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Review article

Emerging viral diseases of fish and shrimp

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Abstract – The rise of aquaculture has been one of the most profound changes in global food production of the past 100 years. Driven by population growth, rising demand for seafood and a levelling of production from capture fisheries, the practice of farming aquatic animals has expanded rapidly to become a major global industry. Aquaculture is now integral to the economies of many countries. It has provided employment and been a major driver of socio-economic development in poor rural and coastal communities, particularly in Asia, and has relieved pressure on the sustainability of the natural harvest from our rivers, lakes and oceans. However, the rapid growth of aquaculture has also been the source of anthropogenic change on a massive scale. Aquatic animals have been displaced from their natural environment, cultured in high density, exposed to environmental stress, provided artificial or unnatural feeds, and a prolific global trade has developed in both live aquatic animals and their products. At the same time, over-exploitation of fisheries and anthropogenic stress on aquatic ecosystems has placed pressure on wild fish populations. Not surprisingly, the consequence has been the emergence and spread of an increasing array of new diseases. This review examines the rise and characteristics of aquaculture, the major viral pathogens of fish and shrimp and their impacts, and the particular characteristics of disease emergence in an aquatic, rather than terrestrial, context. It also considers the potential for future disease emergence in aquatic animals as aquaculture continues to expand and faces the challenges presented by climate change.

disease emergence / shrimp / fish / virus

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1. INTRODUCTION

1.1. The rapid growth of aquaculture

The farming of fish and other aquatic animals is an ancient practice that is believed to date back at least 4 000 years to pre-feudal China. There are also references to fish ponds in The Old Testament and in Egyptian hieroglyphics of the Middle Kingdom (2050–1652 BC). Fish farms were common in Europe in Roman times and a recent study of land forms in the Bolivian Amazon has revealed a complex array of fish weirs that pre-date the Hispanic era [30, 49]. However, despite its ancient origins, aquaculture remained largely a low-level, subsistence farming activity until the mid-20th century when experimental husbandry practices for salmon, trout and an array of tropical fish and shrimp species were developed and adopted. Aquaculture is now a major global industry with total annual production exceeding 50 million tonnes and estimated value of almost US$ 80 billion [32]. With an average annual growth of 6.9% from 1970–2007, it has been the fastest growing animal food-producing sector and will soon overtake capture fisheries as the major source of seafood [31].

1.2. Diversity of farmed aquatic species

In contrast to other animal production sectors, aquaculture is highly dynamic and characterised by enormous diversity in both the range of farmed species and in the nature of production systems. Over 350 different species of aquatic animals are farmed, including 34 finfish (piscean), 8 crustacean and 12 molluscan species each for which annual production exceeds 100 000 tonnes [32]. Aquatic animals are farmed in freshwater, brackishwater and marine environments, and in production systems that include caged enclosures, artificial lakes, earthen ponds, racks, rafts, tanks and raceways. Farming can be a small-scale traditional activity with little human intervention, through to sophisticated industrial operations in which animals are bred and managed for optimal performance and productivity. The diversity of aquaculture species and farming systems also extends geographically from tropical to subarctic climes and from inland lakes and rivers to estuaries and open offshore waters.

Aquaculture production is heavily dominated by China and other developing countries in the Asia-Pacific region which accounts for 89% by volume of global production and 77% by value [31]. The major farmed species are carp, oysters and shrimp of which 98%, 95% and 88% of production, respectively, originates in Asia. By contrast, Atlantic salmon production is dominated by Norway, Chile, the United Kingdom and Canada which together account for 88% by volume and 94% by value [32]. Capture fisheries and aquaculture, directly or indirectly, play an essential role in the livelihoods of millions of people, particularly in developing countries. In 2006, an estimated 47.5 million people were primarily or occasionally engaged in primary production of aquatic animals [31].

1.3. Characteristics of fish and shrimp production systems

Although a significant component of the small-scale aquaculture sector continues to rely on traditional methods of natural recruitment of seed into ponds, modern fish and shrimp production systems more typically involve

a hatchery/nursery phase in which broodstock are spawned or stripped for the collection and hatching of eggs, and in which larvae are nursed through to post-larvae or juvenile stages (i.e., fry, smolt, fingerling) for delivery to farms. Broodstock may be captured from wild fisheries or produced in captivity from mature farmed stock or from closed-cycle breeding and genetic improvement programs. The use of wild broodstock that may be healthy carriers of viral pathogens is arguably the most significant biosecurity risk in aquaculture. Farming systems employed for grow-out may be extensive or intensive. Extensive farming employs fish or shrimp trapped at low density in natural or man-made enclosures utilising natural sources of feed with minimal human intervention. Intensive systems employ medium-to-high stocking densities in cages or ponds and artificial or supplemental feeds. Intensive pond culture usually requires aeration and controlled water exchange to maintain water quality. Super-intensive recirculating aquaculture systems (RAS) are also employed for some species. On-farm biosecurity measures to exclude pathogens and minimise health risks are more commonly employed in intensive and super-intensive systems.

1.4. The decline of capture fisheries

Whilst aquaculture has been on a steady path of expansion, capture fishery production has levelled since 1990 and many of the world's major fisheries have been driven into a state of decline by unsustainable fishing practices and environmental pressures. It has been estimated that 11 of the 15 major fishing areas and 80% of marine fishery resources are currently overexploited or at their maximum sustainable limit [31]. Much of the pressure on wild stocks is due to commercial fishing but the increasing popularity of recreational angling has led to a growing awareness of the need for regulation to ensure marine and inland fishery sustainability. Disease emergence is also a concern in wild fisheries due to environmental pressures, the direct impact of human activities and the risk of pathogen spread from aquaculture [102].

2. HISTORY OF DISEASE EMERGENCE IN FISH AND SHRIMP

Whilst various forms of disease have been reported among aquatic animals for centuries, most were either non-infectious (e.g., tumours), or caused by common endemic pathogens (mainly parasites and bacteria), and thus already known among observers and those engaged in traditional aquaculture. However, during the past century, the rise of novel forms of intensive aquaculture, increased global movement of aquatic animals and their products, and various sources of anthropogenic stress to aquatic ecosystems have led to the emergence of many new diseases in fish and shrimp. In this review, we consider these emerging diseases as: (i) new or previously unknown diseases; (ii) known diseases appearing for first time in a new species (expanding host range); (iii) known diseases appearing for the first time in a new location (expanding geographic range); and (iv) known diseases with a new presentation (different signs) or higher virulence due to changes in the causative agent.

