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REVIEW

A review of the research on introduced freshwater fishes: new perspectives, the need for research, and management implications

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Abstract Although freshwater fishes have a long history of human-induced introduction, recent globalization has accelerated worldwide introduction events even more, and those introduced fish species are now perceived to be a major threat to ecosystems. Over the last two decades, numerous studies have been published on introduced fish species; however, it has been challenging for researchers to understand the magnitude of the impact and the underlying mechanism of invasions. Recently, new perspectives in understanding invasive freshwater fish biology have been presented in a number of studies, which can be largely attributed to advances in analytical techniques and also to a growing need for proactive analysis in management strategies. The aim of this paper is to summarize new ecological perspectives, the need for research, and/or management implications with emphasis on technological advances in, for example, statistics, molecular analysis, modeling techniques, and landscape analysis addressed under the following five categories: introduction pathways, predicting spatial patterns, biotic homogenization, hybridization, and control and eradication. The conservation of native fish fauna and the management of introduced fish species will benefit from combining these new perspectives with fundamental studies such as those on life history and population biology.

Keywords Invasive fishes · Introduction pathways · Spatial patterns · Biotic homogenization · Hybridization · Eradication

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Introduction

It has been widely recognized that the introduction and establishment of nonnative species can have high and potentially adverse effects on individuals, populations, and communities of native species, and those that have been introduced have contributed to the decline or extinction of native species worldwide (Taylor et al. 1984; Coblentz 1990; Lodge 1993; Primack 1998; Townsend 2003). Among 170 extinct animal species listed on the International Union for Conservation of Nature (IUCN) Red List with known causes of extinction, invasive species were cited as the direct cause of extinction in 34 of those cases (Clavero and García-Berthou 2005). Furthermore, the effects of invasives on single species can have a domino effect upon other organisms, resulting in a catastrophic transformation of the entire ecosystem (Primack 1998).

Unlike open terrestrial ecosystems, freshwater ecosystems are more or less closed systems; the connectivity of each pond, lake, and watershed with each other is limited, often creating distinct unique faunas within a small geographical range. However, at the same time, freshwater ecosystems have a close association with human activities such as the use for local water supplies, natural resource development (e.g., aquaculture), commercial navigation, and recreation (Colautti et al. 2003). Among all of the freshwater organisms, fish have a long history of human-induced introduction and translocation, dating back to Roman times (Welcome 1988; Copp et al. 2005). The magnitude of the introduction events was accelerated in the 1800s largely due to improved methods of transportation and was intensified even more in the 1960s due to a greater variety of human activities (e.g., aquaculture, sport fishing, ornamental purposes, and biocontrol) (Welcome 1984, 1988; Fuller 2003). The best known recent cases of devastating impacts on native fish species include, to mention just a few, an introduction of the piscivorous Nile perch (*Lates niloticus*) into Lake Victoria, east Africa, in 1954 (Fryer 1960), which presumably collapsed populations of more than 400 fish species, out of which, 200 species of endemic haplochromine cichlid species were driven to extinction (Kaufman 1992; Witte et al. 1992). An introduction of pikeperch (also called Zander) (*Sander lucioperca*) into Lake Egridir in Turkey in 1955 also exemplifies the severe impact of introduced species, which extirpated five native species including two species of lake endemics and severely decreased the number of the remaining four native species (Crivelli 1995).

Although the negative effects of introduced fish species on native freshwater fish fauna have been indicated by a large number of studies, it has been challenging for researchers to measure the magnitude of the impact and to demonstrate how introduced fishes have affected native fish fauna, largely because data is usually limited and multiple causes and levels of interaction and effect are involved (Simberloff 1981; Helfman 2007). In particular, freshwater habitats have been rapidly modified by human activities in many regions of the world, making it even more difficult to examine whether the decline in native species is indeed caused by introduced species or human disturbances. Fortunately, over the last decade, new perspectives in understanding invasive freshwater fish biology have been provided in a number of studies. This is partly due to advances in technology with statistics, molecular analysis, and landscape analysis and partly due to a growing need for the proactive analysis of the impact of introduced fishes. With the current situation where the management of invasive fish species requires urgent action, reviewing this continuously increasing research compilation should assist in providing biologists and managers with effective ideas and knowledge for conducting future research and establishing priorities in the management of introduced fish species.

