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REVIEW

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Collateral diseases: Aquaculture impacts on wildlife infections

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Abstract

1. Aquaculture is a promising source of fish and other aquatic organisms to ensure human food security but it comes at the price of diverse environmental impacts. Among others, these include diseases which often thrive under the conditions in aquaculture settings and can cause high economic losses. These diseases may also affect wildlife, however, the impacts of aquaculture on disease dynamics in wild species in surrounding ecosystems are poorly understood.
2. In this Review, we provide a conceptual framework for studying the effects of aquaculture on wildlife diseases, and illustrate the different mechanisms identified with examples from the literature. In addition, we highlight further research needs and provide recommendations for management and policy.
3. We identified five potential means by which farmed populations may alter wildlife disease dynamics: (a) farmed species may co-introduce parasites to the new environment, which infect wild conspecifics without infecting other species (intraspecific parasite spillover); (b) these co-introduced parasites from farmed species may infect other wild host species potentially leading to emerging diseases (interspecific parasite spillover); (c) parasites from other wild host species may infect farmed species, amplifying parasite numbers and increasing parasite infections when spilling back to wild hosts (interspecific parasite spillback); (d) farmed species may acquire parasites from wild conspecifics, increasing parasite population size and subsequently raising infection loads in the wild host population (intraspecific parasite spillback); and (e) farmed species may be neither hosts nor parasites, but affect the transmission of parasites between wild host species (transmission interference). Although these mechanisms can alter wildlife disease dynamics, we found large knowledge gaps regarding collateral disease impacts and strong biases in terms of production countries, aquaculture practices and host taxa.
4. *Synthesis and applications*. The strong potential for aquaculture to affect the dynamics of diseases in wildlife populations calls for the consideration of collateral disease impacts in risk assessments and biosecurity protocols regarding aquaculture. In particular, comprehensive parasite inventories of both farmed and wild hosts as well as disease monitoring in wildlife surrounding farms will be necessary to increase our knowledge on aquaculture impacts on wildlife disease and to develop adequate prevention and mitigation measures.

KEYWORDS
aquaculture, biosecurity, disease ecology, environmental impact, risk assessment, wildlife diseases

1 | INTRODUCTION

The per capita consumption of fish and other aquatic animals such as crustaceans and molluscs has considerably increased over the previous decades, reaching a record-high of 20.3 kg per capita per year in 2016 (FAO, 2018). Meeting the global demand for fish and other aquatic food products and ensuring human food security are therefore becoming increasingly challenging (Béné et al., 2015; Jennings et al., 2016). While capture fisheries are unable to keep up with the demand for aquatic food products, aquaculture, i.e. the farming of aquatic organisms, has been responsible for the ever increasing supply for human consumption, with 53 percent of global aquatic food production coming from aquaculture in 2016 (FAO, 2018; Figure 1). Aquaculture is practiced inland, in coastal and in marine environments in a variety of aquaculture systems, ranging from ponds and cages to highly sophisticated water reuse systems (Boyd & McNevin, 2005; Lucas et al., 2019). Like the variety of culture systems, the range of different species produced in these facilities varies extensively. While the bulk of species produced in aquaculture is comprised of fish, many species of other taxa are also farmed, such as crustaceans and molluscs, and their production is increasing as well (Metian et al., 2020).

Although promising from the point of human food security, the rapid growth of aquaculture has also raised concerns about its ecological impacts; ensuring the environmental sustainability of future growth constitutes one of the main challenges for aquaculture (Barrett et al., 2019; Beveridge et al., 1994; Campbell et al., 2019; Costello et al., 2019; Diana, 2009; Hall et al., 2011; Subasinghe et al., 2019; Subasinghe et al., 2009). Among the ecological impacts of aquaculture activities are the widespread use of wild fish as feed for aquaculture stocks (Naylor et al., 2000, 2009; Tacon & Metian, 2009, 2015), the genetic pollution of wild stocks (Cross et al., 2008; Glover et al., 2012; Jørstad et al., 2008; McGinnity et al., 1997), water quality issues such as local eutrophication (Pitta et al., 2009; Price et al., 2015) as well as the introduction of non-native species through escapees from farms or the co-introduction of other species with the translocation of aquaculture stocks (Diana, 2009; Naylor et al., 2001; Peeler et al., 2011; Savini et al., 2010).

Another ecological impact that affects aquaculture itself is related to diseases. The specific nature of aquaculture practices makes farmed aquatic organisms particularly prone to disease outbreaks: (a) the translocation and introduction of aquaculture stocks can lead to the co-introduction of pathogens and parasites (Peeler et al., 2011), (b) the often low genetic diversity of aquaculture stocks can increase the susceptibility of hosts and increase the virulence of pathogens (Kennedy et al., 2016) and (c) stocking densities in aquaculture settings are often much higher than would be found in natural environments which provides excellent conditions for pathogens and parasites to thrive (Krkošek, 2010; Salama & Murray, 2011). Accordingly, disease outbreaks frequently occur in aquaculture settings (Lafferty et al., 2015; Leung & Bates, 2013; Sweet & Bateman, 2015) and there are numerous examples of diseases ravaging farmed salmon (e.g. salmon lice *Lepeophtheirus salmonis* and *Caligus elongatus* (Revie et al., 2002), infectious salmon anaemia (Mullins et al., 1998) and infectious haematopoietic necrosis (Saksida, 2006)), shrimp (e.g. white spot syndrome (Chou et al., 1995) and acute hepatopancreatic necrosis disease (Soto-Rodriguez et al., 2015)) and other cultured organisms (Lafferty et al., 2015). The economic losses associated with such disease outbreaks in aquaculture, including the costs of disease control measures, are enormous. For example, sea lice infections of salmon in Norway generate economic costs equivalent to 9% of farm revenues and have led to damages estimated at >US$ 400 million in 2011 alone (Abolofia et al., 2017). On a global scale, economic losses in aquaculture due to diseases are estimated to amount to at least several billion US$ per year (World Bank, 2014). Due to these considerable economic risks, disease outbreaks represent one of the main obstacles for the sustainable growth of aquaculture (Stentiford et al., 2012; Subasinghe et al., 2019) and the problem has been termed the 'global aquaculture disease crisis' (Stentiford et al., 2017).

