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Non-native aquatic animals introductions have driven disease emergence in Europe

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Abstract :

In this paper it is argued, using examples of disease emergence in aquatic animals in Europe, that the introduction of non-native species drives disease emergence by both extending the geographic range of parasites and pathogens and facilitating host-switching. Enteric red mouth disease and infectious haematopoietic necrosis of salmonids have extended their geographic range from North America to Europe with the import of live fish (*Pimephales promelas*) and rainbow trout eggs, respectively. Host-switching results in disease emergence when previously unidentified commensal organisms or known pathogen switch to new naïve hosts. The most serious endemic diseases of wild aquatic animals in Europe in recent years can be traced to the introduction of non-native species. Across Europe dramatic population declines have occurred in native crayfish (e.g. *Astacus astacus*), oysters (*Ostrea edulis*) and eels (*Anguilla anguilla*), all which can be attributed, in varying degrees, to diseases (crayfish plague, *Bonamia ostreae* and *Anguillicoloides crassus*, respectively) introduced with non-native species. The severe adverse effects at a population level can be attributed to the lack of immunity in the new hosts. The impact of parasites more recently introduced to Europe, *Sphaerothecum destruens* (the rosette agent), and *Batrachochytrium dendrobatidis*, have yet to be fully determined. Both are generalists, with wide host ranges, and may present serious threats to native species. Aquaculture is the key driver for the introduction of non-native species. Most farming systems allow pathogen exchange between farmed and wild populations which underpins host-switching. Subsequently movements of animals between farms may result in the spread of newly emerged diseases. The introduction of non-native aquatic animals drives disease emergence, thus the *ex-ante* assessment of these hazards is severely limited. Generic risk mitigation measures (e.g. movement of disinfected eggs in place of live animals) and improved methods for rapid detection of new diseases are vital.

Keywords : Aquaculture ; Transmission ; Control ; Pathways ; Virulence ; Fish

1. Introduction

Aquaculture production and the range of species farmed (which include crustaceans, molluscs and finfish) have increased significantly over the last two decades (Food and Agriculture Organisation (FAO), <http://www.fao.org/fi/statist/statit.asp> accessed on 15/12/08). Salmonid farming has expanded rapidly in Northern Europe, North America and Chile, mirrored by increases in farmed sea bream (*Sparus aurata*) and seabass (*Dicentrarchus labrax*) in the Mediterranean (Ariel and Olesen 2002). Nevertheless, Asia, and especially China still dominate world-wide farmed fish and shellfish production (FAO 2008). Aquatic animals are mainly farmed for food but also for stock enhancement, recreational fishing and the pet trade. The expansion of aquaculture in recent years has depended on the use of non-native species. Rainbow trout (*Oncorhynchus mykiss*) are indigenous to North America but are now farmed in South America, Europe, Asia and Australia (MacCrimmon 1971). Similarly, the Pacific Oyster *Crassostrea gigas* (Ruesink et al. 2005) has a wide distribution across the globe and is the most important farmed species of shellfish in Europe. The phenomenal growth in penaeid shrimp farming, periodically constrained by disease outbreaks (Hill 2002), has been based on the culture of species outside of their natural range. The trade in ornamental aquatic animals has also resulted in large scale movements of live aquatic animals to countries outside of their natural range (Gozlan 2008). On a similar scale live molluscs and crustaceans, intended for human consumption, are moved internationally.

The economic benefits of non-native introductions are undeniable (Gozlan 2008); however, there are ecological risks. The deliberate or accidental introduction of non-native aquatic animal species has caused a range of environmental impacts (e.g. predation, competition, hybridisation, habitat use) (Ruiz et al. 1997). Codes of practice have been developed to mitigate the likelihood and consequences of non-native species introduction (FAO 2005; FAO and NACA 2000). The environmental threats of non-native aquatic animals motivated the European Commission to pass 'Council Regulation No. 708/2007, which requires that approval to introduce non-native species is supported by a risk assessment.