2.1. Problems associated with emerging diseases

Emerging disease epizootics frequently cause substantial, often explosive, losses among populations of fish and shrimp, resulting in large economic losses in commercial aquaculture and threats to valuable stocks of wild aquatic animals. However, the extent of disease spread and impacts are often exacerbated by other problems that are typically encountered including: (i) delay in developing tools for the confirmatory diagnosis of disease or identification of the causative agent that allows infected animals to go undetected; (ii) poor knowledge of the current or potential host range; (iii) inadequate knowledge of the present geographic range; (iv) no understanding of critical epidemiological factors (replication cycle, mode of transmission, reservoirs, vectors, stability); and (v) poor understanding of differences among strains and/or relationships to established pathogens. Interventions to prevent pathogen spread are also often limited by poor capacity in some developing countries for implementation of effective quarantine and/or biosecurity measures and the illegal or poorly

regulated international trans-boundary movement of live aquatic animals [128, 164].

2.2. Emerging viral diseases of fish

Important emerging viral pathogens of fish are found among many families of vertebrate viruses that are well-known to include pathogens of humans or domestic livestock. However, there are significant differences between the ecology of viral diseases of fish and those of humans or other terrestrial vertebrates. The most significant amongst these differences are that: (i) few fish viruses are known to be vectored by arthropods; (ii) water is a stabilizing medium, but currents are less effective for long range virus transmission than are aerosols; (iii) wild reservoir species are often at very low densities (except for schooling and aggregate spawning stocks); (iv) fish are poikilotherms and temperature has an exceptionally critical role in modulating the disease process by affecting both the replication rate of the virus as well as the host immune response and other physiological factors involved in resistance; (v) few fish viruses are transmitted sexually between adults, although high levels of some viruses are present in spawning fluids and a few viruses are transmitted vertically from adult to progeny, either intra-ovum or on the egg surface. However, as occurs for avian diseases, migratory fish can serve as carriers for long-range dispersal of viral pathogens.

The global expansion of finfish aquaculture and accompanying improvements in fish health surveillance has led to the discovery of several viruses that are new to science. Many of these are endemic among native populations and opportunistically spill-over to infect fish in aquaculture facilities. Other well-characterized fish viruses (e.g., channel catfish virus, *Onchorhynchus masou* virus) can also cause significant losses in aquaculture but do not seem to be increasing significantly in host or geographic range. In the following sections, we consider the major emerging fish virus diseases that cause significant losses in aquaculture and are expanding in host or geographic range (Tab. I). Because of the risk of spread through commercial trade in finfish, many of the diseases are listed as notifiable by the World Organization for Animal Health (OIE).

2.2.1. Infectious haematopoietic necrosis

Infectious haematopoietic necrosis is one of three rhabdovirus diseases of fish that are listed as notifiable by the OIE. Originally endemic in the western portion of North America among native species of anadromous salmon, infectious haematopoietic necrosis virus (IHNV) emerged in the 1970s to become an important pathogen of farmed rainbow trout (*Oncorhynchus mykiss*) in the USA [11, 156]. Subsequently, the virus was spread by the movement of contaminated eggs to several countries of Western Europe and East Asia, where it emerged to cause severe losses in farmed rainbow trout, an introduced species. Similar to other members of the genus *Novirhabdovirus* in the family *Rhabdoviridae*, IHNV contains a negative-sense, single-stranded RNA genome, approximately 11 000 nucleotides in length and encoding six proteins, packaged within an enveloped, bullet-shaped virion [67]. Isolates of IHNV from North America show a strong phylogeographic signature with relatively low genetic diversity among isolates from sockeye salmon (*Oncorhynchus nerka*) inhabiting the historic geographic range of the virus [66]. However, isolates from trout in Europe, Japan or Korea, where the virus is emerging, show evidence of independent evolutionary histories following their initial introduction [29, 64, 106]. The emergence of IHNV in rainbow trout aquaculture is accompanied by genetic changes that appear to be related to a shift in host specificity and virulence [112].

2.2.2. Viral haemorrhagic septicaemia

Viral haemorrhagic septicaemia (VHS) is another emerging disease caused by a fish rhabdovirus. Similar to IHNV in morphology and genome organization, viral haemorrhagic septicaemia virus (VHSV) is also a member of the genus *Novirhabdovirus* [67]. The virus was initially isolated and characterized in Europe where it had become an important cause of loss among rainbow trout reared in aquaculture

Table I. Emerging viral pathogens of finfish.

Virus	Abbreviation	Genome	Taxonomic classification[1]	Known geographic distribution	OIE listed[2]
DNA viruses					
Epizootic haematopoietic necrosis virus and other ranaviruses	EHNV	dsDNA	*Iridoviridae*, *Ranavirus*	Australia, Europe, Asia, North America, Africa	Yes
Red sea bream iridovirus	RSIV	dsDNA	*Iridoviridae*, *Megalocytivirus*	Asia	Yes
Koi herpesvirus	KHV	dsDNA	*Alloherpesviridae*, *Cyprinivirus*	Asia, Europe, North America, Israel, Africa	Yes
RNA Viruses					
Infectious haematopoietic necrosis virus	IHNV	(−) ssRNA	*Mononegavirales*, *Rhabdoviridae*, *Novirhabdovirus*	Europe, North America, Asia	Yes
Viral haemorrhagic septicaemia virus	VHSV	(−) ssRNA	*Mononegavirales*, *Rhabdoviridae*, *Novirhabdovirus*	Europe, North America, Asia	Yes
Spring viraemia of carp virus	SVCV	(−) ssRNA	*Mononegavirales*, *Rhabdoviridae*, *Vesiculovirus*	Europe, Asia, North and South America	Yes
Infectious salmon anaemia virus	ISAV	(−) ssRNA	*Orthomyxoviridae*, *Isavirus*	Europe, North and South America	Yes
Viral nervous necrosis virus	VNNV	(+) ssRNA	*Nodaviridae*, *Betanodavirus*	Australia, Asia, Europe, North America, Africa, South Pacific	No

[1] ICVT, 2009.
[2] OIE, 2009.

[123]. Prior to the 1980s, VHSV was assumed to be largely endemic among native freshwater species of fish in Western Europe where it spilled-over to the introduced, and presumably more susceptible, rainbow trout [156]. Subsequently, an increasing number of virological surveys of anadromous and marine fish in the North Pacific and North Atlantic Oceans revealed a much greater host and geographic range than previously recognized [35, 91, 99, 121], and VHSV was shown to cause significant losses in both cultured and free-ranging species of marine fish [48, 56]. The understanding that VHS appeared to be an emerging disease of marine fish as a result of both greater surveillance efforts and the development of novel forms of marine fish aquaculture was further extended when VHS emerged for the first time in the Great Lakes of North America. The explosive losses among free-ranging native species revealed how devastating the disease can be when first introduced into naive populations of freshwater fish [28, 40, 84].