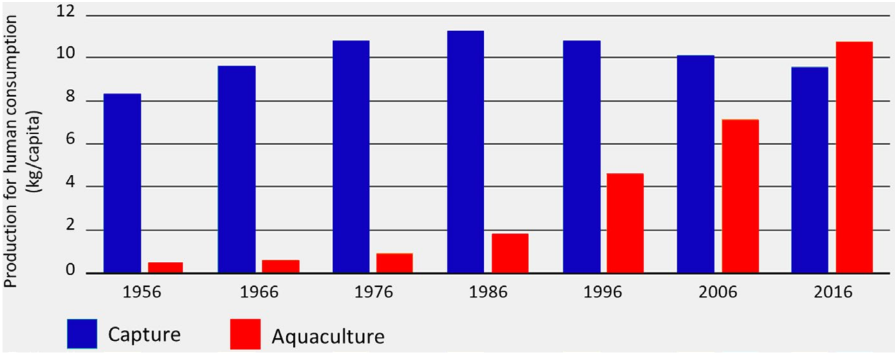

FIGURE 1 Origin of aquatic food production for human consumption over the past five decades, showing the increasing share of aquatic food products originating from aquaculture and capture of wild fish (for commercial, industrial, recreational and subsistence purposes). Data retrieved from FAO (2018)

Given the tremendous economic risks associated with disease outbreaks in farms, it comes as no surprise that diseases in aquaculture have been extensively studied, in particular with respect to the identification and treatment of responsible agents and the prevention of disease outbreaks based on risk assessments and biosecurity protocols (Hine et al., 2012; Subasinghe et al., 2019). However, diseases in aquaculture settings are not necessarily confined to farms themselves but can affect and interact with wild hosts in the vicinity of farms as well, with aquaculture held responsible for several reported cases of wildlife diseases (Diana, 2009; Lafferty et al., 2015). For example, salmon lice originating from farmed salmon in North America have been shown to infect wild juvenile pink salmon *Oncorhynchus gorbuscha* when passing salmon farms during their migration, leading to strong population declines and local risk of extinction of the wild host species (Krkošek et al., 2007). However, studies into the effects of aquaculture on wildlife disease ecology have been few, and the diversity and magnitude of impacts of aquaculture activities on disease dynamics in wild hosts in surrounding ecosystems are generally poorly understood.

This review examines the possible effects of aquaculture on wildlife disease dynamics and provides a conceptual framework for studying the effects of aquaculture on parasite–host interactions, borrowing from mechanisms and conceptual frameworks developed for biological invasions (e.g. Dunn & Hatcher, 2015; Goedknegt et al., 2016; Kelly et al., 2009; Young et al., 2016). As discussed above, aquaculture introduces host or parasite species to environments where they had been absent before. Therefore, many of the mechanisms of parasite and disease exchange between farmed and wild hosts may be similar to interactions between introduced and native hosts and parasites. In the following, we first review the most common methods used in aquaculture to pinpoint possible means of parasite exchange between farmed organisms and wildlife. We then identify the various ways in which these exchanges can affect parasite–host interactions, and illustrate the different mechanisms with examples from the literature. Finally, we highlight further research needs and recommendations for management and policy.

2 | THE MANY FORMS OF AQUACULTURE

Aquaculture is practised in many different ways. Species are cultured in freshwater, brackish and marine environments, with the majority of production coming from inland freshwater facilities (FAO, 2018). According to FAO (2018), based on known and documented practices, there are 598 different species of organisms used in aquaculture, and these include 369 fishes, 109 molluscs, 64 crustaceans, nine other invertebrates, seven amphibians and 40 algae (FAO, 2018). A variety of distinct methods are used for cultivating such a wide range of species. In the following, we describe some of the most commonly used methods, and identify the possible routes of parasite exchange with the environment surrounding the facilities.

2.1 | Ponds

Ponds are the most commonly used system for fish and crustacean aquaculture, with an estimated 11×10^6 ha of global aquaculture pond surface area (Verdegem & Bosma, 2009). Ponds can be constructed in several ways. Watershed ponds are created by building a dam to confine runoff, either from overland flow of rainfall or from an existing stream (Boyd & McNevin, 2005). Ponds may also be excavated or constructed by building an earthen embankment, a so called embankment pond, which is the main type of system used in shrimp farming (Boyd & Clay, 1998; Boyd & McNevin, 2005; Figure 2a). These types of ponds usually require a water supply from an external source such as a stream, well or irrigation system (Boyd & McNevin, 2005). This external water supply offers a potential vector by which parasites from the wild are able to enter the pond system. Additionally, ponds are usually equipped with drainage structures to discharge excess water or to drain them entirely, which is common practice during harvest (Boyd & McNevin, 2005; Verdegem & Bosma, 2009). When inadequate action is taken to disinfect this effluent, drainage of culture ponds has the potential to release parasites of cultured species in the environment, thus offering a mechanism for parasite exchange from farmed to wild organisms (Kurath & Winton, 2011).

