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Introduction of pathogens in European aquatic ecosystems: Attempt of evaluation and realities

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SUMMARY – The multiplicity of fish and shellfish introductions or translocations was amplified in the last few decades and was accompanied by the introduction of pathogens into inland hydrosystems. However, the analysis of pathogens' origins revealed that some paths remain underestimated. The progress in the methodologies and techniques of identification has lead to recent advances in the analysis of pathogen introductions, but with this progress the problem of perception thresholds arose. A review of the literature reveals that almost one hundred pathogen species were introduced into European hydrosystems. The biological characters in favour of the establishment of the pathogens are described. The diversity and the apparent non predictibility of the introduced pathogens' impacts are detailed both in field and theoretical contexts. A conceptual framework of risk analysis and propositions is provided.

Key words: Biological invasions, pathogen spreading, hydrosystem.

RESUME *– "L'introduction d'agents pathogènes dans les écosystèmes aquatiques européens : Essai d'évaluation et réalités". La multiplicité des introductions ou translocations de poissons, mollusques ou crustacés s'est largement amplifiée dans les dernières décennies et s'est accompagnée de multiples introductions d'agents pathogènes dans les hydrosystèmes naturels. L'analyse de la diversité des sources de ces agents pathogènes montre que certaines voies sont encore largement sous-évaluées aujourd'hui. L'amélioration apportée aux méthodologies et aux techniques d'identification a récemment permis un progrès spectaculaire dans la traçabilité des agents pathogènes et dans l'analyse de leurs introductions. Elle apporte, en partie, les clarifications nécessaires pour tenter de faire le bilan des introductions mais pose nettement le problème du seuil de perception de l'intrus. Une revue de la littérature a permis de recenser environ une centaine d'introductions relativement récentes d'agents pathogènes dans les hydrosystèmes naturels européens. Les caractères biologiques* sensu lato *favorables à la naturalisation des agents pathogènes introduits sont présentés. La diversité et la non-prédictibilité des impacts consécutifs à ces introductions sont ensuite détaillés à la lumière des études de terrain et de l'écologie théorique de la relation hôte-pathogène. Un cadre conceptuel d'analyse de risque est succinctement délimité pour évaluer ces introductions et des recommandations sont proposées.*

Mots-clés : *Invasions biologiques, diffusion d'agents pathogènes, hydrosystèmes.*

Introduction

The introduction of fish specimens into aquatic ecosystems is commonplace around the world. The main purposes of these introductions are for aquaculture, reinforcement of natural populations, biological control or recreation activities (exotic fish aquaria, angling, etc.) and have experienced an unprecedented boom (Welcomme, 1986, 1988; Stewart, 1991) over the past 3 decades. The wide introduction of these species is quantified in the detailed analysis by Bartley and Subasinghe (1996), who made a review of 654 introductions of aquatic species, 537 of which were freshwater species. The vast majority of these introductions were finfish, mainly into Europe (178 species), Asia (163) and North and South America (121). Introductions for aquaculture were the most numerous (346 species, 112 of which are farmed intensively); followed by fishery species (121), angling (79) and ornamental species (63).

The taxonomic diversity of the introduced species, particularly in Europe (Cowx, 1997), the high number of introduction events – evaluated in thousands (Welcomme, 1992), worldwide transfers and intrinsic links between aquaculture production systems and aquatic ecosystems confer aquaculture a particular status, that is often considered negative.

In fact, the development of aquaculture production has been accompanied by a remarkable increase of infectious and parasitic diseases in farm species. Among the factors at the source of the emergence of these diseases is the increase in trade of live aquatic species. This means that species which under natural conditions would not co-inhabit the same biocenosis are living together and that pathogens are introduced at the same time.

With aquaculture development, a wider application of sanitary measures and a constant improvement of diagnosis techniques have increased awareness of how important the introduction of pathogens is in the emergence of aquatic animal diseases (Munro and Duncan, 1977; Munro, 1986; Sindermann, 1988, 1992; Stewart, 1991).

Sanitary research targeted on the epizootics of fish farms is recent and is constrained by socio-economic demands. This raises the problem of making an objective balance between how many pathogens have come with the introduced species and how many correspond to the autochthonous species. The evolution of diagnosis methodologies has considerably modified the level of perception of pathogens and diseases; it has notably influenced health legislation and the scope of application of the systems designed to reduce introductions is being considered.

Later on, some selected examples may help to analyse the impacts of the main pathogens introduced, both in aquaculture and in natural populations, and show the methodological difficulties as well as the limitations in our knowledge.

Finally we will give a brief outline of the premises of a risk analysis of the introductions and from it we will deduce some recommendations.

The evaluation of the introduction of pathogens. Truth or myth?

It is necessary here to consider the diversity of sources and the methodological difficulties involved in the detection and identification of pathogens in succession. These pathogens can be introduced in various ways and we will address the range of introduction sources only where the volume of introduction and translocation is particularly high.

The diversity of sources

Aquaculture: A revealer of pathogens

Historically, studies of aquatic animals pathogens were oriented mainly towards the diseases of farm populations and towards the implementation of strategies that would lower economic incidence.

At that time it was generally believed that aquaculture conditions favoured the outbreaks of epidemics and revealed the presence of (pre) existing pathogens in the natural environment of the wild aquatic populations. In fact, rearing high-densities replaces the stress of interspecific competition and predation with ethological stresses that the fish are not used to. Farming in suboptimum temperature conditions, low levels of dissolved oxygen and catabolism waste accumulation as well as repeated handling all lead to a lower efficacy of immune defences (De Kinkelin *et al.*, 1985, 1994); these factors thus favour the emergence of devastating epidemics that are the exacerbated clinical expression of indigenous pathogens.

In this sense, the finding of *Yersinia ruckeri* in France is particularly illustrative. This bacteria was isolated by Rucker in 1966 from systemic infections in farmed rainbow trout in the Hagerman Valley in Idaho, USA (Rucker, 1966). It was reported for the first time in March 1981 in the rainbow trout farms of the south west of France during clinical episodes in young trout where mortalities were reaching between 5 and 10% of the farm stock (Lésel *et al.*, 1983). In the same year, the authors reported the presence of this bacteria in neighbouring farms experiencing clinical episodes of systemic bacteriosis and reported that this disease would have spread further throughout the French river basin network. An introduction route of the pathogen was only shown in 1986 (Michel *et al.*, 1986). These authors described a clinical case of this bacteriosis in minnows (*Pimephales promelas*) that had been imported from the United States at least since 1981 for live-bait fishing.

Finding this bacteria in the farm populations then revealed its introduction in the wild populations of aquatic ecosystems that were in contact with the production systems. Its present cosmopolitan area of distribution englobes a wide diversity of biocenoses, both freshwater and seawater, stretching mainly to the salmon-producing countries. The part that corresponds to the introductions and translocations of fishfarming species or trade in its present geographical distribution remains to be determined.