In recent years, the rate of disease emergence in human (Jones et al. 2008) and animal populations has increased (Daszak et al. 2000), and emerging diseases have become an increasingly important area of research in both human (Krause 1998) and animal health (Daszak et al. 2001b), including aquatic animals (Harvell et al. 1999). Human activities, including the introduction of non-native species, have altered many ecosystems, in some cases seriously reducing ecosystem function (Chapin et al. 2000) and possibly leading to disease emergence (Woolhouse and Gowtage-Sequeria 2005). However, it has been argued that few studies have examined whether or how ecological change may influence disease emergence (Plowright et al. 2008). There is strong evidence that the introduction of pathogens into new areas through human activities (pathogen pollution) is one of the most important factors driving disease emergence in wildlife populations (Daszak et al. 2001a). In this paper disease emergence resulting from the movement of non-native aquatic animal species into Europe are reviewed. The impact of these diseases on native species is considered in the context of generalist and specialist pathogens. The challenges to risk assessment, the management of non-native introductions and disease in wildlife populations are discussed.

In this paper the term parasite will be used as a collective term for pathogens (also known as micro-parasites, such as viruses and bacteria) and macro-parasites, such as nematodes and cestodes.

2. Types of disease emergence

Emerging diseases have been defined as recently increasing in incidence, geographic range or virulence, recently moved into a new host, newly discovered or caused by a newly evolved pathogen (Brown 2000; Daszak et al. 2000). The movement of non-natives may spread identified parasites which are also known as transboundary diseases (Hedrick 1998). Known parasites may also exploit their new environment by switching host (i.e. crossing the species barrier); this may occur with or without evolutionary change through mutation. Commensal micro-organisms (previously unidentified) may emerge as new parasites having switched to a new host (Murray and Peeler 2005). Host switching requires contact between the putative parasites and a new host species. Secondly, host barriers to infection (e.g. immune response) must be overcome and the infection established, before efficiently spreading within the new host population (Parrish et al. 2008). Pathogens may be more virulent (i.e. increase ability to cause disease) in a new host due to a lack of innate immunity (compare with the original host). More virulent parasites may also emerge, without host switching, if conditions favour their selection (see Mennerat et al. 2010 for a discussion on the impact of intensive fish farming on the evolution of virulence). The categories of emerging disease are not mutually exclusive. By switching hosts a parasite may extend its geographic range, through live animal movements of the new host. The introduced original host may act as a reservoir population from which infection can 'spill-over' to sympatric wildlife (Gozlan et al. 2005). In the long term this may allow for evolutionary change to take place which results in host switching or increased virulence (Parrish et al. 2008).

3. What is a non-native aquatic animal species?

Despite attempts to achieve common definitions of terms, difficulties remain due to the combination of ecological and political criteria being used to identify species as 'native' or 'non-native' (Davis and Thompson 2000; Shafland and Lewis 1984). Most scientific publications use national boundaries to determine whether a species is native or non-native, irrespective of its biogeography. The term translocation is often used to differentiate between within- and across-country movements. However, in ecological terms a species moved from one river drainage basin to another within the same country could generate similar ecological outcomes as a species moved across national borders. The International Union for Conservation of Nature (IUCN) and the Convention on Biological Diversity (CBD) recommend that native species are determined at the level of the ecosystem, and not by political borders; both organisations define non-native species as a species introduced outside its natural range (Riley 2005). The same reasoning can be applied to parasites. They also have an original geographic distribution, largely determined by the presence of the natural host(s), with which the parasite has co-evolved.

4. Drivers for the movement of non-native aquatic animals

Aquatic animals may be translocated outside of their natural geographic range for a number of reasons (see Table 1) but aquaculture is the main driver. In addition the movement of aquatic animals, fertilised eggs are moved in large volumes and internationally for salmonid aquaculture. Whilst moving this life stage is safer than moving live animals, the transmission of disease is still possible. It is estimated that over 1 billion ornamental fish comprising more than 4000 freshwater and 1400 marine species from over 100 countries are traded internationally each year (Whittington and Chong 2007). Little is known of their disease

status. Most pet aquatic animals are kept in secure closed systems, however, some are released into the wild and survive (Copp et al. 2007).

Live molluscs and crustaceans, and to a far lesser extent fish, are traded internationally for human consumption. Such animals may be diverted for use in culture, or be disposed of in the aquatic environment potentially leading to the establishment of their parasites. *Volumes of trade.*

5. Emergence of known parasites in new hosts

The large majority of cases of disease emergence in European aquatic animals (Table 2) are attributable to host-switching. *Anguillicoloides crassus* (a nematode) which was introduced to Europe through the importation of Asian eels *Anguilla japonica* from Japan to Germany for fattening and consumption (Koops and Haartmann 1989). Whilst the exotic eels did not escape the parasite succeeded in infecting wild European eels *Anguilla anguilla* (Koops and Haartmann 1989). *A. crassus* first emerged in European eels which had been translocated to Asia (Kirk 2003).