2.2.3. Spring viraemia of carp

Spring viraemia of carp (SVC) is also caused by a fish rhabdovirus (SVCV). However, unlike IHNV and VHSV, SVCV is related to rhabdoviruses in the genus *Vesiculovirus* in having an enveloped, bullet-shaped virion with somewhat shorter morphology and lacking the non-virion gene characteristic of novirhabdoviruses [67]. Initially believed to be endemic among common carp (*Cyprinus carpio*) in Eastern and Western Europe, the disease appeared in the spring to cause large losses among farm-reared carp [2, 156]. More recently, SVCV has emerged in several regions of the world where it has been associated with very large losses in common carp and its ornamental form, the koi carp. These outbreaks have occurred in both farmed and wild fish, suggesting a recent range expansion. The emergence of SVC in North America, Asia and in portions of Europe, formerly free of the virus, appears to be a result of both improved surveillance and the global shipment of large volumes of ornamental fish, including koi carp. Genotyping of isolates of SVCV and a closely related fish rhabdovirus from Europe, pike fry rhabdovirus, from various locations have revealed the isolates form four major genetic clades [127], and that the isolates of SVCV representing the recent emergence and geographic range expansion appear to have links to the spread of the virus within China where common carp are reared in large numbers for food and koi are reared for export [92].

2.2.4. Infectious salmon anaemia

Infectious salmon anaemia (ISA) is an emerging disease of farmed Atlantic salmon (*Salmo salar*) caused by a member of the family *Orthomyxoviridae*. The virus (ISAV) has eight independent genome segments of negative-sense, single-stranded RNA packaged within a pleomorphic, enveloped virion, approximately 100–130 nm in diameter, and is the type species of the genus *Isavirus*. Initially identified as the causative agent of outbreaks and high rates of mortality among Atlantic salmon reared in sea cages in parts of Norway [109], ISAV subsequently emerged to cause losses in other areas of Western Europe where Atlantic salmon are farmed [95]. The virus was also confirmed to be the cause of an emerging hemorrhagic kidney disease of farmed Atlantic salmon along the Atlantic coast of Canada and the USA [82]. Isolates of ISAV form two major genotypes containing isolates from Europe and North America, respectively [62]. More recently, ISAV has caused very extensive losses in the Atlantic salmon farming industry in Chile. Genetic analysis has revealed that the Chilean isolates group with those from Norway and that the virus was likely transferred to Chile sometime around 1996 by the movement of infected eggs [63]. Although principally known as a pathogen of Atlantic salmon, ISAV has been isolated from naturally infected marine species that are apparent reservoirs for virus spill-over to susceptible Atlantic salmon in sea cages [115]. Investigation of virulence determinants of ISAV has also revealed significant differences among isolates [88]. Thus, the emergence of ISA appears to be a response to the farming of a susceptible species in an endemic area, evolution of the virus and

some degree of transmission via the movement of fish or eggs used in aquaculture.

2.2.5. Koi herpesvirus disease

The disease caused by koi herpesvirus (KHV) is amongst the most dramatic examples of an emerging disease of fish. KHV is a member of the genus *Cyprinivirus* in the family *Alloherpesviridae*. Koi herpesvirus disease is relatively host-specific; although other cyprinid species have been shown to be susceptible, only common carp (*C. carpio*) and its ornamental subspecies, the koi carp, have been involved in the explosive losses that have been reported globally in areas where the virus has been first introduced [47]. The enveloped virion of KHV, formally classified as the species *Cyprinid herpesvirus 3*, has a morphology typical of herpesviruses and contains a double-stranded DNA genome of approximately 295 kbp [5]. Molecular analysis has shown little variation among isolates, as might be expected for a virus that is being rapidly disseminated by the global movement of infected fish [37]; however, minor variation has been reported that may reflect at least two independent introductions or emergence events of KHV [68]. A significant problem is that once fish are infected, the virus persists for some period of time in a latent or carrier state without obvious clinical signs [125]. It appears that the movement of such carriers via the extensive trade in cultured ornamental fish has resulted in the rapid appearance of the disease in many regions of the world [41]. In addition, the release or stocking of ornamental fish into ponds and other natural waters has resulted in the introduction of KHV to naive wild populations, where the initial exposure can result in substantial mortality.

2.2.6. Epizootic haematopoietic necrosis and other ranavirus diseases

Epizootic haematopoietic necrosis is caused by a large DNA virus (EHNV) which is classified in the genus *Ranavirus* of the family *Iridoviridae* [152]. Initially discovered in Australia where it was identified as an important cause of mortality among both cultured rainbow trout and a native species, the redfin perch [71], it later became clear that EHNV was but one of a large pool of ranaviruses having a broad host and geographic range that included amphibians, fish and reptiles [53]. Isolated from sub-clinical infections as well as severely diseased fish in either aquaculture or the wild, the genetically diverse, but related, ranaviruses have been given many names in different locations [86]. Although, there is evidence of spread by the movement of infected fish, either naturally or via trade, an important driver of the emergence of ranavirus diseases in finfish aquaculture seems to be the spill-over of virus from endemic reservoirs among native fish, amphibians or reptiles [152]. In this regard, ranaviruses related to the type species, *Frog Virus 3*, have been shown to be an important cause of emerging disease among both cultured and wild amphibian populations and may be associated, at least in some areas, with their global decline [19]. Both the large, unregulated global trade in amphibians and the unintended movement of ranaviruses by humans, including anglers and biologists, have been postulated to be important methods of dissemination of these relatively stable viruses to new aquatic habitats [114].

