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REVIEW PAPER

Current knowledge on non-native freshwater fish introductions

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This review provides a contemporary account of knowledge on aspects of introductions of non-native fish species and includes issues associated with introduction pathways, ecological and economic impacts, risk assessments, management options and impact of climate change. It offers guidance to reconcile the increasing demands of certain stakeholders to diversify their activities using non-native fishes with the long-term sustainability of native aquatic biodiversity. The rate at which non-native freshwater fishes have been introduced worldwide has doubled in the space of 30 years, with the principal motives being aquaculture (39%) and improvement of wild stocks (17%). Economic activity is the principal driver of human-mediated non-native fish introductions, including the globalization of fish culture, whereby the production of the African cichlid tilapia is seven times higher in Asia than in most areas of Africa, and Chile is responsible for *c.* 30% of the world's farmed salmon, all based on introduced species. Consequently, these economic benefits need balancing against the detrimental environmental, social and economic effects of introduced non-native fishes. There are several major ecological effects associated with non-native fish introductions, including predation, habitat degradation, increased competition for resources, hybridization and disease transmission. Consideration of these aspects in isolation, however, is rarely sufficient to adequately characterize the overall ecological effect of an introduced species. Regarding the management of introduced non-native fish, pre-introduction screening tools, such as the fish invasiveness scoring kit (FISK), can be used to ensure that species are not introduced, which may develop invasive populations. Following the introduction of non-native fish that do develop invasive populations, management responses are typified by either a remediation or a mitigation response, although these are often difficult and expensive to implement, and may have limited effectiveness. © 2010 The Authors

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Key words: ecological impact; economy; invasive; management; pathways; risk.

INTRODUCTION

The number of species introduced worldwide has more than doubled (Gozlan, 2008) compared with estimates nearly three decades ago (Williamson & Fitter, 1996), with growth in global trade and human mobility principally responsible (Sala *et al.*, 2000;

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Gozlan, 2008). Biological invasions are now considered a major environmental issue of public concern.

The introduction of a non-native species in an ecosystem is always likely to present an ecological risk if the species is able to integrate itself successfully into the ecosystem (Gozlan & Newton, 2009), resulting in possible detrimental interactions with native species or even on ecosystem functioning. The introduced species could affect biodiversity through predation (Brown & Moyle, 1991; McIntosh & Townsend, 1995; Kitchell *et al.*, 1997; Shurin, 2001; McDowall, 2006; Weyl & Lewis, 2006; Bampfylde & Lewis, 2007; Yonekura *et al.*, 2007), competition (Gurevitch *et al.*, 1992; Fausch, 1998; Potapov & Lewis, 2004; Simon *et al.*, 2004; Caiola & Sostoa, 2005; McDowall, 2006; Zimmerman & Vondracek, 2006; Blanchet *et al.*, 2007), hybridization (Pullan & Smith, 1987; Scribner *et al.*, 2001; Allendorf *et al.*, 2004; Costedoat *et al.*, 2004, 2005; Hänfling *et al.*, 2005; D'Amato *et al.*, 2007), habitat modification (Moyle, 1986; Brown & Moyle, 1991, 1997; Kitchell *et al.*, 1997; Tejerina-Garro *et al.*, 2005; McDowall, 2006) and transmission of a novel disease (Bartley & Subasinghe, 1996; Blanc, 1997, 2001; Daszak, 2000; Gaughan, 2002; Gozlan *et al.*, 2005, 2006). There are many such examples, with some cases causing serious consequences for the conservation of biodiversity (Balirwa *et al.*, 2003; Gozlan *et al.*, 2005; McDowall, 2006). Fishes are among the most introduced group of aquatic animal in the world (*i.e.* 624 species, Gozlan, 2008) and also one of the most threatened, with the total number of threatened fish species reaching 1201 in the year 2007 (IUCN, 2008). Nonetheless, fish species are still introduced around the world because of societal demands for fish products for food aquaculture (51%), ornamental fish (21%), sport fishing (12%) and fisheries (7%) (Gozlan, 2008). While socio-economic forces suggest that the increasing trend of non-native fish introductions will continue, it implies that the associated ecological risks and biodiversity loss will also increase. This is characteristic of many other ecological issues where the needs of societal development do not necessarily converge with conservation interests (Gozlan & Newton, 2009).

When the issue is examined more closely, however, these societal needs for non-native fish can be regulated, and not all non-native fish introductions have ecological implications or loss of biodiversity. While it is crucial to be better able to forecast the risks resulting from a non-native fish introduction, given that risk cannot be totally absent, it is crucial to develop appropriate management tools and mitigation protocols. The current scientific understanding of non-native fish introductions is highly polarized, as many specific terms remain ill-defined, with a lack of common understanding of aspects such as ecological impact. At a time when policies dealing with non-native species are being put in place, it is important that the current understanding of this issue is refined and reframed in a global context of environmental pressures (Gozlan & Newton, 2009).

DEFINITION OF TERMS

As there are so many different terms used to describe biological invasions, it can be difficult to determine whether common thinking is being applied across different terminologies. For example, non-native fish are also termed exotic, non-indigenous, alien, xenic, noxious, weedy, pest and foreign (Peretti, 1998; Daehler, 2001; Occhipinti-Ambrogi & Galil, 2004; Copp *et al.*, 2005a). Additionally, invasive

species is a term that is often used when invasive population would be more appropriate. Despite attempts to achieve common definitions, difficulties remain because of a combination of ecological and political perspectives being used to determine those species that are either native or non-native (Shafland & Lewis, 1984; Davis & Thompson, 2000; Shrader-Frechette, 2001; Copp *et al.*, 2005a). This is evident from the common use of national boundaries to determine whether a species is native or non-native, irrespective of the biogeography of the species concerned. Often, the term translocation is used to differentiate between within and across-border movements. In terms of ecology, this has little relevance, as a species moved from one basin to another basin within the same country could generate similar ecological outcomes (*i.e.* predation, competition, hybridization, habitat use, disease transmission) as a species moved across national borders. The International Union for Conservation of Nature (IUCN) and the Convention on Biological Diversity (CBD) have also called on parties to focus on non-native species at the ecosystem level, rather than the national level, as both organizations define non-native species as a species introduced outside its natural range (Riley, 2005). For these reasons, tight definitions are suggested that are based on the common understanding that species introductions are primarily an ecological issue and as such, definitions should follow an ecological perspective rather than a political one (Table I).

There are some aspects, however, that cannot be successfully defined using an ecological perspective alone (Davis *et al.*, 2001). These require strict policy guidance, for example, the definition of the persistence of a species that may otherwise be considered naturalized. There is no clear ecologically relevant time limit that could be confidently used to set the time limits of when an introduced non-native species could be considered naturalized; hence, a subjective decision is necessary (Davis & Thompson, 2000; Falk-Petersen *et al.*, 2006). This is an important consideration because a species considered as persistent and naturalized may be managed differently to a species that has been introduced more recently.

ENTRY ROUTES AND MECHANISMS

Non-native species have primarily been introduced into new ecosystems through human activity, either deliberately or unintentionally (Vitousek *et al.*, 1997; Koo & Mattson, 2004). Information on the reasons for introductions are, however, far from complete, particularly pre-1900s, and the information available is often vague, indicating no obvious motive. Introductions for aquaculture have always been relatively important but came to the fore in the late 1900s with the development of salmonid aquaculture worldwide, and again in the 1960s and 1970s with the emphasis on tilapiine species and carps, especially in Asia (De Silva *et al.*, 2006).