In this paper, we review scientific publications on introduced freshwater fishes to identify new ecological perspectives, the need for research, and/or management implications, with emphasis on the advances in analytical techniques, highlighting several categories for fields of research that appear to be particularly important for future studies. Five broad categories are specifically addressed: introduction pathways, predicting spatial patterns, biotic homogenization, hybridization, and control and eradication. For introduction pathways, we introduce a molecular technique that has been used to identify the origin and introduction pathways of nonnative fishes. Predicting spatial patterns is covered by introducing analytical techniques that have recently advanced in predicting spatial patterns of introduced fishes. With regards to biotic homogenization, we focus on how the concepts and perspectives have evolved over the last decade. As for the category hybridization, for which numerous case studies have already been reported, we address some issues associated with establishing conservation and management strategies of both parental native species and hybrids using a well-known case study to illustrate this. Lastly, for control and eradication, we review some case studies and discuss the need for research and management implications.

The terms and definitions associated with introduced species follow those of Copp et al. (2005) in which "introduced" refers to nonnative, "exotic" to nonindigenous and alien, whereas "invasive" is used when these species spread and cause significant change in the composition and structure of ecosystem processes or lead to severe economic losses to human activities. Likewise, "native" is referred to in this context as indigenous.

Introduction pathways

One of the most fundamental pieces of information necessary for research and management of introduced species is the knowledge of their introduction pathways. Knowing how a particular species has been introduced from its origin to a local fish community could help explain the current distribution patterns and predict how the species may expand its range in the near future. For example, in a survey on 14 introduced freshwater fishes in Flanders, Verreycken et al. (2007) examined distribution of each species along with its historical pathway of introduction, reporting the current status and future potential range expansion of those fishes, some of which seemed to be related to their introduction pathways. Nakajima et al. (2008) also summarized the current distributions of introduced fishes in the northern Kyushu region in Japan, showing their introduction pathways. Their study revealed that patterns in the introduction of the 23 nonnative fishes found in the region could be attributed to a variety of pathways, including both intentional and accidental introductions that may vary both spatially and temporally, providing essential information for the establishment of a practical management scheme that could be implemented to prevent further introduction events.

Although it is often difficult to reveal the origins and pathways of the introduction of nonnative species when literature information is not available, recent advances in molecular biology now make it possible to deal with the problem. For example, the bluegill sunfish (*Lepomis macrochirus*) is among the most notorious invasive aquatic species in Japan and is now very widespread nationwide. Although it is widely known that the species was first introduced from Guttenberg, Iowa, USA, in 1960 (Maruyama et al. 1987), it has not been confirmed as to whether any other introduction events were involved after the initial event because, unfortunately, there have been no other official records of introductions of the species. However, Kawamura et al. (2006) recently used polymerase chain reaction–restriction fragment length polymorphism (PCR-RFLP) analyses of mitochondrial DNA (mtDNA) and were able to reveal that all bluegill sunfish in Japan originated from the 15 individuals that were first introduced from Guttenberg. Other case examples include studies on introduced salmonid species (e.g., Quinn et al. 1997; Riva Rossi et al. 2004) and translocated species in Japan (see review by Mukai 2007). These studies have proven the effectiveness of molecular techniques for identifying the origin and introduction pathways of nonnative freshwater fishes and providing insight into how those nonnatives expanded their range.