It has been suggested that gaffkaemia (caused by *Aerococcus viridans*) was introduced to the UK with the import of live North American lobsters *Homarus americanus* for human consumption (Alderman, 1996). The imported lobsters were held in open seawater holding facilities which allowed the bacteria to spill over into the wild native lobster population (Alderman, 1996). The disease sporadically affects native European lobsters (Stebbing et al, submitted for publication).

The introduction of a large number of macro-parasites to the UK due to ornamental fish introductions has been reviewed by Kennedy (1993). However, none is yet to cause serious disease epidemics, their impact in native species has been confined to localised mortalities. By contrast, one of the most emerging important diseases affecting wild Atlantic salmon (*Salmo salar*) is caused by a macroparasites, *Gyrodactylus salaris*. Emergence occurred in the early 1970s following its introduction to Norway from Sweden with Atlantic salmon smolts destined for aquaculture (Mo 1994). The parasite was first described from Atlantic salmon in a hatchery on the Baltic coast of Sweden (Malmberg 1957). For many years, there were occasional findings of the parasite in Swedish salmon farms but no observations of severe disease, or findings in wild fish (Malmberg and Malmberg 1991). The switch from its original host, a Baltic strain of Atlantic salmon to Atlantic strains of Atlantic salmon resulted in disease emergence and illustrates the need to use the term of non-native with an ecological perspective. Whilst Baltic and Atlantic strains of Atlantic salmon meet the criteria necessary to class them as a single species, they have been geographically separated for thousands of years. Genetic differences have arisen, some of which are due to co-evolution with parasites. Thus movement of animals from a geographically isolated to another population of the same species (e.g. Atlantic salmon from Sweden to Norway, see Table 1) may carry a similar risk of parasite introduction as a non-native introduction. These movements may not be scrutinised to the same degree of introductions of non-native species, and are likely to be more frequent.

The international trade in amphibians for food, as zoo animals, pets, laboratory animals and biological control has been implicated in the spread of spread the fungus *Batrachochytrium dendrobatidis* (Daszak et al. 2003). The fungus is consistently carried by the North American bullfrogs (*Lithobates catesbeianus*, previously *Rana catesbeiana*) (Garner et al. 2006). It was detected in the UK in 2004 in an introduced population of North American bullfrogs in Kent (Cunningham et al. 2005) and is known to be established in at least five other

European countries (Garner et al. 2005). The fungus has a wide host range which explains its success in establishing in so many countries (Daszak et al. 1999).

The introduction of ranaviruses (family *Iridoviridae*) to Europe is also likely to have been due to imports of amphibians for ornamental purposes; the virus has been detected in frogs imported to the UK for the ornamental trade (Barry Hill, pers comm.). It emerged in Europe by host switching to native amphibians toads (*Bufo bufo*) in the UK (Hyatt et al. 2000) and the edible frog (*Rana esculenta*) in Croatia (Fijan et al 1991). Outside of Europe, trade in ornamental fish has been associated with the introduction of iridoviruses into Australia (Whittington and Chong 2007).

The ornamental trade has resulted in the accidental introduction of hitchhiker (or non-target species) which may also carry non-native parasites. *Pseudorasbora parva*, the topmouth gudgeon, was accidentally introduced to Europe from Asia with imports of carp (*Cyprinus carpio*) for ornamental purposes (Pinder and Gozlan 2003). It has recently been shown to be a healthy carrier of the rosette agent *Sphaerothecum destruens* (Gozlan et al., 2005; Gozlan et al., 2006). It appears that the parasite was introduced to the UK with topmouth gudgeon and but its presence only became apparent once it had infected sunbleak (*Leucaspis delineatus*) in which it appears to cause wasting and reduced fecundity (Gozlan et al., 2005; Gozlan et al., 2006).