2.2 | Cages and net pens

Another frequently used aquaculture system is the use of enclosures situated in natural bodies of water, usually cages or net pens (Figure 2b). These enclosures can be as small as 1 m^3 or as large as 1,000 m^3 and are stocked with fish densities ranging from <20 to over 200 kg/m^3 (Schmittou, 1993). Atlantic salmon *Salmo salar*, the most common marine aquaculture species, are usually grown out in enclosures at sea, but the method can also be applied to other species such as marine shrimps (FAO, 2018; Paquotte et al., 1998). Because cages and net pens are placed directly in the natural environment and allow for free water exchange with the surrounding environment, the chance of parasite exchange between wild and farmed fish stocks is particularly high for these types of systems (Johansen et al., 2011). Furthermore, the likelihood of fish escaping from net pens is high, and escapes are known to occur on a regular basis (Diana, 2009; Johansen et al., 2011). In addition, cages and net pens attract aggregations of wild fish seeking food or shelter, further increasing the risk of parasite exchange between farmed and wild fish and between neighbouring farms (Dempster et al., 2009; Johansen et al., 2011).

2.3 | Flow through raceways

A system often used for farming rainbow trout is a raceway supplied with water originating from a natural water source such as a

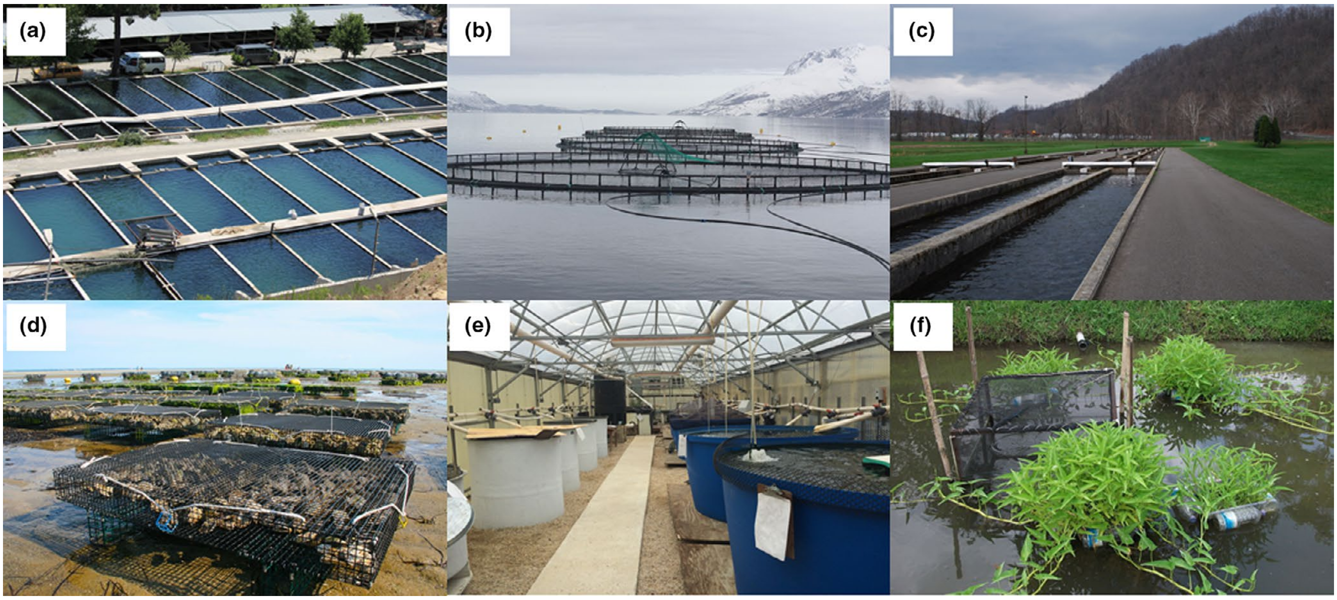

FIGURE 2 Examples of the various methods used for aquaculture: (a) fish farming in ponds, (b) marine cage aquaculture facility, (c) freshwater flow-through raceway system, (d) off-bottom oyster cages, (e) indoor recirculating aquaculture system (RAS), and (f) small scale integrated multi-trophic aquaculture (IMTA) system in a freshwater pond. Photo credits: (a) Vera Kratochvil, Wikimedia Commons, Public Domain, (b) Thomas Bjørkan, Wikimedia Commons, CC BY-SA 3.0, (c) Brian M. Powell, Wikimedia Commons, CC BY-SA 3.0, (d) Pixabay, Public Domain, (e) Narek Avetisyan, Wikimedia Commons, CC BY-SA 4.0, (f) Saifullahrony, Wikimedia Commons, CC BY-SA 3.0 [Colour figure can be viewed at wileyonlinelibrary.com]

spring, stream or lake (Boyd & McNevin, 2005). They are usually made of concrete and positioned in series, in which the water from the upper units flows into the units below (Figure 2c). Water exchange occurs via gravity flow at a rate of approximately two or three times the volume of a culture unit per hour and from the lowermost unit it is discharged into a natural body of water (Boyd & McNevin, 2005). These raceways generally harbour higher stock densities than ponds, ranging from 80 to 160 kg/m^3 for rainbow trout (Soderberg, 1994). High stocking densities along with the release of effluent into natural waterbodies provide risks of parasite exchange with wild populations, and could be cause for concern.

