 1995. Responses of oxygen consumption, ammonia-N excretion and urea-N excretion of *Penaeus chinensis* exposed to ambient ammonia at different salinity and pH levels. Aquaculture 136, 243–255. https://doi.org/10.1016/0044-8486(95)01060-2.

Chen, S.M., Chen, J.C., 2003. Effects of pH on survival, growth, molting and feeding of giant freshwater prawn *Macrobrachium rosenbergii*. Aquaculture 218, 613–623. https://doi.org/10.1016/S0044-8486(02)00265-X.

Chen, Y.Y., Chen, J.C., Tseng, K.C., Lin, Y.C., Huang, C.L., 2015. Activation of immunity, immune response, antioxidant ability, and resistance against *Vibrio alginolyticus* in white shrimp *Litopenaeus vannamei* decrease under long-term culture at low pH. Fish Shellfish Immunol. 46, 192–199. https://doi.org/10.1016/j.fsi.2015.05.055.

Cheng, W., Chen, S.M., Wang, F.I., Hsu, P.I., Liu, C.H., Chen, J.C., 2003a. Effects of temperature, pH, salinity and ammonia on the phagocytic activity and clearance efficiency of giant freshwater prawn *Macrobrachium rosenbergii* to *Lactococcus garvieae*. Aquaculture 219, 111–121. https://doi.org/10.1016/S0044-8486(03)00017-6.

Cheng, W., Liu, C.H., Chen, J.C., 2002b. Effect of nitrite on interaction between the giant freshwater prawn *Macrobrachium rosenbergii* and its pathogen Lactococcus garvieae. Dis. Aquat. Organ. 50, 189–197. https://doi.org/10.3354/dao050189.

Cheng, W., Liu, C.-H., Hsu, J.-P., Chen, J.-C., 2002a. Effect of hypoxia on the immune response of giant freshwater prawn *Macrobrachium rosenbergii* and its susceptibility to pathogen *Enterococcus*. Fish Shellfish Immunol. 13, 351–365. https://doi.org/10.1006/fsim.2001.0411.

Cheng, W., Liu, C.H., Kuo, C.M., 2003b. Effects of dissolved oxygen on hemolymph parameters of freshwater giant prawn, *Macrobrachium rosenbergii* (de Man). Aquaculture 220, 843–856. https://doi.org/10.1016/S0044-8486(02)00534-3.

Chong-Robles, J., Charmantier, G., Boulo, V., Lizárraga-Valdéz, J., Enríquez-Paredes, L.M., Giffard-Mena, I., 2014. Osmoregulation pattern and salinity tolerance of the white shrimp *Litopenaeus vannamei* (Boone, 1931) during post-embryonic development. Aquaculture 422–423, 261–267. https://doi.org/10.1016/j.aquaculture.2013.11.034.

Chou, H.-Y.Y., Huang, C.-Y.Y., Wang, C.-H.H., Chiang, H.-C.C., Lo, C.-F.F., 1995. Pathogenicity of a baculovirus infection causing White Spot Syndrome in cultured penaeid shrimp in Taiwan. Dis. Aquat. Organ. 23, 165–173. https://doi.org/10.3354/dao023165.

Corsin, F., Turnbull, J.F., Hao, N.V., Mohan, C.V., Phi, T.T., Phuoc, L.H., Tinh, N.T.N., Morgan, K.L., 2001. Risk factors associated with White Spot syndrome virus infection in a Vietnamese rice-shrimp farming system. Dis. Aquat. Organ. 47, 1–12. https://doi.org/10.3354/dao047001.

Côté, I., Lightner, D.V., 2010. Hyperthermia does not protect Kona stock *Penaeus vannamei* against infection by a Taura syndrome virus isolate from Belize. Dis. Aquat. Organ. 88, 157–160. https://doi.org/10.3354/dao02131.

da Silva, S.M.B.C., Rocha, J.L., Martins, P.C.C., Gálvez, A.O., dos Santos, F.L., Andrade, H.A., Coimbra, M.R.M., 2015. Experimental infection of infectious myonecrosis virus (IMNV) in the Pacific white shrimp *Litopenaeus vannamei* (Boone, 1931). Aquac. Int. 23, 563–576. https://doi.org/10.1007/s10499-014-9836-9.

De Freitas Rebelo, M., Rodriguez, E.M., Santos, E.A., Ansaldo, M., 2000. Histopathological changes in gills of the estuarine crab *Chasmagnathus granulata* (Crustacea-Decapoda) following acute exposure to ammonia. Comp. Biochem. Physiol. – C Pharmacol. Toxicol. Endocrinol. 125, 157–164. https://doi.org/10.1016/S0742-8413(99)00093-6.

de la Vega, E., Hall, M.R., Degnan, B.M., Wilson, K.J., 2006. Short-term hyperthermic treatment of Penaeus monodon increases expression of heat shock protein 70 (HSP70) and reduces replication of gill associated virus (GAV). Aquaculture 253, 82–90. https://doi.org/10.1016/j.aquaculture.2005.07.041.

Defur, P.L., 1988. Systemic respiratory adaptations to air exposure in intertidal decapod crustaceans. Integr. Comp. Biol. 28, 115–124. https://doi.org/10.1093/icb/28.1.115.

Didar-Ul Islam, S.M., Bhuiyan, M.A.H., 2016. Impact scenarios of shrimp farming in coastal region of Bangladesh: an approach of an ecological model for sustainable management. Aquac. Int. 24, 1163–1190. https://doi.org/10.1007/s10499-016-9978-z.

Direkbusarakom, S., Danayadol, Y., 1998. Effect of oxygen depletion on some parameters of the immune system in black tiger shrimp (*Penaeus monodon*). Adv. Shrimp Biotechnol. Proceedings to the special session on shrimp biotechnology. In: 5th Asian Fisheries Forum, Chiengmai, Thailandpp. 147–149.

Du, Huahua, Dai, Wei, Han, Xinyan, Li, Weifen, Xu, Yaxiang, Xu, Zirong, 2008. Effect of low water temperature on viral replication of white spot syndrome virus in *Procambarus clarkii*. Aquaculture 277 (3-4), 149–151. https://doi.org/10.1016/j.aquaculture.2008.03.003.

Elliot, S.L., Blanford, S., Thomas, M.B., 2002. Host-pathogen interactions in a varying environment: temperature, behavioural fever and fitness. Proc. R. Soc. B Biol. Sci. 269, 1599–1607. https://doi.org/10.1098/rspb.2002.2067.