Predicting spatial patterns

While the number of studies on introduced species has grown dramatically over the last 30 years, not many of them have been effectively utilized in management practices. In fact, the biggest problem associated with introduced species is probably that by the time one recognizes the introduced species as being invasive, they are already so well established and so widely spread that it is virtually impossible to take any practical actions to eliminate them. Recently, in a response to a growing concern over economic and ecological costs caused by invasive species, research efforts have focused on more predictive and proactive approaches specifically to predict which species will be introduced and successfully established and which factors will be associated with their establishment (Kolar and Lodge 2001). Such studies predicting species invasions have been conducted in terms of the relationship of the fish with humans, species biological characteristics, the characteristics of the introduction locality (i.e., site characteristics), and propagule pressure, generally considering some combinations of these components (e.g., Kolar and Lodge 2001; Ruesink 2005; Moyle and Marchetti 2006). Whereas these components are all important in predicting the general characteristics of successful invasions, many studies have focused more on investigating which site characteristics can support the introduction and establishment of nonnative species, the second component mentioned above, which can further lead to the prediction of spatial patterns of range expansion after establishment. Three factors associated with site characteristics are considered to favor the introduction and establishment of nonnative species, namely, similarity to source areas, human-induced disturbances, and low native species richness (Moyle and Marchetti 2006). Here, we review some of the studies investigating site characteristics, focusing on recent developments in analytical techniques.

Multivariate statistical analysis has been intensively applied for a wide variety of ecological studies. For studying introduced fish, the technique has been used to examine a range of site characteristics that influence introduction and establishment. For example, Fausch et al. (2001) used a principle components analysis (PCA) and a multivariate analysis of variance (MANOVA) to demonstrate that a successful invasion by rainbow trout (*Oncorhynchus mykiss*) was related to the timing and extent of high-flow events that were similar to those at the source areas. Multivariate analytical techniques can benefit further from the use of a geographic information system (GIS), which not only allows researchers to incorporate environmental data at various spatial scales but also to include human-induced disturbances that provide introduced generalist fishes with favorable habitats through habitat modification and alteration. For example, by using a PCA and canonical correspondence analysis (CCA) together with a GIS technique, Brasher et al. (2006) were able to investigate 23 species (16 of them introduced) and 18 physical or environmental variables and demonstrate that Hawaiian streams with altered habitats characterized by urbanization and development can be more successfully established by introduced species. Gido et al. (2004), by using a multiple regression and a GIS technique, also found that high human population density was a significant variable that could predict the higher number of introduced species across the 949 sites in the Great Plains region of North America. They speculated, however, that the result may have been caused by higher propagule pressure (i.e., a high introduction event) that can be associated with highly populated areas rather than caused by habitat modifications.

Recently, ecological niche modeling (also referred to as species' distribution modeling or predictive habitat distribution modeling) has been receiving increasingly more attention for its wide variety of ecological applications, including conservation and management planning (Guisan and Thuiller 2005). Compared with multivariate analytical techniques, ecological niche models more explicitly aim to predict the future distribution and spatial patterns of the range expansion. The result is generally drawn on GIS maps by relating species occurrence data (i.e., presence/absence or abundance) to suites of environmental variables (Peterson and Vieglais 2001; Pearson 2007). For example, in producing a predictive distribution map by using one of the ecological niche modeling approaches, namely, the artificial neural network (ANN), Vander Zanden et al. (2004) were able to identify lakes across southern Canada that are "vulnerable" because they exhibit conditions that would make ideal habitats for invasive smallmouth bass (*Micropterus dolomieu*), although the species has not yet been observed there. Céréghino et al. (2005) used a similar approach to show on maps the occurrence probabilities of ten nonnative fish species of southwest France.

A number of ecological niche models have been proposed (see reviews by Guisan and Thuiller 2005), such as the genetic algorithm for rule-set prediction (GARP) (Stockwell and Peters 1999; also see Peterson and Vieglais 2001), ecological-niche-factor analysis (ENFA) (Hirzel et al. 2002), and maximum entropy (MAXENT) (Phillips et al. 2006). Although numerous case studies using ecological niche models have been reported for a variety of taxa, there have been surprisingly few studies conducted on invasive fish (but see examples discussed above). This is surprising given that once an aquatic invader becomes established, its range expansion is generally unavoidable (Vander Zanden et al. 2004), and proactive analyses such as predicting occurrences and distribution should be particularly important to prevent the further invasion and range expansion of introduced fishes.