2.2.7. Red sea bream iridoviral disease and other megalocytivirus diseases

Another group of emerging iridoviruses causes disease in marine as well as freshwater fish species [19]. Initially identified in 1990 as the cause of high rate of mortality among cultured red sea bream (*Pagrus major)* in southwestern Japan [54], the causative agent termed red sea bream iridovirus (RSIV) was shown to affect at least 31 species of marine fish cultured in the region [60, 89]. Antigenic and molecular analyses revealed the causative agent of these outbreaks differed from other known fish iridoviruses [69, 103]. Soon, reports began to emerge that similar viral diseases in new hosts and other geographic areas of Asia were associated with novel iridoviruses including: infectious spleen and kidney necrosis iridovirus (ISKNV) from cultured mandarinfish (*Sinaperca chuatsi*) in southern China, sea bass (*Lateolabrax* sp.) iridovirus (SBIV)

from Hong Kong, rock bream (*Oplegnathus fasciatus)* iridovirus (RBIV) from Korea and the orange-spotted grouper (*Epinephelus coiodes*) iridovirus (OSGIV) from China [27, 45, 83, 94]. Sequence analysis showed these and several additional, but related, viruses formed a novel group and have been assigned to the genus *Megalocytivirus* in the family *Iridoviridae,* with ISKNV as the type species [27, 46, 69, 83]. In addition to causing outbreaks associated with severe necrosis and high mortality in a wide range of cultured marine fish, these viruses have emerged to affect freshwater species such as the African lampeye (*Aplocheilichthys normani*) and dwarf gourami (*Colisa lalia*) in which they have caused additional losses [132]. Molecular epidemiological studies have shown that megalocytiviruses form at least three genetic lineages. There is evidence that some of the initial outbreaks in marine species were due to spill-over from viruses endemic among free-ranging fishes; in other cases, there are clear links to the international movement of both marine and ornamental fish [132, 150, 152].

2.2.8. Viral nervous necrosis and other nodavirus diseases

Viral nervous necrosis (VNN) has emerged to become a major problem in the culture of larval and juvenile marine fish worldwide [101]. Initially described as a cause of substantial mortality among cultured barramundi (*Lates calcarifer*) in Australia where the disease was termed vacuolating encephalopathy and retinopathy, the condition was shown to be caused by a small, icosahedral virus that resisted cultivation in available cell lines, but appeared similar to picornaviruses [38, 100]. Around the same time, efforts to expand marine fish aquaculture in other regions of the world revealed disease conditions associated with similar viruses in larvae or juveniles from a range of species including turbot (*Scophthalmus maximus*) in Norway [8], sea bass (*Dicentrarchus labrax*) in Martinique and the French Mediterranean [12], and parrotfish (*Oplegnathus fasciatus*) and red-spotted grouper (*Epinephelus akaara*) in Japan [97, 163]. In Japan, the disease was termed nervous necrosis and the virus infecting larval striped jack (*Pseudocaranx dentex*), now assigned as the species *Striped jack nervous necrosis virus* (SJNNV), was shown to be a putative member of the family *Nodaviridae* [98]. Following isolation in cell culture [34], sequence analysis of the coat protein gene supported the creation of a novel genus, *Betanodavirus*, within the family *Nodaviridae* to include isolates of fish nodaviruses from various hosts and geographic locations [104, 105]. These and other phylogenetic analyses [23, 122, 139] revealed that genetic lineages of the betanodaviruses show low host specificity and generally correspond to geographic location, indicating they emerged due to spill-over from reservoirs that include a broad range of wild marine fish, although some isolates revealed links to commercial movement.

2.3. Emerging viral diseases of shrimp

Shrimp is the largest single seafood commodity by value, accounting for 17% of all internationally traded fishery products. Approximately 75% of production is from aquaculture which is now almost entirely dominated by two species – the black tiger shrimp (*Penaeus monodon)* and the white Pacific shrimp (*Penaeus vannamei*) that represent the two most important invertebrate food animals [32]. Disease has had a major impact on the shrimp farming industry. Since 1981, a succession of new viral pathogens has emerged in Asia and the Americas, causing mass mortalities and threatening the economic sustainability of the industry [148]. Shrimp are arthropods and most shrimp viruses are either related to those previously known to infect insects (e.g., densoviruses, dicistroviruses, baculoviruses, nodaviruses, luteoviruses) or are completely new to science and have been assigned to new taxa (Tab. II).

Several important characteristics are common to shrimp diseases and distinguish them from most viruses of terrestrial or aquatic vertebrates. Firstly, as invertebrates, shrimp lack the key components of adaptive and innate immune response mechanisms (i.e., antibodies, lymphocytes, cytokines, interferon) and, although Toll-like receptors have been identified, there

Table II. Emerging viral pathogens of marine and freshwater shrimp.

Virus	Abbreviation	Genome	Taxonomic classification[1]	Year emerged	Known geographic distribution	OIE listed disease[2]
DNA viruses						
Monodon baculovirus	MBV	dsDNA	*Baculoviridae*	1977	Asia-Pacific, Americas, Africa	No
Baculoviral midgut gland necrosis virus	BMNV	dsDNA	*Baculoviridae*	1971	Asia, Australia	No
White spot syndrome virus	WSSV	dsDNA	*Nimaviridae*, *Whispovirus*	1992	Asia, Middle-East, Mediterranean, Americas	Yes
Infectious hypodermal and haematopoietic necrosis virus	IHHNV	ssDNA	*Parvoviridae*, *Densovirus*	1981	Asia-Pacific, Africa, Madagascar, Middle-East, Americas	Yes
Hepatopancreatic parvovirus	HPV	ssDNA	*Parvoviridae*, *Densovirus*	1983	Asia-Pacific, Africa, Madagascar, Middle-East, Americas	No
RNA viruses						
Yellow head virus	YHV	(+) ssRNA	*Nidovirales*, *Roniviridae*, *Okavirus*	1990	East and Southeast Asia, Mexico	Yes
Taura syndrome virus	TSV	(+) ssRNA	*Picornavirales*, *Dicistroviridae*	1992	Americas, East and Southeast Asia	Yes
Infectious myonecrosis virus	IMNV	(+) ssRNA	Totivirus (unclassified)	2002	Brazil, Indonesia, Thailand, China	Yes
Macrobrachium rosenbergii nodavirus	MrNV	(+) ssRNA	Nodavirus (unclassified)	1995	India, China, Taiwan, Thailand, Australia, Caribbean	Yes
Laem-Singh virus	LSNV	(+) dsRNA	Luteovirus-like (unclassified)	2003	South and Southeast Asia	No
Mourilyan virus	MoV	(−) ssRNA	Bunyavirus-like (unclassified)	1996	Australia, Asia	No

[1] ICTV, 2009.
[2] OIE, 2009.

is little evidence that they are involved in antiviral immunity [70, 160]. RNA interference (RNAi) does appear to have a role in the antiviral defensive response of shrimp and there is evidence that viral proteins can induce a short-lived protective immunity [57, 118]. However, as is the case for insects, the response of shrimp to viral infection is poorly understood and the subject of intensive research. The second distinguishing feature is that most of the major pathogenic viruses cause very low level persistent infections that can occur at moderate to very high prevalence in apparently health shrimp populations [16, 51, 108, 133, 145]. Almost all shrimp pathogens are transmitted vertically (but usually not transovarially) and disease is the result of a massive viral amplification that follows exposure to various forms of environment or physiological stress [22, 81, 113, 119]. Stressors can include handling, spawning, poor water quality or abrupt changes in temperature or salinity. Shrimp viruses can also commonly be transmitted horizontally and, once viral loads are high and disease is manifest, horizontal transmission of infection is accompanied by transmission of disease. The third significant characteristic is a logical consequence of the former two in that shrimp commonly can be infected simultaneously or sequentially with multiple viruses [33], or even different strains of the same virus [50]. These characteristics present a very different landscape for the interaction of pathogen and host and significant challenges for diagnosis, detection, pathogen exclusion and the use of prophylactics in health management. Viruses listed by the OIE as causing notifiable diseases of marine and freshwater shrimp are reviewed briefly in this section.