Ellis, R.P., Urbina, M.A., Wilson, R.W., 2017. Lessons from two high CO_2 worlds – future

oceans and intensive aquaculture. Glob. Chang. Biol. 23, 2141–2148. https://doi.org/10.1111/gcb.13515.

Esparza-Leal, H.M., Magallon-Barajas, F.J., Portillo-Clark, G., Perez-Enriquez, R., Alvarez-Ruiz, P., Escobedo-Bonilla, C.M., Mendez-Lozano, J., Manon-Rios, N., Valerio-Garcia, R.C., Hernandez-Lopez, J., Vibanco-Perez, N., Casillas-Hernandez, R., 2010. Infection of WSSV-negative shrimp, *Litopenaeus vannamei*, cultivated under fluctuating temperature conditions. J. World Aquac. Soc. 41, 912–922. https://doi.org/10.1111/j.1749-7345.2010.00434.x.

Fan, X., Thirunavukkarasu, K., Weaver, R.F., 1996. Temperature-sensitive mutations in the protein kinase-1 (pk-1) gene of the *Autographa californica* nuclear polyhedrosis virus that block very late gene expression. Virology 224, 1–9. https://doi.org/10.1006/viro.1996.0500.

FAO, 2016. The state of world fisheries and aquaculture 2016. Contributing to food security and nutrition for all, Rome, pp. 200.

FAO, 2009. How to feed the world in 2050, in: Rome: High-Level Expert Forum, 2009.

Ferreira, N.C., Bonetti, C., Seiffert, W.Q., 2011. Hydrological and water quality indices as management tools in marine shrimp culture. Aquaculture 318, 425–433. https://doi.org/10.1016/j.aquaculture.2011.05.045.

Fischer, E.M., Knutti, R., 2015. Anthropogenic contribution to global occurrence of heavy-precipitation and high-temperature extremes. Nat. Clim. Chang. 5, 560–564. https://doi.org/10.1038/nclimate2617.

Fisher, B., Naidoo, R., Guernier, J., Johnson, K., Mullins, D., Robinson, D., Allison, E.H., 2017. Integrating fisheries and agricultural programs for food security. Agric. Food Secur. 6, 1–7. https://doi.org/10.1186/s40066-016-0078-0.

Flegel, 2012. Historic emergence, impact and current status of shrimp pathogens in Asia. J. Invertebr. Pathol. 110, 116–173. https://doi.org/10.1016/j.jip.2012.03.0.

Flegel, T.W., 2009. Review of disease transmission risks from prawn products exported for human consumption. Aquaculture 290, 179–189. https://doi.org/10.1016/j.aquaculture.2009.02.036.

Flegel, T.W., 2006. Detection of major penaeid shrimp viruses in Asia, a historical perspective with emphasis on Thailand. Aquaculture 258, 1–33. https://doi.org/10.1016/j.aquaculture.2006.05.013.

Flegel, T.W., Sritunyalucksana, K., 2011. Shrimp molecular responses to viral pathogens. Mar. Biotechnol. 13, 587–607. https://doi.org/10.1007/s10126-010-9287-x.

Flegel, T.W., 2019. A future vision for disease control in shrimp aquaculture. J. World. Aquac. Soc. 50, 249–266. https://doi.org/10.1111/jwas.12589.

Food and Agriculture Organization of the United Nations Statistics Division (FAOSTAT), 2017. FAO yearbook: Fishery and aquaculture statistics. 2015, FAO Annual Yearbook. https://doi.org/10.5860/CHOICE.50-5350.

Fouzi, M., Shariff, M., Omar, A.R., Md Yusoff, F., Tan, S.W., 2010. TaqMan real-time PCR assay for relative quantification of White Spot Syndrome Virus infection in *Penaeus monodon* Fabricius exposed to ammonia. J. Fish Dis. 33, 931–938. https://doi.org/10.1111/j.1365-2761.2010.01200.x.

Furtado, P.S., Campos, B.R., Serra, F.P., Klosterhoff, M., Romano, L.A., Wasielesky, W., 2014. Effects of nitrate toxicity in the Pacific white shrimp, *Litopenaeus vannamei*, reared with biofloc technology (BFT). Aquac. Int. 23, 315–327. https://doi.org/10.1007/s10499-014-9817-z.

Gao, H., Kong, J., Li, Z., Xiao, G., Meng, X., 2011. Quantitative analysis of temperature, salinity and pH on WSSV proliferation in Chinese shrimp *Fenneropenaeus chinensis* by real-time PCR. Aquaculture 312, 26–31. https://doi.org/10.1016/j.aquaculture.2010.12.022.

Garcia, S.M., Rosenberg, A.A., 2010. Food security and marine capture fisheries: characteristics, trends, drivers and future perspectives. Philos. Trans. R. Soc. Lond. B Biol. Sci. 360, 2869–2880. https://doi.org/10.1098/rstb.2010.0171.

Gitterle, T., Gjerde, B., Cock, J., Salazar, M., Rye, M., Vidal, O., Lozano, C., Erazo, C., Salte, R., 2006. Optimization of experimental infection protocols for the estimation of genetic parameters of resistance to White Spot Syndrome Virus (WSSV) in *Penaeus (Litopenaeus) vannamei*. Aquaculture 261, 501–509. https://doi.org/10.1016/j.aquaculture.2006.07.017.

Godoy-Lugo, J.A., Miranda-Cruz, M.M., Rosas-Rodriguez, J.A., Adan-Bante, N.P., Icedo-Garcia, R., Sonanez-Organis, J.G., 2019. Hypoxia inducible factor -1 regulates WSSV-induced glycolytic genes in the white shrimp *Litopenaeus vannamei*. Fish Shellfish Immunol. 92, 165–171. https://doi.org/10.1016/j.fsi.2019.05.040.

Granja, C.B., Aranguren, L.F., Vidal, O.M., Aragón, L., Salazar, M., 2003. Does hyperthermia increase apoptosis in White Spot Syndrome Virus (WSSV)-infected *Litopenaeus vannamei*? Dis. Aquat. Organ. 54, 73–78. https://doi.org/10.3354/dao054073.

Granja, C.B., Vidal, O.M., Parra, G., Salazar, M., 2006. Hyperthermia reduces viral load of White Spot Syndrome Virus in *Penaeus vannamei*. Dis. Aquat. Organ. 68, 175–180. https://doi.org/10.3354/dao068175.