Biotic homogenization

Over the past decade, increasing attention has been given to a biological phenomenon known as biotic homogenization (McKinney and Lockwood 1999). Biotic homogenization (or taxonomic homogenization) increases the taxonomic similarity in the composition of communities, for the most part as a result of the introduction of nonnative species and loss of native species, both of which are facilitated by habitat modifications (McKinney and Lockwood 1999; Rahel 2002; Olden et al. 2004), and the growing number of studies reflect an increasing concern over a decline in biodiversity.

Initially, the homogenization of freshwater fish faunas received less attention compared with that of plants and birds, for example (Scott and Helfman 2001). However, the number of studies on this has been gradually increasing: for example, Radomski and Goeman (1995), Rahel (2000), Scott and Helfman (2001), Marchetti et al. (2001), Rahel (2002), Walters et al. (2003), Olden and Poff (2003, 2004), Taylor (2004), Marchetti et al. (2006), and Olden et al. (2006) for North American fish faunas, Clavero and García-Berthou (2006) for Iberian Peninsula fish faunas, and Leprieur et al. (2008) for European fish faunas. A common approach for the quantitative analysis of homogenization has been to investigate temporal changes in compositional similarity between a pair of fauna over a certain period of time. Rahel (2000), for example, calculated the similarity of fish assemblages between each pair of states in the contiguous United States for two time periods, before and after European settlement, demonstrating that present fish faunas are more homogenized across the United States. The study also showed that pairs of states now have 15.4 more common species on average than they did in the past and that 89 pairs of states that formerly had no common species now share an average of 25 common species. In addition, he pointed out that introductions, most of which were intentional for angling or aquaculture purposes, were the cause of homogenization rather than extirpations.

Several authors point out that urbanization (or habitat alteration) is one of the environmental drivers causing biotic homogenization (McKinney and Lockwood 1999; Rahel 2002; McKinney 2006), which encourages the establishment of nonnative species not only by introducing them through human activities but also by providing them with favorable habitats, as discussed in the above section (McKinney 2006). For example, increased levels of sedimentation associated with urbanization homogenized highland stream fish assemblages in northern Georgia, USA, by creating more hospitable environments for the cosmopolitan, nonnative species (Walters et al. 2003).

The concept of homogenization should, however, be applied with caution in conservation or management. There is consistent agreement among conceptual and empirical studies that biotic homogenization can be promoted and regulated by interactions among native species, nonnative species, and the environment (e.g., habitat alteration from urbanization). However, interactions of these three drivers of homogenization are complex, and the underlying mechanisms remain only partially understood (Rahel 2002; Olden and Poff 2004). Olden and Rooney (2006) admonished researchers that one cannot predict a priori as to whether a pair of communities will undergo homogenization or differentiation. For example, there can be some points over the homogenization process where the extinction of native species and invasion of nonnative species can in fact decrease homogenization and increase differentiation (see Scott and Helfman 2001; Olden and Poff 2003; Rooney et al. 2007). Marchetti et al. (2001) showed the evidence of homogenization of Californian fish faunas by investigating historic (i.e., before the Californian gold rush) and present fish assemblages, but the extent to which fish assemblages became more similar differed depending on the geographical scale (i.e., between aquatic zoogeographic provinces/watersheds within the same aquatic zoogeographic province/individual stream reaches). The dependence of homogenization and differentiation on a spatial scale was also reported by Taylor (2004) for the Canadian freshwater fish faunas. Furthermore, Marchetti et al. (2006) found urbanization to be associated with the differentiation in fish assemblages between watersheds within Californian provinces despite the fact that a strong positive correlation was found between urbanization and both the endangering of native fish and the invasion of nonnative fish within watersheds. They warned that the relationship between urbanization and homogenization is much more complicated than we would expect and may be spatial-scale dependent. These studies highlight the need for conservation biologists and managers to consider what the main drivers of biotic homogenization or differentiation have been in the past.