2.4 | Mollusc and seaweed culture

Bivalve molluscs and seaweeds are generally produced in coastal waters, although there are a few species which are cultured in ponds. Bivalves and seaweed are either grown out on the bottom (on-bottom culture), or by so called off-bottom culture in which spat or seaweed propagules are fixed to longlines, rafts or racks for grow-out (Boyd & McNevin, 2005; Figure 2d). The latter method is deemed more efficient as it eliminates the limiting effects of benthic predators and impaired sediment quality while permitting three-dimensional use of the water column (Boyd & McNevin, 2005). Because culture occurs directly in natural coastal waters, parasites can be exchanged between farmed and wild populations, seemingly without any restriction.

2.5 | Recirculating aquaculture systems

Recirculating aquaculture systems (RAS) are closed culture systems in which waste water is treated and subsequently re-used to allow for a more efficient use of water and a greater fish production per volume of water (Figure 2e). Waste water from culture units usually passes into a sedimentation basin, where coarse solid waste is removed. Subsequently the water is purified naturally or through technologically more complex purification systems (Boyd & McNevin, 2005). As a result, waste water volume released into the environment is greatly reduced (Boyd & McNevin, 2005; Edwards, 2015), lowering the chances of parasites from culture organisms being released into the wild.

2.6 | Integrated multi-trophic aquaculture

In some cases, extractive species such as bivalve molluscs or seaweeds are used as a means of removing excess nutrients and other waste, both in closed RAS and open systems such as cages or net pens (Figure 2f). These extractive species are then harvested as well. This use of multiple species of different trophic levels in a single culture system is known as integrated multi-trophic aquaculture (IMTA). Although this relatively new approach has been the subject of ongoing research and many of these are positive about its potential, there is some debate regarding the efficiency of bivalves in capturing organic wastes from fish cultures, especially in open systems (Edwards, 2015). In IMTA systems, extractive species have the potential to change parasite–host interactions, as they have been shown to be capable of reducing free-living parasite stages in the water, so called transmission interference (Burge, Closek, et al., 2016; Molloy et al., 2011). However, the addition of more species to a farm could also lead to the introduction of additional parasites along with these extractive species, with the potential to infect native hosts. In addition, there is a possibility for amplification of already pre-existing parasite populations (Burge, Closek, et al., 2016; Kelly et al., 2009).

3 | AQUACULTURE IMPACTS ON WILDLIFE DISEASES

Considering the aforementioned possibilities of parasite exchange between aquaculture farms and surrounding wildlife, and the numerous examples of cultured species escaping and becoming invasive, aquaculture has the potential to alter parasite–host interactions and diseases in wildlife inhabiting the environment surrounding farms. In the following, we identify the different mechanisms by which aquaculture affects wildlife parasite–host interactions and diseases and provide examples of their occurrence from the literature. By doing so, we provide a conceptual framework for studying the effects of aquaculture on wildlife diseases (Figure 3). The mechanisms presented are not mutually exclusive, it is possible that several or even all of the different mechanisms occur in a specific aquaculture setting. For our review, we extensively searched the literature for studies on aquaculture disease impacts on wildlife using Web of Science and Google Scholar, as well as by scanning existing reviews and books on aquatic diseases and aquaculture. Although we did not conduct a formal meta-analysis, we believe that we have found the majority of existing studies and we thus consider our overview of examples to be reasonably representative.

3.1 | Interspecific parasite spillover

Whenever a species is taken from its environment and transported to a new one, there is a possibility of transporting parasites along with them. In invasion ecology, the process of introducing a parasite along with its host is known as parasite co-introduction (Goedknegt et al., 2016; Lymbery et al., 2014). This principle can be applied to aquaculture as well. When a parasite is co-introduced with a host species to an environment which is inhabited by other naive potential host species, there is a possibility of the parasite switching hosts. The switch from the original host to naive wild host species is known in invasion ecology as parasite spillover (Kelly et al., 2009). When aquaculture species are farmed in systems that allow for water exchange with the environment, interspecific spillover events to wild species are known to occur (Peeler et al., 2011). A similar phenomenon can be observed in domestic animals when parasites spill over from domestic animals to wildlife populations living in proximity (Daszak et al., 2000). There are numerous examples of diseases from aquaculture farms affecting