Thus, the advance in knowledge has shown how important the wild populations are in the contamination of aquaculture populations, and more generally, in keeping disease endemic.

Conversely, the pathogens of the aquaculture animals may have influenced the infectious flora and the parasite fauna of the wild populations.

Aquaculture: A source of pathogenic agents

The rapid development of the aquaculture farming industry has been accompanied by a growth in the number of isolated pathogens and severity of associated diseases. The lack of proportion between the number of diseases described in fish farms and the apparent absence of diseases in the wild has been the origin of recent awareness of the potential transfer of aquaculture animal diseases to wild populations. However, most authors do not consider this hypothesis to be very important, arguing that the pathogens already existed in the wild populations, and that aquaculture simply revealed the pathogens that were already in the environment (Hastein and Linstad, 1991). In fact, disease is the result of a complex interaction between host, environment and pathogen (De Kinkelin *et al.*, 1985).

Therefore, there are numerous potential interactions between wild populations and farms, to name just a few:

(i) Aquaculture systems are very rarely closed and the water leaving the farms can carry pathogens over long distances. It has been shown that the infectious pancreatic necrosis virus could be detected in the effluents several kilometres downstream from a salmon farm (Munro and Duncan, 1977).

(ii) Fish introduction, transport, contact with fish that have escaped from farms or contact with contaminated material are also potential sources of pathogens for wild populations.

(iii) Reinforcements of free populations without sanitary control are likewise sources of pathogens, particularly formidable in the case of vertically transmitting pathogens.

The multiplicity and diversity of contact opportunities between farmed and wild populations make it probable for pathogens to be introduced from farms into freshwater ecosystems.

However, the farmed populations are focalizing the major part of the available means to study aquatic animal pathogens and subject to regular surveillance made compulsory by the health protection regulations. These regulations are periodically updated according to the acquired scientific knowledge and it can be considered that the pathogens in these populations are amongst the best known. On the other hand, in spite of an important contribution from biologists, there is still less knowledge of infectious fauna and parasites of wild fish species.

Aquarium fish: An underestimated source

Hundreds of species of ornamental fish are exported worldwide from South East Asia: Malaysia, Singapore and Thailand being the main suppliers. The identity of pathogens and their virulence in aquarium species raised or captured in natural environments has not received as much attention as needed (Hedrick, 1996). In fact, Kennedy (1993) examining the introduction, dispersal and colonisation by helminths and parasite crustaceans in the British Isles, showed that for 16 introduced species, 70% of the helminths had been introduced with ornamental fish.

Iridoviruses were isolated very recently in several species (*Poecilia reticulata* and *Labroides dimidatus*) of tropical ornamental fish (Hedrick and McDowell, 1995). These virions isolated in ornamental fish had a comparable morphology and antigens common to the iridovirus already described in sheatfish, *Silurus glanis* (Ahne *et al.*, 1989) and the black bullhead, *Ictalurus melas* (Pozet *et al.*, 1992) in Europe, the pike, *Perca fluviatilis* (Langdon and Humphrey, 1987), and the rainbow trout, *Oncorhynchus mykiss* (Langdon *et al.*, 1988) in Australia. The primers developed for the pike virus have allowed a PCR amplification to be made of a fragment of genomic DNA of the iridovirus of ornamental fish. Furthermore, a study of the virulence of this isolate has shown how sensitive the rainbow trout is. According to Hedrick and McDowell (1995), the iridovirus of the wild or farmed species and the isolates of ornamental fish belonged to the *Ranavirus* genus. Their present geographical distribution would come from a parallel introduction with the ornamental fish.

Aquarium fish are therefore ideal sources of pathogens because of the taxonomic diversity of the imported species and their provenances. However, their real contribution in the introduction of pathogens is largely unknown as they are not the object of specific sanitary surveillance in Europe.

Problems in the detection of introduced pathogens

Limitations in detection of pathogens through their effects

In the natural environment, epidemics are only perceived after inducing ethological modifications or if there are high mortalities in the populations. In fact, diseased or dead animals are rapidly destroyed by predators or necrophages. Their disappearance is all the more rapid as it is the young age classes that are often the most affected. This is why the impact of an introduced pathogen very often goes unnoticed. A good example is the typical case of the infectious pancreatic necrosis that causes mortalities in young fry whereas the adults are receptive but not sensitive (Wolf, 1988). As in many parasitoses, young Atlantic salmon fry are much more sensitive than older cohorts to gyrodactylosis caused by *Gyrodactylus salaris* (Johnsen and Jensen, 1992).

Furthermore, the observed effects – brutal and massive mortalities – are often attributed to other causes, particularly pollution. In Norway, the mortalities in wild Atlantic salmon populations were attributed for several years to industrial pollution when they were really caused by the monogene *G. salaris* (Johnsen and Jensen, 1986). Thus, the detection of introduced pathogens in free populations is difficult and exceptional.

Detection: Which hosts?

Investigation of pathogens based on clinical symptoms is a traditional animal health procedure. However, the development of research on the host – pathogen relationship has shown that the specificity of the viruses, bacteria and parasites is very variable and difficult to predict (Combes, 1995). Thus the birnavirus which is responsible for infectious pancreatic necrosis was isolated in numerous fish species, in molluscs and even crustaceans even though it was estimated to be only present in some salmonid species (Wolf, 1988). Numerous reservoir species of this virus never showed clinical symptoms but these asymptomatic carriers contribute to their natural or anthropic dispersal. The detection of sub-clinical carriers was not done systematically and the techniques or means set up for the diagnosis are not always sensitive enough in many laboratories.

Likewise, the distribution of parasites in a host population is normally aggregated: a large majority of slightly infested hosts do not even show clinical symptoms.

The range of hosts of *Yersinia ruckeri* includes 9 salmonid species, 11 non-salmonid species including *Anguilla anguilla, Acipenser baeri, Carassius auratus, Lota lota, Pimephales promelas, Pollachius virens, Scophthalmus maximus* and *Thymallus thymallus*, 3 bird species and 2 mammal species as well as a crustacean species (Furones *et al.*, 1993).

This illustrative case has displayed the role of wild species in the spreading of pathogens. It also raises the issue of including these multiple host-species that belong to very different taxonomic groups in legislations that will regulate their introduction, transfer and trade.

One of the major difficulties involved in establishing a realistic balance lies in the fact that the concept of specificity has been considered very differently in these unrelated systematic groups and that in-depth research in this field of bacteria and virus is recent.

Detection: Which pathogens?

The detection and identification of pathogens are based on the use of morphological, biochemical, immunochemical, and population genetics criteria as well as the more recent criteria of molecular biology. The evolution of techniques and knowledge in the detection and the systematics of the pathogenic agents modify the thresholds of perception and will be determining factors in all regulations of introductions.

For the sake of continuity, we will take up the example of *Y. ruckeri* but there are multiple models, both in microbial agents and in parasites.