Non-native species are reared locally in farms or imported from abroad for business reasons based on the most cost-efficient species in terms of production costs to output revenues, resistance to environmental stressors (*e.g.* pollution or parasites), and pre-existing knowledge of rearing methodologies and technologies. This includes the genetic improvement of farmed species, promotion of specific pathogen-resistant stocks and stock enhancement practices and ease of reproduction. Within this category, freshwater fishes such as tilapias (*Oreochromis* spp.), Chinese and Indian carps and African catfish make huge contributions to aquaculture outside their natural

TABLE I. Terms and definition based on an ecological approach to fish introduction*

Term	Definition
Native	A species that occurs naturally in a specific water (<i>i.e.</i> rivers, lakes, ponds, <i>etc.</i>)
Non-native (encompassing exotic, non-indigenous and alien)	A species <i>introduced</i> outside its natural <i>range</i>
Range	The geographical distribution of a species
Introduction	The deliberate or accidental release into the wild of a <i>non-native</i> species
Translocation	The human-assisted movement of fish within a specific water (<i>i.e.</i> rivers, lakes, ponds, <i>etc.</i>)
Stocking	The release of a species into a specific water (<i>i.e.</i> river, lake, pond <i>etc.</i>) following its initial <i>introduction</i>
Establishment	The process whereby an <i>introduced</i> species reproduces and forms self-sustaining populations (<i>i.e.</i> not relying on further introductions)
Naturalization	The process whereby an <i>established</i> species develops persistent populations
Dispersal	The natural dissemination (<i>i.e.</i> non-human assisted) of a species from its point of <i>introduction</i>
Colonization	The natural <i>dispersal</i> of an established population resulting in its <i>range</i> expansion
Spreading	A species expanding its <i>range</i> (can be human assisted or natural)
Invasion	The process whereby an <i>introduced</i> species has <i>established</i> populations, <i>spread</i> rapidly and presents a risk to <i>native</i> species
Lag phase	The delay between <i>introduction</i> and <i>invasion</i>

*Despite the desire to see the terms used for non-native introductions defined according to ecological processes only, when referring to non-native fish introduction this review encompasses both the ecosystem and national boundaries, as much of the published literature is set at this level.

distribution range (De Silva *et al.*, 2006). All have led to a high number of escapes from aquaculture installations and the establishment of natural breeding populations.

The introduction of non-native fish species to modify wild stocks is an important fisheries management intervention that essentially responds to three perceived needs: (1) establishment of new fisheries, (2) enhancement of existing fisheries and (3) fill a vacant niche. The main motives behind stock enhancement are the desire to improve fishery performance because the social and economic values of fisheries are huge, especially as demand for fishery products and improved leisure access increases. Indeed, Cambray (2003) suggests that species introductions arising from recreational fishing practices are one of the principal causes of environmental degradation resulting in loss of biodiversity, and that it requires a global solution. For example, total expenditure on recreational fishing across Europe currently exceeds €25 billion per year (Arlinghaus *et al.*, 2002; Cooke & Cowx, 2006). Introductions of fishes for sport fishing include species (principally salmonids) valued for their sporting qualities and meat. Among these, the most widely dispersed are the rainbow trout *Oncorhynchus mykiss* (Walbaum), brown trout *Salmo trutta* L.,

brook trout *Salvelinus fontinalis* (Mitchill) and, among centrarchids, largemouth bass *Micropterus salmoides* (Lacépède). Similarly, North American catfish species, such as black bullhead *Ameiurus melas* (Rafinesque), brown bullhead *Ameiurus nebulosus* (LeSueur) and channel catfish *Ictalurus punctatus* (Rafinesque), as well as the European catfish *Silurus glanis* L., have been introduced into ponds throughout Europe for sport fishing. Many fish species, including tilapias, carps and coregonids, have been introduced worldwide to create new fisheries and enhance commercial yields or create subsistence fisheries, especially in impoverished water bodies, and in some cases to establish new communities, such as in newly inundated reservoirs that have no indigenous pelagic species. Perhaps, the most iconic examples are the introductions of Nile perch *Lates niloticus* (L.) into Lake Victoria to enhance fishery yield (Ogutu-Ohwayo & Hecky, 1991; Matsuishi *et al.*, 2006) and Lake Tanganyika sardine *Limnothrissa moidon* (Boulenger) into Lake Kariba or Lake Kivu (Marshall, 1995).

More recently, non-native fish species (6%) have been intentionally introduced into open waters to manipulate the ecosystem through physical (bioengineering) or biological actions (predation on another species) to control unwanted organisms (biocontrol; Ciruna *et al.*, 2004a), especially mosquito fishes *Gambusia affinis* (Baird & Girard) and *Gambusia holbrooki* Girard, for mosquito control (Kumar & Hwang, 2006), grass carp *Ctenopharyngodon idella* (Valenciennes), for macrophyte control, and silver carp *Hypophthalmichthys molitrix* (Valenciennes), for controlling phytoplankton. While these introductions appear to have been highly successful, particularly relative to more costly and environmentally unacceptable alternatives such as insecticides and herbicides, the effect on the recipient ecosystems has yet to be fully evaluated, but evidence suggests such effects can be detrimental. There is also a lack of certainty about the level of biological control that will be achieved and over what time scale (Wittenberg & Cock, 2001), causing considerable controversy over the concept of biocontrol as a management tool in freshwater ecosystems. For example, Chinese carps, native species of eastern Asia, have been introduced throughout the world to control excessive aquatic plant growth, but they have often failed to achieve their intended objective and displaced native fish species of greater commercial value [*e.g.* bighead carp *Hypophthalmichthys nobilis* (Richardson) in the Danube Delta] or been the source of new parasite fauna that has affected native species (*e.g.* *Ergasilus* sp. from grass carp into U.K. waters, Cowx, 1997). In some cases, indiscriminate exploitation of aquatic vegetation has resulted in the destruction of important habitats and food organisms (Cudmore & Mandrak, 2004). Similarly, mosquito fishes are aggressive foragers, feeding on a variety of prey, including the eggs, fry and larvae of native biota (Goodsell & Kats, 1999). Intentional introduction into the wild is fraught with risks if not regulated correctly because the invasive species and their associated fauna are introduced directly into open water bodies, and rarely held in aquaculture quarantine facilities.

High volumes of ornamental fish are imported into western industrialized countries, especially from South-east Asia, Africa and South America (Keller & Lodge, 2007). These non-native species are reared in local farms or imported from abroad for ornamental or aesthetic reasons, such as private or public aquaria or gardens, for example, goldfish *Carassius auratus* (L.) and koi carp *Cyprinus carpio carpio* L., cichlid fishes *Symphysodon discus* Heckel (discus), *Pterophyllum* sp. (scalar) and the poeciliid fish *Xiphophorus* sp. (platy) (Copp *et al.*, 2005b). It is unlikely that many of these fishes could survive and spread as invasive alien species in temperate waters

because of their particular ecological and physiological requirements (warm water >15 °C), although *C. auratus* is an exception. Some species, however, find ideal conditions in lower latitudes (*e.g.* southern Europe or the southern U.S.A.) where water temperatures do not fall below the lower temperature thresholds, or are able to tolerate the ambient conditions. Furthermore, some species find refuge in waters artificially warmed by effluent discharge, for example, downstream of power stations and other industrial facilities.

Several species have also been imported and stocked live for use in research. This is mainly for new, non-indigenous species imported for experimental aquaculture trials, *e.g.* crossbreeding with native and non-native fishes (Colombo *et al.*, 1998), or for biocontrol assays or other research issues, *e.g.* bio-essays conducted with alien species to stop bioinvasion by other alien species. Generally, the risk of dispersal is minimal because the research institute applies quarantine measures to experimental trials, which are conducted in closed systems and not in open waters (Colombo *et al.*, 1998).

Perhaps, the category that causes greatest concern is accidental introductions. Nearly 8% of introductions are accredited to this mode. Although not specified, escape from aquaculture installations is probably a main cause, and this in turn has led to diffusion along water courses. Similarly, dispersal through ballast water disposal is another mechanism contributing to accidental introductions. Shipping accounts for 25% of the recorded introductions of freshwater organisms in Europe (Gollasch, 2007), mainly *via* ship ballast water and hull fouling (Bax *et al.*, 2001). It is estimated that $\geq 10\ 000$ species of marine organisms may be transported around the world in ships' ballast water each week (Carlton, 1999), but movements of freshwater fishes are less common. Prominent examples are the introductions of ruffe *Gymnocephalus cernuus* (L.) and round goby *Neogobius melanostomus* (Pallas) into the Great Lakes of North America (Scott & Crossman, 1973; Grigorovich *et al.*, 2003; Holeck *et al.*, 2004). With the extensive development of inter-catchment transfers of water resources that now take place, it is likely that dispersion of species by this mechanism will increase in the future. Accidental introductions that result from contaminants within batches of other fishes that are being deliberately imported or released are particularly problematic. For example, recreational anglers have been responsible for the direct translocation of fish species (West *et al.*, 2007), including the transfer of common carp either by accident, ignorance or deliberately to new fishing areas (McDowall, 1996; Koehn, 2004). The cyprinid, topmouth gudgeon *Pseudorasbora parva* (Temminck & Schlegel), which was initially discovered in Europe in a fish farm facility in Romania in 1961, is presumed to have been introduced as a contaminant of a consignment of Chinese carps and is a prominent example of an accidental introduction as it is now found throughout eastern, central and western Europe (Holcík, 1991; Gozlan *et al.*, 2002). The use of live finfish as live bait can also lead to the introduction of non-native alien species (Lintermans, 2004; Kerr *et al.*, 2005), and examples include introduced *G. cernuus* into parts of northern England outside its native range (Drake, 2005). Similarly, the enrichment of the Irish cyprinid fauna has been related to the release of bait species by recreational anglers targeting pike *Esox lucius* L. (Caffrey *et al.*, 2008). These mechanisms probably contribute to indiscriminate, inter-river basin dispersal and potentially account for the rapid expansion of the range of many non-native species.

