



## Ghoti

### Ghoti papers

Ghoti aims to serve as a forum for stimulating and pertinent ideas. Ghoti publishes succinct commentary and opinion that addresses important areas in fish and fisheries science. Ghoti contributions will be innovative and have a perspective that may lead to fresh and productive insight of concepts, issues and research agendas. All Ghoti contributions will be selected by the editors and peer reviewed.



### Etymology of Ghoti

George Bernard Shaw (1856-1950), polymath, playwright, Nobel prize winner, and the most prolific letter writer in history, was an advocate of English spelling reform. He was reportedly fond of pointing out its absurdities by proving that 'fish' could be spelt 'ghoti'. That is: 'gh' as in 'rough', 'o' as in 'women' and 'ti' as in palatial.

## Scientific uncertainty and the assessment of risks posed by non-native freshwater fishes

F Leprieur<sup>1</sup>, S Brosse<sup>2</sup>, E García-Berthou<sup>3</sup>, T Oberdorff<sup>1</sup>, J D Olden<sup>4</sup> & C R Townsend<sup>5</sup>

<sup>1</sup>IRD – Institut de Recherche pour le Développement (UR131), Antenne au Muséum National d'Histoire Naturelle, 43 rue Cuvier, 75231 Paris cedex, France; <sup>2</sup>Laboratoire d'Ecologie Fonctionnelle, U.M.R 5245, C.N.R.S – Université Paul Sabatier, 118 route de Narbonne, F-31062 Toulouse cedex 4, France; <sup>3</sup>Institut d'Ecologia Aquàtica, Universitat de Girona, E-17071 Girona, Catalonia, Spain; <sup>4</sup>School of Aquatic & Fishery Sciences, University of Washington, Box 355020, Seattle, WA 98195-5020, USA; <sup>5</sup>Department of Zoology, University of Otago, P.O. Box 56, Dunedin, New Zealand

### Abstract

The introduction of non-indigenous plants, animals and pathogens is a pressing global environmental challenge. Although not all introduced species become established and the fraction of those that do often have little appreciable effect on their new ecosystems, many others exert significant ecological, evolutionary and economic impacts. Stimulating further debate, Gozlan [Fish and Fisheries (2008) Vol. 9, pp. 106–115] argued that the majority of intentional freshwater fish introductions associated with aquaculture (fish species providing societal benefits) have not been reported as having an ecological impact. We find little to argue with his suggestion that low risk of ecological impact coupled with high market value encourages further introductions. But do we have an adequate understanding of the ecological risks associated with fish introductions to support such decisions? Indeed, resource managers and decision makers require some scientific knowledge to support their management actions; without this information, a precautionary approach is the only sensible course of action. The precautionary approach implies that the lack of scientific certainty is reason enough for postponing intentional introduction of non-

### Correspondence:

F Leprieur, IRD – Institut de Recherche pour le Développement (UR131), Antenne au Muséum National d'Histoire Naturelle, 43 rue Cuvier, 75231 Paris cedex, France  
Tel.: 003140793745  
Fax: 0033140793771  
E-mail: leprieur@mnhn.fr

Received 14 Apr 2008  
Accepted 22 Oct 2008

native species to avoid potentially serious or irreversible harm to the environment. Here, we suggest that we actually know very little about ecological impacts associated with fish introductions and that it would be therefore wholly inappropriate to equate a lack of data with a conclusion of 'no impact'. We discuss four major challenges for enhancing the assessment of risks posed by non-native freshwater fishes in the face of scientific uncertainty and highlight research opportunities and some alternative approaches for confronting these challenges in the future.

**Keywords** Aquaculture, ecological impacts, invaders, non-native fish, precautionary approach, species introductions

---

## Introduction

The accidental or deliberate introduction of species outside their native range is considered one of the leading threats to contemporary biodiversity (Vitousek *et al.* 1997; Sala *et al.* 2000). But should non-native species introductions always be viewed as undesirable (a question debated by Brown and Sax 2004; Cassey *et al.* 2005; Warren 2007; Richardson *et al.* 2008), particularly because not all introduced species become invasive and successful invaders do not invariably have negative ecological and/or economic impacts (Williamson 1996; Jeschke and Strayer 2005; Ricciardi and Kipp 2008)? In a recent article aimed at stimulating further debate, Gozlan (2008) sought to explore the threats posed by introduced freshwater fishes. Based on his analysis of datasets from the Food and Agriculture Organization (FAO) and from FishBase, he concluded that the majority of intentional freshwater fish introductions associated with aquaculture, and its societal benefits, have not been reported as having an ecological impact. Consequently, Gozlan (2008) advocated the protection of introductions that have beneficial outcomes and a more systematic ban of species or families of fish presenting a higher historical risk.