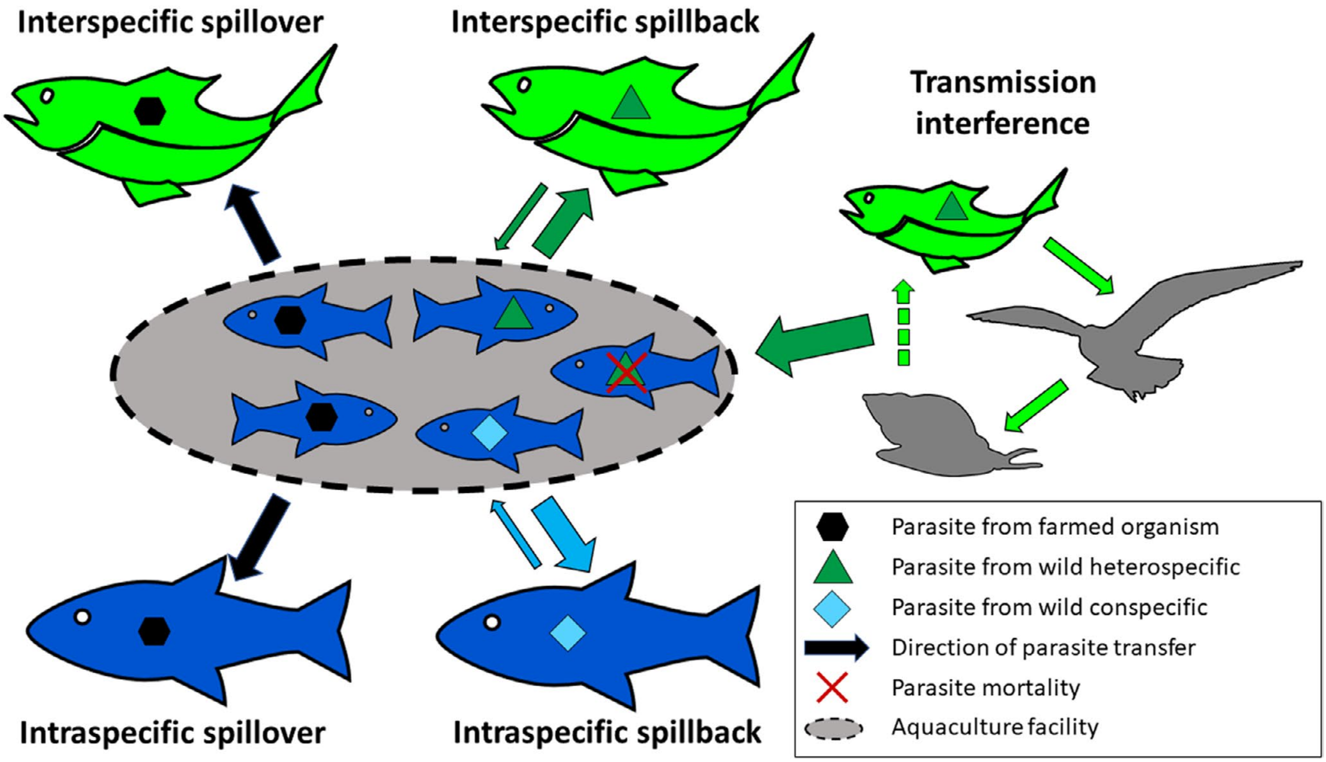

FIGURE 3 Conceptual framework showing the five different mechanisms through which aquaculture activities can affect diseases in wildlife in the environment surrounding aquaculture facilities. See main text for further details and examples of each of these mechanisms [Colour figure can be viewed at wileyonlinelibrary.com]

wild populations. Out of 35 interspecific spillover events of invasive parasites to native species in marine ecosystems listed in a review by Goedknegt et al. (2016), aquaculture was named as the most likely vector for 20, and five more were caused by stocking for fisheries. One example of such an interspecific spillover event involves the parasitic copepod *Mytilicola orientalis*, co-introduced to Europe with the Pacific oyster *Crassostrea gigas* imported for aquaculture. This parasite has been found in wild populations of several native bivalve species such as blue mussels *Mytilus edulis*, common cockles *Cerastoderma edule* and Baltic tellins *Macoma balthica*, indicating an interspecific spillover effect (Goedknegt et al., 2017). Another example involves infectious hypodermal and haematopoietic necrosis virus (IHHNV) in penaeid shrimps in the Gulf of California. This disease probably did not occur in wild shrimp populations in this region prior to 1987, but has become established in wild populations of Pacific blue shrimp *Penaeus stylirostris* and possibly other native shrimp species, following importation of *Penaeus vannamei* postlarvae to local shrimp farms (Pantoja et al., 1999).

Although many of the aforementioned interspecific spillover events of aquaculture parasites are the result of escaping culture species or close contact between farmed and wild populations in open farm systems, direct contact between species might not always be necessary for parasite spillover to occur. The parasitic swimbladder nematode *Anguillicoloides crassus* which affects eels (*Anguilla* spp.) was co-introduced in Europe with Japanese eel *Anguilla japonica* in the 1980s and spilled over to native European eel *Anguilla anguilla*, spreading rapidly across the continent (Kennedy & Fitch, 1990; Kirk, 2003; Koops & Hartmann, 1989). The spread of *A. crassus* was mainly due to the transport of live eels, which may have escaped (Kennedy & Fitch, 1990; Koops & Hartmann, 1989). However, infective stages of this parasite are capable of surviving and remaining infective for up to 2 weeks in the water column and introductions in Britain occurred mainly along the routes of lorries transporting eels, which exchange water several times during transport (Kennedy & Fitch, 1990). Therefore it is possible that at certain locations *A. crassus* interspecific spillover into European eels occurred via infective stages that were flushed out with waste water (infecting freshwater copepod intermediate hosts), rather than direct contact between eels (Kennedy & Fitch, 1990; Kirk, 2003; Peeler et al., 2011). Furthermore, *Anguilla japonica* has also been responsible for the interspecific spillover of two monogeneans *Pseudodactylogyrus anguillae* and *P. bini* to European eel *Anguilla anguilla* and American eel *Anguilla rostrata* in Europe and the US, respectively (Hayward et al., 2001; Morozińska-Gogol, 2009).