At the outset, it was accepted that *Yersinia ruckeri* was a homogeneous taxon but a wide variability of biochemical and serological features soon became evident.

Biochemical criteria

Yersinia ruckeri is currently identified when examining the specific biochemical profiles using rapid and classical methods such as the API 20 E and API 50 CH systems. However, the profiles obtained are characterised by a great variability, which makes their interpretation delicate in different laboratories and makes it necessary to resort to conventional methods, which are more laborious and costly.

Immunochemical criteria

The study of antigenic properties of the whole cell has led to the identification of 5 serotypes besides the initial Hagerman serotype. Based on a technique of immunoenzymatic detection of lipopolysaccharides, the serovars 2, 4, 5 and 6 were identified through serotype II (Pyle and Schill, 1985). In 1990, Davies described 5 new other serotypes of *Yersinia ruckeri* of which the taxonomic relations are, however, near to the first classification.

The serology of *Yersinia ruckeri* is therefore more complex than had originally been imagined. The recent typology of Davies allowed him to show that the 5 serotypes are present in Europe and in North America. On the contrary, only serotype 01 was identified in Australia and in South Africa (Davies, 1990).

These results show that the North American and European bacterias are similar, which confirms the epidemiological data on the American origin of the European isolates and indicates that the populations of bacteria in Australia and in South Africa are relatively isolated.

The study of pathogenic mechanisms and differential virulence of the serotypes of *Y. ruckeri* is presently in full development. Research has shown that the strains of certain serotypes are strongly virulent whereas others are not so or not at all virulent (Davies, 1991).

This advance in knowledge raises the question of what analysis to chose: should we consider that the presence of new serotypes means introductions?

Molecular criteria

Can the problem of detecting on a serotype scale be addressed through the analysis of genes on a molecular scale?

The first detection of the viral haemorragic septicemia virus in the United States was reported in 1988, in Pacific salmon (Batts *et al.*, 1993). At that time it was thought that this virus was the first isolate of an introduction from a European source. Given the economic importance of this virus in Europe, eradication measures were taken and the fish that were present in the natural environment were destroyed. However this virus was isolated again in other sites, which suggests that its dissemination had not been contained.

The use of DNA/DNA hybridisation techniques shows that the North American isolate was different from the European viruses and that it was native in the wild populations of cod and herrings from the State of Washington to Alaska.

The recent availability of the appropriate molecular techniques has shown introduction of pathogens with a level of analysis of unsuspected scope. These progresses reveal the considerable diversity of pathogens in correlation with the extreme biodiversity of their hosts. The previous data emphasises how difficult it is to select criteria for the legislations, which aim to restrict introductions and trade between geographical zones.

The recent availability of sophisticated tools has led to the comparison of pathogens at gene level. Knowledge has thus been gained of taxonomy, pathogenic mechanisms and the genetic evolution of these agents in natural environments and in farming, making it easier to trace the spreading of pathogens. Furthermore, the real introductions of pathogens can be distinguished from native agents in emergence in the importing country. This likewise allows unjustified sanitary measures and barriers to international trade to be lifted.

Detection: What methodologies?

As has been described above, the detection of pathogens calls for ever more sophisticated direct identification techniques (enzyme-linked immunosorbent assays, monoclonal antibodies, DNA probes and gene amplification using PCR); detection can also be made through the immune response of the hosts.

The respective interest of these methodologies, always discussed case by case, can be illustrated by an example of the infectious hematopoietic necrosis virus (IHNv). This rhabdovirus of salmonids was considered to be localised on the West Coast of USA and the northern coast of the Far East. It was reported for the first time in Europe in the North of France in 1987 (De Kinkelin *et al.*, 1987). As being an exotic and reputedly contagious virus, the prophylaxis and sanitary police measures were rapidly applied to limit its spreading. These measures are mainly the prohibition of the sale of live fish, total destruction of farmed fish and wild populations when justified. An eradication programme financed by a contribution from the State of several million francs was set up in three farms and has given excellent results at the head of the water basin (Hattenberger-Baudouy *et al.*, 1995).

However, the implementation of a diagnosis method based on an agglutination microtechnique has shown the contamination of a fourth farm situated downstream from the others. In this farm, as there was no clinical disease, the virus was not eradicated. In fact, in France IHN is defined as a reputedly contagious disease under two conditions: the existence of clinical signs and the positive result of the virology diagnosis (Decree of 3 Sept. 85, Orders of 16 and 25 March and 9 Nov. 1987). This new diagnosis technique has managed to detect the presence of asymptomatic carriers in sub-adults and adults when isolation of the virus using the classical techniques was not possible until the reproduction period (once the clinical stage that mainly affects the young age classes is over, the virus undergoes an eclipse stage before it is found again in the sexual products at reproduction).

This example clearly shows the limitations of the direct diagnosis methodology based on the isolation of the virus in cell cultures (associated to an immunological identification). It is however the only method admitted internationally in the sanitary controls and therefore in trade regulation.

These improvements in the detection and in the identification of the pathogens render it necessary to make adjustments in the regulations in order to restrict trade between geographical zones and thus restrict introductions.

The main introductions and translocations of pathogens in the European freshwater hydrosystems and estuaries

A balance could be presented of the agents introduced into the French or European continental aquatic ecosystems (Table 1), but it is certainly biased because of lack of knowledge of the pathogen fauna of fish in the natural environment and because it mainly concerns pathogens of species of aquacultural interest.

Table 1. Major introductions and translocations of pathogens in inland European aquatic ecosystems. After many contributions in Hoffman, 1970; Bauer and Hoffman, 1976; Odening, 1989; Bauer, 1991; Anderson, 1992; Lom and Dykova, 1992; Kennedy, 1993; Moravec, 1994; Williams and Jones, 1994