In order to deal with complex interactions among drivers causing homogenization and to understand the underlying mechanisms, the development of theoretical models appears to be an effective means. Olden and Poff (2003, 2004) developed a predictive model that describes a variety of invasion–extirpation scenarios and tested it using empirical data for freshwater fish faunas in the United States. They demonstrated that different rates and patterns of species invasions and extirpations that are both spatially and taxonomically dependent can lead to various levels of biotic homogenization and differentiation. The development of such theoretical models will most certainly provide insight into the drivers of homogenization and differentiation and provide a means to forecast future patterns of biotic homogenization, which can be applied in conservation and management planning.

Given that quantifying the impact of nonnative fish species on native species, communities, and ecosystems is still challenging despite the urgent need for the implementation of management programs, the concept of biotic homogenization, especially quantitative estimates of homogenization and theoretical models, can be an effective way to measure the impact of biological invasions on biodiversity. Empirical studies conducted at various places with different temporal and spatial scales should be encouraged not only to deepen our understanding of the current patterns and impacts of homogenization but also to validate theoretical models.

Hybridization

Hybridization is one of the most detrimental effects from the introduction and establishment of nonnative species on native species. Hybridization has long been recognized among many taxa, including plants, mammals, reptiles, amphibians, and fish. Over the last two decades in particular, the increased availability of informative genetic markers have enabled researchers to investigate not only the occurrence of hybridization but also the extent of introgression (hybrids backcrossing with one or both of the parental species), which is often difficult on morphological grounds alone (Rhymer and Simberloff 1996).

For freshwater fishes, numerous cases have been documented in the literature (see Rhymer and Simberloff 1996; Epifanio and Nielsen 2000; Helfman 2007), and yet less attention has been paid to the severity of ecological impact from hybridization despite the fact that it can cause extinction of a species, subspecies, or populations in the form of genetic extermination (Rhymer and Simberloff 1996). Because hybrid F1 are known to be generally less fertile, and even in cases where F1 are fertile and happen to backcross with a parental population (i.e., introgression), those hybrids are still assumed to have reduced fitness (Mallet 2005) and thus cause little ecological impact. However, it is a well-known phenomenon that fitness equals or exceeds that of parental types, called hybrid vigor (Rhymer and Simberloff 1996; Rosenfield et al. 2004), accelerating further introgression until there are no individuals of the native species with their original genome. When introgression has occurred among the individuals of a rare species whose number and distribution were already limited—often due to habitat destruction and disappearance—the situation becomes even more problematic (Allendorf et al. 2001), with various conservation and management concerns arising for both the parental native species and the hybrids. Conservation of a parental native species may benefit from increasing intraspecific genetic exchange, which may, however, also pose the potential dangers of both intra- and interspecific hybridization. Additionally, the treatment of hybrids has been reevaluated for the possible importance of the ecological and evolutionary role of hybrids (Rhymer and Simberloff 1996; Epifanio and Nielsen 2000). These conservation and management issues have been addressed in reviews (e.g., Rhymer and Simberloff 1996; Epifanio and Nielsen 2000; Allendorf et al. 2001) but have rarely been applied to individual case studies and discussed (but see Rosenfield et al. 2004). Here we review a well-documented case of hybridization and its subsequent genetic introgression in the Japanese rosy bitterling (*Rhodeus ocellatus kurumeus*) and discuss the problems associated with establishing conservation and management goals.