6. Emergence of new parasites

Only one example of a new parasite emerging as a non-native introduction to Europe was identified. *Bonamia oestreae* emerged in *Ostrea edulis* Europe during the late 1970s and early 1980s (Elston et al. 1986). Later the parasite was discovered in Californian, where studies indicated it originated (Elston et al. 1986). It is believed that the parasite was introduced into France and Spain with spat of *O. edulis*, the European flat oyster, produced in a hatchery in California (USA) (Comps et al. 1980). *O. edulis* was first introduced from Holland into the west coast of USA at the end of the 1940s (Loosanoff 1955). Thus the parasite was introduced into Europe through the reintroduction of a native species from outside its natural geographic range. When an aquatic animal species is moved outside its natural range not only may it introduce parasites to a range of new potential hosts, the non-native species is itself exposed to a new range of potential parasites. The case of *O. edulis*, illustrates that the reintroduction of a species back to its country of origin carries a similar risk of parasite introduction as a truly non-native species. It is reasonable to assume switching from its original host, possibly *Crassostrea virginica* (O.I.E. 2009), underpinned emergence in *O. edulis*.

7. Geographic spread of known parasites

There are a few examples of diseases which spread to Europe years after they initially emerged in other parts of the world. *Yersinia ruckeri* (the bacteria causing enteric redmouth in salmonids) emerged in rainbow trout production in the 1950s in the US. It appears to have spread initially to France (Lesel et al. 1983) with the importation of minnows (*Pimephales promelas*) which were used for live-baiting in the early 1980s (Michel et al. 1986). The pathogen has become established in rainbow trout culture throughout Europe (Horne and Barnes 1999).

Similarly IHNV emerged in salmonids production in Oregon in the 1950s (Wolf 1988) and was introduced to Europe in the 1980s. On this occasion the route of introduction appears to

have been the import of rainbow trout eggs for use in aquaculture (Bovo et al. 1987). The hypothesis has been supported by molecular epidemiology studies showing that all European IHNV isolates belong to one of the four North American genogroups, and suggest a single introduction (Enzmann et al. 2005).

The haplosporidian parasite *Haplosporidium nelsoni* was first identified in 1993 in *C. gigas* collected in two bays in France (Renault et al. 2000). *H. nelsoni* is suspected to have been introduced into France with spat and adult Pacific oysters imported from Japan and British Columbia (Canada) respectively in the 1970s. There is no recorded spread to native European species.

8. Routes of establishment

Following emergence, the likelihood that the parasite establishes and spreads will partly be determined by how the host population is maintained. Compared with other routes of parasite introduction (e.g. fish carcasses), non-native species introduction is likely to result in parasite establishment since the parasite is introduced with its host. Establishment of the parasite in native species requires contact (direct or via water) between a potential new host and the infected non-native species. This may occur if the non-native species is deliberately (e.g. for recreational fishing or biological control) or accidentally (e.g. escapees) introduced into a wild environment. Escapes from aquaculture or ornamental facilities have been well documented for many non-native species, which may have been deliberately (i.e. target species) or accidentally (hitchhiker or non-target species) introduced. Rainbow trout escapees from aquaculture are commonly found around farms. Deliberate (and often illegal) introductions of aquatic animals into the wild also take place, and have been particularly well documented for ornamental fish (Copp et al., 2007).

The open design of many aquaculture systems permits the exchange of parasites between farmed and wild aquatic animal populations without direct contact between hosts (Kent 2000). Thus, whilst species introduced for aquaculture may be kept in conditions which prevent their escape, excreted parasites will be disseminated via water currents exposing endemic species in the vicinity (e.g. downstream of a farm using river water). Following introduction, *A. crassus* and *A. viridans* both succeeded in establishing in wild native species, whilst their non-native hosts (*A. japonicus* and *H. americanus*) did not establish in the wild. Land based recirculation systems are the exception; effluent is disinfected, e.g. by ozone treatment, from which the likelihood of parasite dissemination is very low.