Family	Host species	Code†	Pathogenic agent	Area of origin	Area of introduction	Date	References
Cyprinidae	*Cyprinus carpio*	1	*Rhabdovirus carpio* (VVPC)	Asia	URSS	1915	Bauer and Faktorovitch, 1969
					England	1979	Bucke and Finlay, 1979
		5	*Hoferellus cyprini* (syn. *Mitraspora cyprini*)				Plehn, 1924
		5	*Sphaerospora renicola*	East Asia	Europe	1950	Csaba *et al.*, 1984
					Germany	1988	
		5	*S. molnari*	Asia	Europe	1960	Dykova and Lom, 1988
		5	*S. carassi*	Asia	Poland	1993	Pojmanska and Chabros, 1993
		5	*Thelohanellus hovorka*	East Asia	Eastern Europe	1979	Dykova and Lom, 1988
		8	*Philometroides cyprini* (syn. *P. lusiana*)	East Asia	Latvia		Vismanis, 1962
		9	*Diplozoon nipponicum*	Asia	France	1983	Denis *et al.*, 1983
		9	*Dactylogyrus extensus*	Europe	Jersey	1986	Mueller and van Cleave, 1932
		9	*D. vastator*	Asia	Europe		
					Ireland	1966	
		9	*D. minutus*	Asia-Central Europe			Rogers, 1967
		9	*D. wegeneri*	Asia?	Europe		Price and Mizelle, 1964
		9	*Gyrodactylus katharineri*	Asia	Russia-Western Europe	1960s-1970s	Rogers, 1968
		9	*G. cyprini*	Asia	Russia-Western Europe	1960s-1970s	Rogers, 1968
		9	*G. medius*	Asia	Russia-Western Europe	1960s-1970s	
		9	*G. sprostonae*	Asia	Russia-Western Europe	1960s-1970s	
		9	*G. kherulensis*	Asia	Russia-Western Europe	1980s	
		9	*G. shulmani*	Asia	Russia-Western Europe	1980s	
		9	*G. stankovici*	Asia	Russia-Western Europe	1980s	
		10	*Sanguinicola inermis*		England	1977	
		11	*Khawia sinensis*	East Asia	East Germany	1974	Dubinina in Bauer, 1987
		11	*Bothriocephalus acheilognathi* (= *B. opsariichthydis, B. gowkongensis)*	East Asia	Rumania-Danube		Molnar, 1970
					West Germany		Korting, 1975
					England	1979	Chubb, 1980
					France	1983	Denis *et al.*, 1983
		12	*Argulus japonicus*	Japan	Great Britain		Rushton-Mellor, 1992
	Ctenopharyngodon idella	9	*Dactylogyrus lamellatus*		Europe		Molnar, 1972
		9	*D. ctenopharyngodonis*		Europe		
		9	*Gyrodactylus ctenopharyngodonis*		Europe		
		10	*Amurotrema dombrovskajae*		European Russia		
		11	*Bothriocephalus acheilognathi*	Taiwan	Europe, North America, Japan	1970	Hoffman, 1976
		11	*Khawia sinensis*	East Asia			

Table 1 (cont.). Major introductions and translocations of pathogens in inland European aquatic ecosystems. After many contributions in Hoffman, 1970; Bauer and Hoffman, 1976; Odening, 1989; Bauer, 1991; Anderson, 1992; Lom and Dykova, 1992; Kennedy, 1993; Moravec, 1994; Williams and Jones, 1994

Family	Host species	Code[†]	Pathogenic agent	Area of origin	Area of introduction	Date	References
Cyprinidae (cont.)	*Hypophthalmichthys molitrix*	5	*Chloromyxum barki*		Germany		
		9	*Dactylogyrus hypophthalmichthys*	Asia-Central Europe			Musselius *et al.*, 1973
		9	*D. chenshuchenae*				
		9	*D. skrjabini*				
		9	*D. suchengtai*				
		9	*Gyrodactylus sprostonae*				
	Carassius auratus	9	*Dactylogyrus anchoratus*	Asia	Europe		Mueller, 1936
					Great Britain	1972	
		9	*D. formosus*	Asia	Europe		
		9	*D. vastator*	Asia	Europe, Ireland		Paperna, 1964
		9	*D. baueri*	Asia	Europe		
		9	*Gyrodactylus elegans*	Asia	Europe		Malmberg, 1962
		12	*Lernea cyprinacea*	Asia	Great Britain	1960s	
		8	*Philometra sanguinea*	Japan	North America		Hoffman, 1970
		2	*Yersinia ruckeri*		Europe		McArdle and Dooley-Martin, 1985
				Finland	Norway		Sparboe *et al.*, 1986
		7	*Trichodina reticulata*	Asia?	Europe		Lom and Hoffman, 1964
		7	*Trichodinella subtilis*	Asia?	Europe		Lom and Hoffman, 1964
	G. carassius	5	*Sphaerospora carassi*	Japan or China	Poland		Bykovskaya and Pavlovskaya, 1962
	Aristichthys nobilis	9	*Dactylogyrus aristichthys*				
	Abramis brama	12	*Tracheliastes maculatus*	Europe	England	1990	
		12	*Ergasilus briani*		England	1982	Fryer and Andrews, 1983
		12	*E. sieboldi*		England, Jersey	1967	
	(?)	12	*Neoergasilus japonicus*		England	1980	
	Leuciscus idus	12	*Tracheliastes polycolpus*		Scotland	1933	
	Leuciscus leuciscus	12	*Tracheliastes polycolpus*		England	1961	
	Tinca tinca	11	*Monobothrium wageneri*		England	1992	
	Pimephales promelas	2	*Yersinia ruckeri*	USA	Europe	1981	Michel *et al.*, 1986
	Various Cyprinidae	9	*Gyrodactylus sprostonae*	Asia	Russia, Western Europe	1960s-1970s	Rogers, 1968
		9	*G. shulmani*	Asia	Russia, Western Europe	1980s	
		11	*Bothriocephalus acheilognathi*	East Asia	England	1979	
Salmonidae	*Oncorhynchus mykiss*	1	Rhabdovirus (IHNV)	North Pacific	France	1987	De Kinkelin, 1987
					Italy	1987	Bovo *et al.*, 1987
		5	*Myxobolus aeglefini*	USA	Germany, Denmark, France	*Circa* 1900	
		5	*Myxobolus cerebralis* (syn. *Myxosoma cerebralis*)	Europe	Sweden		Hoffman *et al.*, 1962

Table 1 (cont.). Major introductions and translocations of pathogens in inland European aquatic ecosystems. After many contributions in Hoffman, 1970; Bauer and Hoffman, 1976; Odening, 1989; Bauer, 1991; Anderson, 1992; Lom and Dykova, 1992; Kennedy, 1993; Moravec, 1994; Williams and Jones, 1994