Diseases that occur in a novel species after an interspecific spillover event are known as emerging diseases, and can have devastating consequences (Daszak et al., 2000). Due to the fact that naive hosts do not have a co-evolutionary history with the novel parasite, they can be particularly vulnerable, leading to negative effects on the new host species, communities and even entire ecosystems (Goedknegt et al., 2016). This can be especially dangerous if the parasite does not cause high mortality rates in its original host, but does so in the novel host, while the original host remains present as a reservoir of the disease. For instance, the crayfish plague, a fungal disease caused by *Aphanomyces astaci*, spilled over from American signal crayfish *Pacifastacus leniusculus* to European crayfish *Astacus astacus*. While *P. leniusculus* rarely succumbs to the disease, it causes extremely high mortality rates in *A. astacus*, threatening the latter species with extinction (Alderman, 1996; Peeler et al., 2011).

3.2 | Intraspecific parasite spillover

Many cultured species are not bred in captivity, but larvae or juveniles are caught from the wild and transported to aquaculture facilities for grow-out (Boyd & McNevin, 2005). If these juveniles are infected, parasites are co-introduced to the farm environment, potentially leading to disease outbreaks within the farmed stock. In invasions, co-introduced parasites do not always lead to infections in wild native hosts by switching hosts, but affect only the invader (Goedknegt et al., 2016). In the same way, outbreaks of co-introduced parasites in aquaculture species do not have to lead to interspecific spillover in other wild species. However, a co-introduced parasite is likely to spread to neighbouring wild populations of the same species, as it does not need to cross the species barrier. For example, ostreid herpesvirus OsHV-1 μVar has recently been co-introduced to European oyster aquaculture with imports of Pacific oysters *C. gigas* from East-Asia, causing up to 90% mortality in farmed oyster, but has so far only affected this species in Europe (Goedknegt et al., 2016; Mineur et al., 2015). However, this virus has been found in wild (invasive) populations of *C. gigas* in the Dutch Wadden Sea (Gittenberger et al., 2016), although mortalities in wild populations are unknown. Similarly, intraspecific spillover was the source of bonamiasis outbreaks in European flat oysters *Ostrea edule*, caused by the parasitic protozoan *Bonamia ostreae*. The parasite is invasive and reached Europe via oyster transports from Europe to North America and back to France, bringing the parasite with them and spilling over to wild oyster populations (Chew, 1990; Engelsma et al., 2014). Intraspecific parasite spillover has also been observed in fish aquaculture. The monogenean parasite *Gyrodactylus salaris* which infects Atlantic salmon *S. salar* has been introduced to Norwegian waters with translocated salmon from hatcheries in the Baltic Sea, where salmon populations are tolerant or resistant to infections. In contrast, Norwegian salmon populations proved to be highly susceptible to the parasite and high mortalities in wild salmon populations have occurred (Bakke et al., 2007; Johansen et al., 2011; Johnsen & Jensen, 1992). This example shows that intraspecific spillover events can have important ecological implications as they can have an intense regulatory effect on the population dynamics of affected wild populations, which in turn may alter competitive interactions between affected hosts and other wild species (Goedknegt et al., 2016).

3.3 | Interspecific parasite spillback

In addition to wild species acquiring parasites from cultured species, parasites from wild species in the proximity of aquaculture farms may also spillover into cultured species, a phenomenon similar to the 'reverse spill-over' of parasites from wild populations to susceptible domesticated animals (Daszak et al., 2000). When aquaculture species are competent hosts for wild parasites, they could amplify parasite populations, which can subsequently spill back into wild hosts, increasing the number of parasite infections in wild host species (Goedknegt et al., 2016; Kelly et al., 2009; Leung & Bates, 2013). This is because the high stocking densities used in aquaculture can increase local host densities and thus boost parasite propagule production, which in turn can increase the risk for wild hosts to become infected. For example, the shell boring polychaete *Polydora ciliata* which infects the shells of wild molluscs in European seas has been acquired by the Pacific oyster *C. gigas* which is cultured in oyster farms and has also spread outside farms. In the wild, the parasite is more prevalent in Pacific oysters than in blue mussels *M. edulis* (Goedknegt et al., 2019), potentially leading to an interspecific spillback effect for wild mussels (Goedknegt et al., 2019). Another example comes from Atlantic salmon *S. salar* which is cultured along the Chilean Pacific coast and has become infected with copepods *Caligus rogercresseyi* and nematodes *Hysterothylacium aduncum* originating from a wide range of wild host species (Sepúlveda et al., 2004). Due to the high infection levels, it is likely that these parasites spill back to wild hosts, leading to increased infection levels in wild host populations. Likewise, American brine shrimp *Artemia franciscana* have been commercially imported from North America to the southern Iberian Peninsula where they escaped aquaculture farms and entered habitats with wild native *Artemia* populations (Green et al., 2005). Here, the invasive brine shrimp became infected with a variety of native cestodes that cause high infection prevalences in wild brine shrimp (*A. parthenogenetica* and *A. salina*; Georgiev et al., 2007). These examples indicate that interspecific parasite spillback can have large consequences for wild species and that the effects may not only originate from the aquaculture farms themselves but also from populations that escaped from these facilities.