9. Parasite dissemination following introduction

The movement of live animals is generally the most important for widespread, long distance dissemination of parasites (Peeler et al. 2004). The scale of impact of new and introduced pathogens will in large part be determined by the extent of its geographic distribution. The movement of live fish is an integral part of many production systems. In Europe rainbow trout production is organised around specialist hatcheries that supply juvenile fish ("fingerlings") to a large number of producers for on-growing. Detailed investigations (Johnsen and Jensen 1988) concluded that nearly all Norwegian rivers affected by *G. salaris* could be traced to the release of salmon from one Norwegian hatchery where the parasite was first discovered in 1975, the accidental release of infected fish from a truck transport, or with secondary spread to neighbouring watercourses via short-distance migrations through brackish water. Similarly *A. crassus* has been spread through eel restocking programmes and movement of wild caught eels for farming (Kirk 2003). Whilst crayfish plague was introduced in the 1860s

(probably through the discharge of ballast water or import of fish carrying fungal spores in their gut), the spread of crayfish plague in Europe accelerated once signal crayfish (the non-native host) were brought to Europe to be farmed in the 1960s (Alderman, 1996). Topmouth gudgeon, a healthy carrier of the rosette agent *Sphaerothecum destruens* (Gozlan et al., 2005) has become the most invasive fish species in Europe, with what has become a pan European distribution, through movement of other species (e.g. carp) to fisheries and for ornamental purposes (Pinder and Gozlan 2003).

Shellfish farming is also based on large-scale animal movements. Oyster farmers transfer oyster batches between areas to optimize yields. Moreover movements of oyster spat (authorised and illegal), produced naturally and in hatcheries also occur between European countries. This has resulted in the rapid and widespread distribution of *B. ostreae* throughout European shellfish production areas and natural beds (McArdle et al. 1991). Recently the emergence of a new strain of oyster herpes virus 1 disease in France, which was associated with high levels of summer mortality in *C. gigas* (Pepin et al. 2009) spread to Jersey (Reid, A. pers comm.) and Ireland (Geoghagen, F., pers. com.) through movements of live oysters for relaying. Oysters may also be moved accidentally spreading disease. Two loughs in Ireland, Lough Foyle and Lough Swilly, have recently been found to be positive for *Bonamia ostreae* (Culloty and Mulcahy 2007). An epidemiological investigation concluded that a batch of mussels containing flat oyster spat was the likely route of introduction (Culloty and Mulcahy 2007); an example of a hitch-hiker (non-target organism) spreading disease within a country. Boats and equipments can also disseminate parasites in oysters attached to the hulls or carried by dredges (Howard 1994). Sharing equipment between sites is thought to have resulted in the spread of IHN virus in France and in British Columbia (Hattenberger-Baudouy et al. 1995; St-Hilaire et al. 2002). *Anguilloides crassus* was also probably spread to the UK via the movement of transport lorries from mainland Europe to collect elvers, which were carrying free living larval stages (Kennedy and Fitch 1990)

Slaughterhouses and processing plants may also be hubs of disease dissemination (Munro et al. 2003). Parasites can be disseminated locally if discharged effluent is not disinfected. Observational studies (Jarp and Karlsen 1997) revealed that distance to slaughterhouses were an important risk factor for infectious salmon anaemia (ISA) in farmed Atlantic salmon in Norway. There is inconclusive evidence that waste from imported crustacean resulted in white spot syndrome virus (WSSV) introduction, possibly via birds scavenging landfill sites (Vanpatten et al. 2004).

10. Generalist versus specialist parasites and the impact of emerging diseases

Disease spread and emergence due to the movement of non-natives has disproportionately affected wild, not farmed, aquatic animal populations in Europe over recent years. The lack of natural immunity to introduced parasites has resulted in population declines and the total or virtual elimination of susceptible hosts at a local or wider scale. Atlantic salmon populations have been severely depleted in over 45 rivers in Norway due to *G. salaris* (though elimination of the parasites has been achieved in some rivers) (pers. comm. T.A. Mo). Native European crayfish, *Astacus astacus* L., have been virtually eliminated from large parts of Europe due to crayfish plague carried by signal crayfish, *Pacifastacus leniusculus* (Dana 1852) (Alderman 1996). *B. ostreae* has significantly contributed to the virtual elimination of native oysters from many regions of Europe (and their replacement by the Pacific oyster, *C. gigas*) (Culloty et al. 1999). *A. crassus* causes a debilitating infection in the swimbladder of European eels and may have has an important role to play in the dramatic decline in numbers over the last 20 years. It is certainly possible that infected eels are less likely to reach the Sargasso Sea to spawn. However, the decline of eels is at least partially

due to a number of inter-related factors, including pollution, barriers to upstream migration and over-exploitation (Kirk 2003; Naismith and Knights 1990).