A cyprinid subspecies, the Japanese rosy bitterling, *R. o. kurumeus*, endemic to creeks and small rivers in western Japan (Nakamura 1955), is now on the brink of extinction, largely due to hybridization with its consubspecific, the Chinese rosy bitterling (*R. o. ocellatus*). In 1991, *R. o. kurumeus* was designated as critically endangered by the Japanese Ministry of the Environment. Whereas *R. o. ocellatus* has invaded all over Japan since its accidental introduction from China in 1942 (Nakamura 1955; Nagata and Nishiyama 1976), *R. o. kurumeus* has been restricted to small, isolated impoundments on the Honshu and Shikoku islands (Kawamura 2005; Miyake et al. 2007). Individuals that appeared to be hybrids from their morphological characteristics of both subspecies began being found in the mid-1970s (Kanoh 2002). These two subspecies were originally similar in morphology and yet distinguishable, but now the occurrence of hybrids with various degrees of introgression makes it difficult to identify each subspecies and their hybrids. Based on morphological characteristics, the hybrids have already replaced many populations of *R. o. kurumeus* within its former distribution range (Nagata 1980), which was further confirmed by an allozyme analysis (Ueno 1987; Nagata et al. 1996), an RFLP analysis of mtDNA, and a random amplified polymorphic DNA (RAPD)-PCR analysis of genomic DNA (Kawamura et al. 2001a). Furthermore, extremely low genetic diversity was found in many populations of *R. o. kurumeus* restricted to impoundments where there was no substantial movement of individuals between impoundments (Hosoya 1997; Kawamura et al. 2001b; Kawamura 2005).

In order to avoid the risk of inbreeding depression, it is imperative to maintain a viable population size, and the removal of concrete walls was suggested to encourage the gene flow among impoundments (Kawamura 2005). However, this kind of conservation action also has the potential danger of increasing intersubspecific gene flow (i.e., hybridization with *R. o. ocellatus*), because geographic isolation has greatly contributed to the current reproductive isolation of the remaining *R. o. kurumeus*. Moreover, the fitness decline observed among *R. o. kurumeus* populations in experiments were not improved in intrasubspecific hybrids between subpopulations but were improved between populations from different regions (Kawamura 2005). This may indicate that an introduction of individuals from populations in other regions could be an option, although one might then argue that this action is against the general treatment and agreement in conservation genetics that genetic variation among populations should be maintained (Frankham et al. 2002). In other words, it may cause intrasubspecific hybridization. In addition to the careful consideration and constructive discussion regarding the potential danger of both intra- and intersubspecific hybridization, a more comprehensive and detailed molecular analysis is necessary to reveal the genetic relatedness among all remaining populations, using informative molecular markers such as microsatellite markers.

It is justifiable that most attention on the conservation of *R. o. kurumeus* has so far focused on the protection of remaining populations from the invasion of *R. o. ocellatus*. However, biologists, managers, and conservationists should, at least, start discussing the treatment of hybrids for the following reasons. First, many impoundments are now inhabited only by hybrids that retain more or less unique genetic information of native *R. o. kurumeus*. Second, habitats of freshwater fish including those hybrids are now greatly disturbed throughout Japan due to, for example, development, degraded water quality, and introduction of piscivorous fish such as largemouth bass (*M. salmoides*) and bluegill sunfish (*L. macrochirus*). Third, those hybrids can be assumed to have the same or a similar ecological role in the ecosystems as that of native *R. o. kurumeus*. Finally, the historical role of hybridization as an evolutionary process has been recently recognized (Allendorf et al. 2001). Rosenfield et al. (2004) state that hybridization and genetic introgression are always best avoided, but once introgression has occurred, the management response to hybrids depends on one's conservation goal. We recommend that studies on population dynamics, interaction with other organisms, and life history should be conducted for both hybrids and *R. o. kurumeus* to evaluate whether the ecological roles of disappearing populations could be revived by hybrids in those ecosystems that are no longer inhabited by *R. o. kurumeus*.