2.3.1. White spot syndrome

White spot syndrome first emerged in Fujian Province of China in 1992 [165]. It was soon after reported in Taiwan and Japan and has since become panzootic throughout shrimp farming regions of Asia and the Americas [148]. It is the most devastating disease of farmed shrimp with social and economic impacts over 15 years on a scale that is seldom seen, even for the most important diseases of terrestrial animals. White spot syndrome virus (WSSV) is a large, enveloped, ovaloid DNA virus with a flagellum-like tail and helical nucleocapsid that has been classified as the only member of the new family *Nimaviridae*, genus *Whispovirus* [144, 158]. The ~ 300 kbp viral genome contains at least 181 ORF, most of which encode polypeptides with no detectable homology to other known proteins [142, 159]. Although first emerging in farmed kuruma shrimp (*Penaeus japonicus*), WSSV has a very broad host range amongst decapod crustaceans (e.g., marine and freshwater shrimp, crabs, lobsters, crayfish, etc.), all of which appear to be susceptible to infection [72]. However, susceptibility to disease varies and some crustacean species have been reported to develop very high viral loads in the absence of clinical signs [162]. All farmed marine (penaeid) shrimp species are highly susceptible to white spot disease, with mass mortalities commonly reaching 80–100% in ponds within a period of 3–10 days [20, 77]. Persistent, low level infections in shrimp and other crustaceans occur commonly, sometimes at levels that are not detectable, even by nested PCR. The amplification of viral loads and onset of disease can be induced by environmental or physiological stress [80, 113], or at ambient temperatures below 30 °C [39, 143].

WSSV was not known prior to its emergence in China and the original source of infection has not been determined. However, the spread of infection throughout most of Asia during the mid-1990s and subsequently to the Americas from 2001 was explosive and was almost certainly the consequence of a prolific international trade in live shrimp and other crustacean seed and broodstock [76]. The susceptibility of all decapods and absence of evidence of replication in other organisms suggests the virus is of crustacean origin but it remains a mystery why a virus with such broad host range and ease of transmission was not long established globally in crustacean populations prior to the advent of aquaculture [148].

2.3.2. Taura syndrome

Taura syndrome first emerged in white Pacific shrimp (*P. vannamei*) farms on the

Taura River near Guayaquil in Ecuador in 1992, almost simultaneously with the emergence of WSSV in kuruma shrimp in China [43]. The disease spread rapidly throughout most shrimp farming regions of Central and South America [75]. In 1998, it was detected in Taiwan and has now spread throughout much of Asia [140]. Taura syndrome virus (TSV) is a small, naked (+) ssRNA virus that is currently classified as an unassigned species in the family *Dicistroviridae*, order *Picornavirales* [21]. The most closely related known viruses include insect viruses in the genus *Cripavirus* such as cricket paralysis virus and drosophila C virus [21, 87]. Acute, transitional (recovery) and chronic phases of TSV infection have been described [44]. Mortalities in the acute phase can be as high as 95% but surviving shrimp remain infected and a potential source of virus transmission. The susceptible host range of TSV is far more restricted than that of WSSV but includes most farmed marine shrimp species. However, susceptibility to disease varies and virulence varies for different strains of the virus. Other crustaceans including freshwater shrimp and crabs appear to be resistant to disease but may be potential carriers [61]. Birds and water-boatmen (*Trichocorixa reticulata*) have been proposed as possible mechanical vectors [14, 36, 126]. The focal origin of the TSV panzootic and absence of evidence of infection prior to the first outbreak suggest that, as for WSSV, penaeid shrimp are not the natural host. The rapid spread of TSV in the Americas and then to Asia has also been attributed to the international trade in live shrimp.

2.3.3. Yellow head disease

Yellow head virus (YHV) is the most virulent of shrimp pathogens, commonly causing total crop loss within several days of the first signs of disease in a pond. It first emerged in black tiger shrimp (*P. monodon*) in Central Thailand in 1990 and has since been reported in most major shrimp farming countries in Asia, including India, Indonesia, Malaysia, the Philippines, Sri Lanka, Vietnam and Taiwan [17, 145]. There is also a recent unconfirmed report that YHV is present in farmed *P. vannamei* and *P. stylirostris* in Mexico [25]. YHV is an enveloped, rod-shaped (+) ssRNA virus with a helical nucleocapsid and prominent glycoprotein projections on the virion surface [157]. The particle morphology and organisation and expression strategy of the ~ 26 kb genome indicate that it is most closely related to vertebrate coronaviruses, toroviruses and arteriviruses, and it has been classified within the order *Nidovirales* in the family *Ronivirus*, genus *Okavirus* [147]. It is now known that YHV is one of a complex of six closely related viruses infecting *P. monodon* shrimp [153]. Gill-associated virus (GAV) is a far less virulent virus that emerged to cause mid-crop mortality syndrome in farmed *P. monodon* in Australia in 1996 [124]. However, the prevalence of GAV infection in healthy *P. monodon* broodstock and farmed shrimp in Australia has been reported to approach 100% and, although disease can be transmitted by injection or exposure *per os* to moribund shrimp, outbreaks in ponds are most likely the result of amplification of viral loads as a consequence of environmental stress. The other four known genotypes in the complex have been detected only in healthy *P. monodon* in Asia and, although they occur at high prevalence in many locations, they are not known to be associated with disease [153]. Many other penaeid and palemonid shrimp species have been shown to be susceptible to experimental infection with YHV or GAV, but yellow-head-complex viruses are detected rarely in other penaeid shrimp species and *P. monodon* appears to be the natural host [148]. Nevertheless, the very high virulence of YHV for penaeid shrimp does suggest that this genotype may enter ponds via an alternative reservoir host. Homologous genetic recombination is also a feature of the yellow head complex. A recent study has indicated that ~ 30% of yellow-head-complex viruses detected in *P. monodon* from across the Asia-Pacific region are recombinants [154]. The prevalence and geographic distribution of these recombinant viruses suggests that aquaculture and the international trade in live shrimp are the source of rapidly increasing viral genetic diversity.