The potential impact of more recently introduced parasites, *Sphaerothecum destruens* and *Batrachochytrium dendrobatidis* cannot yet be fully assessed. However, both are generalist pathogens, with wide host ranges, which is a serious cause for concern. The consequences of generalism on pathogenicity are important but often overlooked (Yamamoto and Kilistoff 1979). Generalist pathogens are more likely to emerge through host-switching (Woolhouse and Gowtage-Sequeria 2005). The existence of functional fitness trade-offs for generalists should favour the evolution of specialists exploiting narrower niches. Many studies have highlighted that in single host parasites the trade-off between virulence and transmissibility determines the optimum level of virulence (Davies et al. 2001). In multi-host pathogens, depending on the level of virulence and transmissibility in each host, the introduction of a second host with a different susceptibility can lead to a change of virulence of the pathogen and thus could alter its potential transmissibility to the first host and the outcome of infection (Woolhouse et al. 2001). *Sphaerothecum destruens* (rosette agent) illustrates the potential threat of a generalist parasite. This intracellular parasite was recently discovered in Europe (Gozlan et al. 2005) and appears to infect wild and captive salmonid and cyprinid fish (Gozlan et al. 2009). Topmouth gudgeon is an invasive healthy carrier (i.e. reservoir host) of *S. destruens*, in which the parasite may persist whilst causing localized outbreaks of variable and unpredictable timing and magnitude in other susceptible species. The sunbleak contributes little to *S. destruens* fitness, and there should not be a selective constraint on *S. destruens* virulence in sunbleak because the topmouth gudgeon is present as a healthy carrier. This may explain why the parasite, within three years of introduction, has led to localised population extinctions of sunbleak (Gozlan et al. 2005). In addition, a number of cyprinid species have been shown under experimental conditions to be susceptible to *S. destruens* (Gozlan et al. 2009) though to date there is no evidence that these populations are regulated by the parasite in Europe.

Similar arguments may also be advanced for *B. dendrobatidis*, the cause of chytridiomycosis, a fungal disease which has been the cause of dramatic declines of a wide range of amphibian populations (Hyatt et al. 2000) in Australia and Central America (Daszak et al. 2001a). It has been detected in Europe (Garner et al. 2005) and has been associated with localised mortalities, e.g. natterjack toads (*Epidalea (Bufo) calamita*) in Cumbria, UK (Cunningham et al. 2005) but to date has not been associated with population declines.

11. The limits of risk assessment and risk mitigation

The likelihood of parasite introduction and spread with the introduction of a non-native aquatic animal species should be an integral part of a risk assessment protocol undertaken to support decision making about species introduction (FAO, 1995; FAO and NACA, 2000; Anon., 2001). However, the usefulness of risk assessment for disease introduction is limited by hazard identification (the first step). As currently applied risk assessment does not attempt to account for unidentified hazards. Parasites introduced by non-native species are very often unidentified hazards because, as discussed above, it is the non-native introduction that drives disease emergence (e.g. *G. salaris*, *A. crassus* and *A. astaci* were only recognised as pathogenic following a non-native introduction). Whittington and Chong (2007) made a similar point by highlighting the significant difficulties in undertaking disease import risk assessments for ornamental fish; a large number of imported species and sources, combined with little disease information. The situation may be further complicated by the presence of non-target, non-native species which themselves may carry parasites; rosette agent infections of the topmouth gudgeon being an example. It has been suggested that historical evidence on the frequency of disease emergence could be used to provide an

estimate of the risk of unidentified hazards for use in an import risk analysis (Gaughan 2002); but this is not currently acceptable under international trade agreements (WTO 1995). The risk assessment required by the EC regulation 708/2007 will also only assess identified parasites.

Control of diseases in wild populations is extremely problematic and elimination is generally considered impossible; an exception being localised control of *G. salaris* and *S. destruens* (Britton et al. 2008; Britton et al. 2009) through the elimination of host fish species in some lakes and rivers by chemical treatment. The control of introduced parasites can be particularly problematic once established in a wild endemic population, or in a highly successful invasive species (e.g. signal crayfish, *Pacifastacus leniusculus*). Parasites with multiple host species, such as *Batrachochytrium dendrobatidis*, create further challenges. Effective disease control requires a high level of understanding of the dynamics of infectious disease in multihost populations (Cleaveland et al. 2001), especially when some species act as reservoir populations where the pathogen can be permanently maintained and difficult to detect (e.g. *S. destruens* in top mouth gudgeon) (Haydon et al. 2002).