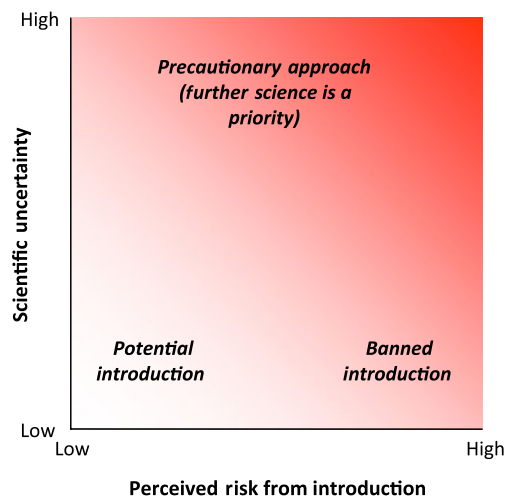
There are three major strands to sustainability issues – ecological, social and economic – and all three sciences have a vital role in the debate, but the ecologist's primary function is to help human society understand the ecological ramifications of a particular course of action (Townsend 2008). Gozlan (2008) reminds us of this political reality and we find little to argue with his suggestion that low risk of ecological impact coupled with high market value lends support to further introduction.

Moreover, we acknowledge that the scientific community must take a balanced view and avoid promoting a xenophobic attitude toward non-native species (Simberloff 2003). The major issue for us is whether we currently have adequate understanding of the ecological risks associated with fish introductions. It is true that science has markedly increased our knowledge of the patterns and implications of species invasions in freshwater ecosystems. Recent decades have seen tremendous progress in invasive species research, management and policy and much has been learned (Lodge *et al.* 2006; Keller *et al.* 2007; Vander Zanden and Olden 2008). Yet what remains unknown is formidable and much is left for future study and analysis. At the same time, managers and decision makers continue to ask for more information on the risk of invasion from human activities (e.g. aquaculture, live food trade, aquarium trade) for species and places that are poorly understood. A skeptic could argue that science may be less effective at reducing uncertainty than it is capable of making us more aware of what we still do not know. Against this background of available information on one hand and knowledge gaps on the other, decision makers need to know when they have enough science to support their management actions and when more information is warranted.

Given that only a fraction of introductions result in severe ecological impacts (Williamson 1996; Ricciardi and Kipp 2008), the challenge is to develop risk assessments that are highly predictive of extreme, rare events (Franklin *et al.* 2008). A balanced and objective approach to the costs and benefits of non-native species introductions is essential and we strongly encourage the development of realistic simulation models,

experiments and well-designed mechanistic and comparative studies aimed at determining the magnitude of the impact of potential invaders on recipient ecosystems. However, from a practical point of view, we have to grapple with the uncertainties stemming from incomplete knowledge of past effects and future risks associated with the non-native species under consideration.

The relationship between scientific uncertainty and potential harm from non-native species introduction can be visualized in two dimensional space (Fig. 1). First, in cases where sufficient scientific knowledge is already available to be confident of high environmental harm, the introduction of a proposed non-native species should be banned (high risk, low scientific uncertainty). For example, the New Zealand government decided not to import channel catfish (*Ictalurus punctatus*) for aquaculture based on an assessment of the environmental risks posed (Townsend and Winterbourn 1992). At the other extreme, when both perceived risk and scientific uncertainty are low, species introduction for aquaculture or conservation purposes can be more safely considered (lower right quadrant of our conceptual model). Between these two extremes, when baseline knowledge about the impacts of a given non-native species is lacking (high scientific uncertainty), regardless of the degree of perceived harm from introduction, we strongly recommend applying a 'precautionary' approach (sensu United Nations Environmental Programme (UNEP) 1992).



**Figure 1** Conceptual model illustrating the relationship between scientific uncertainty and potential harm from non-native species introduction.

The precautionary approach implies that the lack of scientific certainty is a reason for postponing intentional introduction of non-native species to avoid potentially serious or irreversible harm to the environment. One of the central tenets of the precautionary approach is that effective environmental measures need to be based upon actions that take a long-term approach and that anticipate impacts on the basis of scientific knowledge (United Nations Environmental Programme (UNEP) 1992). Considering a non-native species as a potential candidate for introduction when there is high scientific uncertainty is a risky approach, given that eradication of a species, once established, may be impossible or likely to be associated with high collateral damage (Lodge *et al.* 1998). In addition, intensive management actions and high economic costs are often associated with control and prevention measures to limit secondary spread and further impacts (Vander Zanden and Olden 2008).

There is a pressing need to identify and fill the key knowledge gaps that currently limit our ability to make generalizations about the risks posed by non-native freshwater fish introductions and, consequently, to effectively make decisions regarding the importation and management of non-native species. In the following sections, we discuss four major challenges (i.e. knowledge gaps) for advancing the assessment of risks posed by non-native freshwater fishes in the face of scientific uncertainty and highlight research opportunities and some alternative approaches for confronting these challenges.