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. https://doi.org/http://dx.doi.org/10.1016/S0022-2011(03)00068-5.

Gunalan, B., Soundarapandian, P., Dinakaran, G.K., 2010. The effect of temperature and pH on WSSV Infection in cultured marine shrimp *Penaeus monodon* (Fabricius). Middle-East J. Sci. Res. 5, 28–33.

Guo, H., Xian, J.A., Li, B., Ye, C.X., Wang, A.L., Miao, Y.T., Liao, S.A., 2013. Gene expression of apoptosis-related genes, stress protein and antioxidant enzymes in hemocytes of white shrimp *Litopenaeus vannamei* under nitrite stress. Comp. Biochem. Physiol. – C Toxicol. Pharmacol. 157, 366–371. https://doi.org/10.1016/j.cbpc.2013.03.001.

Han, S. yin, Wang, B. jie, Liu, M., Wang, M. qiang, Jiang, K. yong, Liu, X. wei, Wang, L., 2018. Adaptation of the white shrimp Litopenaeus vannamei to gradual changes to a low-pH environment. Ecotoxicol. Environ. Saf. 149, 203–210. https://doi.org/10.1016/j.ecoenv.2017.11.052.

Henry, R.P., Kormanik, G. a, Smatresk, N.J., Cameron, J.N., 1981. The role of CaCO3

dissolution as a source of HCO3- for the buffering of hypercapnic acidosis in aquatic and terrestrial decapod crustaceans. J. Exp. Biol. 94, 269–274.

Henry, R.P., Lucu, Č., Onken, H., Weihrauch, D., 2012. Multiple functions of the crustacean gill: Osmotic/ionic regulation, acid-base balance, ammonia excretion, and bioaccumulation of toxic metals. Front. Physiol. 3, 431. https://doi.org/10.3389/fphys.2012.00431.

Herreid, C.F., 1980. Hypoxia in invertebrates. Comp. Biochem. Physiol. – Part A Physiol. 67, 311–320. https://doi.org/10.1016/S0300-9629(80)80002-8.

Hopkins, J.S., Stokes, A.D., Browdy, C.L., Sandifer, P.A., 1991. The relationship between feeding rate, paddlewheel aeration rate and expected dawn dissolved oxygen in intensive shrimp ponds. Aquac. Eng. 10, 281–290. https://doi.org/10.1016/0144-8609(91)90017-E.

Inouye, T., Miwa, S., Oseko, N., Nakano, H., Kimura, T., Momoyama, K., Hiraoka, M., 1994. Mass mortalities of cultured kuruma shrimp Penaeus japonicus in Japan in 1993: electron microscopic evidence of the causative virus. Fish Pathol. 29, 149–158. https://doi.org/10.3147/jsfp.29.149.

Jenny, J.P., Francus, P., Normandeau, A., Lapointe, F., Perga, M.E., Ojala, A., Schimmelmann, A., Zolitschka, B., 2016. Global spread of hypoxia in freshwater ecosystems during the last three centuries is caused by rising local human pressure. Glob. Chang. Biol. 22, 1481–1489. https://doi.org/10.1111/gcb.13193.

Jensen, F.B., 1990. Sublethal physiological changes in freshwater crayfish, Astacus astacus, exposed to nitrite: haemolymph and muscle tissue electrolyte status, and haemolymph acid-base balance and gas transport. Aquat. Toxicol. 18, 51–60. https://doi.org/10.1016/0166-445X(90)90035-N.

Jiang, G., Yu, R., Zhou, M., 2004. Modulatory effects of ammonia-N on the immune system of Penaeus japonicus to virulence of White Spot Syndrome Virus. Aquaculture 241, 61–75. https://doi.org/10.1016/j.aquaculture.2004.08.020.

Jiang, N., Pan, X., Gu, Z., Liu, W., Si, K., Zhou, Yong, Zhou, Yongze, Zhai, L., Fan, Y., Zeng, L., 2019. Proliferation dynamics of WSSV in crayfish, Procambarus clarkii, and the host responses at different temperatures. J. Fish Dis. 42, 497–510. https://doi.org/10.1111/jfd.12942.

John, C.V., Coles, S.L., Abozed, A., 1990. Seasonal cycles of temperature, salinity and water masses of the Western Arabian Gulf. Oceanol. Acta 13, 273–281.

Joseph, A., Philip, R., 2007. Acute salinity stress alters the haemolymph metabolic profile of Penaeus monodon and reduces immunocompetence to White Spot Syndrome Virus infection. Aquaculture 272, 87–97. https://doi.org/10.1016/j.aquaculture.2007.08.047.

Karunasagar, Indrani, Otta, S.K., Karunasagar, Iddya, 1997. Histopathological and bacteriological study of White Spot Syndrome of Penaeus monodon along the west coast of India. Aquaculture 153, 9–13. https://doi.org/10.1016/S0044-8486(97)00011-2.

Kathyayani, S.A., Poornima, M., Sukumaran, S., Nagavel, A., Muralidhar, M., 2019. Effect of ammonia stress on immune variables of Pacific white shrimp Penaeus vannamei under varying levels of pH and susceptibility to White Spot Syndrome Virus. Ecotoxicol. Environ. Saf. 184, 109626. https://doi.org/10.1016/j.ecoenv.2019.109626.

Kawahigashi, D., 2017. New paradigm for controlling AHPND in intensive culture systems: what works, what doesn't, and why, in: FAO Second International Technical Seminar/Workshop on Acute Hepatopancreatic Necrosis Disease (AHPND) There Is a Way Forward! FAO Technical Cooperation Programme: TCP/INT/3501 and TCP/INT/3502, Bangkok, Thailand 23-25 June 2016. p. 33.

Kay, B.H., Jennings, C.D., 2002. Enhancement or modulation of the vector competence of Ochlerotatus vigilax (Diptera: Culicidae) for Ross River Virus by temperature. J. Med. Entomol. 39, 99–105. https://doi.org/10.1603/0022-2585-39.1.99.

Khan, M.I.R., 2018. Shrimp Toilet: A novel way for disposal of organic waste in Aquaculture systems.

Korkut, G.G., Noonin, C., Söderhäll, K., 2018. The effect of temperature on White Spot Disease progression in a crustacean, Pacifastacus leniusculus. Dev. Comp. Immunol. 89, 7–13. https://doi.org/10.1016/j.dci.2018.07.026.