In all the above cases, aquaculture plays a major role in the provision of stocking material. This is either through artificial rearing of the material or acting as growing-on facilities before fish being stocked into the wild. The propensity for non-native species interactions is high in these activities and not least because the species are stocked directly into open or semi-enclosed environments. Consequently, the risks of dispersal of the target species are high, as well as those of accompanying non-target species. There is potential for the transfer of new pathogens, viruses, bacteria, fungi, parasites and other organisms to new areas where they may not be pathogenic under normal environmental conditions for native species. The risks are also high because aquaculture facilities play an intermediary role when novel species are brought into a country before being stocked out. If health checks and inspections are weak, and quarantining not used, then the risks of transfer of pathogens or contamination of material by alien invasive species are high.

Drivers of use of non-native freshwater fish species are essentially direct interventions by humans, but they should also include upstream and downstream activities allied to fisheries and the potential for invasion and subsequent colonization of already established populations. In the former case, it should be recognized that these drivers operate both within and outside the law. There are many instances where fishes are moved illegally, but always for one of the purposes outlined above (Minchin & Rosenthal, 2002).

ECOLOGICAL IMPACT

In the last decade, the profile of non-native species has been strongly advocated as a driver of biodiversity loss but 'there is a growing minority of ecologists who question whether there is strong evidence that non-native species are a direct cause of native population decline' (Didham *et al.*, 2005; Sagoff, 2007; Gozlan, 2008, 2009; Gozlan & Newton, 2009). Often, non-native species introductions are correlated with other drivers of environmental change, such as habitat modifications (Moyle, 1986; Brown & Moyle, 1991, 1997; Kitchell *et al.*, 1997; Tejerina-Garro *et al.*, 2005; McDowall, 2006) and management practices (Bain, 1993; Wootton, 1994; Whittier & Kincaid, 1999; Caissie, 2006; Lewin *et al.*, 2006). It remains very difficult to distinguish the primary cause of environmental change and what is actually co-occurrence, which by definition represents an association (Didham *et al.*, 2005).

A further issue is the lack of common understanding of what actually represents an ecological impact (Simberloff, 2003, 2007; Sagoff, 2005, 2007; Brown, 2007; Gozlan, 2008). For some, the mere act of introducing a non-native species into an ecosystem is a source of ecological impact (*i.e.* guilty before proven innocent; Simberloff, 2007), whereas for others, the need to define this nebulous and ill-defined concept of ecological impact is fundamental to progress contemporary thinking and develop more robust policies on non-native species (Sagoff, 2007).

Freshwater ecosystems and their fish assemblages present a particularity since drainage basins may be considered 'biogeographic' islands. The obstacles to natural fish migration between hydrographic catchments over large temporal scales imply that extinction and speciation processes are largely specific to each basin. In this context, understanding of what constitutes a harmful biological introduction is crucial to the preservation of freshwater ecosystems and their biodiversity (Copp *et al.*, 2005a). There are several key aspects often considered in association with non-native fish

introductions: predation, habitat degradation, competition for resources, hybridization and disease transmission. According to a recent report to the European Commission (2008), and in agreement with Gozlan (2008, 2009), consideration of these aspects in isolation is insufficient to characterize the ecological impact of an introduced fish. Instead, there is a requirement for the above key aspects to be associated with a quantifiable and significant decline of biological or genetic diversity threatening long-term integrity of native species. The question is not about ecological changes as changes are inevitable when any species is introduced and established in a naïve ecosystem, but rather if these changes lead to a *measurable loss of diversity or change in ecosystem functioning*. Only in this case can fish species introduction be considered harmful.

Foraging habits are often one of the first ecological aspects studied for any introduced non-native fish (Brown & Moyle, 1991; McIntosh & Townsend, 1995; Kitchell *et al.*, 1997; Shurin, 2001; McDowall, 2006; Weyl & Lewis, 2006; Bampfyld & Lewis, 2007; Yonekura *et al.*, 2007). Foraging, however, is a difficult ecological aspect to characterize in the context of overall ecological impact. Although diet overlap and prey–predator relationships are strong indicators of species interactions and of the trophic position attributed to the introduced species, these are not necessarily indicators of loss of biological diversity or profound changes in ecosystem function (Isumbisho *et al.*, 2006). The real tipping point indicator of a significant ecological impact in the system is when gradual changes in environmental parameters resulting from non-native interactions lead to discontinuous changes in ecosystem functioning. This is characterized by the loss of ecosystem resilience to disturbances and the loss of its capacity to maintain its functioning, structure, various feedbacks and service provisions (Folke *et al.*, 2004). Ecosystems with less functional duplication are more vulnerable to disturbance (Schindler, 1990), and in some cases introduced fish could diminish the overall resilience of the ecosystem through modification of the trophic structure (Folke *et al.*, 2004). Most studies on non-native introductions, however, only identify initial effects of alteration (Moretto *et al.*, 2008; Smith *et al.*, 2009), cover a relatively short period (Gozlan *et al.*, 2003; Encina *et al.*, 2004; Jordan *et al.*, 2004; Buria *et al.*, 2007) or do not explicitly identify effects on other ecosystem processes (Zaret & Paine, 1973; Bradford, 1989; Nelva, 1997) or changes in ecosystem function (Xie & Chen, 1999; Moyle & Davis, 2000; Bernardo *et al.*, 2003; Holcik, 2003; Russell *et al.*, 2003; Olsen & Belk, 2005). Even studies that characterize interactions between non-native and native fauna rarely discuss these processes in the global context of ecosystem functioning (McIntosh & Townsend, 1995; Chapleau *et al.*, 1997; Funk & Dunlap, 1999; Ling, 2004; Maezono *et al.*, 2005).

A quantitative understanding of long-term changes occurring in food-web structure and functioning is a good way to characterize the long-term implications of non-native fish introductions (Ogutu-Ohwayo & Hecky, 1991; Vander Zanden *et al.*, 2003; Eby *et al.*, 2006). The increasing use of stable isotopes (*e.g.* ^{15}N , ^{13}C) to characterize food-web structure now allows their routine use for long-term monitoring of changes in ecosystem functioning that result from introductions (Vander Zanden *et al.*, 1999). Several studies have integrated this methodology into the study of non-native ecological impacts and provide useful insights into the role played by various fish introductions to the overall ecosystem (Buktenica *et al.*, 2007). Introductions of fish can alter food-web structure and ecosystem functioning through top-down or bottom-up mechanisms, or through consumer and resource co-limitation

(Eby *et al.*, 2006; Cucherousset *et al.*, 2007). Outcomes range from changes in trophic efficiency (Matyas *et al.*, 1998; Parker *et al.*, 2001; Shurin, 2001; Angeler *et al.*, 2002; Isumbisho *et al.*, 2006; Reissig *et al.*, 2006) to changes in biogeochemical cycling in the aquatic system itself (Kyle *et al.*, 2001; Lung'ayia *et al.*, 2001; Schindler *et al.*, 2001; McIntyre *et al.*, 2007). This, however, could also include the flux of nutrients with the riparian terrestrial ecosystem (Cole *et al.*, 2000; Duarte & Prairie, 2005), which could lead to overall changes in the resilience of ecosystems.