#### Scientific research may be limited for invasive species of concern

The invasion process can be divided into four stages – introduction, establishment, spread and integration/impact. Invasion research, whether on plants or animals, has been unevenly divided between these stages (Puth and Post 2005). The question of impact, which is a crucial stage when evaluating potential harm, has been rarely examined (Parker *et al.* 1999; D'Antonio and Kark 2002; Puth and Post 2005). For instance, using the United Nations Food and Agriculture Organization's Database of Invasive Aquatic Species (DIAS)\*, both García-Berthou *et al.* (2005) and Bartley (2007) highlighted that very little documentation exists on the actual impact of many introductions. Of 3141

\*<http://www.fao.org/fishery/dias>

introduction records in the DIAS database, whether the species succeeded in establishing is unknown in 13.9% of cases and whether the species had ecological effects is unknown in 80% of cases (García-Berthou *et al.* 2005). Moreover, García-Berthou (2007) questioned whether the DIAS database is suitable for examining ecological effects, being based on subjective answers to questionnaires. For instance, DIAS version 1.3 reported 85 established (or probably established) mosquitofish introductions (including *Gambusia affinis* and *G. holbrooki*) of which only six had adverse ecological effects, one had 'positive' effects, 76 had no data and two were 'undecided'. The equivalent results for brown trout (*Salmo trutta*, including subspecies) were 9, 4, 24 and 3 (for a total of 40 established introductions). We do not believe that these statistics can reflect the true frequency of impacts of these two widely introduced species, shown to have widespread ecological impacts (Townsend and Simon 2006; Alcaraz *et al.* 2008) but only in the few places where they have been intensively studied (generally in developed countries).

In this context, the results obtained by Gozlan (2008) should be interpreted with caution. To identify the ecological impacts associated with a given introduced species, Gozlan (2008) conducted a literature survey based on scientific reports and publications (peer reviewed or not). The assumption of Gozlan (2008) that over the 54-year period encompassed by his database, 'an undisputed ecological impact following a freshwater fish introduction would have been picked up in scientific literature' is patently incorrect. Tellingly, Gozlan (2008) uses the word 'quantifiable' in his definition of an ecological impact, but the key word should be 'quantified'. There is no doubt that impacts are quantifiable; the issue is whether actual effects have, in fact, commonly been quantified. Indeed, there are at least two main reasons for our ignorance of the true ecological consequences of non-native species. First, the required scope of research for any given species is large. At one extreme, for example, understanding of the impacts of *Salmo trutta* on certain endemic galaxiid fish in New Zealand and of the changes to energy and nutrient flux mediated through a trout-related trophic cascade (Townsend 2003), has involved more than 23 researchers, more than 20 peer-reviewed articles and taken more than 10 years (with 30+ person years of research) (C.R. Townsend pers.comm.). Second, the complaint of Coblentz

(1990) still holds, that funds are rarely forthcoming for the 'luxury' of investigations of introduced species that have no likelihood of removal. For both these reasons, ecological impacts of non-native species including freshwater fish remain poorly investigated (Parker *et al.* 1999; Simberloff 2006; García-Berthou 2007) and so we cannot properly judge the general importance of introduced species in threatening native biodiversity and ecosystem services.

Although we agree that not all introduced fish species become invasive and hence cause negative ecological impacts (Williamson 1996; Jeschke and Strayer 2005; Ricciardi and Kipp 2008), our clear conclusion is that we actually know very little about impacts and it would be dangerous and wholly inappropriate to equate a lack of data with 'no impact'. This problem is further compounded by two factors. First, past studies of species introductions have largely emphasized invader impacts of particular taxa, focusing on conspicuous species or species that cause dramatic ecological impacts (Parker *et al.* 1999). Based on an extensive literature review, both Gherardi (2007) and Pyšek *et al.* (2008) found that our current scientific understanding is severely biased toward a very small number of species with imminent or realized ecological impacts (i.e. those species for which funding is more likely to be obtained). As a result, the literature contains many 'confirmatory' papers (repeats of research conducted in other regions), which is useful for managing species in a certain locality, but contributes little to our understanding of potential impacts of the literally thousands of other non-native species. Second, impact studies have rarely been performed in locations where species introductions are most prevalent (Pyšek *et al.* 2008). According to De Silva *et al.* (2006), there had not been a single dedicated study on impacts of any of the introduced fish species in Asia, while this region is the greatest importer of non-native fishes, especially for aquaculture purposes (Bartley *et al.* 2005; Gozlan 2008). Indeed, although there have been many comprehensive scientific surveys on freshwater fish in Asia, research has mostly focused on the biology and status of economically important fish (Yan *et al.* 2001). In Cambodia, Nuov *et al.* (2005) acknowledged that no study has documented whether introduced fish have altered aquatic habitats or had other impacts on local species and populations. Overall, very little is known in Asia on the

ecological impacts of non-native fishes including species introduced for aquaculture (Yan *et al.* 2001; Bartley *et al.* 2005; De Silva *et al.* 2006).