Kramer, L.D., Hardy, J.L., Presser, S.B., 1983. Effect of temperature of extrinsic incubation on the vector competence of Culex tarsalis for Western Equine Encephalomyelitis Virus. Am. J. Trop. Med. Hyg. 32, 1130–9. https://doi.org/ajtmh.1983.32.1130.

Kuhn, D.D., Smith, S.A., Boardman, G.D., Angier, M.W., Marsh, L., Flick, G.J., 2010. Chronic toxicity of nitrate to Pacific white shrimp, Litopenaeus vannamei: Impacts on survival, growth, antennae length, and pathology. Aquaculture 309, 109–114. https://doi.org/10.1016/j.aquaculture.2010.09.014.

Kulkarni, G.K., Joshi, P.K., 1980. Some aspects of respiratory metabolism of a penaeid prawn, Penaeus japonicus (Bate) (Crustacea, Decapoda, Penaeidae). Hydrobiologia 75, 27–32. https://doi.org/10.1007/BF00006558.

Kumar, V., Roy, S., Meena, D.K., Sarkar, U.K., 2016. Application of probiotics in shrimp aquaculture: Importance, mechanisms of action, and methods of administration. Rev. Fish. Sci. Aquac. 24, 342–368. https://doi.org/10.1080/23308249.2016.1193841.

Kumaran, M., Kumar, J.A., Anand, P., Paul, J., 2015. Training needs of extension personnel in Pacific white shrimp (Litopenaeus vannamei) farming. Fish. Technol. 52, 265–270.

Kumlu, Metin, Türkmen, S., Kumlu, Mehmet, 2010. Thermal tolerance of Litopenaeus vannamei (Crustacea: Penaeidae) acclimated to four temperatures. J. Therm. Biol 35, 305–308. https://doi.org/10.1016/j.jtherbio.2010.06.009.

Lara, G., Krummenauer, D., Abreu, P.C., Poersch, L.H., Wasielesky, W., 2017. The use of different aerators on Litopenaeus vannamei biofloc culture system: effects on water quality, shrimp growth and biofloc composition. Aquac. Int. 25, 147–162. https://doi.org/10.1007/s10499-016-0019-8.

Le Moullac, G., Soyez, C., Saulnier, D., Ansquer, D., Avarre, J.C., Levy, P., 1998. Effect of hypoxic stress on the immune response and the resistance to vibriosis of the shrimp Penaeus stylirostris. Fish Shellfish Immunol. 8, 621–629. https://doi.org/10.1006/fsim.1998.0166.

Lehmann, M., Schleder, D.D., Guertler, C., Perazzolo, L.M., Vinatea, L., 2016. Hypoxia

increases susceptibility of Pacific white shrimp to White Spot Syndrome Virus (WSSV). Arq. Bras. Med. Vet. Zootec. 68, 397–403. https://doi.org/10.1590/1678-4162-7942.

Lemonnier, H., Bernard, E., Boglio, E., Goarant, C., Cochard, J.C., 2004. Influence of sediment characteristics on shrimp physiology: pH as principal effect. Aquaculture 240, 297–312. https://doi.org/10.1016/j.aquaculture.2004.07.001.

Li, C.C., Chen, J.C., 2008. The immune response of white shrimp Litopenaeus vannamei and its susceptibility to Vibrio alginolyticus under low and high pH stress. Fish Shellfish Immunol. 25, 701–709. https://doi.org/10.1016/j.fsi.2008.01.007.

Lightner, D.V., 2011. Virus diseases of farmed shrimp in the Western Hemisphere (the Americas): a review. J. Invertebr. Pathol. 106, 110–130. https://doi.org/10.1016/j.jip.2010.09.012.

Lin, Y.-R., Hung, H.-C., Leu, J.-H., Wang, H.-C., Kou, G.-H., Lo, C.-F., 2011. The role of aldehyde dehydrogenase and hsp70 in suppression of White Spot Syndrome Virus replication at high temperature. J. Virol. 85, 3517–3525. https://doi.org/10.1128/JVI.01973-10.

Lin, Y.C., Chen, J.C., Li, C.C., Morni, W.Z., Suhaili, A.S.N., Kuo, Y.H., Chang, Y.H., Chen, L.L., Tsui, W.C., Chen, Y.Y., Huang, C.L., 2012. Modulation of the innate immune system in white shrimp Litopenaeus vannamei following long-term low salinity exposure. Fish Shellfish Immunol. 33, 324–331. https://doi.org/10.1016/j.fsi.2012.05.006.

Liu, B., Yu, Z.M., Song, X.X., Guan, Y.Q., Jian, X.F., He, J.F., 2006. The effect of acute salinity change on White Spot Syndrome (WSS) outbreaks in Fenneropenaeus chinensis. Aquaculture 253, 163–170. https://doi.org/10.1016/j.aquaculture.2005.08.022.

Liu, C.H., Chen, J.C., 2004. Effect of ammonia on the immune response of white shrimp Litopenaeus vannamei and its susceptibility to Vibrio alginolyticus. Fish Shellfish Immunol. 16, 321–334. https://doi.org/10.1016/S1050-4648(03)00113-X.

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. Sen, Wang, C.H., Kou, G.H., 1996. White Spot Syndrome Baculovirus (WSBV) detected in cultured and captured shrimp, crabs and other arthropods. Dis. Aquat. Org. 27, 215–225. https://doi.org/10.3354/dao027215.

Lu, X., Kong, J., Luan, S., Dai, P., Meng, X., Cao, B., Luo, K., 2016. Transcriptome analysis of the hepatopancreas in the pacific white shrimp (Litopenaeus vannamei) under acute ammonia stress. PLoS ONE 11 (10), e0164396. https://doi.org/10.1371/journal.pone.0164396.

MacKay, R.D., 1974. A note on minimal levels of oxygen required to maintain life in Penaeus schmitti. Proc. Annu. Meet. - World Maric. Soc. 5, 451–452. https://doi.org/10.1111/j.1749-7345.1974.tb00213.x.

Mallasen, M., Valenti, W.C., 2006. Effect of nitrite on larval development of giant river prawn Macrobrachium rosenbergii. Aquaculture 261, 1292–1298. https://doi.org/10.1016/j.aquaculture.2006.07.048.

Martínez-Palacios, C.A., Ross, L.G., Jiménez-Valenzuela, L., 1996. The effects of temperature and body weight on the oxygen consumption of Penaeus vannamei, Boone, 1931. J. Aquat. Trop. 11, 59–65.