While shifts in the trophic structuring of food webs may be relatively easy to characterize, more subtle changes resulting from competition between species of similar trophic level can also occur following an introduction. For example, *S. trutta* introduced to New Zealand streams have out-competed and displaced native top predator species of the Galaxiidae family, with their distribution now restricted to *S. trutta*-free reaches (McDowall, 2006). In addition, through changes of invertebrate and algal production, significant changes in nutrient cycling and, in particular, nitrate were identified (Simon *et al.*, 2004), although the full implications of these changes in the functioning of the ecosystem remain unclear. Trophic interactions of this type, however, are not always apparent following the introduction of a non-native fish, as shown in a study of competition between *O. mykiss* and Atlantic salmon *Salmo salar* L., where intraspecific competition was found to be greater than interspecific [reference Hearn & Kynard (1986) in Fausch, 1998].

It is also important to consider that quantitative measures of *in situ* competition are complex and often influenced by other factors, including temperature and habitat (Gurevitch *et al.*, 1992; Fausch, 1998; Potapov & Lewis, 2004). Nonetheless, if non-native fish introductions were to have a significant ecological impact on native species and ecosystems through interspecific competition, then an unequivocal measure of the effects should be measurable and would need characterization. Despite the importance of laboratory experimentation in highlighting competitive interactions (Caiola & Sostoa, 2005; Zimmerman & Vondracek, 2006), field studies are key in providing a more holistic vision of non-native species-induced ecological impact emerging from competitive forces (Blanchet *et al.*, 2007).

Despite hybridization being a common phenomenon in fishes (*i.e.* more than in other vertebrates), loss of genetic integrity is often reported as a potential ecological impact associated with the introduction of non-native fishes (Hänfling *et al.*, 2005). Hybrid zones, characterized by relatively small areas where genetically distinct species meet and mate, are often exacerbated by limited spawning habitat, are common in freshwater ecosystems and are synonymous with clines (Scribner *et al.*, 2001). Hybridization does not necessarily result in the loss of species diversity, as illustrated by the colonization by the non-native nase *Chondrostoma nasus* (L.) through a man-made canal into the Rhône catchment where the French nase *Chondrostoma toxostoma* (Vallot) occurred naturally. These two species have hybridized for decades creating a hybrid zone, while at the same time maintaining pure-bred populations within the same hydrosystem (Costedoat *et al.*, 2004; Costedoat *et al.*, 2005). Although the process of hybridization has been greatly enhanced by human activities, especially through aquaculture, habitat modifications and fish introductions (Scribner *et al.*, 2001), the link with the loss of global fish biodiversity is still rarely demonstrated. Hybridization that results from non-native fish introductions may be considered as an additional stressor on already fragile populations of species that have a limited distribution and could, in some cases, lead to loss of genetic

integrity (Allendorf *et al.*, 2004; Hänfling *et al.*, 2005; D'Amato *et al.*, 2007). The great difficulty is to put these local hybridization events in the context of global fish species conservation. For example, hybridization between crucian carp *Carassius carassius* (L.) and the introduced *C. auratus* and *C. carpio* is commonplace (Hänfling *et al.*, 2005; Smartt, 2007), affecting 38% of *C. carassius* populations in the U.K. It is still unclear, however, what this figure represents in the overall global distribution of *C. carassius* and whether it represents a significant threat to the conservation of this species. It is also difficult to discriminate between the importance of the time of introduction and habitat availability in these hybridization processes, as it may explain, for example, why levels of hybridization between *C. carassius* and *C. carpio* vary significantly between locations (Pullan & Smith, 1987; Hänfling *et al.*, 2005). Hybridization related to non-native fish introductions only accounts for 17% of known hybridization (Scribner *et al.*, 2001) and *c.* 4% of all non-native fish introductions in the world. Therefore, this issue appears relatively limited when looking at ecological impacts associated with global non-native fish introductions, but it could be greater at the local scale (Allendorf, 1991; Allendorf *et al.*, 2004; D'Amato *et al.*, 2007). In some cases, local adaptations could be lost through introgressive hybridization with introduced species and could potentially decrease their chance of long-term persistence (Allendorf *et al.*, 2004).

Among non-native fish introductions, those that may have the most severe ecological consequences are engineer species that directly modify their ecosystem, generating cascading effects (Crooks, 2002). These effects are often achieved through a change in physical habitat, and consequences are typically proportional to long-term stability and complexity of the ecosystem (Brown & Moyle, 1991; Power, 1992; Fuselier, 2001; McDowall, 2006). A change in habitat, and particularly macrophytes or phytoplankton community or biomass, would typically result in a substantial modification of ecosystem function, with long-term implications for many species and the overall integrity of the ecosystem. This is well illustrated by the worldwide introduction of *C. carpio* (Khan *et al.*, 2003; Koehn, 2004; Pinto *et al.*, 2005), a species that modifies aquatic ecosystems through its foraging behaviour, resulting in uprooted plants and the re-suspension of sediments. The knock-on effect is increased turbidity, which prevents plant re-growth and affects phytoplankton biomass. Such trophic cascade is largely influenced by the density of *C. carpio* and the type of macrophytes present (Miller & Crowl, 2006), and produces direct effects on macrophyte, invertebrate and plankton diversity, and indirect effects *via* changes in water chemistry, turbidity and wind effect. Despite the recorded ecological impacts of *C. carpio* on habitat, the species is now widely distributed, with populations in Northern Europe principally maintained by regular stockings, as their reproduction is inhibited by the requirement for sustained temperatures above 20 °C (McDowall, 1996). Habitat modification of this type is also observed, albeit to a lesser degree, following the introduction of other fish species, both within and beyond their native ranges [*e.g.* common bream *Abramis brama* (L.)], but is mainly associated with benthivores.

In the same way that a non-native engineer fish can modify habitat, habitat itself could be engineered to favour native species to the detriment of those introduced, or to at least promote their coexistence. For example, following the introduction of *G. affinis* in Utah, U.S.A., populations of the native least chub *Iotichthys phlegethontis* (Cope) declined, mainly through habitat degradation but also as a result of the introduced *G. affinis* that use the same spawning habitat (Ayala *et al.*, 2007). A

detailed field study of habitat use of these two species, however, highlighted subtle differences resulting from the evolutionary history of both species and characterized the need for habitat management to promote deeper, cooler habitats that would support the coexistence of the species, as opposed to warm, shallow and marsh habitats that favour *G. affinis* (Ayala *et al.*, 2007). Pro-active habitat management is a powerful tool with significant implications for ecosystem function and should not be underestimated as an effective tool to limit the effects of introduced non-native fishes (Brown & Moyle, 1991; Maret *et al.*, 2006). In some cases, such as the least chub, habitat management could be used to enhance pockets of conservation interest targeted to a particularly vulnerable native species or group of species (Ayala *et al.*, 2007). In many places, habitat changes are happening whether non-native fish are introduced, and the desire to maintain or restore a pristine habitat in the sense of original habitat all too often is reminiscent of Plato's myth of the cave where the vision of this pristine lost environment provides a distorted view of a changing reality.

As mentioned before, aquaculture has been the main source of non-native fish introductions worldwide (Bartley & Subasinghe, 1996; Blanc, 1997, 2001; Gozlan, 2008) and has been followed by increased introduction and translocation of infectious pathogens in freshwater ecosystems (Blanc, 1997; Gozlan *et al.*, 2006). The strong correlation between source of host and source of pathogen indicates that aquaculture not only facilitates disease emergence but may also act as a source of pathogen introduction. This account, however, is possibly biased towards pathogens of aquaculture species due to limited knowledge of the pathogenic fauna of wild fishes. Many fish disease specialists believe that introduced hosts act as a reservoir population from which infection can spill-over to sympatric wildlife. Pathogen pollution, which would otherwise fail to persist, instead underpins the emergence of disease in naïve populations (Daszak, 2000; Gaughan, 2002; Gozlan *et al.*, 2005, 2006). Although there are numerous examples of disease emergence after species introduction, there are likely to be many more that have not been identified. Epidemics in the wild that cause high mortality or changes in fish behaviour are easily characterized, but are less easily identified when they cause long-term gradual population declines. It is relatively complex to link fish population decline with pathogen infection in wild populations because diseased or dead animals are rapidly consumed by predators or necrophages. This is one of the reasons why the effect of an introduced pathogen might very often go unnoticed. This link should become more obvious when developments in sampling protocols and diagnostic techniques enable better characterization of emerging infectious pathogens (Bull, 1994; Vanderploeg *et al.*, 2002; Gozlan *et al.*, 2005; Murray & Peeler, 2005).