More observational and experimental studies on the potential ecological impacts associated with fish introductions are therefore urgently needed (García-Berthou 2007), especially in the understudied regions of the world such as Africa and Asia (Pyšek *et al.* 2008). Among the different approaches to assess the impacts of non-native fish introductions (i.e. correlative, comparative and experimental), few impact studies have focused on the link between the impact mechanism and impact manifestation (Taylor *et al.* 1984; Parker *et al.* 1999; Corfield *et al.* 2008). In contrast, evidence of impacts is mostly based on correlative data or perceptions, which may not provide accurate impact assessments for non-native species, especially those with limited distributions (Corfield *et al.* 2008). Indeed, the major limitations of the correlative approach are the absence of requisite controls and the lack of consideration of other potential sources of perturbation, such as habitat modification and pollution (Taylor *et al.* 1984). Recently, Kats *et al.* (2006) proposed a study plan for the invasion ecology of exotic crayfish in California involving a multi-stage mechanistic approach that combined landscape-level and GIS-based distributional analyses, controlled experiments in mesocosms and field experiments and surveys. We endorse the design of such mechanistic approaches that link cause with effect at different stages of the invasion process. This would help to reduce the uncertainty surrounding the potential impacts of non-native fishes significantly.

#### **The research timetable may have been too short to reveal impacts associated with an invasive species**

The phenomenon of lag times (i.e. the time interval between two stages considered together) has become an increasingly recognized aspect of the invasion process, from arrival to impact (Williamson 1996; Crooks 2005). According to Richardson *et al.* (2008), 'All introduced species must be considered potential invaders, as many lie dormant for years or decades, starting to invade and cause damage only when certain conditions for reproduction or spread are realized' (p. 296). Thus, for example, the study of 193 boreal lakes in northern Sweden revealed that the time lag between the first record of brook trout (*Salvelinus fontinalis*) and the

subsequent extinction of brown trout (*Salmo trutta*) was two decades on average (Spens *et al.* 2007). It is also noteworthy that no effects of other drivers of extinction were detected by Spens *et al.* (2007). The converse may also hold: a number of case-studies of non-native species have shown initial ecological impacts, but have reported integration into the new environment without long-term adverse effects (Arthington and Mitchell 1986; Garton *et al.* 1993). Such temporal aspects of the impacts of non-native species have been largely unexplored and Strayer *et al.* (2006) reported, on the basis of a literature survey, that most studies are of short duration (<1 year) and 40% did not record the time since invasion. A better understanding of the phenomenon of lag times, through long-term studies (McCarthy *et al.* 2006), is needed if we are to make accurate assessments of the risks posed by non-native species.

#### **Research has rarely considered the interactive effects among invasive species and other drivers of native species decline**

Despite recent efforts to predict successful freshwater fish invaders, our ability to forecast the impact of non-native freshwater fish on recipient ecosystems is still limited (García-Berthou 2007; Vander Zanden and Olden 2008). Success in predicting the undesired consequences of non-native species is complicated by the fact that many ecosystems increasingly support multiple invasive species. Complex interactions among this 'cocktail' of invaders can lead to a diversity of outcomes for native species and ecosystems, many of which are difficult to predict *a priori* (Byers *et al.* 2002). Invaders can negatively affect the ecological effects of one another through competition and/or predation (Ross *et al.* 2004), have no effect on each other (Cope and Winterbourn 2004) or exhibit facilitative interactions increasing their ecological impacts or promoting establishment and spread (Ricciardi 2003). Because of the potentially complex interactions among co-invaders, experimental studies may be particularly well suited for identifying how invaders interact and their joint consequences for native communities and ecosystems (Johnson *et al.* 2008). Furthermore, field-based efforts need to be supplemented with experiments that examine the individual and combined effects of multiple invaders at several ecological scales ranging from individual organisms to whole ecosystems (Ricciardi 2003).

Another significant limitation is that environmental change (e.g. habitat degradation, land-use change, climate warming) and species invasion can have additive, synergistic or antagonistic effects on native species and ecosystems (Didham *et al.* 2007; Brook 2008; Rahel and Olden 2008), but such interactions have only rarely been explored (Ruiz *et al.* 1999; Leprieur *et al.* 2006). The term 'synergistic' describes the simultaneous action of separate processes that have a greater total effect than the sum of individual effects alone. This means that the per capita ecological impact of an invasive species can increase via an interactive effect with another factor (see Didham *et al.* 2007).