2.3.4. Infectious hypodermal and haematopoietic necrosis

Infectious hypodermal and haematopoietic necrosis was first detected in Hawaii in 1981, causing mass mortalities in blue shrimp (*Penaeus stylirostris*) farmed in super-intensive raceways [74]. Infectious hypodermal and haematopoietic necrosis virus (IHHNV) is a small, naked, ssDNA virus that has been classified with several insect viruses in the family *Parvoviridae*, genus *Brevidensovirus* [21]. Following its initial detection in Hawaii, IHHNV was found to be widely distributed in both *P. stylirostris* and *P. vannamei* shrimp throughout farming regions of the Americas and in the wild shrimp population of the Gulf of California where some reports suggest that it may have contributed to the collapse of the capture fishery [96, 111]. Although it does not cause mortalities in *P. vannamei*, IHHNV has been shown to reduce growth by up to 30% and cause deformities of the rostrum and anterior appendages in a condition called "runt deformity syndrome" [59]. In Asia, IHHNV is endemic and occurs commonly in *P. monodon* shrimp which appears to be the natural host and in which it does not cause disease and has no impact on growth or fecundity [18, 155]. Four genotypes of IHHNV have been identified of which two have been shown to be integrated into host genomic DNA and experimental transmission studies suggest they may not be infectious for *P. monodon* or *P. vannamei* shrimp [65, 135, 136]. The other two genotypes can be transmitted horizontally by injection, ingestion or exposure to infected water, or vertically from infected females [73]. Genetic evidence suggests that *P. monodon* imported from the Philippines were the source of the epizootic in the Americas, indicating that disease emergence has been the consequence of an expanded host range providing opportunities for pathogenicity and a vastly expanded geographic distribution [134].

2.3.5. Infectious myonecrosis

Infectious myonecrosis is the most recently emerging of the major viral diseases of marine shrimp. It first appeared in farmed *P. vannamei* shrimp at Pernambuco in Brazil in 2002 and has subsequently spread throughout coastal regions of north-east Brazil and to Indonesia, Thailand and Hainan Province in China [4, 79, 120]. The original source of infection is unknown but the trans-continental spread has almost certainly been due to the voluminous trade in *P. vannamei* broodstock. Shrimp with the acute form of the disease display various degrees of skeletal muscle necrosis, visible as an opaque, whitish discolouration of the abdomen [137]. Surviving shrimp progress to a chronic phase with persistent low-level mortalities. Infectious myonecrosis virus (IMNV) is a small, naked, icosahedral, dsRNA virus that is most closely related to members of the family *Totiviridae*, genus *Giardiavirus* [116]. The only other known members of this family infect yeasts and protozoa. Several farmed marine shrimp species have been reported to be susceptible to infection but disease has only been reported in white Pacific shrimp [137]. The increasingly common practice in parts of Asia of co-cultivation of white Pacific shrimp and black tiger shrimp is likely to present opportunities for adaptation and further spread of the disease.

2.3.6. White tail disease

White tail disease is an emerging infection of the giant freshwater shrimp *Macrobrachium rosenbergii*. It was first reported in 1995 from the island of Guadeloupe and then nearby Martinique in the French West Indies, and has since been reported from China, Taiwan, Thailand, India and Australia [6, 110, 117, 141, 161]. The disease can affect larvae, postlarvae and early juvenile stages, causing up to 100% mortalities within 5–7 days of the first gross signs which include a white or milky appearance of abdominal muscle [42, 117]. Adults are resistant to the disease but can be persistently infected and transmit the infection vertically. Marine shrimp (*Penaeus monodon*, *P. japonicus* and *P. indicus*) have been shown to be susceptible to infection but did not develop disease, and artemia and some species of aquatic insects appear to be vectors [130, 131]. White tail disease is caused by a

small, naked (+) ssRNA virus that has been named *Macrobrachium rosenbergii* nodavirus (MrNV). Sequence alignments indicate that it is related to but distinct from nodaviruses of insects (genus *Alphanodavirus*) and nodaviruses of fish (genus *Betanodavirus*) [9]. A very small satellite virus (extra small virus, XSV) appears to be universally associated with natural MrNV infections but is not the direct cause of disease [117]. As the native endemic range of *Macrobrachium rosenbergii* is restricted to south and south-east Asia, the wide geographic distribution of the disease most likely has been due to the movement of stock for aquaculture purposes. Nevertheless, the detection in 2007 of a distinct strain of MrNV in *Macrobrachium rosenbergii* broodstock captured from the remote Flinders River in western Queensland, Australia [110], where there is a long-standing enforced prohibition on the importation of live crustaceans, suggests that the virus is a natural infection of freshwater shrimp. *Penaeus vannamei* nodavirus (PvNV) is a distinct but related virus that was detected in 2004 in cultured marine shrimp in Belize displaying the gross signs of white tail disease [138].

3. IMPACTS OF EMERGING DISEASES OF FISH AND SHRIMP

3.1. Economic and social impacts

The impacts of emerging diseases of aquatic animals have been substantial; all have affected livelihoods locally and many have impacted on regional or national economies. The most devastating economic and social impacts have been in shrimp aquaculture for which it was estimated in 1996 that the global direct and indirect costs of emerging diseases had reached $US 3 billion annually or 40% of the total production capacity of the industry [55, 85]. The most significant production losses have immediately followed the emergence of each of the major pathogens, with ensuing periods of poor productivity and reduced rates of industry expansion during which pathogens have been identified and characterised, diagnosis and detection methods developed, and improved biosecurity measures implemented [10, 148]. In many cases, impacts have continued for many years, particularly for small low-income farmers in developing countries who lack the knowledge, skill and resources to respond effectively. WSSV has been by far the most devastating of the shrimp pathogens. It has been estimated that the impact of WSSV in Asia alone during the 10 years after its emergence in 1992 was $US 4–6 billion [78]. In the Americas, the emergence of WSSV in 1999–2000 resulted in immediate losses estimated at $US 1 billion. The combined impacts of TSV and IHHNV on aquaculture and wild shrimp fisheries in the Americas have been estimated at $US 1.5–3 billion [44, 78]. The consequences of disease emergence for some countries have been so severe that shrimp production has never fully recovered. Beyond the direct effects on production and profitability, disease impacts on the income and food-security of small-holder shrimp farmers and the job security of workers on larger farms and in feed mills and processing plants, with a flow-on effect to the sustaining local communities [148].