Control and eradication

Contrary to a growing body of ecological studies on introduced freshwater fishes, to date, surprisingly little has been reported on control and eradication measures in the scientific literature. In part, this is due to the fact that such management actions on introduced fish have not been fully implemented in many countries. Even in countries that do already take management action, in fact, effective control and eradication measures have not been established. In addition, much of the information on control and eradication measures is often only available in "grey literature" (Simberloff 2002), probably because eradication measures are often conducted by local citizens and nongovernment organizations, for example. Here, we focus on some of the eradication techniques and practices reported in scientific publications.

The use of piscicide rotenone and antimycin has been one of the most commonly applied chemical eradication measures worldwide (Meronek et al. 1996; Rowe 2001).

The rotenone application on the eradication of the invasive topmouth gudgeon (*Pseudorasbora parva*) in England and evaluation of the program were recently reported by Britton and Brazier (2006). The gudgeon appeared to have been accidentally introduced into a recreational fishery located in the Lake District in England in 2000. The fishery was seasonally connected to a catchment that was of high conservation concern. After removal of the nontarget species, rotenone was applied to the fishery to eradicate the gudgeon in 2005, and postapplication fish sampling as an evaluation of the eradication program suggested that there were no more gudgeon present. Another case study on the use of rotenone was reported by Lintermans (2000), in which rotenone was applied to eradicate rainbow trout (*O. mykiss*) from one section of a small stream in southeastern Australia in the hope that the native galaxiid species, *Galaxias olidus*, would recolonize this section. After the rotenone treatment, the stream-gauging weir was augmented with a heavy steel grill to function as a barrier to prevent the trout from reentering the section. However, *G. olidus* was expected to recolonize the section from a connected trout-free stream. By monitoring the recolonization of *G. olidus* both above and below the barrier over four successive years, it was revealed that trout had been successfully eradicated and a breeding population of *G. olidus* had established themselves upstream of the weir.

Nonchemical control and eradication exercises can be employed in various ways such as removals using casting nets, gill nets, and traps (Knapp and Matthews 1998); electrofishing (Copp et al. 2007; Marr 2008); drain-down methods (Copp et al. 2007); and an electric barrier (Stokstad 2003). However, the effectiveness of each method has not yet been fully understood. Knapp and Matthews (1998) assessed the effectiveness of the physical removal of nonnative brook trout (*Salvelinus fontinalis*) and rainbow trout (*O. mykis*) by gill netting from a small subalpine lake in the Sierra Nevada in California, USA, which was originally “fishless” before the trout introduction. It took approximately 2 years to completely eradicate the brook trout and 3 years for the rainbow trout.

These studies highlight the need for careful consideration on a number of aspects such as the type (e.g., ponds, lakes, rivers) and morphometry of the waterbody (e.g., area size, depth, width of inlets and outlets), connectivity with other waterbodies, presence of native species and their current status, biology of target nonnative species (e.g., life history traits, estimated number of each age group), expected effects of the measure (i.e., number control or complete eradication), possibility of recolonization of the target species, negative impacts associated with the measure, postpractice monitoring and evaluation, and costs. Particularly, the use of rotenone and antimycin should be treated with extra caution due to their lethal effects on nontarget organisms (Knapp and Matthews 1998), and although these chemicals could be used in a community-poor environment, they should certainly not be used in a community-rich environment. As for the above case studies on the application of rotenone, there were no native species of conservation concern that existed in either of the fisheries studied or the stream. Further, connectivity of the stream was effectively taken into account in the Australian case, as to which native species can naturally recolonize the rotenone-applied section from another stream, whereas target nonnative species were prohibited from reentering the section by an augmented stream-gauging weir. Knapp and Matthews (1998) suggest that lake morphometry and total area of stream spawning habitat were important factors for eradicating trout by gill netting from high mountain lakes in the Sierra Nevada. More importantly, the above studies conducted postpractice monitoring and evaluation, which are often overlooked but can maximize the knowledge gained from the management practice, improving the effectiveness of future management and avoiding the repetition of costly mistakes (Gehrke 2001).