Rahel and Olden (2008) discuss how climate change may affect aquatic invasive species via modified water temperature, reduced ice cover in lakes, altered streamflow regimes, increased salinity and increased water-development activities in the form of canal and reservoir construction. For example, global climate change is projected to cause warmer water temperatures in northern-latitude lakes of Canada providing more suitable thermal conditions for non-native warmwater fish species, such as smallmouth bass (*Micropterus dolomieu*) to thrive (Sharma *et al.* 2007). Such species may prey on or compete for food resources with native fishes leading to the decline or loss of native fish populations (Jackson and Mandrak 2002). In this case, declines in native species and loss of populations would be the result of the synergistic effects of climate warming and species invasion.

Another complex outcome, an antagonistic interaction, occurs if adverse impacts of non-native introductions and another stressor act in opposition to each other. An example concerns the native fish *Galaxias anomalus* in New Zealand (Leprieur *et al.* 2006). The presence of the introduced brown trout and reduced stream discharge (because of the abstraction for irrigation) are both stressors with negative effects on *G. anomalus*. However, the native species actually benefits from discharge reduction, because it can cope with this adverse factor better than brown trout. Many other interactive effects of invasive species with climate change, whether synergistic or antagonistic, are also to be expected, but Brook (2008) noted that between 1980 and 2007 only 34 published papers explored the interaction between biological invasions and climate change. Our ecological understanding of the interactions among multiple drivers of global change is still in its infancy and presents a

fundamental challenge when assessing the real risk posed by non-native species introductions.

#### **Long-term implications of non-native fish introductions remain uncertain**

Understanding to what extent freshwater fish introductions have long-term consequences for biodiversity is crucial to the adoption of sound and effective conservation strategies. Recently, Sax and Gaines (2008) explored this question for plants and vertebrates by analysing patterns of invasion and extinction on islands over the past few hundreds years. They examined, in particular, whether a saturation point (i.e. the number of species a locality of region can support) was reached by the gradual addition of non-native plants and discussed their results in the light of two major community ecology theories: Island Biogeography Theory (IBT) (MacArthur and Wilson 1967) and Stochastic Niche Theory (SNT) (Tilman 2004). IBT suggests that the number of species on islands (i.e. the saturation point) represents a dynamic balance between colonization (plus speciation) and extinction and predicts increasing species richness with increasing island size and decreasing species richness with greater distance from a colonization source (mainland). According to IBT, once the saturation point is reached, the addition of new colonizing species results in the extinction of previously established species. In contrast, SNT suggests that the number of species in a given locality (or region) may not be fixed within strict boundaries. According to SNT, establishment success of new colonizing species will become progressively less likely as species richness increases because of decreasing resource availability (Stachowicz and Tilman 2004). This implies that newly colonizing species are not likely to displace already established species (i.e. low risk of extinction). As pointed out by Sax and Gaines (2008), IBT and SNT provide two contrasting views of the long-term consequences of species introductions, in relation to the likelihood of future native species extinctions. Unfortunately, Sax and Gaines (2008) did not provide support for either theory because current data are insufficient to distinguish between these two different views of the long-term consequences of species introductions.

In the case of freshwater fishes, we also lack data on long-term trends in non-native fish introductions and fish extinctions in freshwater ecosystems that would allow the predictions of IBT and SNT to

be tested. However, several expectations can be proposed on the basis of previous studies of large-scale patterns and processes relating to freshwater fish diversity. For strictly freshwater fishes, river basins (flowing into the ocean) can be considered as biogeographical islands with specific species pools (Oberdorff *et al.* 1997) because dispersion between river basins is limited over large temporal scales because of the impassable barriers (ocean or land). A consequence of these barriers to dispersion is that river basins can be considered as non-equilibrated islands in which species extinctions (related to historical events) are not fully balanced by colonization from neighbouring river basins (Oberdorff *et al.* 1997; Reyjol *et al.* 2007; Tedesco *et al.* 2005). The implication is that river basins are very likely to be unsaturated with species and thus more susceptible to the establishment of non-native species because ecological space should be less densely packed and interspecific competition should be less intense (Hutchinson 1959). From the few studies of riverine fish communities at the local (reach or site) scale (i.e. local-regional species richness relationships, see Cornell and Lawton 1992), the emerging pattern is that few of these communities are truly saturated (Hugueny and Paugy 1995; Angermeier and Winston 1998; Oberdorff *et al.* 1998). Furthermore, two analyses of human-induced colonization patterns in river basins (Gido and Brown 1999; Smith *et al.* 2004), showed that the riverine fish communities were not saturated at this larger scale either, and are capable of achieving higher species richness if the pool of potential colonisers is artificially increased by the direct introduction or colonization of other species. An implication of these studies is that species introductions might have impacts on fish communities that are smaller than would be expected if the saturation point had already been reached. However, we should keep in mind that human-mediated species introduction and extinction processes act at different time scales (Sax *et al.* 2002). Indeed, species extinctions might take many decades to come to completion and such time-lags could create a large extinction-debt that will be paid in future (Sax and Gaines 2008).