The introduction of non-native species clearly has potential economic benefits (Gozlan 2008). However, given the limitations of risk assessment, it is important that risk mitigation measures to reduce the likelihood of parasite transmission are thoroughly explored to minimise the potential costs that may occur from disease. Whittington and Chong (2007) recommend limiting the number of ornamental species traded and the countries of origin. Other options include quarantining non-native species with native species. Research is needed to establish the duration and conditions of quarantine most likely to reveal putative parasites. However, quarantine cannot offer a high likelihood of detection. Notwithstanding the example of IHN virus introduction to Europe via rainbow trout eggs, the movement of gametes is invariably considerably safer than moving live animals. Few aquatic animal diseases are transmitted via true intra-ovum infections, and surface disinfection (e.g. using iodine) can reduce the risk of contamination to a negligible level (the introduction of IHN virus was probably a failure to properly disinfect the eggs). Establishing a non-native species by introducing fertilised eggs instead of adult animals should always be considered.

12. Conclusion

Aquaculture and the ornamental aquatic animal trade are the key drivers for the introduction of non-native aquatic animal species. The movement of live animals is the main route of spread of disease. However, the introduction of non-native species also drives the emergence of new diseases and known diseases in new hosts by bringing parasites into contact with new potential hosts, thus facilitating host-switching. Generalist parasites, able to jump the species barrier, are more likely to emerge, compared with single host parasites. Endemic species of aquatic animals (especially wild populations) become exposed to introduced parasites due to the open nature of aquaculture production systems. Once emerged parasites have been disseminated through the large-scale movements of animals for aquaculture. The presence of the natural host facilitates emergence of disease in naïve native populations and in the longer terms may allow emergence through evolutionary change in the introduced parasite. Although there are numerous examples of disease emergence after species introduction, there are probably many more that have not been identified. Slow emergence through evolutionary changes may not so easily be associated with non-native introductions. Developments in sampling protocols and diagnostic techniques will enable better characterisation of emerging infectious pathogens. These improved methods will also underpin measures to control non-native pathogens through surveillance to establish free zones and effective legislation to prevent the movement of animals from infected areas.

The serious adverse consequences of the introduction of parasites introduced to naive wild European aquatic animals are well documented. The impact of recent parasite introductions in amphibians is currently unfolding. Rising water temperatures, due to climate change, will increase the likelihood that introduced ornamental species, and their parasites can survive in Europe. Successful control of parasites is very unlikely once established in wild populations, thus changes generally are permanent and irreversible. It must be recognised that introducing non-native species carries a risk of non-native parasite introduction that, *ex-ante*, cannot be fully assessed. Without improved risk mitigation (quarantine, introduction of fertilised eggs) disease emergence as a result of non-native species introduction will continue with potentially serious consequences for wild aquatic animal populations.

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Tables

Table 1 Reasons for the introduction of non-native aquatic animal species to Europe

Reason for introduction	Example
Aquaculture	Introduction of signal crayfish (<i>Pacifastacus leniusculus</i>) rainbow trout (<i>Oncorhynchus mykiss</i>) to Europe from N. America
Slaughter and human consumption	Establishment of Pacific oysters (<i>Crassostrea gigas</i>) in Norway, following its introduction for human consumption
Ornamental aquatic animal trade	Goldfish (<i>Carasius auratus</i>), orfe (<i>Leuciscus idus</i>), bitterling (<i>Rhodeus amarus</i>) and pumpkinseed (<i>Lepomis gibbosus</i>) are now established in the wild in the UK following introduction for ornamental purposes
Recreational fishing	Introduction of European catfish (<i>Silurus glanis</i>) and zander (<i>Sander lucioperca</i>) to the UK
Biological control	Grass carp (<i>Ctenopharyngodon idella</i>) introduced to control weed in the UK
Laboratory use	Historical trade (international) in the African clawed toad (<i>Xenopus laevis</i>) for pregnancy testing
Accidental	Mitten crabs (<i>Eriocheir sinensis</i>) to Europe (from Asia via ballast water) Topmouth gudgeon (<i>Pseudorasbora parva</i>) in Europe as 'hitchhikers' from Asia with Chinese carps for aquaculture