Mayo, M.A., 2002a. Virus taxonomy – Houston 2002. Arch. Virol. 147, 1071–1076. https://doi.org/10.1007/s007050200036.

Mayo, M.A., 2002b. A summary of taxonomic changes recently approved by ICTV. Arch. Virol. 147, 1655–1663. https://doi.org/10.1007/s007050200039.

McCoid, V., Miget, R., Finne, G., 1984. Effect of environmental salinity on the free amino acid composition and concentration in penaeid shrimp. J. Food Sci. 49, 327–330. https://doi.org/10.1111/j.1365-2621.1984.tb12413.x.

McGraw, W., Teichert-Coddington, D.R., Rouse, D.B., Boyd, C.E., 2001. Higher minimum dissolved oxygen concentrations increase penaeid shrimp yields in earthen ponds. Aquaculture 199, 311–321. https://doi.org/10.1016/S0044-8486(01)00530-0.

McNamara, J.C., Moreira, G.S., Souza, S.C.R., 1986. The effect of salinity on respiratory metabolism in selected ontogenetic stages of the freshwater shrimp Macrobrachium olfersii (Decapoda, palaemonidae). Comp. Biochem. Physiol. – Part A Physiol. 83, 359–363. https://doi.org/10.1016/0300-9629(86)90590-6.

Menz, A., Blake, B.F., 1980. Experiments on the growth of Penaeus vannamei Boone. J. Exp. Mar. Bio. Ecol. 48, 99–111. https://doi.org/10.1016/0022-0981(80)90010-6.

Metzger, R., Sartoris, F.J., Langenbuch, M., Pörtner, H.O., 2007. Influence of elevated CO_2 concentrations on thermal tolerance of the edible crab Cancer pagurus. J. Therm. Biol 32, 144–151. https://doi.org/10.1016/j.jtherbio.2007.01.010.

Mikulski, C.M., Burnett, L.E., Burnett, K.G., 2000. The effects of hypercapnic hypoxia on the survival of shrimp challenged with Vibrio parahaemolyticus. J. Shellfish Res.

Millamena, O.M., 1990. Organic pollution resulting from excess feed and metabolite build-up: effect on Penaeus monodon postlarvae. Aquac. Eng. 9, 143–150. https://doi.org/10.1016/0144-8609(90)90001-G.

Miranda-Cruz, M.M., Poom-Llamas, J.J., Godoy-Lugo, J.A., Ortiz, R.M., Gómez-Jiménez, S., Rosas-Rodríguez, J.A., Morán-Palacio, E.F., Soñanez-Organis, J.G., 2018. Silencing of HIF-1 in WSSV-infected white shrimp: Effect on viral load and antioxidant enzymes. Comp Biochem. Physiol. Part - C Toxicol. Pharmacol. 213, 19–26. https://doi.org/10.1016/j.cbpc.2018.07.004.

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. https://doi.org/10.31.47/jsfp.33.95.

Montgomery-Brock, D., Tacon, A.G.J., Poulos, B., Lightner, D., 2007. Reduced replication of Infectious Hypodermal And Hematopoietic Necrosis Virus (IHHNV) in Litopenaeus vannamei held in warm water. Aquaculture 265, 41–48. https://doi.org/10.1016/j.aquaculture.2007.01.025.

Morgan, D., McMahon, B., 1982. Acid tolerance and effects of sublethal acid exposure on iono-regulation and acid-base status in two crayfish Procambarus clarki and Orconectes rusticus. J. Exp. Biol. 97, 241–252.

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 Viremia (PAV), by some chemical and physical treatments. Fish Pathol. 33, 65–71.

https://doi.org/10.3147/jsfp.33.65.

Navarro-Nava, F., Castro-Longoria, R., Grijalva-Chon, J.M., Ramos-Paredes, J., De la Rosa-Vélez, J., 2011. Infection and mortality of *Penaeus vannamei* at extreme salinities when challenged with Mexican Yellow Head Virus. J. Fish Dis. 34, 327–329. https://doi.org/10.1111/j.1365-2761.2011.01236.x.

Nhan, D.K., Milstein, A., Verdegem, M.C.J., Verreth, J.A.V., 2006. Food inputs, water quality and nutrient accumulation in integrated pond systems: A multivariate approach. Aquaculture 261, 160–173. https://doi.org/10.1016/j.aquaculture.2006.07.015.

Nicholls, N., Baek, H.J., Gosai, A., Chambers, L.E., Choi, Y., Collins, D., Della-Marta, P.M., Griffiths, G.M., Haylock, M.R., Iga, N., Lata, R., Maitrepierre, L., Manton, M.J., Nakamigawa, H., Ouprasitwong, N., Solofa, D., Tahani, L., Thuy, D.T., Tibig, L., Trewin, B., Vediapan, K., Zhai, P., 2005. The El Nino - Southern Oscillation and daily temperature extremes in east Asia and the west Pacific. Geophys. Res. Lett. 32, 1–4. https://doi.org/10.1029/2005GL022621.

O'Brien, C.J., 1994. The effects of temperature and salinity on growth and survival of juvenile tiger prawns *Penaeus esculentus* (Haswell). J. Exp. Mar. Bio. Ecol. 183, 133–145. https://doi.org/10.1016/0022-0981(94)90161-9.

Oseko, N., 2006. Occurrence and prevention of White Spot Syndrome (WSSV) in Malaysia, in: Proceedings from the 32nd Edition, National Research Institute of Aquaculture. 422–431.

Pan, L.Q., Zhang, L.J., Liu, H.Y., 2007. Effects of salinity and pH on ion-transport enzyme activities, survival and growth of *Litopenaeus vannamei* postlarvae. Aquaculture 273, 711–720. https://doi.org/10.1016/j.aquaculture.2007.07.218.

Park, J.H., Lee, Y.S., Lee, S., Lee, Y., 1998. An infectious viral disease of penaeid shrimp newly found in Korea. Dis. Aquat. Organ. 34, 71–75. https://doi.org/10.3354/dao034071.

Peinado-Guevara, L.I., López-Meyer, M., 2006. Detailed monitoring of White Spot Syndrome Virus (WSSV) in shrimp commercial ponds in Sinaloa, Mexico by nested PCR. Aquaculture 251, 33–45. https://doi.org/10.1016/j.aquaculture.2005.05.022.