Family	Host species	Code†	Pathogenic agent	Area of origin	Area of introduction	Date	References
Salmonidae (cont.)	*Oncorhynchus mykiss* (cont.)	5	*Sphaerospora renicola*	North America?	Europe	1970	Plehn, 1924
					Germany	1988	
		5	*S.* sp.		Europe	1988	Hedrick *et al.*, 1988 Odening *et al.*, 1988
		11	*Proteocephalus neglectus*		Central Europe		Priemer, 1980
	Oncorhynchus kisutch (eggs)	4	*Loma salmonae*	North America	France	1970s	Lom and Dykova, 1992
		2	*Renibacterium salmoninarum*	USA	France	1975	De Kinkelin, 1975
	Salmo salar	9	*Gyrodactylus salaris*	Sweden and Finland	Norway	1975	Johnsen, 1978
		9	*Diplozoon tetragonopterini*		Europe		Sterba, 1957
		2	*Aeromonas salmonicida*	Scotland	Norway		Anon., 1986b
		5	*Sphaerospora renicola*	North America?	Europe	1970	
					Germany	1988	
	Salmo trutta fario	5	*S. renicola*	North America?	Europe	1970	
					Germany	1988	
	Salmonidae	11	*Eubothrium crassum*				
		11	*Triaenophorus nodulosus*				
		11	*T. crassus*				
Anguillidae	*Anguilla anguilla*	9	*Pseudodactylogyrus anguillae*	Japan, China, Taiwan, Australia	Eastern Europe	1970s	Golovin, 1977; Molnar, 1983
					France	1984	Lambert *et al.*, 1984
		9	*P. bini*	Japan, China, Taiwan, Australia	Eastern Europe	1970s	Golovin, 1977; Molnar, 1983
		8	*Anguillicola crassus*	Japan, China	Germany	1982	Neuman, 1985
					France	1984	Dupont and Petter, 1988
					England	1987	Kennedy and Fitch, 1989
					Corsica	1994	Roche and Blanc (unpublished)
		8	*A. novaezelandiae*		Italy	1982	Paggi *et al.*, 1982; Moravec and Tarashchewski, 1988
Centrarchidae	*Micropterus salmoides*	9	*Urocleidus principalis*	USA	England	1969	Maitland and Price, 1969
		9	*U. (Haplocleidus) furcatus*	USA	Western Germany		Reichenbach-Klinke, 1966
		9	*U. helicis*	USA	Italy		Ghittino, 1965
	Lepomis gibbosus	9	*Urocleidus dispar*	USA	Rumania		Roman, 1953
					Czechoslovakia		Vojtek, 1958
		9	*U. similis*	USA	Rumania		Roman, 1953
					Czechoslovakia		Vojtek, 1958

Table 1 (cont.). Major introductions and translocations of pathogens in inland European aquatic ecosystems. After many contributions in Hoffman, 1970; Bauer and Hoffman, 1976; Odening, 1989; Bauer, 1991; Anderson, 1992; Lom and Dykova, 1992; Kennedy, 1993; Moravec, 1994; Williams and Jones, 1994

Family	Host species	Code[†]	Pathogenic agent	Area of origin	Area of introduction	Date	References
Ictaluridae	*Ictalurus nebulosus*	9	*Cleidodiscus pricei*		Ukraine, Belorussia, Hungary		Molnar, 1968
		9	*Gyrodactylus stankovici*	Asia	Russia, Western Europe	1980s	
Siluridae	*Silurus glanis*	11	*Proteocephalus osculatus*		Great Britain (fish farm)		
Gasterosteidae	*Gasterosteus aculeatus*	9	*Gyrodactylus gasterostei*		Austria	19th century	Ahnelt *et al.*, 1995
"Aquarium fish"	*Lebistes reticulatus*	9	*Gyrodactylus bullatarudis*		Germany		Reichenbach-Klinke, 1960
	Monocirrhus polyacanthus	8	*Filaria* sp.	South America	Germany		Geuss, 1958
	Colisa labia	8	*Clinostomum* sp.	India, Africa	Europe		Reichenbach-Klinke, 1960
	Polypterus senegalensis	9	*Macrogyrodactylus polypteri*	West Africa	Sweden		
Ostreidae	*Ostrea edulis*	6	*Bonamia ostreae*	North America	France	1979	Comps *et al.*, 1980
Astacidae	*Astacus astacus*	3	*Aphanomyces astaci*	North America	Europe	19th century	
	Austropotamobius pallipes	3	*Aphanomyces astaci*	USA, Europe	England	End 1970s (1983)	Murren, 1986

[†] 1 = Virus; 2 = Bacteria; 3 = Eumycota; 4 = Microspora; 5 = Myxozoa; 6 = Acetospora; 7 = Ciliophora; 8 = Nematoda; 9 = Monogenea; 10 = Digenea; 11 = Cestoda; 12 = Crustacea.

Among the numerous conclusions that can be drawn from this balance, as it is incomplete we will simply underline the following points:

(i) From the point of view of the host species, there is a strong correlation between the number of introductions of host-species and the number of pathogens introduced. In cyprinids, for example, 54 species were introduced or transferred in Europe (Cowx, 1997) and 54 species of pathogens were introduced and naturalised in the European hydrosystems. This apparent correlation should not disguise the fact that 45 species of pathogens are reported in only 4 host species. This probably means that the number of pathogens introduced was underestimated.

(ii) From the point of view of pathogens, it is essential to take into account the specificity and complexity of the biological cycle in order to explain naturalisation. The direct cycle confers pathogens a capital advantage which, in general terms, counterbalances the specificity. The heteroxenous agents use a wide diversity of intermediate invertebrate hosts and therefore can become more easily established than those which have more specific intermediate hosts.

(iii) From the point of view of receiving biocenoses: there should be a compromise between the diversity of species, favourable to the establishment of pathogens, and the density of receiving hosts, advantageous for transmission. Thus, the simplified biocenoses characterised by very strong densities, such as those observed in aquaculture, are favourable to the naturalisation of pathogens.

This balance will have to evolve in the short term as diagnostic techniques improve, in particular the criteria used in systematics. An objective balance of the introduction of pathogens today seems, therefore, to be a myth.

The impacts of introduced pathogens: Limitations of knowledge

It seems difficult to make an objective balance of the introduction of pathogens in aquatic ecosystems as knowledge is constantly being updated. However, some selected examples will help present the wide diversity of their impacts, both in aquaculture and in free populations given their inseparable links. The limit of our empirical knowledge could be partly enlightened by theoretical studies on the role of pathogens in conservation biology.

Impacts on aquaculture

Setbacks in the creation of aquaculture farms

Attempts at introducing rainbow trout for cage farming in a volcanic lake in the high altitudes of the Azores archipelago failed due to population explosions of the parasite *Argulus foliaceus* (Menezes *et al.*, 1990). The ichthyological constitution of the population in the lake, originally devoid of fish, is well known: carp, introduced in 1890, at the same time as the crustacean parasite, followed by river perch in 1898, pike around 1950 and the rainbow trout in 1987. At present, prevalences in each species are: 18, 40, 57 and 100% respectively.

The population explosion of the parasite following the heavy introduction of trout not only immediately halted attempts at farming trout causing serious mortalities but also induced a decrease in the catches of other fish.

This example illustrates the stabilising role of the co-evolution of the host and parasite during the fluctuations of abundance of their populations (Lambert, 1997). Furthermore, it shows the importance of being acquainted with the parasite fauna in the ecosystem that hosts the introduced species and the effects on the host communities in the receiving ecosystem.

Socio-economic consequences

The socio-economic impacts of introduced pathogens are rarely established, not even in aquaculture production, due to the following difficulties:

(i) Estimation of the economic losses based on the evaluation of the volume of disease-free production.

(ii) Estimation of the social cost that includes mainly the retraining of staff, conversion of the production processes, transformation and marketing system as well as the loss of image of a production basin.