The global economic losses in fish aquaculture due to infectious diseases are of a lesser magnitude, but still highly important in several ways and can be crippling for farmers. Not only are many individual animals of greater commercial value (e.g., koi carp) but the disruption of consistent production schedules by companies engaged in intensive aquaculture can result in loss of market share. The emergence of ISAV in Scotland in 1998–1999 is estimated to have cost the industry ~ $US 35 million and resulted in an ongoing annual loss of $US 25 million to the industries in Norway and Canada. The estimated cost of the emergence of KHV in Indonesia was in excess of $US 15 million during the first 3 years [10], with ongoing socio-economic impacts on low-income, small-holder farmers.

3.2. Environmental impacts

Environmental impacts of emerging diseases of aquatic animals have been both direct and indirect. Disease can impact directly on wild populations and the ecosystem by changing

host abundance and predator/prey populations, reducing genetic diversity and causing local extinctions [7]. The emergence of pilchard herpesvirus in Australasia during the 1990s was one of the most dramatic examples of large-scale impact on ecosystems. Commencing in March 1995, mass mortalities occurred in wild pilchard (*Sardinops sagax neopilchardus*) populations across 5 000 km of the Australian coastline and 500 km of the coastline of New Zealand [58]. The epizootic subsided in September 1995 but a second more severe wave of mortalities occurred between October 1998 and April 1999 with vast numbers of pilchards washed onto southern Australian beaches and mortality rates in pilchard populations as high as 75% [151]. The causative agent was identified as a previously unknown fish herpesvirus, but the source of the epidemic has never been identified [52]. Beyond the direct impact on pilchard populations, wider secondary impacts on piscivorous species were observed. Penguins suffered increased mortalities and failed to breed due to food shortage [24]. The contribution of pilchards to the diet of the Australian gannet (*Morus serrator*) declined from 60% to 5% following the mortality event and was compensated by feeding on species with lower calorific value [15]. As pilchards are important prey for seabirds, fish and marine mammals, other secondary impacts were likely. The recent introduction of VHSV to the Great Lakes Basin has also resulted in large-scale mortalities and spread to at least 25 native freshwater fish species with potential for similar broader environmental impacts [1].

Despite their panzoootic distribution in aquaculture systems and wide crustacean host range, direct environmental impacts of shrimp viruses have not been commonly observed. It has been reported that IHHNV impacted on wild *P. stylirostris* fisheries in the Gulf of Mexico following its introduction in 1987 [96] but rigorous environmental assessments of the impact of this or other shrimp pathogens have not been conducted. Indirect environmental impacts of disease in shrimp aquaculture are more clearly evident. These include the destruction of mangrove habitats due to pond abandonment and relocation to new sites, soil salinisation in inland areas due to avoidance of disease-prone coastal zones, and use of antibiotics, disinfectants and other chemicals to prevent or treat disease in ponds [3, 93, 148]. Difficulties in managing disease in native Asian marine shrimp species have also led to an extraordinary shift in production since 2001 to imported *P. vannamei* for which SPF stock are readily available [13]. The natural habitat of this species is the west coast of Central America but it now accounts for 67.1% of total farmed shrimp production in Asia [32], representing a massive species translocation for which the impacts on local biodiversity remain uncertain.

4. FACTORS CONTRIBUTING TO DISEASE EMERGENCE IN AQUATIC ANIMALS

The increasing rate of emergence of diseases of fish and shrimp has been driven primarily by anthropogenic influences, the most profound of which have been associated with the global expansion of aquaculture. Farming of aquatic animals commonly involves displacement from their natural habitat to an environment that is new and sometimes stressful, the use of feeds that are sometimes live and often unnatural or artificial, and culture in stocking densities that are much higher than occur naturally. This has provided opportunities for exposure to new pathogens and conditions that can compromise defensive responses and facilitate pathogen replication and disease transmission [146, 148]. Most importantly, the growth in aquaculture and increasing international trade in seafood has resulted in the rapid movement of aquatic animals and their products, with associated risks of the trans-boundary movement of pathogens [129]. Other diseases have been spread by natural or unintentional movement of infected hosts or amplified by invasive species, while anthropogenic environmental pressures have caused changes in the severity of several endemic diseases. Better surveillance activities based upon novel and more sensitive tools and their application in new species and geographic areas have also contributed to an apparent expansion of host or geographic range, sometimes dramatically.

4.1. Activities related to the global expansion of aquaculture

Emerging viral diseases of fish or shrimp are usually caused either by (i) viruses that naturally infect the target species but are unobserved or not normally pathogenic in wild or unstressed populations, or (ii) the spill-over of viruses from other species that may not be encountered naturally. Virus infections occur commonly in apparently healthy populations of wild fish and shrimp and, although disease outbreaks may occasionally occur, these often pass undetected and are not essential to sustain the natural cycle of transmission [149]. In shrimp, IHHNV, yellow-head-complex viruses and possibly MrNV appear to be naturally endemic in healthy wild populations and have emerged as significant pathogens only as a consequence of aquaculture practices. In the case of IHHNV, disease emergence has been due to the translocation of the natural host, *P. monodon*, from the Philippines to Hawaii and the Americas for use in aquaculture breeding programs, allowing spill-over into susceptible western hemisphere shrimp species [134]. For viruses in the yellow head complex, the natural prevalence can approach 100% in some healthy wild *P. monodon* populations but stressful culture conditions, in combination with yet uncharacterised virulence determinants, appear to trigger disease outbreaks [26, 145, 153]. Similarly, the emerging fish pathogen ISAV is endemic at relatively high prevalence in wild salmonid populations in Norway and Canada but has been associated with disease only in farmed Atlantic salmon. It has been suggested that intensive culture serves to provide concentrations of susceptible animals in which virulent strains of ISAV emerge due to a combination of high mutation rate and increased opportunity for virus replication [63]. Other major emerging pathogens are clearly not naturally endemic in aquaculture species but have spilled-over into both farmed and wild populations as a consequence of the exposure opportunities provided by the rapid growth of a large and diverse industry. WSSV, TSV and IMNV each appear to have been initially introduced to shrimp populations from unidentified sources that could potentially include experimental live or frozen feeds or co-inhabitants of terrestrial pond environments such as insects or aquatic invertebrates. Nevertheless, each of these viruses now occurs commonly as low-level persistent infections in healthy shrimp populations and disease outbreaks are precipitated by environmental stresses associated with aquaculture. In the case of WSSV, aquaculture has also provided opportunities for spread of infection to a very wide range of new wild crustacean hosts in which the virus has now become endemic across a vast coastal area of Asia and the Americas.