Pequeux, A., 1995. Osmotic regulation in crustaceans. J. Crustac. Biol. 15, 1–60. https://doi.org/10.1163/193724095X00578.

Perez-Velazquez, M., González-Félix, M.L., Jaimes-Bustamente, F., Martínez-Córdova, L.R., Trujillo-Villalba, D.A., Davis, D.A., 2007. Investigation of the effects of salinity and dietary protein level on growth and survival of pacific white shrimp *Litopenaeus vannamei*. J. World Aquac. Soc. 38, 475–485. https://doi.org/10.1111/j.1749-7345.2007.00121.x.

Persson, M., Cerenius, L., Soderhall, K., 1987. The influence of haemocyte number on the resistance of the freshwater crayfish, *Pacifastacus leniusculus* Dana, to the parasitic fungus *Aphanomyces astaci*. J. Fish Dis. 10, 471–477. https://doi.org/10.1111/j.1365-2761.1987.tb01098.x.

Peterson, C.H., Fronc, K., 2007. Fishing for consumers: Market-driven factors affecting the sustainability of the fish and seafood supply chain, in: Globalization: Effects on Fisheries Resources. Cambridge University Press, pp. 424–452.

Piamsomboon, P., Inchaisri, C., Wongtavatchai, J., 2016. Climate factors influence the occurrence of White Spot Disease in cultured penaeid shrimp in Chanthaburi province. Thailand. Aquac. Environ. Interact. 8, 331–337. https://doi.org/10.3354/aei00176.

Ponce-Palafox, J., Martinez-Palacios, C.A., Ross, L.G., 1997. The effects of salinity and temperature on the growth and survival rates of juvenile white shrimp, *Penaeus vannamei*, Boone, 1931. Aquaculture 157, 107–115. https://doi.org/10.1016/S0044-8486(97)00148-8.

Pradeep, B., Rai, P., Mohan, S.A., Shekhar, M.S., Karunasagar, I., 2012. Biology, host range, pathogenesis and diagnosis of White Spot Syndrome Virus. Indian J. Virol. 23, 161–174. https://doi.org/10.1007/s13337-012-0079-y.

Rachalewski, M., Kobak, J., Szczerkowska-Majchrzak, E., Bącela-Spychalska, K., 2018. Some like it hot: factors impacting thermal preferences of two Ponto-Caspian amphipods *Dikerogammarus villosus* (Sovinsky, 1894) and *Dikerogammarus haemobaphes* (Eichwald, 1841). PeerJ 6, e4871. https://doi.org/10.7717/peerj.4871.

Racotta, I.S., Hernández-Herrera, R., 2000. Metabolic responses of the white shrimp, *Penaeus vannamei*, to ambient ammonia. Comp. Biochem. Physiol. Part A Mol. Integr. Physiol. 125, 437–443. https://doi.org/10.1016/S1095-6433(00)00171-9.

Rahman, M.M., Corteel, M., Dantas-Lima, J.J., Wille, M., Alday-Sanz, V., Pensaert, M.B., Sorgeloos, P., Nauwynck, H.J., 2007a. Impact of daily fluctuations of optimum (27 degrees C) and high water temperature (33 degrees C) on *Penaeus vannamei* juveniles infected with White Spot Syndrome Virus (WSSV). Aquaculture 269, 107–113. https://doi.org/10.1016/j.aquaculture.2007.04.056.

Rahman, M.M., Corteel, M., Wille, M., Alday-Sanz, V., Pensaert, M.B., Sorgeloos, P., Nauwynck, H.J., 2007b. The effect of raising water temperature to 33 degrees C in *Penaeus vannamei* juveniles at different stages of infection with White Spot Syndrome Virus (WSSV). Aquaculture 272, 240–245. https://doi.org/10.1016/j.aquaculture.2007.07.228.

Raj, S., Vijayan, K.K., Alavandi, S.V., Balasubramanian, C.P., Santiago, T.C., 2012. Effect of temperature and salinity on the infectivity pattern of white spot syndrome virus (WSSV) in giant tiger shrimp *Penaeus monodon* (Fabricus, 1837). Indian J. Fish. 59, 109–115.

Ramos-Carreño, S., Valencia-Yáñez, R., Correa-Sandoval, F., Ruíz-García, N., Díaz-Herrera, F., Giffard-Mena, I., 2014. White Spot Syndrome Virus (WSSV) infection in shrimp (*Litopenaeus vannamei*) exposed to low and high salinity. Arch. Virol. 159, 2213–2222. https://doi.org/10.1007/s00705-014-2052-0.

Randall, D.J, Tsui, T.K.N, 2002. Ammonia toxicity in fish. Mar. Pollut. Bull. 45 (1-12), 17–23. https://doi.org/10.1016/S0025-326X(02)00227-8.

Renaud, M.L., 1986. Detecting and avoiding oxygen deficient sea water by brown shrimp, *Penaeus aztecus* (Ives), and white shrimp *Penaeus setiferus* (Linnaeus). J. Exp. Mar. Bio. Ecol. 98, 283–292. https://doi.org/10.1016/0022-0981(86)90218-2.

Reyes, A., Salazar, M., Granja, C., 2007. Temperature modifies gene expression in

subcuticular epithelial cells of White Spot Syndrome Virus-infected *Litopenaeus vannamei*. Dev. Comp. Immunol. 31, 23–29. https://doi.org/10.1016/j.dci.2006.05.003.

Reynolds, W.W., Casterlin, M.E., Covert, J.B., 1976. Behavioural fever in teleost fishes. Nature 259, 41–42. https://doi.org/10.1038/259041a0.

Rodríguez-Ramos, T., Espinosa, G., Hernández-López, J., Gollas-Galván, T., Marrero, J., Borrell, Y., Alonso, M.E., Bécquer, U., Alonso, M., 2008. Effects of *Echericha coli* lipopolysaccharides and dissolved ammonia on immune response in southern white shrimp *Litopenaeus schmitti*. Aquaculture 274, 118–125. https://doi.org/10.1016/j.aquaculture.2007.10.049.

Romano, N., Zeng, C., 2007. Ontogenetic changes in tolerance to acute ammonia exposure and associated gill histological alterations during early juvenile development of the blue swimmer crab, *Portunus pelagicus*. Aquaculture 266, 246–254. https://doi.org/10.1016/j.aquaculture.2007.01.035.