The development of the parasite diseases of the common oyster, *Ostrea edulis*, is interesting to point out here. *Bonamia ostreae*, one of the two pathogens responsible for these parasite epizootics was detected for the first time on the island of Tudy (Brittany) in June 1979 (Comps *et al.*, 1980; Pichot *et al.*, 1980) following heavy mortalities. It was rapidly identified in most of the shellfish centres of Brittany. This parasite had probably been introduced into France in the 1960s with the importations of seed from hatcheries on the West Coast of USA (Grizel *et al.*, 1988). In fact the identity of *B. ostreae* with parasite forms identified since 1963 in California (Katkansky *et al.*, 1966; Katkansky and Warner, 1970) was demonstrated by morphological and epidemiological studies (Elston, 1980; Elston *et al.*, 1986) and by serological studies (Mialhe, in Grizel *et al.*, 1988).

A detailed analysis was made of the estimated economic losses due to the development of parasitic epizootics of the common oyster (Meuriot and Grizel, 1984). The production of common oysters peaked in the 1970s to almost 20,000 tonnes but did not even reach 2500 tonnes in 1982. In a matter of years the oyster culture in Brittany, which was practically a monoculture of the common oyster, was oriented towards the production of the cupped oyster *Crassostrea gigas* (Fig. 1). The direct economic losses caused by these parasitic epizootics were assessed at 175 million 1983 francs per year, during the eight years needed for the reconversion, that is an accumulated reduction in wealth of 1.3 thousand million 1983 francs, about three times the total amount of losses caused by the oil slick from the Amoco-Cadiz shipwreck as the authors reported (Fig. 1). The social cost cannot be analysed as precisely but the direct loss of employment has been assessed at 10% of the total number of salaries in the production system of Brittany.

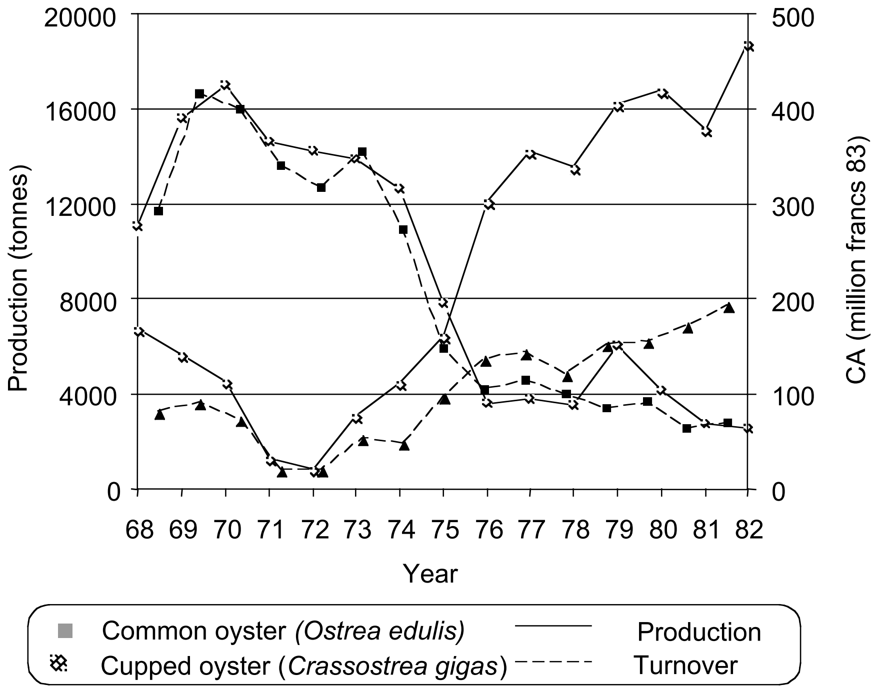

Fig. 1. Productions and turnover rates associated with the farming of the common oyster (*Ostrea edulis*) and the cupped oyster (*Crassostrea gigas*) in Brittany (after Meuriot and Grizel, 1984).

The consequences of introducing pathogens or hosts into geographical zones where certain parasites are autochthonous can affect the healthiness of staple foods.

Potential consequences on human health

The introduction of the brown trout, *Salmo trutta,* into the region of Santa Elvira in Chile for farming, like the rainbow trout in the High Rock Lake of Canada, failed because of nematode parasitism by the *Contracaecum* genus (Dick *et al.*, 1987; Torres and Cubillos, 1987). In the latter case, the strong density of introduced trout caused an increase in the density of pelicans (*Pelecanus erythrorhynchos*) definitive hosts of the parasite, and in the mean parasite intensity in the local populations of minnows and trout. The larval stages of this parasite can induce gastric ulcer formation in humans (Miegeville *et al.*, 1986; Chord-Auger, 1994), which has led to the withdrawal of foodstuffs and the halt of all aquaculture production and fishing in the regions concerned.

Impacts on the free populations

Demographic impacts

The impacts on the survival of fish populations are rarely quantified, except in the particular case of lake ecosystems, or populations targeted for fishing or long-term scientific studies.

However the great disproportion in numbers between the introduction events and the studies aiming to characterise these demographic effects in wild populations is noteworthy.

The introduction of *Anguillicola crassus* has had direct effects on the survival of eel populations but these have only been precisely quantified in Lake Balaton in Hungary, where this fish is the object of a specific fishery (Ashworth and Blanc, 1997).

These effects seem difficult to predict in relation to the date of introduction: the massive mortalities of *Orestias agassi*, a species of commercial interest of lake Titicaca, evaluated at 18 million individuals, were only observed about 30 years after the introduction of the ciliate parasite *Ichthyophthirius multifiliis* (Wurtsbaugh and Tapia, 1988).

In certain conditions the influence of introduced pathogens may lead to the virtual extinction in the region of the host species.

The first sign of the monogenean parasite *Gyrodactylus salaris* in Norway dates from 1975 when it was introduced following translocations of salmon and rainbow trout from Swedish or Finnish hatcheries (Johnsen and Jensen, 1991). The Norwegian authorities rapidly set up a health monitoring programme of infested areas, extended later on under the form of a descriptive epidemiological study in most of the salmon rivers of Norway.

More than 210 rivers were investigated between 1980 and 1982. These studies determined the impact of the parasite on the wild salmon populations. For example, the monitoring by means of electrofishing in the reference stations of the Lakselva River showed that the prevalence reached an average of 35% in the same year of introduction. In 1976, more than 95% of the parr population was infested and, in 1977, most salmons had been eliminated by this parasite (Johnsen and Jensen, 1986): the parr density, consisting of between 20 and 70 individuals/100 m^2, was reduced to almost zero (Johnsen and Jensen, 1991).

In the other infested rivers, the scenario was probably similar as shown by the statistics of anadromous migrating adult salmon captures, meaning a drastic decline in contaminated areas (Fig. 2). This parasitosis, eliminating juvenile populations, directly affected the global fecundity of the salmon populations. According to the parasitologists and biologists involved with the study of salmon population dynamics, the mortality of juveniles and parrs was more than 90%, causing them to become practically extinct in continental environments, and leading in the short term to a probable loss of the majority of the adult stocks (Johnsen and Jensen, 1986).