The discovery of an infectious agent implicated in the decline of the endangered sunbleak *Leucaspis delineatus* (Heckel) has highlighted the potential for the spread of fish pathogens *via* the introduction of non-native invasive fish species. In this case, *P. parva* was found to be a healthy host of the rosette agent *Sphaerothecum destruens* (Gozlan *et al.*, 2005), a micro-parasite identified in North America, as affecting a large range of salmonid species, particularly Chinook salmon *Oncorhynchus tshawytscha* (Walbaum) and *S. salar*. The pathogen causes a chronic disease in *L. delineatus* and has been related to the decline of sunbleak across Europe and the concomitant spread of *P. parva* (Gozlan *et al.*, 2005, 2009). This is typically the worst case scenario where a non-species-specific pathogen is associated with an invasive

healthy carrier and is allowed to be associated with the aquaculture trade, thus accelerating its further dispersal. Despite causing mass mortality, this pathogen is still difficult to characterize in wild populations as a result of the chronic nature of the infections, but nonetheless appears to pose a substantial threat to fish biodiversity (Gozlan *et al.*, 2005).

The introduction of *Anguillicolloides crassus* in Europe in the early 1980s is another compelling example of a disease being spread as a result of global non-native fish movements and introductions for aquaculture purposes (Ashworth & Blanc, 1997; Kirk, 2003). Originating from Asia, *A. crassus* is a nematode that can severely impair swimbladder function and has been causing serious losses in intensive European eel *Anguilla anguilla* (L.) production. An expanding *Anguilla* spp. trade has promoted the global distribution of the parasite in Europe and North Africa as well as in the eastern part of North America, where infected American eels *Anguilla rostrata* (LeSueur) have been found (Kirk, 2003). The majority of *A. crassus* records come from aquaculture facilities, as it is easier to detect dead or diseased *Anguilla* spp. in cultured populations. It seems, however, that in the few cases of host-mortality reported in wild populations (Ashworth & Blanc, 1997), high losses resulted from a combination of high-density *Anguilla* spp. stocks and adverse environmental stressors (*i.e.* high temperatures and low dissolved oxygen levels).

Owing to diagnostic limitations, it remains difficult to clarify the extent of pathogen introductions associated with non-native fish introduction. Torchin *et al.* (2003), however, specifically tested the hypothesis that hosts were less parasitized in their introduced range than those in their natural range, leading to demographic release in the host population and facilitating invasion. It was concluded that this may be as a result of reduced probability of introduction (few host population founders), absence of intermediate host in the introduced range and host specificity limitations; non-native fish were less burdened with parasites in the novel environment (Torchin *et al.*, 2003). Few studies have been conducted on the effects of pathogens on free-living hosts. Furthermore, the number of studies examining the role of disease in structuring fish populations is even more limited, particularly in relation to introduced pathogens. Those pathogens that are studied tend to be the ones that affect immediately and negatively host population dynamics, usually in the form of epidemics. Future pathogen-related issues are likely to come from aquaculture semi-open systems, with these facilities increasing the probability of introduction through high densities of hosts and their frequent introduction. These types of facilities are the main entrance of non-native fish introductions, and intensive aquaculture conditions such as high stocking densities, accumulation of waste, handling and poor water quality all serve to compromise immunity and favour disease emergence (Blanc, 2001; Gozlan *et al.*, 2006).

A principal concern regarding non-native fish introductions is uncertainty about whether a particular introduction into a particular ecosystem will have no detrimental effect on its ecology and the long-term sustainability of its biodiversity (Simberloff & Stiling, 1996b; Clavero & García-Berthou, 2005). Even when a species has been introduced for decades with no obvious effect, the existence of a lag phase following introduction means that effects may still become apparent subsequently. Many conservation ecologists believe that ecological impacts following introduction of non-native fish species are unavoidable and even if it seems that there are no effects, this is because they have yet to be quantified (Simberloff, 2003; Ricciardi, 2004). It

may be considered easier to demonstrate a correlation between ecological changes and non-native fish introductions rather than the absence of changes, and according to the 'guilty before proven innocent approach', there is always the possibility that changes have occurred but are yet to be detected (Simberloff, 2007). This is the most commonly accepted view among scientists with interests in biological invasions, but has a tendency to skew observations towards introduced fishes generating ecological problems and serves to reinforce the notion that outcomes of non-native introductions are generally detrimental (Brown, 2007; Sagoff, 2007; Gozlan, 2008). It also means that in the management of introduced fishes, it is difficult to prioritize efforts to those species that are most ecologically damaging, as the majority have to be considered as detrimental to receiving ecosystems (Gozlan, 2009).

It is intuitive to consider that the integration of a species in an ecosystem will induce changes in the system and its biodiversity, particularly as the introduced species commences its basic biological functioning (foraging, reproduction and habitat utilization). If the measure of ecological impact is based on the characterization of changes in the system, then it is correct to assume that ecological impacts following introductions of non-native fishes are unavoidable. The question is whether this is a realistic approach to the problem or whether should there be more discrimination when looking at the effect of non-native fish introductions. Given that many freshwater ecosystems are undergoing radical changes because of anthropogenic pressures such as habitat degradation, impoundments, gravel extraction, change in land use and climate change (Francis & Schindler, 2006; Kruk, 2007; Hoagstrom *et al.*, 2008; Seilheimer *et al.*, 2009), then it is against this back-drop that the effect of introduced non-native fishes should be measured.

In a recent review of the demonstrated effects of non-native fish introduction worldwide, Gozlan (2008) came to similar conclusions as Simberloff (2007) and the 'tens rule' of Williamson & Fitter (1996). This predicted that 10% of all introductions will become established, and that 10% of those established will become pests. Thus, for every 100 non-native fish species introduced, 99 will not be associated with serious ecological impacts. Notwithstanding, when an ecological problem occurs at a meso-scale, there could be serious consequences for local biodiversity. This is seen with the introduction of the *L. niloticus* in Lake Victoria (Goldschmidt *et al.*, 1993; Kitchell *et al.*, 1997; Pringle, 2005) and *S. trutta* in New Zealand (Townsend, 1996; McDowall, 2003). Biological and behavioural differences between family and species of fish, however, allow some level of discrimination between those non-native fish introductions presenting a high risk of ecological impact and those that are likely to prove relatively benign (Kolar & Lodge, 2002; Gozlan, 2008). It is not as if the 1% of species presenting ecological risk is random, and so tools are being developed to screen effects of future non-native introductions. In the meantime, future efforts to limit losses of global aquatic biodiversity resulting from non-native fish introductions need to be focused on aquatic areas of high conservation value that are also characterized by a high risk of non-native species introduction. These could easily be identified because the major pathways for fish introductions are known and are related to some human activities (Copp *et al.*, 2007).

ECONOMIC IMPLICATIONS

An aspect associated with the movement of non-native species that is often neglected are the socio-economic implications of their use and spread. Economic activity, particularly globalization through trade, is the fundamental human cause of non-native introductions (Perrings *et al.*, 2000, 2002; Pimentel, 2002; Koo & Mattson, 2004; Taylor & Irwin, 2004; Pimentel *et al.*, 2005). The general consensus is that non-native invasive species have a negative economic effects. This is, however, very much a misconception as there are both direct (*e.g.* revenue and food security *v.* cost of eradication and control and loss of biodiversity) and indirect (wider benefits to society *v.* loss of ecosystem goods and services), positive and negative, and social and economic effects of introduced non-native species (Gozlan & Newton, 2009). If the socio-economic dimension is reviewed, the typical picture of high number of ecologically adverse effects arising from non-native species is potentially very different (Table II). Unfortunately, the economic implications of species introductions have rarely been evaluated because of problems associated with determining environmental costs arising from a lack of adequate data and approaches for meaningful comparisons, for example, how to value ecosystem services and products. Information is often fragmented or anecdotal, but the literature is replete with evidence of the positive and negative effects of non-natives. For example: (1) *c.* 17% of the world's finfish production is due to non-native species; (2) production of the African cichlid *Oreochromis* spp. is much higher in Asia (>1.6 million t in 2005) than in most areas of Africa (245 000 t); and (3) introduced salmonid fishes in Chile support a thriving aquaculture industry that is responsible for *c.* 30% of the world's farmed salmonids and directly employs *c.* 30 000 people.