Ruiz-Velazco, J.M.J., Hernández-Llamas, A., Gomez-Muñoz, V.M., Magallon, F.J., 2010. Dynamics of intensive production of shrimp *Litopenaeus vannamei* affected by White Spot Disease. Aquaculture 300, 113–119. https://doi.org/10.1016/j.aquaculture.2009.12.027.

Sahoo, A.K., Patil, P., Shankar, K.M., 2005. White spots? A loaded question for shrimp farmers. Curr. Sci. 88, 1914–1917.

Sahu, B.C., Adhikari, S., Mahapatra, A.S., Dey, L., 2013. Carbon, nitrogen, and phosphorus budget in scampi (*Macrobrachium rosenbergii*) culture ponds. Environ. Monit. Assess. 185, 10157–10166. https://doi.org/10.1007/s10661-013-3320-2.

Saksena, D.N., Gaidhane, D.M., Singh, H., 2006. Limnology of Kharland (saline) ponds of Ratnagiri, Maharashtra in relation to prawn culture potential. J. Environ. Biol. 27, 49–53.

Selvam, D.G., Mujeeb Rahiman, K.M., Mohamed Hatha, A.A., 2012. An investigation into occasional White Spot Syndrome Virus outbreak in traditional paddy cum prawn fields in India. Sci. World J. 2012, 1–11. https://doi.org/10.1100/2012/340830.

Shikata, M., Sano, Y., Hashimoto, Y., Matsumoto, T., 1998. Isolation and characterization of a temperature-sensitive mutant of *Bombyx mori* nucleopolyhedrovirus for a putative RNA polymerase gene. J. Gen. Virol. 79, 2071–2078. https://doi.org/10.1099/0022-1317-79-8-2071.

Sonanez-Organis, J.G., Peregrino-Uriarte, A.B., Gomez-Jimenez, S., Lopez-Zavala, A., Forman, H.J., Yepiz-Plascencia, G., 2009. Molecular characterization of hypoxia inducible factor-1 (HIF-1) from the white shrimp *Litopenaeus vannamei* and tissue-specific expression under hypoxia. Comp. Biochem. Physiol. C-TOXICOLOGY Pharmacol. 150, 395–405. https://doi.org/10.1016/j.cbpc.2009.06.005.

Souza, A.T., Ilarri, M.I., Campos, J., Marques, J.C., Martins, I., 2011. Differences in the neighborhood: Structural variations in the carapace of shore crabs *Carcinus maenas* (Decapoda: Portunidae). Estuar. Coast. Shelf Sci. 95, 424–430. https://doi.org/10.1016/j.ecss.2011.06.021.

Stentiford, G.D., Lightner, D.V., 2011. Cases of White Spot Disease (WSD) in European shrimp farms. Aquaculture 319, 302–306. https://doi.org/10.1016/j.aquaculture.2011.06.032.

Stentiford, G.D., Neil, D.M., Peeler, E.J., Shields, J.D., Small, H.J., Flegel, T.W., Vlak, J.M., Jones, B., Morado, F., Moss, S., Lotz, J., Bartholomay, L., Behringer, D.C., Hauton, C., Lightner, D.V., 2012. Disease will limit future food supply from the global crustacean fishery and aquaculture sectors. J. Invertebr. Pathol. 110, 141–157. https://doi.org/10.1016/j.jip.2012.03.013.

Tacon, A.G., Jory, D., Nunes, A., 2013. Shrimp feed management: issues and perspectives. On-Farm Feeding and Feed Management in Aquaculture. 481–488.

Tendencia, E.A., Bosma, R.H., Usero, R.C., Verreth, J.A.J., 2010. Effect of rainfall and atmospheric temperature on the prevalence of the Whitespot Syndrome Virus in pond-cultured *Penaeus monodon*. Aquac. Res. 41, 594–597. https://doi.org/10.1111/j.1365-2109.2009.02336.x.

Tendencia, E.A., Verreth, J.A.J., 2011. Temperature fluctuation, low salinity, water microflora: Risk factors for WSSV outbreaks in *Penaeus monodon*. Isr. J. Aquac. Bamidgeh. 63, 548.

Tseng, I.T., Chen, J.C., 2004. The immune response of white shrimp *Litopenaeus vannamei* and its susceptibility to *Vibrio alginolyticus* under nitrite stress. Fish Shellfish Immunol. 17, 325–333. https://doi.org/10.1016/j.fsi.2004.04.010.

United Nations, 2015. World Population Prospects - Population Division, World Population Prospects - 2015 Revision. https://doi.org/10.1108/09574099810805708.

Van Thuong, K., Van Tuan, V., Li, W., Sorgeloos, P., Bossier, P., Nauwynck, H., 2016. Effects of acute change in salinity and moulting on the infection of white leg shrimp (*Penaeus vannamei*) with White Spot Syndrome Virus upon immersion challenge. J. Fish Dis. 39, 1403–1412. https://doi.org/10.1111/jfd.12471.

Vaseeharan, B., Ramasamy, P., Wesley, S.G., Chen, J.C., 2013. Influence of acute salinity changes on biochemical, hematological and immune characteristics of *Fenneropenaeus indicus* during White Spot Syndrome Virus challenge. Microbiol. Immunol. 57, 463–469. https://doi.org/10.1111/1348-0421.12057.

Verbruggen, B., Bickley, L.K., van Aerle, R., Bateman, K.S., Stentiford, G.D., Santos, E.M., Tyler, C.R., 2016. Molecular mechanisms of White Spot Syndrome Virus infection and perspectives on treatments. Viruses. 8 (1), 23. https://doi.org/10.3390/v8010023.

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 Aquac. Soc. 32, 364–372. https://doi.org/10.1111/j.1749-7345.2001.tb00462.x.

Vinatea, L., Muedas, W., Arantes, R., 2011. The impact of oxygen consumption by the shrimp *Litopenaeus vannamei* according to body weight, temperature, salinity and stocking density on pond aeration: a simulation. Acta Sci. Biol. Sci. 33. https://doi.org/10.4025/actascibiolsci.v33i2.7018.

Wang, A.L., Wang, W.N., Wang, Y., Shang, L.X., Liu, Y., Sun, R.Y., 2003. Effect of dietary vitamin C supplementation on the oxygen consumption, ammonia-N excretion and Na+/K+ATPase of *Macrobrachium nipponense* exposed to ambient ammonia.

Aquaculture 220, 833–841. https://doi.org/10.1016/S0044-8486(02)00536-7.