Genetic impacts

Chevassus and Dorson (1990) presented numerous examples of genetic variability of the sensitivity of fish populations to infectious pathogens such as parasites. Wakelin (1978, 1992) pointed out that the genetic differences of the hosts could play a critical role in the nature and outcome of helminthiasis.

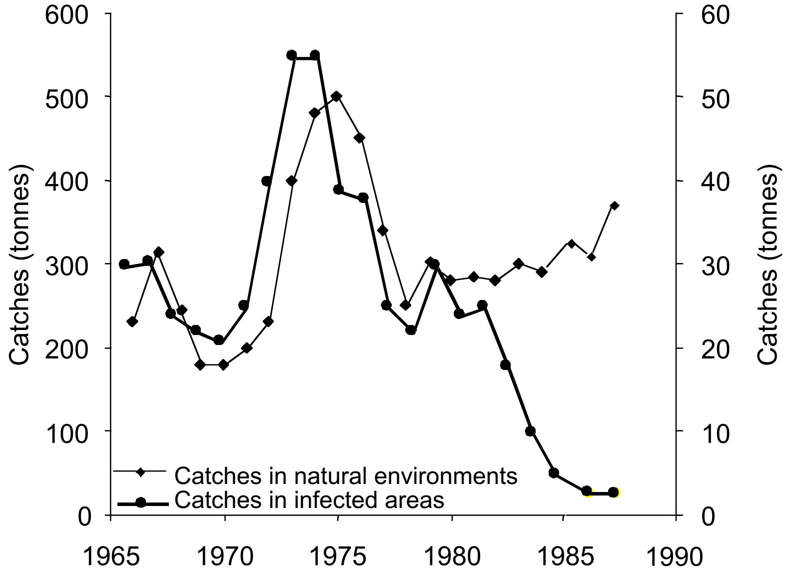

Fig. 2. Total river fishing catches of salmon in Norway compared with the total catches of salmon in infested rivers (after Johnsen and Jensen, 1986).

The genetic studies of the Atlantic salmon populations have shown the existence of two main stocks, the East-Atlantic stock which notably includes the Norwegian populations and those of the British Isles and the Baltic stock (Stahl, 1987). The experimental studies show that the salmon originating from the Neva River in Baltic Russia was receptive, but naturally resistant to *Gyrodactylus salaris* infection. It can be considered today that the Baltic stock is resistant to that parasitosis. In fact, the parasite intensity (number of parasites per fish) is limited to less than 15; furthermore, these fish eliminate almost the whole parasite population in about 35 days. In the East-Atlantic salmon (Norwegian or Scottish strain), the parasite intensities increase exponentially until they eradicate almost all the fish (Bakke, 1991). There is therefore no regulation of the growth of the parasite population in these host populations.

Hybridization was considered with introgression of the resistance character or selective rearing of the survivors of a given population that can confer resistance against *G. salaris* to populations that could possess features that one would wish to retain (Bakke, 1991).

This use of naturally established genetic resistance in certain salmon populations or in certain individuals of sensitive populations at the same time shows the importance of experimental studies aimed at identifying disease-resistance characters (Dorson *et al.*, 1991, 1995) and the importance of conserving genetic diversity. In the prolongation of these studies, it is necessary to outline the future route of estimating the genetic diversities of the host and parasite populations in their relations with the stability and the evolution of interaction between the two populations.

Contribution of the theoretical studies to an improved impact assessment

The previous examples have shown that infectious and parasitic diseases are the results of the introduction of pathogens, which lead to mortality on a short time scale. These mortalities are frequently interpreted as the result of an imbalance in the interaction between the host and the parasite and we can be questioned about this interaction in the long term.

Even though infectious and parasitic diseases are, by definition, associated with the morbidity and mortality of the hosts, it is generally admitted that a well-adapted pathogen does not kill its host in order to prevent its own eradication.

At present, this theory is starting to be strongly questioned as the theoretical studies indicate that many co-evolutionary routes are likely to be followed according to the relationships between pathogenicity of the pathogen and its transmission efficacy (May and Anderson, 1990). These evolutive routes may be in a steady state, either real and permanent or fictitious, obtained by an indefinite co-evolution, a cyclical variation of the host and parasite populations or the eventual elimination of one of the two.

In fact, the evolutionary processes that lead to the maintenance of virulence could be genetically linked to other components of the parasite fitness. The numerical ecology equations can be used to illustrate the role of this balance in the fitness of the parasite (Ebert and Herre, 1996). For a parasite that is transmitted horizontally in an originally parasite-free population, fitness can be described by the parasite reproduction success Ro ($Ro = \beta(N)/\mu + \alpha + \partial$, with β = transmission rate, function of host density; α = virulence; μ = mortality rate of a non-infected host; ∂ = recovery rate).

In the absence of genetic correlation between the parameters of this equation, Ro is higher when the virulence of the pathogen approaches zero. As the authors point out, this is unlikely; a positive relationship between α and β or negative between α and ∂ maximises Ro and hence the fitness of the parasite for different levels of virulence.

As pointed out by Combes (1995), the key concept is that of host-parasite compatibility during the moment of transfer. If there is a good compatibility, the introduction of the host in a contaminating biocenosis, or of a pathogen in contact with the receptive host, will mean an immediate and massive pathogenic effect and an evolutionary pressure will be exerted on the host populations. On the other hand, if the compatibility is weak, the selection pressure will be exerted on the parasite populations that will become more and more virulent and the pathogenic effect will increase.

It is likely, however, that this effect will come about unpredictably, a real time bomb, in relation with ecological factors (Schrag and Wiener, 1995) and, furthermore it will be transitory on the scale of an isolated host-parasite system.

Such systems do not exist in the natural environment and therefore a multiple host-parasite system should be considered. The participation of a second receptive host-species, where the pathogen would be less virulent, could lead to the extinction of the former since the density-dependent regulations cannot be implemented in the first system.

The evaluation of the impact of a pathogen in the host populations, rather than on an individual scale, is difficult to undertake, especially in the long term. The ideal impact studies should involve an association of observational studies of the pathogen or diseases, of experimental investigations analysing the populational impact of the parasite and parallel theoretical studies of modelling the dynamics of the resulting host-parasite interaction. In a review of the literature regarding studies of impacts of pathogens on the fecundity of vertebrate hosts, only one study associates these three perspectives. Furthermore, out of a total of 130 studies on the survival of vertebrate hosts, only seven concerning mostly terrestrial vertebrates, integrate all of these perspectives and, only one makes a detailed study of the impact of a parasite nematode on both the fecundity and survival of its host at a populational level (Grenfell and Gulland, 1995).