The economic and social benefits accrued from non-native fish introductions must be weighed up against the environmental as well as the detrimental social and economic implications of introduction of non-native fishes (Gozlan & Newton, 2009). Pimentel *et al.* (2000, 2005) provided examples of these issues, although mainly for the U.S.A. For example, despite the conservative economic losses due to non-native fishes, estimated to be *c.* US\$5.4 billion annually, there are positive gains, as illustrated with sport fishing supported by introduced fishes contributing \$69 billion annually to the economy of the U.S.A. (Bjergo *et al.*, 1995). Despite these figures, there is a lack of precise data on the economic costs of non-native invasive species in inland fisheries.

One aspect that is not covered by these examples is the high cost of eradication or control of non-native species should they exhibit negative effects on the recipient ecosystem (Shaw & Seiger, 2002). Once established, invasive species can

TABLE II. Effects of introduced fish on ecological and socio-economic (in brackets) environments by reason for the introduction. Data represent number of records from Froese & Pauly (2009). Others include accidents, bait, forage, to fill niche, research and diffusion

Effect	Fishing	Aquaculture	Ornamental	Biocontrol	Unknown	Others
Adverse	36 (2)	78 (8)	17 (5)	23 (9)	13 (0)	40 (12)
Beneficial	16 (87)	52 (283)	11 (42)	11 (19)	3 (10)	6 (15)
Unknown	28 (16)	76 (49)	9 (9)	8 (2)	21 (3)	
Not indicated	196 (299)	949 (815)	169 (150)	106 (122)	459	283

be extremely difficult and costly to control or eradicate. For example, after opening the St Lawrence Seaway, sea lamprey *Petromyzon marinus* L. has dispersed through the Great Lakes of North America, affecting fisheries that generate up to \$4 billion for the region economy annually, offering recreational angling opportunities for five million people and providing 75 000 jobs (Lovell & Stone, 2005). To protect these fisheries, a number of control methods for *P. marinus* have been in force for many years, including lampricide for larval control, barriers, traps and a sterile male release programme (Great Lakes Fishery Commission, 2009). Estimates for this control action vary but are likely in the region of US\$10 million spent annually for control and research and another US\$10 million on fish stocking (Lovell & Stone, 2005). Without this control, lost fishing opportunities and indirect economic effects are estimated at US\$500 million annually (OTA, 1993). It is often argued that prevention, control and eradication of invasive species should be international and most certainly a global public good because of the high costs involved (Perrings *et al.*, 2002). There is, therefore, a need for optimal policies regarding invasive non-native species that minimize the likelihood of their entry (or for deliberately introduced species, their escape into unintended habitats), taking into account the costs of prevention, and policies that minimize the damage they consequently cause, bearing in mind costs of control or eradication. There are, however, challenges with efforts to control or prevent invasive aquatic species and these include the high level of scientific uncertainty surrounding: (1) the likelihood of species entry; (2) their invasiveness and (3) the identification of specific economic, environmental and social effects potentially caused by the species.

HOW ARE RISKS ASSESSED?

To justify measures to mitigate threats to biodiversity (CBD, 2001), protocols were needed to assess the risks of non-native species introductions. Protocols were adapted from environmental risk analysis (Calow, 1998) to assess the risks posed by non-native species, in particular plants and their pests (Tucker & Richardson, 1995; Panetta *et al.*, 2001), and then fishes using qualitative and semi-quantitative elements (Kohler & Stanley, 1984; US_ANS_Task_Force, 1996; Kahn *et al.*, 1999). More recent approaches have been quantitative (Kolar & Lodge, 2002), using classification and regression tree (CART) decision-tree analysis of ecological and biological characteristics of existing non-native species to predict future invasive species from the same donor region. Other recent approaches (US_ANS_Task_Force, 1996; Copp *et al.*, 2005b) employ multistep frameworks, such as that developed in the U.K. specifically for freshwater fishes (Copp *et al.*, 2005b), and then more generally for all plants and animals (Baker *et al.*, 2008). The U.K. frameworks combine the quantitative decision-making tools required under the World Trade Organization Sanitary and Phytosanitary (SPS) Agreement (www.wto.org) and the qualitative decision-support systems espoused by the guidelines of international policy and principles on alien species (*e.g.* Convention on Biological Diversity, CoP6 Decision VI/23, 2002). For the pre-screening (hazard identification) phase, the *Weed Risk Assessment*, WRA (Pheloung *et al.*, 1999), was converted into a fish invasiveness scoring kit (FISK), and similar tools for other aquatic taxa (Cefas, 2010), which identify potentially invasive organisms for full risk assessment. Pre-screening tools such as these are not 100% reliable (Smith *et al.*, 1999; Gordon *et al.*, 2008), but they represent relatively

simple, bibliographic-based, objective tools to facilitate the decision-making process and also help identify gaps in knowledge.

In these non-native species risk analyses, the underlying premise is that only adverse effects are assessed. Consideration of positive (beneficial) effects (Gozlan, 2008; Gozlan & Newton, 2009) by environmental managers takes place as part of the decision-making process. Where information is scarce or lacking, the precautionary approach may be applied (FAO, 1995), but this is not always the case, such as in the invasive species environmental impact assessment (ISEIA; Branquart *et al.*, 2007) scheme developed in Belgium. This screening system, which helps managers prioritize species according to their relative risk and their stage of invasion, relies on a relatively simple algorithm. In the case of crayfishes (Astacidea), the outcomes were similar in most cases to those from a WRA-type tool (E. Tricarico, L. Vilizzi, F. Gherardi & G. Copp, unpubl. data), whereas for freshwater fishes, the ISEIA scheme underestimated the risk of most species relative to FISK (Table III). FISK is based on 49 questions and has been calibrated and validated against independent assessments of invasive status, whereas the ISEIA scheme classifies species using four scores of which two are the maximum values from eight questions and this system is as yet not calibrated. Adequate interrogation is an important consideration in the risk-screening process and must be balanced against the available financial resources. In other words, schemes that classify species from a limited number of questions may reduce the time (and cost) of assessments but at the expense of accuracy in identifying potential invaders (Table III).

The precautionary approach has now been integrated into numerous disciplines associated with risk analysis and management beyond the marine fisheries area. The effectiveness of the precautionary approach has been addressed directly in relatively few areas, and these are related to fisheries management or food safety. In fisheries

TABLE III. Comparison of invasiveness risk scores for fresh and brackishwater fishes using the adapted invasive species environmental impact assessment (ISEIA) scheme (Parrott *et al.*, 2009) and the fish invasiveness scoring kit (FISK) screening tool whereby H is high risk, M is medium risk, L is low risk, with lower and middle ranks of FISK referring to a score's relative position (lower or intermediate 1/3) within that risk rank

Species	Common name	ISEIA scheme	FISK invasiveness risk	
			Mean score	Rank
<i>Acipenser ruthenus</i>	Sterlet	L	16.0	Lower H
<i>Ameiurus melas</i>	Black bullhead	M	28.8	Middle H
<i>Hypophthalmichthys nobilis</i>	Bighead carp	L	24.3	Lower H
<i>Catostomus commersoni</i>	White sucker	L	23.0	Lower H
<i>Ctenopharyngodon idella</i>	Grass carp	L	24.0	Lower H
<i>Cyprinella lutrensis</i>	Red shiner	L	18.0	Lower H
<i>Gambusia holbrooki</i>	Eastern mosquitofish	M	21.0	Lower H
<i>Hypophthalmichthys molitrix</i>	Silver carp	L	22.8	Lower H
<i>Misgurnus fossilis</i>	Weatherfish	L	12.5	Lower H
<i>Neogobius melanostomus</i>	Round goby	H	29.5	Middle H
<i>Pimephales promelas</i>	Fathead minnow	L	19.0	Lower H
<i>Proterorhinus marmoratus</i>	Tube-nose goby	H	18.5	Lower H

management, appreciation of the precautionary approach is equivocal but generally positive (Essington, 2001; Piet & Rice, 2004; Aprahamian *et al.*, 2006), whereas in food safety these principles are not viewed as particularly helpful (Hanekamp *et al.*, 2003). No published studies have been found that specifically assess the effectiveness of the precautionary approach with regard to non-native species.