Consequently, two major research gaps must be filled to improve our understanding of the long-term consequences of non-native fish introductions. First, time-lags for species extinction (Brooks *et al.* 1999), which have rarely been examined for freshwater fishes (but see Morita and Yamamoto 2002), need

to be better understood. Second, although species-level extinctions following fish introductions have rarely been reported at the regional scale, population-level extinctions can occur at smaller spatial scales particularly when exotic species reduce native species to a few population fragments in small refuges (Chapman *et al.* 1996; Labbe and Fausch 2000; Leprieur *et al.* 2006; Pyke 2008). Thus, future research should concentrate on how non-native species change both the abundance and distribution of native species because the magnitude of ongoing declines will help predict likely future extinctions.

## Conclusion

Recent decades have witnessed tremendous progress in the science and management of invasive fish species, yet many challenges remain. What is the likelihood that an introduced species will establish a non-native population? Which species are likely to cause ecological and/or economic damage if provided with the opportunity? We continue to learn more about these issues, but clear and complete answers remain elusive because of the complexity of the scientific questions and management options. Clearly, new strategies are needed that account for the scientific uncertainty in the invasion process. Our objective was to add clarity to the issues of scientific uncertainty and the risks associated with non-native fish introductions. We have stressed, in particular, that the results obtained by Gozlan (2008) should be interpreted with caution because our clear conclusion is that we actually know very little about ecological impacts associated with fish introductions and that it would be therefore dangerous and wholly inappropriate to equate a lack of data with 'no impact'. Based on our assessment, we suggest that uncertainties that result from a lack of knowledge can be partially overcome through targeted research. We have discussed what we view as fruitful areas of research to reduce uncertainty when assessing the risks posed by non-native freshwater fishes.

## Acknowledgements

We are grateful to five anonymous reviewers for their helpful comments on a previous manuscript and Tony Pitcher for considering our original submission.