3.4 | Intraspecific parasite spillback

Aquaculture species are not always newly introduced to an area, wild species are also commonly farmed locally. This leads to unnaturally high local densities of wild species within, for example, cages or net pens, while wild conspecifics live at much lower densities in the surrounding waters. This is for instance the case in the farming of salmon species, where the species farmed also naturally occur in the wild. Many disease outbreaks in salmon farms may have been acquired through exchanges with wild salmon populations, although it is often not clear whether disease originated from farmed or wild stocks. However, when a parasite is transferred from wild to farmed salmon stock it could be amplified during an outbreak in the farm, due to the high stocking densities, and subsequently spill back high numbers of infective stages to the wild population, similar to the interspecific spillback previously described, except without the need for a shift in host species. Such intraspecific spillback events are known for salmon lice *L. salmonis* and sea lice *Caligus* spp., which are naturally occurring parasites of salmonids. They can be exchanged between wild salmonids, such as the pink salmon *Oncorhynchus gorbuscha*, and farmed conspecifics along the Pacific coast of North America. Juvenile pink salmon in close proximity to salmon farms have been shown to have high rates of lice infestation, higher than those in areas without salmon aquaculture, leading to high juvenile mortality (Krkošek et al., 2007). Similar effects occur in salmon lice in farmed Atlantic salmon *S. salar* in Europe where these parasites are naturally present in wild Atlantic salmon populations. They are known to cause massive outbreaks in salmon farms and there is evidence that they subsequently cause elevated infection levels in wild salmon populations (Costello, 2009; Thorstad & Finstad, 2018; Torrissen et al., 2013). Likewise, intraspecific spillover may also affect the oyster *Ostrea chilensis*, native to New Zealand, which is cultured in Foveaux Strait between the South Island and Stewart Island in New Zealand, where wild populations also exist. Cultured oysters have experienced epizootics of the parasite *Bonamia exitiosa*, which have been catastrophic for the industry and will most likely have affected wild populations as well (Cranfield et al., 2005). Although the evidence for intraspecific spillover events is limited, spillback effects from farmed to wild conspecifics are very likely as there is no threshold for host switching that needs to be overcome, and this may be a highly underestimated effect of aquaculture on parasite–host dynamics in wildlife. Like interspecific parasite spillback between different species, intraspecific parasite spillback has the potential to induce high mortalities in wild populations, and in doing so, negatively affect wild ecosystem functioning.

3.5 | Transmission interference

One subtle effect of cultivated species on wild parasite–host interactions does not involve acting as a host or a parasite. Instead they might disturb wild parasite transmission from one host to the next, so called transmission interference (Burge, Closek, et al., 2016; Goedknegt et al., 2016; Thieltges et al., 2009). In general, many farmed and wild species that do not act as a host for a particular parasite can be so called dead-end hosts, predate on infective stages or interfere in other ways (see review by Thieltges et al., 2008). An aquaculture species which has been shown to interfere with the transmission of wild parasites is the Pacific oyster *C. gigas*, which can remove the free-living infective larval stages of wild trematode parasites affecting blue mussels *M. edulis* by filter feeding, without being infected itself (Goedknegt et al., 2015; Thieltges et al., 2009; Welsh et al., 2014). Pacific oysters are also extensively cultured in open systems in coastal waters. It is possible that oysters in farm cultures filter infective larval stages of parasites in the same way their escaped counterparts have been shown to do. This could lead to lower infection levels in wild blue mussels in close vicinity of the farm. The extent to which filter feeding organisms can remove infective stages of parasites depends on a number of factors such as the prey size range of the filter-feeder, the transmission mode and host specificity of a particular parasite (Burge, Closek, et al., 2016). Whether such transmission interference by aquaculture farms truly occurs remains unknown, as it is yet to be studied. If it is the case, it could lead to substantial increases in the wild host population, especially if a heavy parasite burden is lifted due to the interference. This way, transmission interference has the potential to change the local communities surrounding the aquaculture facility and affect both the farm and wild ecosystem. In a similar way, certain aquaculture practises themselves, such as parasite control treatments or effluents dispersing from farms into ecosystems, may affect parasite transmission in wild hosts. However, such indirect effects of parasite control treatments on wildlife diseases are beyond this review.

4 | COLLATERAL DISEASE RISK, RESEARCH NEEDS AND RECOMMENDATIONS FOR MANAGEMENT AND POLICY

The chances of the above mechanisms occurring in a specific aquaculture facility and causing collateral disease risk for wildlife depend on the interactions between farmed and wild populations. In closed systems, where effluent water is kept to a minimum, parasite exchange between farm and wild populations is unlikely to play a major role. In pond systems, interactions are more likely, as pond water is often released in the environment during harvest or heavy rainfall. Aquaculture systems that are partially or entirely open such as raceways, cages, net pens and coastal mollusc cultures pose the highest risk for parasite exchange between farmed and wild populations, through any of the five mechanisms in our conceptual framework. These systems allow for free flow of water potentially containing infective stages and have a high risk of escapes that may establish wild populations.