MANAGEMENT: REMEDIATION AND MITIGATION

The effective management of non-native fishes begins with preventing introductions, as this optimizes the potential to minimize subsequent adverse effects and their associated costs (Myers *et al.*, 1998, 2000; Simberloff, 2002), and is complementary to the precautionary principle (Sandin, 1999; Foster *et al.*, 2000). Although managers might intuitively be expected to choose the prevention of introductions as their preferred form of management, Finnoff *et al.* (2007) argued that instead, managers frequently wait until non-native species have been introduced and only then act to limit their effect (Leung *et al.*, 2002; Carlton & Ruiz, 2005). This relates to a perception that post-introduction management is a safer choice than prevention because its productivity is relatively less risky, *i.e.* even with strict and expensive prevention protocols in place, introductions still occur. Some introductions are intentional, making use of species predicted to produce substantial economic returns and societal benefits (Gozlan, 2008). Accidental introductions do, however, also occur; as these are less likely to have been subject to risk assessment, they may be most damaging ecologically. These introductions occur through, for example, a breach of biosecurity at aquaculture or research facilities, and through the introduction of a contaminant or hitch-hiking species (Copp *et al.*, 1993, 2006).

When measures to prevent unregulated fish introductions fail, then management interventions, using appropriate remediation and mitigation tools, are required if the ability of that species to establish and cause detrimental effects is to be minimized or eliminated (Lodge *et al.*, 2006). Remediation is the process whereby the introduced species is completely removed from the recipient ecosystem, such as through eradication, whereas mitigation concedes that either the introduced species cannot be eradicated or its effect is insufficient to warrant such an approach. Consequently, the role of mitigation is to control and contain the species so that the provision of, for example, essential ecosystem services can be maintained in their presence. The initial steps of any management intervention are the detection of the introduced species followed by determination of the level of risk they pose to the recipient water body, the wider environment and socio-economic considerations. This risk-based management approach is necessary (Andersen *et al.*, 2004) because: (1) non-native fishes differ in their likelihood of becoming invasive and incurring ecological impact; (2) recipient ecological communities differ in their vulnerability to invasion and the values society attaches to them; (3) non-native fishes and their recipient ecosystems differ in their susceptibility to prevention and control; and (4) there is a requirement for scarce resources to be allocated among existing and potential invaders through a process of balancing disparate risks, costs and benefits that are not uniformly distributed under conditions of scientific uncertainty.

Consequently, risk management decisions on introduced non-native fishes rarely consider scientific evidence in isolation, but also rely on legal, economic, administrative, social and cultural factors to determine the most appropriate, dispassionate

and rational response (Andersen *et al.*, 2004). Typical remediation and mitigation responses (as summarized in Zavaleta *et al.*, 2001; Simberloff, 2002; Britton *et al.*, 2008) include the following: (1) eradication: the complete elimination of the non-native fish population whereby only re-introduction could allow their return; (2) crisis management: no action is taken on that species until the development of a major pest issue at which point major management interventions are initiated; (3) sustained control: the population is routinely suppressed by regular management actions; and (4) do-nothing: considered a justifiable default option when assessment demonstrates that the likely effect of the species will be socially acceptable, the cost of control exceeds the value of their effects or there are no existing management techniques available.

The reason why preventing unwanted fish introductions is so important is that there is a paucity of techniques that can adequately control their distribution and dispersal in open systems. While there are effective interventions for closed systems, such as enclosed ponds, these are generally lethal, designed to incur maximum mortality rates in the target fishes, for example, the application of biocides such as rotenone (Meadows, 1973; Ling, 2002; Allen *et al.*, 2006; Britton & Brazier, 2006; Rayner & Creese, 2006). As these techniques are generally non-host specific, collateral damage in non-target species may be considered inevitable (Meadows, 1973; Rayner & Creese, 2006). Consequently, some sections of society may find their use ethically questionable (Barr *et al.*, 2002; Sheail, 2003; Philip & Macmillan, 2005; Fraser *et al.*, 2006; Bremner & Park, 2007). Furthermore, the eradication of introduced fishes is also viewed by many as a controversial and almost impossible goal due to its high expense and difficulty of success (Myers *et al.*, 1998; Simberloff, 2002; Britton *et al.*, 2008). Although eradication has been used effectively against populations of invasive species, the chance of success is usually directly proportional to the spatial extent of dispersal (Culver & Kuris, 2000; Anderson, 2005; Rayner & Creese, 2006), with eradication of fishes most effective in relatively small, closed, sparsely vegetated water bodies, particularly when rotenone is used (Lozano-Vilano *et al.*, 2006; Britton *et al.*, 2009).

Where eradication is a remediation tool that aims to eliminate the population completely, mitigation tools, such as use of control and containment techniques, aim to suppress the introduced fish and facilitate the continued provision of ecosystem services, while generally acknowledging that eradication may be impossible to achieve. In the control and containment of non-native fish populations, small-scale eradications can be integrated into the approach whereby populations are eliminated from waters from which there is a high chance of their dispersal into fluvial environments (Britton *et al.*, 2008, 2009). Alternative management options, however, also exist. The physical removal of the introduced species from infected waters using methods such as seining, electrofishing and gillnetting reduces their abundance in the site and enables all non-target species to be returned (Knapp & Matthews, 1998; Britton *et al.*, 2009). A further method is biocontrol, which relies upon natural enemies to attack the introduced non-native species (Secord, 2003). Classical biocontrol introduces a natural enemy from the natural range of the species to control it in its new environment, whereas augmentative biocontrol enhances populations of native predators, parasites and pathogens to improve their regulation of the introduced species (Secord, 2003). The aim is to take advantage of negative species interactions to reduce the survivorship or reproduction of the introduced species. Although rarely

capable of eliminating the target species, biocontrol can suppress the population to a socio-economic or ecologically acceptable level with only a minimal input of effort (Gause, 1969). Their ecological effects, however, are likely to be irreversible; once an introduced biological agent has established, only eradication may remove it.

Although these eradication and control methods have the potential to manage the dispersal of introduced non-native fishes, all have controversial elements. To overcome some of the more contentious aspects of these methods, novel techniques are being developed and tested. For example, to control introduced species that have predominantly genetic, but environmentally reversible, sex determination, such as many fishes, models have been developed and tested, which use carriers of Trojan Y-chromosomes (individuals that are phenotypically sex reversed from their genotype) (Gutierrez & Teem, 2006; Cotton & Wedekind, 2007). They demonstrate that repeated introduction of YY females into wild populations may produce extreme male-biased sex ratios and the eventual elimination of XX females, thus leading to population extinction in the target species (Gutierrez & Teem, 2006). There are a series of issues, however, that remain unresolved; for example, little is known about the relative performance of genetically manipulated individuals in the wild, or about the sex determining systems of many invasive species (Cotton & Wedekind, 2007). Introductions of inducible fatality genes have also been mooted (neutral genes that become lethal when activated by an external agent or stimulus) but are problematic in that they must become fixed or achieve high frequencies in the population before activation (Muir & Howard, 2004).

A more practical technique may involve the complementary use of pheromones (Burnard *et al.*, 2008). Most fishes rely on pheromones (chemical signals released by conspecifics) to mediate social behaviours, with three categories discerned based on their function: antipredator cues, social cues and reproductive cues (Sorensen & Stacey, 2004; Burnard *et al.*, 2008). Each of these categories comprises pheromones that can induce primer effects (developmental and endocrinological changes) and releaser effects (strong behavioural changes). The pheromones that have been chemically identified are very potent; in combination with their specificity, this provides them with considerable potential for use in controlling introduced non-native fishes (Burnard *et al.*, 2008). Already successfully used within integrated control programmes for sea lamprey *P. marinus* in the North American Great Lakes (Jones *et al.*, 2003), pheromone cues have been used to simultaneously exploit multiple weaknesses in the life history of the species while recognizing their stock–recruitment relationships. Sorensen & Stacey (2004) recommended that their use involves a variety of pheromones to supplement and increase the efficiencies of other control strategies, for example, to: (1) facilitate trapping efficiency (Twohey *et al.*, 2003a, b); (2) disrupt or reduce reproductive success (Carde & Minks, 1997; Wyatt, 2003); (3) disrupt movement and migrations (Li *et al.*, 2003; Sorensen & Vrieze, 2003); and (4) promote the success of sterilized fish and to repel others from sensitive areas (Maniak *et al.*, 2000).