## References

- Alcaraz, C., Bisazza, A. and García-Berthou, E. (2008) Salinity mediates the competitive interactions between invasive mosquitofish and an endangered fish. *Oecologia* **155**, 205–213.
- Angermeier, P.L. and Winston, M.R. (1998) Regional influences on local diversity in stream fish communities of Virginia. *Ecology* **79**, 911–927.
- Arthington, A.H. and Mitchell, D.S. (1986) Aquatic invading species. In: *Ecology of Biological Invasions* (eds R.H. Groves and J.J. Burdon). Cambridge University Press, New York, pp. 34–53.
- Bartley, D. (2007) An ecosystems approach to risk assessment of alien species and genotypes in aquaculture. In: *Ecological and Genetic Implications of Aquaculture Activities* (ed. T.M. Bert). Springer Verlag, Berlin, pp. 35–52.
- Bartley, D.M., Bhujel, R.C., Funge-Smith, S., Olin, P.G. and Phillips, M.J. (2005) International mechanisms for the control and responsible use of alien species in aquatic ecosystems. *Report of an Ad Hoc Expert Consultation*. Xishuangbanna, People's Republic of China, 27–30 August 2003. FAO, Rome, pp. 195. Available at: <http://www.fao.org/docrep/009/a0113e/a0113e00.htm>
- Brook, B.W. (2008) Synergies between climate change, extinctions and invasive vertebrates. *Wildlife Research* **35**, 249–252.
- Brooks, T.M., Pimm, S.L. and Oyugi, J.O. (1999) Time lag between deforestation and bird extinction in tropical forest fragments. *Conservation Biology* **13**, 1140–1150.
- Brown, J.H. and Sax, D.F. (2004) An essay on some topics concerning invasive species. *Austral Ecology* **29**, 530–536.
- Byers, J. E., Reichard, S. H., Randall, J. M. *et al.* (2002) Directing research to reduce the impacts of nonindigenous species. *Conservation Biology* **16**, 630–640.
- Cassey, P., Blackburn, T.M., Duncan, R. and Chown, S. (2005) Concerning invasive species: reply to Brown and Sax. *Austral Ecology* **30**, 475–480.
- Chapman, L.J., Chapman, C.A., Ogutu-Ohwayo, R., Chandler, M., Kaufman, L. and Keiter, A. (1996) Refugia for endangered fishes from an introduced predator in Lake Nabugabo, Uganda. *Conservation Biology* **10**, 554–561.
- Coblentz, B.E. (1990) Exotic organisms: a dilemma for conservation biology. *Conservation Biology* **4**, 261–265.
- Cope, N.J. and Winterbourn, M.J. (2004) Competitive interactions between two successful molluscan invaders of freshwaters: an experimental study. *Aquatic Ecology* **38**, 83–91.
- Corfield, J., Diggles, B., Jubb, C., McDowall, R. M., Moore, A., Richards, A. and Rowe, D. K. (2008) Review of the impacts of introduced ornamental fish species that have established wild populations in Australia. *Prepared for the Australian Government Department of the Environment, Water, Heritage and the Arts*. pp. 277. Available at: <http://www.environment.gov.au/biodiversity/invasive/publications/ornamental-fish.html>
- Cornell, H.V. and Lawton, J.H. (1992) Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *Journal of Animal Ecology* **61**, 1–12.
- Crooks, J.A. (2005) Lag times and exotic species: the ecology and management of biological invasions in slow motion. *Écoscience* **12**, 316–329.
- D'Antonio, C. and Kark, S. (2002) Impacts and extent of biotic invasions in terrestrial ecosystems. *Trends in Ecology and Evolution* **17**, 202–204.
- De Silva, S., Nguyen, T., Abery, N. and Amarasinghe, U. (2006) An evaluation of the role and impacts of alien finfish in Asian inland aquaculture. *Aquaculture Research* **37**, 1–17.
- Didham, R.K., Tylianakis, J.M., Gemmill, N.J., Rand, T.A. and Robert, M. (2007) Interactive effects of habitat modification and species invasion on native species decline. *Trends in Ecology and Evolution* **20**, 470–475.
- Franklin, J., Sisson, S.A., Burgman, M.A. and Martin, J.K. (2008) Evaluating extreme risks in invasion ecology: learning from banking compliance. *Diversity and Distributions* **14**, 581–591.
- García-Berthou, E. (2007) The characteristics of invasive fishes: what has been learned so far? *Journal of Fish Biology* **71**(Suppl. D), 33–55.
- García-Berthou, E., Alcaraz, C., Pou-Rovira, Q., Zamora, L., Coenders, G. and Feo, C. (2005) Introduction pathways and establishment rates of invasive aquatic species in Europe. *Canadian Journal of Fisheries and Aquatic Sciences* **65**, 453–463.
- Garton, D.W., Berg, D.J., Stoeckmann, A.M. and Haag, W.R. (1993) Biology of recent invertebrate invading species in the Great Lakes: the spiny water flea, *Bythotrephes cederstroemi*, and the zebra mussel, *Dreissena polymorpha*. In: *Biological Pollution: The Control and Impact of Invasive Exotic Species* (ed. B. N. McKnight). Indiana Academy of Science, Indianapolis, pp. 63–84.
- Gherardi, F. (2007). Measuring the impact of freshwater NIS: what are we missing? In: *Biological Invaders in Inland Waters: Profiles, Distribution, and Threats* (ed. F. Gherardi). Springer, Dordrecht, pp. 437–462.
- Gido, K.B. and Brown, J.H. (1999) Invasion of North American drainages by alien fish species. *Freshwater Biology* **42**, 387–399.
- Gozlan, R.E. (2008) Introduction of non native freshwater fish: is it all bad? *Fish and Fisheries* **9**, 106–115.
- Hugueny, B. and Paugy, D. (1995) Unsaturated fish communities in African rivers. *American Naturalist* **146**, 162–169.
- Hutchinson, G.E. (1959) Homage to Santa Rosalia, or why are there so many kinds of animals? *American Naturalist* **93**, 245–249.
- Jackson, D.A. and Mandrak, N.E. (2002) Changing fish biodiversity: predicting the loss of cyprinid biodiversity