Amongst finfish pathogens, the ranaviruses and nodaviruses provide good examples of the emergence of disease due to spill-over from wild reservoirs. Prior to the availability of large populations of susceptible species reared in aquaculture, the betanodaviruses were endemic but undetected among free-ranging populations of marine fish and various ranaviruses were present in a broad range of native species that included fish, amphibians and reptiles. The introduction of these viruses to commercial aquaculture and the ensuing emergence of disease were likely due to the use of open water supplies and wild-caught broodstock.

The intentional or unintentional movement of infected hosts or pathogens by individuals or companies involved in global aquaculture or the ornamental fish trade has also been an important driver of viral disease emergence in aquatic animals [150]. Exotic viruses translocated into new geographic areas have spread to cause major disease outbreaks in populations of both native and cultured species and the trans-boundary movement of aquatic animals continues to be one of the greatest threats to the productivity and profitability of aquaculture worldwide. For finfish, this is exemplified by the spread of IHNV to Europe and Asia via the shipment of contaminated eggs of trout and salmon, the global spread of SVCV and KHV via the ornamental fish trade and the introduction of the pilchard herpesvirus into native populations of pilchards in Australia via baitfish. For shrimp, the prolific international trade in live broodstock has been the major driver of the explosive trans-boundary

spread of emerging viral pathogens. The rapid spread of WSSV throughout Asia and then to the Americas has been attributed to the movement of live crustaceans [78]. The magnitude of this problem is most clearly exemplified by the mass translocation of many hundreds of thousands of white Pacific shrimp broodstock from the Americas to Asia, accompanied by the introduction of TSV, IMNV and possibly other exotic pathogens [13]. The international trade in frozen commodity shrimp and shrimp products has also been recognised as a potential mechanism of trans-boundary spread of disease [76]. Several reports have indicated the presence of infectious WSSV and YHV in frozen commodity shrimp imported to the USA and Australia [90, 107]. However, it is yet to be established that the trade in infected frozen product has contributed to disease outbreaks in wild or cultivated shrimp [33b].

4.2. Improved surveillance

Apparent changes in the prevalence and distribution of viral diseases of fish and shrimp can also be attributed to improved surveillance as a result of the availability of new cell lines for virus isolation and characterization, the development of more sensitive molecular diagnostic methods, enhanced testing activity in natural ecosystems and greatly improved aquatic animal health diagnostic capability in some developing countries. For some viral pathogens, the availability of improved detection and surveillance capabilities has resulted in reports of a greater host or geographic range than previously known; in other cases, diseases in different species or geographic regions have been shown to be due to the same or similar viruses. For fish diseases, this is exemplified by development of the salmon head kidney (SHK) cell line to detect and characterize ISAV in Norway which subsequently led to the identification of potential carriers and the observation that emerging diseases of Atlantic salmon in Canada and Chile were due to isolates of the same virus [82]. Enhanced surveillance activities also resulted in the detection and isolation of VHSV from normal returning adult salmon on the west coast of North America in 1988. While initially appearing as a large geographic range expansion, increased surveillance activities showed that VHSV is naturally endemic in the North Pacific and North Atlantic Oceans among a wide range of marine species [121]. Similarly, investigations in Australia have identified that several viruses that were previously assumed to be exotic, occur commonly in healthy shrimp populations [110]. The increasing number of previously unknown viruses that have been identified through enhanced surveillance of healthy wild fish and shrimp populations illustrates how little is currently known of the aquatic virosphere.

4.3. Natural movement of carriers

The emergence of some viral diseases of fish and shrimp has occurred through expansion of the known geographic range via the natural movement of infected hosts, vectors or carriers with subsequent exposure of naive, and often highly susceptible, species. While the mechanism is not known with certainty, it is considered plausible that VHSV was introduced to the Great Lakes Basin of North America via the natural movement of fish up the Saint Lawrence River from the near shore areas of the Atlantic coast of Canada. The initial introduction of the virus into the Great Lakes preceded the emergence of massive epidemics among several species by at least two years. This has given rise to speculation that a single introduction of VHSV resulted in infection of the most susceptible species such as the native muskellunge (*Esox masquinongy*) or the invasive round gobi (*Neogobius melanostomus*) which could amplify the virus sufficiently to increase the infection pressure on a broad range of naive species within the larger ecosystem [40].

4.4. Other anthropogenic factors

The emergence of viral disease in aquatic systems can also been driven by anthropogenic factors unrelated to aquaculture such as the movement of pathogens or hosts via ballast water in ships, movement of bait by anglers and unintentional movement in other biotic or abiotic vectors. The environmental impacts of

increasing global population such as increasing loads of pollutants, contaminants and toxins in aquatic habitats also threaten the health and disease-resistance of both native and farmed fish populations. Finally, water diversions, impoundments, cooling water inputs and other water-use conflicts can result in environmental changes that may be detrimental to the health of aquatic species.

5. FUTURE DISEASE EMERGENCE RISKS

The increasing global population, increasing demand for seafood and limitations on production from capture fisheries will inevitably lead the continued global expansion of aquaculture with associated risks of disease emergence and spread. Africa, in particular, which currently contributes less than 1.3% of global aquaculture production [32], offers significant development opportunities for aquaculture but also presents a rich biodiversity that may be the source of emergence of new aquatic animal pathogens. There are also disease emergence risks associated with the increasing diversity of farmed species, the introduction of species into new farming areas and the increasing trend amongst small-holder farmers in some countries towards polyculture or alternate cropping of several fish and crustacean species to improve productivity.

As is the case for terrestrial pathogens, climate change also looms as a likely future driver of disease emergence in aquatic animals. Climate change and variability are likely to bring ecological disturbance on a global scale that will influence the suitability of aquaculture farming sites and has potential to influence the growth rate of pathogens and the host immune response to infection, generate thermal stress that will increase susceptibility to disease, change the distribution of vectors, carriers and reservoirs and the density or distribution of susceptible wild species, and alter the physical habitat and farming practices in ways that affect disease ecology. Nevertheless, there is a growing awareness of the importance of emerging diseases of aquatic animals and it is likely that the risks of future disease emergence will be mitigated somewhat by the development of improved diagnostic methods and surveillance efforts, increased regulatory oversight of aquaculture with greater levels of health inspection for fish, shrimp and their products involved in international trade, and the development of novel vaccines and therapeutics.

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