Wang, F.I., Chen, J.-C., 2006. Effect of salinity on the immune response of tiger shrimp *Penaeus monodon* and its susceptibility to *Photobacterium damselae* subsp. damselae. Fish Shellfish Immunol. 20, 671–681. https://doi.org/10.1016/S0044-8486(02)00536-7.

Wang, L.-U., Chen, J.-C., 2005. The immune response of white shrimp *Litopenaeus vannamei* and its susceptibility to *Vibrio alginolyticus* at different salinity levels. Fish Shellfish Immunol. 18, 269–278. https://doi.org/10.1016/j.fsi.2004.07.008.

Wang, W.N., Wang, A.L., Chen, L., Liu, Y., Sun, R.Y., 2002. Effects of pH on survival, phosphorus concentration, adenylate energy charge and Na+-K+ ATPase activities of *Penaeus chinensis* Osbeck juveniles. Aquat. Toxicol. 60, 75–83. https://doi.org/10.1016/S0166-445X(01)00271-5.

Wang, Y.G., Hassan, M.D., Shariff, M., Zamri, S.M., Chen, X., 1999. Histopathology and cytopathology of White Spot Syndrome Virus (WSSV) in cultured *Penaeus monodon* from peninsular Malaysia with emphasis on pathogenesis and the mechanism of white spot formation. Dis. Aquat. Organ. 39, 1–11. https://doi.org/10.3354/dao039001.

Westbrook, C.J., Reiskind, M.H., Pesko, K.N., Greene, K.E., Lounibos, L.P., 2010. Larval environmental temperature and the susceptibility of *Aedes albopictus* Skuse (Diptera: Culicidae) to Chikungunya virus. Vector borne zoonotic Dis. 10, 241–247. https://doi.org/10.1089/vbz.2009.0035.

Whiteley, N.M., Scott, J.L., Breeze, S.J., Cann, L.M.C., 2001. Effects of water salinity on acid-base balance in decapod crustaceans. J. Exp. Zool. 204, 1003–1011.

Wickins, J.F., 1984. The effect of reduced pH on carapace calcium, strontium and magnesium levels in rapidly growing prawns (*Penaeus monodon* fabricius). Aquaculture 41, 49–60. https://doi.org/10.1016/0044-8486(84)90389-2.

Withyachumnarnkul, B., Boonsaeng, V., Chomsoong, R., Flegel, T.W., Muangsin, S., Nash, G.L., 2003. Seasonal variation in White Spot Syndrome Virus-positive samples in broodstock and post-larvae of *Penaeus monodon* in Thailand. Dis. Aquat. Organ. 53, 167–171. https://doi.org/10.3354/dao053167.

Wurts, W.A., 1992. Pond pH and ammonia toxicity. World Aquac. 34, 20–21.

Wyban, J., Sweeney, J., 1991. Intensive shrimp production technology: the Oceanic Institute shrimp manual., in: Argent Chemical Laboratories, Redmond, Washington.

Wyban, J., Walsh, W.A., Godin, D.M., 1995. Temperature effects on growth, feeding rate and feed conversion of the Pacific white shrimp (*Penaeus vannamei*). Aquaculture 138, 267–279. https://doi.org/10.1016/0044-8486(95)00032-1.

Wyban, J.A., Pruder, G.D., Leber, K.M., Burzell, L., 1989. Paddlewheel effects on shrimp growth, production and crop value in commercial earthen ponds. J. World Aquac. Soc. 20, 18–23. https://doi.org/10.1111/j.1749-7345.1989.tb00519.x.

Xian, J.-A., Wang, A.-L., Chen, X.-D., Gou, N.-N., Miao, Y.-T., Liao, S.-A., Ye, C.-X., 2011. Cytotoxicity of nitrite on haemocytes of the tiger shrimp, *Penaeus monodon*, using flow cytometric analysis. Aquaculture 317. https://doi.org/10.1016/j.aquaculture.2011.03.026.

Xue, S., Wei, J., Li, J., Geng, X., Sun, J., 2017. Effects of total ammonia, temperature and salinity on the mortality and viral replication of WSSV-infected Chinese shrimp (*Fenneropenaeus chinensis*). Aquac. Res. 48, 236–245. https://doi.org/10.1111/are.12877.

You, X. xin, Su, Y. quan, Mao, Y., Liu, M., Wang, J., Zhang, M., Wu, C., 2010. Effect of high water temperature on mortality, immune response and viral replication of WSSV-infected Marsupenaeus japonicus juveniles and adults. Aquaculture. 305, 133–137. https://doi.org/10.1016/j.aquaculture.2010.04.024.

Yu, Z., Li, C., Guan, Y., 2003. Effect of salinity on the immune responses and outbreak of White Spot Syndrome in the shrimp *Marsupenaeus japonicus*. Ophelia. 57, 99–106. https://doi.org/10.1080/00785236.2003.10409507.

Yuan, K., Yuan, F.H., He, H.H., Bi, H.T., Weng, S.P., He, J.G., Chen, Y.H., 2017. Heat shock 70 kDa protein cognate 5 involved in WSSV toleration of *Litopenaeus vannamei*. Dev. Comp. Immunol. 72, 9–20. https://doi.org/10.1016/j.dci.2017.02.003.

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. https://doi.org/10.1577/1548-8667(1998)010<0405:WSSVIO>2.0.CO;2.

Zhang, J.S., Li, Z.J., Wen, G.L., Wang, Y.L., Luo, L., Zhang, H.J., Dong, H.B., 2016. Relationship between White Spot Syndrome Virus (WSSV) loads and characterizations of water quality in *Litopenaeus vannamei* culture ponds during the tropical storm. Iran. J. Vet. Res. 17, 210–214.

Zhao, J.H., Lam, T.J., Guo, J.Y., 1997. Acute toxicity of ammonia to the early stage-larvae and juveniles of *Eriocheir sinensis* H. Milne-Edwards, 1853 (Decapoda: Grapsidae) reared in the laboratory. Aquac. Res. 28, 517–525. https://doi.org/10.1111/j.1365-2109.1997.tb01070.x.

Zhou, J., Wang, W.N., Wang, A.L., He, W.Y., Zhou, Q.T., Liu, Y., Xu, J., 2009. Glutathione S-transferase in the white shrimp *Litopenaeus vannamei*: Characterization and regulation under pH stress. Comp. Biochem. Physiol. - C Toxicol. Pharmacol. 150, 224–230. https://doi.org/10.1016/j.cbpc.2009.04.012.