After 10 years of in-depth observational studies, completed by experimental and theoretical studies, Hudson and Dobson (1991) have shown that the nematode *Trichostrongylus tenuis* was the main responsible factor in the cyclical collapse of the grouse populations (*Lagopus lagopus scotti*), a game bird of a great economic interest for the region. In fact, when the nematode become abundant in the two intestinal caeca of the host (several tens of thousands per host individual), the fecundity of the female grouse strongly decreases – down to half, and causes the grouse populations to collapse almost to extinction. A mathematical model of host – parasite interaction including ecological factors has been developed for managing the parasite population using helminthicide-covered gravel.

The impact of the pathogens can therefore be considerable in the host populations but it may likewise have later repercussions on the whole ecosystem.

Blanc (1994) has shown the invasion into the European eel's food network of the parasite nematode *Anguillicola crassus*, recently introduced in Europe. It is thought today that the parasites could manipulate or even condition the trophic chains.

A series of long-term studies in a fresh-water fishery suggests that the parasites could determine the structure of the fish communities (Burrough *et al.*, 1979; Kennedy and Burrough, 1981). In a surveyed ecosystem, the competitive interaction between the roach, *Rutilus rutilus*, and the rudd *Scardinius erythrophtalmus*, was disturbed by the introduction of the pseudophyllidean cestode *Ligula intestinalis*.

Before the arrival of the parasite, the rudds were relatively unabundant whereas the roach densities were high enough, leading to growth inhibition and stunting in roach population. The introduction of the parasite involved a reduction in the roach density and an increase in rudd density. This was likewise confirmed by a decrease in the stunting level observed in roach, indicating a reduction in intraspecific competition. The advanced hypothesis is that the introduction of the parasite has led to a fall in roach density due to the mortality induced or by a reduction in fecundity.

The role of infectious pathogens and parasites in the regulation or in the depression of the growth rates of their vertebrate hosts has therefore been introduced by theoretical ecological studies. The mode of action of the pathogens can be a long-term impact through an endemic and stable infection or through recurrent epidemics interrupted with non-predictable latency periods.

It is still however difficult, even exceptional, to measure the impact of pathogens, both in host populations and in an ecosystem. It is necessary to point out, furthermore, that this impact is probably underestimated as few long-term studies have taken interest in the impact of the wide diversity of pathogens that can be observed in host – multiple parasite systems characteristic of natural hydrosystems.

It does seem, however, with further study on impact, more can be discovered about the ecological importance and the evolutionary weight of the pathogens in metazoans and how ecosystems are structured.

Likewise, the introduction of pathogens is the subject for a whole study. We have insisted on the fact that these new associations could have devastating effects. It must be pointed out that this is not the general case, as shown by the experimental studies. The new associations are often not so virulent, are less infectious and less well-adjusted than between the same parasite strain and the host to which it is adapted (Ebert and Herre, 1996). Experimental results indicate, furthermore, that the capacity of a parasite to exploit a new host decreases with its biosystematic – therefore genetic – distance, from the host to which the pathogen is adapted. The local adaptation could be understood as an extension of the specificity of the pathogen on a micro-evolutionary scale.

The study of the mechanisms at the origin of the devastating introductions, which is, the expression of virulence in these new associations and of its evolution, is a capital issue in understanding the impact of pathogens in host populations; it is also an opportunity to practise good science and good conservation biology.

Conclusions and recommendations

Ecological changes of anthropogenic origin, such as the introduction of pathogens, very often linked to the introduction of hosts, are among the most interesting interactions between agrosystems and environment to be surveyed. The interest of applied results his in the great diversity of thresholds of the new relationship between the host and the pathogen, of its multiplicity and the non-predictability of impacts. Even moreso since the ecological factors of the anthropic hydrosystems or agrosystems can modulate these thresholds and contribute to an amplification of impacts from the interior of the initial disturbance. The theoretical interest concerns both the fundamental ecology and the evolutionary and conservation biologies.

Today, important mutations in the social and political factors have resulted from the conclusion of the GATT Uruguay Round in 1986. It has led to an international agreement to remove the trade barriers in agriculture products, except in situations where such trade would threaten human, animal or plant health of the importing country has been proved. The analysis of the problems due to introduction of species shows that under this agreement more introductions could be made. Therefore it would now be valuable to integrate the environmental dimension into this agreement. Indeed, if the hazards of introducing pathogens are effectively linked to voluntary introductions of host species, our attempt to make a balance on an intracontinental or regional scale shows that the host-species translocations are also responsible for the introduction of new pathogens. From the point of view of the introduction of pathogens, there is a continuum between introductions and translocations of host-species. Furthermore, this continuum is largely perceptible in the particular case of the hydrosystems (Haury and Pattee, 1997). A certain number of actions could be recommended:

(i) The case of the voluntary introductions, subject to notification, of small numbers of new host-species should comply with, for example, the directives of international organisations such as the "Code of practice to reduce the risks of adverse effects arising from the introduction and transfers of marine species" developed by the working group of the International Council for the Exploration of the Sea on the introductions and transfers of sea organisms [1993, revised in 1994; see also (De Kinkelin and Hedrick, 1991; Bartley, 1996)]. Among the multiple schemes proposed, a choice should be made according to the characteristics of the species whose introduction is envisaged and of the potential pathogens.

(ii) In the case of the translocations of host-species there should be a risk analysis of the concomitant introduction of the pathogens in order to provide the decision-makers and managers of the environmental patrimony with the means to evaluate the possible threat the concerned ecosystems by the proposed translocation. An advantage of this analysis is that the grounds for the decision are transparent.

The risk analysis is based on:

(i) The identification of danger: at this vital stage, it is essential to use the health surveillance systems of the source countries, the databases of the international organisations such as the OIE and the knowledge of the veterinarians and the field biologists. This stage would avoid making same mistakes that have been made in other countries.

(ii) Risk evaluation: the knowledge of the ecology of the pathogen – host interaction in the original country should allow a probabilistic estimation of an identified risk. To this regard, research on the regulation of the pathogen populations and the modelling of their distribution on the scale of biocenosis (multi-host-species system) have contributed to significant progress (Blanc, 1994). Risk assessment should likewise take into consideration the importance of the harmful effects underlined by the contribution of the theoretical studies in pathogen-multi-host systems. We propose that the rare endemic species or original species of the host ecosystem should be the object of a systematic reinforced protection, based mainly on the experimental studies of receptivity/sensitivity. Furthermore, certain hydrosystems could be declared to be of scientific interest and benefit from a reserve status. It is likewise necessary to develop theoretical and applied studies to improve the knowledge of the long-term effects of an introduced pathogen, in order to define a real predictive risk management programme.

In the near future, methodological and conceptual progress will be made in the field of risk analysis linked to the introductions of pathogens and how they may be related with field epidemiology, environmental experimentation, numerical ecology of pathogens and conservation biology.

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