Table 2 Important parasite introductions to Europe via the translocation of non-native aquatic animal species

Infectious agent (disease)	European host	Origin of infection	Year	Non-native species introduction	Impact	Type of emerging disease
Bacteria						
<i>Yersinia ruckeri</i> (Enteric red mouth)	Wide host range (salmonids and non-salmonids)	N. America	1981	Minnows (<i>Pimephales promelas</i>) imported from the US to France for live-baiting (Michel et al. 1986).	Serious disease in rainbow trout production in Europe, causing a high level of morbidity and significant costs of control	New geographic area
<i>Aerococcus viridans</i> (Gaffkaemia)	European lobster (<i>Homarus gammarus</i>)	N. America	1978	Live American lobsters (<i>Homarus americanus</i>) (Alderman 1996)	No observed impact on wild populations. Clinical disease observed in facilities holding wild caught animals	New host
Viruses						
<i>Infectious haematopoietic necrosis</i>	A number of salmonid species	N. America	1987	Rainbow trout (<i>Oncorhynchus mykiss</i>) eggs (Bovo et al. 1987)	Mortality and morbidity in farmed rainbow trout. No impact observed in wild populations	New geographic area
<i>Ranavirus</i>	Amphibians, reptiles and fish	Unknown, probably N. America	~ 1992	Imported amphibians (B. Hill, pers. comm.).	Common frog mortalities in the UK and localised population declines (Teacher et al. 2010)	New host
Fungal and oomycete infections						
<i>Aphanomyces astaci</i> (Crayfish plague)	European crayfish species (e.g. <i>Astacus fluviatilis</i> , <i>Astacus astacus</i>)	N. America	1860s	Introduction probably mechanical (ballast water or fish vectors) (Alderman 1996); reintroduction via signal crayfish imports from N. America in 1960s)	High mortality of native European crayfish, and extinction from much of their original range	New host
<i>Batrachochytrium dendrobatidis</i>	Wide host range (>13 amphibian families)	Unknown (probably the Americas)	~ 1998	Potential routes of introduction to Europe include movement of amphibians for: pet trade, zoo animals; food trade; laboratory animals (Daszak et al. 2003)	Localised mortality events in amphibians populations (Garner et al. 2005)	New host
Parasites						
<i>Sphaerothecum destruens</i>	A number of cyprinid and salmonid species	Unknown, probably Asia	2005	Topmouth gudgeon (<i>Pseudorasbora parva</i>) (Gozlan et al. 2005)	High mortality of cyprinids in particular sunbleak (<i>L. deloneatus</i>) and salmonids in the US and salmonids in the US	New host
<i>Bonamia oestræ</i>	<i>Ostrea edulis</i>	N. America	Late 1970s	<i>O. oedulis</i> ² reintroduced from N. America	Decimation of native oysters (<i>O. edulis</i>) in Europe	New disease

Table 2 continued

Infectious agent (disease)	European host	Origin of infection	Year	Non-native species introduction	Impact	Type of emerging disease
<i>Gyrodactylus salaris</i>	Atlantic salmon (<i>Salmo salar</i>)	Sweden	1973	Baltic strains of Atlantic salmon (Johnsen and Jensen 1991)	Reduction of over 95% in wild Atlantic salmon populations in 45 affected rivers in Norway	New host
<i>Anguillicoloides crassus</i>	European eel (<i>Anguilla anguilla</i>)	Japan	mid 1970s	Asian eels (<i>Anguilla japonicus</i>) (Koops and Haartmann 1989)	Mortality in infected European eels, potential significant contribution to the decline of eel populations.	New host
<i>Haplosporidium nelsoni</i>	None— Download PDF (243.7 KB) or recorded spread from the introduced host	Japan	1993	Pacific oysters (<i>Crassostrea gigas</i>) (Renault et al. 2000)	No observed impact, recorded at low prevalence	New geographic area
<i>Candidatus Xenohaliotis californiensis</i>	European abalone (<i>Haliotis tuberculata</i>)	N. America	1988	Red abalone (<i>Haliotis rufescens</i>) (Balseiro et al. 2006)	Mortality juvenile abalone in Galicia, Spain	New host

^a *O. edulis* is a native species to Europe that was translocated to N. America from where it was reintroduced to France