Although the various aquaculture practices probably have different impacts on the collateral disease risk for wildlife, there is very limited research on this issue to date. A recent global meta-analysis of the wider impacts of aquaculture activities on the environment included only 22 studies regarding potential disease transmission between farmed and wild populations, most of which were about sea lice (Barrett et al., 2019). Only 11 of those studies actually investigated changes in infection levels in wild fish associated with farms, all of which found higher infection levels in the presence of active fish farms (Barrett et al., 2019). There are most likely more diseases in wildlife that can be affected by aquaculture practices but the extent of these collateral disease effects remains elusive, mainly due to the lack of baseline information on background prevalence of parasites and diseases in wildlife (Lafferty et al., 2015). An important step will thus be to identify the parasite communities in wildlife surrounding aquaculture facilities prior to stocking. In addition to parasite screenings of aquaculture stocks to be introduced, such comprehensive inventories could (a) indicate potential candidates for spillover and spillback scenarios for which further experimental work on transmission and host specificity could evaluate the risk of disease exchange, and (b) establish baselines to monitor ensuing changes in disease prevalence in the course of aquaculture activities. Unfortunately, parasites and diseases are generally difficult to detect in natural ecosystems but emerging technologies such as environmental DNA (eDNA) are promising tools in addition to traditional methods of parasite detection, such as histology (Bass et al., 2015; Burge, Friedman, et al., 2016; Gomesa et al., 2017). Given the likelihood of farm–wildlife disease exchanges and the potentially dramatic effects of collateral diseases on wildlife, we propose to implement wide-scale parasite and disease screenings of wildlife surrounding proposed farm sites prior to aquaculture activities in risk assessments and biosecurity protocols. Biosecurity measures are already generally in place for aquaculture activities (Arthur et al., 2009; Hine et al., 2012; Subasinghe & Bondad-Reantaso, 2006; Subasinghe et al., 2019) but they currently mainly focus on the health of stocks and specific parasites relevant for the farmed species. Adding a stronger wildlife perspective to aquaculture biosecurity and identifying the potential for farm–wildlife disease exchange prior to stocking activities would strongly help to reduce the risk for parasite spillover and spillback scenarios and associated collateral disease impacts.

The establishment of reliable baseline information on background prevalence of parasites and diseases in wildlife in the vicinity of farms would also allow to monitor changes in wildlife diseases once aquaculture activities have started. If implemented in biosecurity protocols, wildlife disease monitoring would make the early detection of collateral disease impacts possible and thus help to initiate containment and eradication or mitigation measures to reduce further impact. Disease monitoring should include both farmed and wild hosts so that the exchange between farmed stocks and surrounding wildlife can be quantified. Any disease monitoring should ideally be further supplemented by monitoring of the population dynamics of wildlife potentially at risk of collateral disease impacts so that any effects on host populations can be detected. This in turn may then initiate further experimental research into the underlying mechanisms.

A general implementation of collateral disease impacts in aquaculture biosecurity protocols would also help to redress the current knowledge gaps in regard to the pervasiveness and magnitude of collateral disease impacts and the biases in existing information in regard to producing nations and culture systems. This bias also exists for aquaculture impacts in general. The global meta-analysis by Barrett et al. (2019) noted that research effort on interactions between wildlife and aquaculture is not equally distributed among producing countries and significantly correlated with a country's developmental index and the size of its aquaculture industry. However, several major producing countries did not follow this trend. China, by far the largest aquaculture producer in the world, was not represented in the relevant English-language studies found in the analysis, as were other major Asian producers. This is in line with our experience, as we did not find a single English-language study on diseases in wildlife related to aquaculture activities from China. According to the analysis of Barrett et al. (2019), research effort into the general environmental effects of aquaculture was also biased regarding production systems, with sea cages being overrepresented and freshwater systems being clearly underrepresented. The high representation of sea cages is not surprising, however, considering the open nature of those systems, allowing for interactions between farm and wildlife populations. The same pattern is also true for disease related studies as we could only trace very few studies regarding inland freshwater aquaculture. Finally, our current knowledge on the collateral disease effect of aquaculture activities is also biased with respect to the host taxa covered by existing studies. Most studies to date have focused on fish (mainly on salmon species) and to a lesser extent on crustaceans and molluscs as sources of farm-wildlife disease transfers. Hence, studies are needed that widen the taxonomic scope of aquaculture impacts on wildlife diseases.

5 | CONCLUSIONS

This review demonstrates that aquaculture activities can have an array of effects on wildlife diseases in the surrounding environment. The conceptual framework developed here provides a basis for further studies on the impacts of aquaculture on wildlife disease ecology and we propose to integrate collateral disease impacts in risk assessments and biosecurity protocols regarding aquaculture.

The risk of disease transfers related to aquaculture activities echoes similar risks in other food production environments such as agriculture and livestock management. There is a wealth of information on disease exchanges between natural ecosystems and crops or livestock (Blitzer et al., 2012; Daszak et al., 2000; Power & Mitchell, 2004). For example, many natural populations of animals serve as reservoirs for livestock diseases, such as badgers for tuberculosis in cattle in the UK (Donnelly et al., 2003) and bison that may transmit brucellosis to livestock in the US (Dobson & Meagher, 1996), creating conditions for spill back into wild host populations. Similarly, plant pathogens might transfer to cultivated crops and spill back when their wild hosts spread into cultivated areas, such as the transfer of crown rust and stem rust from wild to cultivated oats in Australia (Burdon et al., 1983; Oates et al., 1983). Examples of parasite spillover from cultivated to natural systems have also been documented (reviewed by Blitzer et al., 2012). For instance, foot-and-mouth-disease in domestic cattle in Mongolia caused an outbreak in wild gazelles (Nyamsuren et al., 2006). Parasite spillover from agriculture settings can also cause problems for nature conservation when co-introduced parasites infect vulnerable and rare species (Blitzer et al., 2012), e.g. when parasites spillover from commercial pollinators to infect wild bees (Lipa & Triggiani, 1988; Otterstatter & Thomson, 2007). These examples from terrestrial ecosystems demonstrate that more research on similar interactions between aquaculture activities and aquatic wildlife is warranted. Given that the impact of aquaculture is expected to rapidly intensify with the expanding global aquaculture production, increased research efforts into the risks of collateral diseases are urgently needed.

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AUTHORS' CONTRIBUTIONS

All authors designed the study and contributed to the writing led by M.M.B.; all authors revised the manuscript and gave final approval for publication.

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For this review article no new data have been used.

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