Control and containment of an introduced fish can also be achieved through the construction of barriers to prevent their upstream dispersal. Examples of physical barriers include the construction of low head barriers to prevent *P. marinus* from reaching spawning grounds in the Great Lakes system (Great Lakes Fishery Commission, 2009). These block the passage of lampreys, but allow desirable fishes to pass. Their location downstream of spawning grounds prevents access to suitable

spawning habitat, eliminating larval lamprey production and the subsequent need for lampricide treatment. Electric and hydroacoustic barriers have also been used to prevent the movement of invading fishes. Experiments in the U.S.A. revealed that a cross-channel air bubble curtain barrier containing pneumatically generated sound signals randomly selected from a predetermined frequency range was 95% successful in repelling the movements of bighead carp *Hypophthalmichthys nobilis* (Taylor *et al.*, 2005). Introductions of non-native species are generally easier and cheaper to control and eradicate when their distribution is still highly localized (IUCN, 2000; Manchester & Bullock, 2000; Genovesi, 2005; Cacho *et al.*, 2006). This has given rise to the development of the three-step management concept of 'rapid detection, rapid assessment, rapid response' (Myers *et al.*, 2000; Zavaleta *et al.*, 2001; Zavaleta, 2002; Anderson, 2005). A major problem with the concept is that the ability to detect a newly introduced species is compromised by its limited distribution, as the effort required for detection is usually inversely proportional to population size (Hayes *et al.*, 2005). Hence, networks designed to detect new introductions rapidly must maximize their effectiveness by emphasizing their work on high-priority targets, such as high-risk locations, high-value resources, important pathways and populations and species of most specific concern (Lodge *et al.*, 2006). When a non-native fish is detected soon after introduction and has yet to establish a sustainable population and disperse, then cost-effective options are likely to still be available; if eradication is identified as an appropriate response, then it carries relatively little risk due to the chemical or mechanical control efforts remaining highly localized (Genovesi, 2005). If, however, the introduced species has already established a sustainable population, then options for management are already constrained, particularly if that species is now spreading. Its control or eradication is now more difficult and expensive due to the increased spatial and temporal extent of application, and there is a corresponding increase in the risk of failure (Genovesi, 2005; Rayner & Creese, 2006). If the introduced species is only acted upon when it is highly invasive and spreading rapidly, then realistic opportunities for control may be slim, and mitigation schemes that compensate for the presence of the species may be the only appropriate management option. Other issues that should be considered are as follows. (1) Resources: eradication exercises are often expensive and it is vital to determine who is to meet the economic and manpower costs. (2) Opposition: even during the early stages of an invasion by a non-native species, eradication attempts remain controversial. (3) Inadequate legislation: facilitating the rapid initiation of eradication exercises is their basis in legislation; where detection of a new introduction requires an effective response that has a basis in law, there is an increased chance of an eradication attempt being initiated quickly. (4) Invasion pathway remains open: unless the pathway by which the invader arrived has been closed, for example, through increasing the biosecurity of an aquaculture facility, then re-introduction of the non-native species remains a possibility. (5) Feasibility of eradication: feasibility can be determined by analysis of logistics, the biological characters of the species concerned, the water characteristics and the management required to achieve eradication. (6) Presence of protected species: consideration must be given over the presence in the receiving water body of any native species with legal protection or high conservation status that would be adversely affected by any eradication attempt. (7) Resource value: if receiving water is an exploited fishery of high societal and economic value, assessment must be made of how this will be affected by the eradication attempt.

CONCLUSIONS AND PERSPECTIVES

The subject of regulating the introduction and presence of non-native fishes in nature is sensitive and difficult to review, as it falls between socio-economic drivers, conservation practitioners and a wide range of academic disciplines that often ignore each other in their respective conclusions. In this review, a pragmatic approach has been taken to the neo-paradox, resulting from post mid-twentieth century economic development, that, despite knowledge of potential adverse effects on recipient ecosystems, economic drivers are still pushing for further introductions (Gozlan & Newton, 2009). For example, the European aquaculture sector is fairly limited compared with Asia and is under pressure from the European Commission to expand. An option is market diversification, whereby an increased range of species are cultured. As the majority of these species are likely to originate from outside Europe, this will increase the risk of new introductions arising through lapses in the biosecurity of aquaculture sites.

Understanding and acknowledging this paradox are crucial to regulate adverse species introductions successfully, as it enables market diversification to proceed in conjunction with robust risk-assessment tools, more efficient mitigation and, ultimately, the more efficient regulation of future introductions. Pragmatically, the absolute zero risk advocated by some conservationists is an unrealistic position that to date has not been efficient in prohibiting the introduction of fish species worldwide or limiting their adverse effects. Policy advisors are not in a position to ignore the risk, but neither are they in a position to limit trade based on the precautionary approach, as policy makers are often unable to wait for complete scientific answers before policy development and implementation. This review has revealed that manipulating ecosystems can never be considered risk free, and increased international regulation structured around sound risk assessment tools is a major step forward in regulating future fish introductions. Risk assessments are developed and based on current knowledge, where level of risk is constantly updated based on current scientific understanding of the effects of non-native species on ecosystems. Limiting and managing risk is key and as highlighted in Gozlan (2008), the risk is not evenly distributed across species and ecosystems. This review argues that, although mostly empirical, scientists today have a greater understanding of the risks associated with each species introduction. A perspective from this review is that by combining the economic values of species on a global scale with their associated level of ecological risk, those of low ecological risk and high economic value [*i.e.* sterlet sturgeon *Acipenser ruthenus* L.; coho salmon *Oncorhynchus kisutch* (Walbaum); catla *Catla catla* (Hamilton)] can be teased out (Fig. 1). In addition to the use of standardized, robust risk assessment as a basis of future fish species introductions, there is an associated need to support up-to-date research on the ecological implications of non-native species, in particular in the causal relationship between species introductions and loss of biodiversity. An understanding of the processes involved will refine the risk analysis tools and limit the risk of adverse effects. This is particularly relevant in the context of climate change where the equilibrium of ecosystems will be modified and consequently, the potential effect of fish introductions.

It has also emerged from this review that one of the greatest risks associated with this global movement and introduction of species is the introduction of non-native

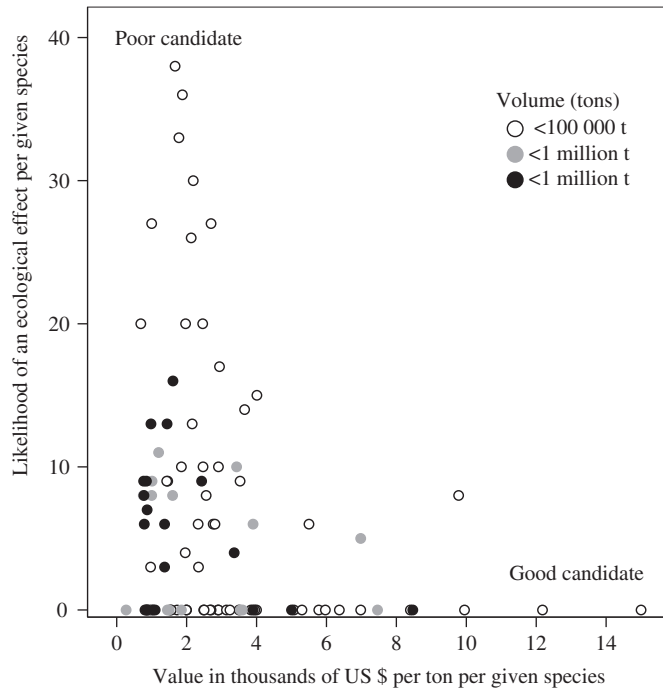


FIG. 1. Relationship between economic value and likelihood of ecological effect per given species. ○, species production in tonnes strictly <100 000; ●, >100 000 but <1 000 000 and ●, strictly >1 000 000 (from Gozlan, 2008).

infectious agents. This is where the magnitude of risk is the greatest and where monitoring and future efforts should concentrate.

Finally, maps of conservation hot spots should be drawn based on a combination of predictors of future introductions (*e.g.* human population density, aquaculture activity) and risk level of incurring losses to local–global biodiversity (*e.g.* number of critically endangered species). This would accelerate prioritization of the areas at national and global levels where risks of future introductions should be minimized, such as those where endemic species are at risk and the intensity of introductions of non-native species has been limited.

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