Unfortunately, case studies on failed control and eradication measures are rarely reported in scientific publications; however, such information would also be highly beneficial for designing and implementing effective management strategies.

Conclusions and recommendations for further research

Despite its long history, the introduction of nonnative freshwater fishes has finally been recognized as a major threat to freshwater ecosystems, and a large number of well-researched case studies have been reported over the last two decades. However, these studies also highlight the difficulties in demonstrating whether introduced species are indeed a direct or indirect cause of the decline of native species, and if so, how introduced species interact with or affect native species. Case studies discussed in this review suggest novel approaches in which recent advances in technology, such as in statistics, molecular analysis, and GIS analysis, can be used in introduced fish studies (see summary in Table 1) and foster new research perspectives. These studies also indicate research needs and management implications, especially in the control and eradiation of introduced fishes, which have not been implemented successfully in many nations. Even where some practical actions have been promoted, science and government or community-based management has not been integrated. Effective management planning will require a tremendous improvement in the connection to scientific studies that deepen our understanding of the factors facilitating the

Table 1 Examples of recently developed analytical techniques on introduced freshwater fishes discussed in this review

Category	Techniques	Purposes	References	Methods
Introduction pathways	Molecular analysis	To identify the origins and pathways of nonnative species	Kawamura et al. (2006)	PCR-RFLP analysis of mtDNA
Predicting spatial patterns	Multivariate analysis	To statistically examine the relationship between species occurrences or assemblages and multiple environmental characteristics	Brasher et al. (2006), Gido et al. (2004)	PCA, CCA, Multiple regression
	GIS analysis	To incorporate landscape elements as environmental variables into the analysis	Brasher et al. (2006), Gido et al. (2004)	Quantifying landscape elements and incorporating human impacts
	Ecological niche modeling	To predict spatial patterns often using GIS maps	Vander Zanden et al. (2004), Céréghino et al. (2005)	ANN
Biotic homogenization	Similarity analysis	To investigate the extent of biotic homogenization	Radomski and Goeman (1995), Rahel (2000), Scott and Helfman (2001), Marchetti et al. (2001), Rahel (2002), Walters et al. (2003), Olden and Poff (2003, 2004), Taylor (2004), Clavero and García-Berthou (2006), Marchetti et al. (2006), Olden et al. (2006), Leprieur et al. (2008)	Quantification of temporal changes in compositional similarity between a pair of fauna
Hybridization	Molecular analysis	To examine occurrences of hybridization and the extent of introgression	Ueno (1987), Nagata (1996), Kawamura et al. (2001a, b)	Allozyme analysis, RFLP analysis of mtDNA, RAPD-PCR analysis of genomic DNA

GIS geographic information system, *PCR-RFLP* polymerase chain reaction–restriction fragment length polymorphism, mtDNA mitochondrial DNA, *CCA* canonical correspondence analysis, *ANN* artificial neural network, *RAPD* random amplified polymorphic DNA

introduction and establishment of nonnative fishes and their impacts on native communities.

Although we did not review the fundamental ecological and biological studies that describe the nature of introduced fishes, such as life history, population dynamics, and physiology, these studies serve as the basis for other applied studies and management planning. In addition, there are some categories within the research field on introduced fish studies that were not discussed in this review but have shown recently developed perspectives and research needs. For example, studies on interactions between climate change and introduced species have received more attention recently, as climate change might facilitate the expansion of introduced species and also exacerbate the effects of them (see Rahel et al. 2008).

Nowadays, even more fish species are expected to be introduced and become invasive with the acceleration of globalization. Lessons that have been learnt from previous studies are that it requires time, cost, and effort to eradicate introduced fishes or even to prevent their further range expansion. Recent technological advances and new ecological perspectives discussed in this paper could be integrated in a proactive research and management practices for preventing and controlling introduced fishes.

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