- due to global climate change. In: *Fisheries in a Changing Climate* (ed. N.A. McGinn). American Fisheries Society Symposium 32, American Fisheries Society, Bethesda, Maryland, pp. 89–98.
- Jeschke, J.M. and Strayer, D.L. (2005) Invasion success of vertebrates in Europe and North America. *Proceedings of the National Academy of Sciences of the United States of America* **102**, 7198–7202.
- Johnson, P.T.J., Olden, J.D., Solomon, C. T. and Vander Zanden, M.J. (2008) Community and ecosystem effects of invasive predators and herbivores in an experimental aquatic system. *Oecologia* (in press).
- Kats, L., Pintor, L., Sih, A. and Kerby, J. (2006) *Aquatic Nuisance Species: A Multi-stage Approach to Understanding the Invasion Ecology of Exotic Crayfish in Northern and Southern California*. California Sea Grant College Program. Research Completion Reports. Paper Coastal06\_01. Available at: [http://repositories.cdlib.org/csgc/rcr/Coastal06\\_01](http://repositories.cdlib.org/csgc/rcr/Coastal06_01), November 2008.
- Keller, R.P., Lodge, D.M. and Finnoff, D.C. (2007) Risk assessment for invasive species produces net bioeconomic benefits. *Proceedings of the National Academy of Sciences of the United States of America* **104**, 203–207.
- Labbe, T.R. and Fausch, K.D. (2000) Dynamics of intermittent stream habitat regulate persistence of a threatened fish at multiple scales. *Ecological Applications* **10**, 1774–1791.
- Leprieur, F., Hickey, M.A., Arbuckle, C.J., Closs, G.P., Brosse, S. and Townsend, C.R. (2006) Hydrological disturbance benefits a native fish at the expense of an exotic fish in a New Zealand River catchment. *The Journal of Applied Ecology* **43**, 930–939.
- Lodge, D.M., Stein, R.A., Brown, K.M., Covich, A.P., Bronmark, C., Garvey, J.E. and Klosiewski, S.P. (1998) Predicting impact of freshwater exotic species on native biodiversity: challenges in spatial scaling. *Australian Journal of Ecology* **23**, 53–67.
- Lodge, D.M., Williams, S.L., MacIsaac, H. *et al.* (2006) Biological invasions: recommendations for U.S. policy and management. *Ecological Applications* **16**, 2035–2054.
- MacArthur, R.H. and Wilson, E.O. (1967) *The Theory of Island Biogeography*. Princeton landmarks in biology with a new preface by EO Wilson, 2001, University Press Princeton, Princeton.
- McCarthy, J.M., Hein, C.L., Olden, J.D. and Vander Zanden, M.J. (2006) Coupling long-term studies with meta-analysis to investigate impacts of non-native crayfish on zoobenthic communities. *Freshwater Biology* **51**, 224–235.
- Morita, K. and Yamamoto, S. (2002) Effects of habitat fragmentation by damming on the persistence of stream-dwelling charr populations. *Conservation Biology* **16**, 1318–1323.
- Nuov, V., Viseth, H. and Vibol, O. (2005) Present status of alien species in aquaculture and aquatic ecosystem in Cambodia. In: *International Mechanisms for the Control and Responsible Use of Alien Species in Aquatic Ecosystems* (Report of an Ad Hoc Expert Consultation. Xishuangbanna, People's Republic of China, 27–30 August 2003). (eds D.M. Bartley, R.C. Bhujel, S. Funge-Smith, P.G. Olin and M.J. Phillips). FAO, Rome, pp. 195.
- Oberdorff, T., Hugueny, B. and Guégan, J.-F. (1997) Is there an influence of historical events on contemporary fish species richness in rivers? Comparisons between Western Europe and North America *Journal of Biogeography* **24**, 461–467.
- Oberdorff, T., Hugueny, B., Compin, A. and Belkessam, D. (1998) Non-interactive fish communities in the coastal streams of North-Western France. *Journal of Animal Ecology* **67**, 472–484.
- Parker, I.M., Simberloff, D., Lonsdale, W.M. *et al.* (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions* **1**, 3–19.
- Puth, L. and Post, D. (2005) Studying invasion: have we missed the boat? *Ecology Letters* **8**, 715–721.
- Pyke, G.H. (2008) Plague minnow or mosquito fish? A review of the biology and impacts of introduced *Gambusia* species. *Annual Review of Ecology, Evolution, and Systematics* (in press).
- Pyšek, P., Richardson, D.M., Pergl, J., Jarošík, V., Sixtová, Z. and Weber, E. (2008) Geographical and taxonomic biases in invasion ecology. *Trends in Ecology and Evolution* **23**, 237–244.
- Rahel, F.J. and Olden, J.D. (2008) Assessing the effects of climate change on aquatic invasive species. *Conservation Biology* **22**, 521–533.
- Reyjol, Y., Hugueny, B., Pont, D. *et al.* (2007) Patterns in species richness and endemism of European freshwater fish. *Global Ecology and Biogeography* **16**, 65–75.
- Ricciardi, A. (2003) Predicting the impacts of an introduced species from its invasion history: an empirical approach applied to zebra mussel invasions. *Freshwater Biology* **48**, 972–981.
- Ricciardi, A. and Kipp, R. (2008) Predicting the number of ecologically harmful species in an aquatic system. *Diversity and Distributions* **14**, 374–380.
- Richardson, D.M., Pyšek, P., Rejmánek, M., Simberloff, D. and Mader, A.D. (2008) Biological invasions – the widening debate: response to Charles Warren. *Progress in Human Geography* **32**, 295–298.
- Ross, D.J., Johnson, C.R., Hewitt, C.L. and Ruiz, G.M. (2004) Interaction and impacts of two introduced species on a soft-sediment marine assemblage in SE Tasmania. *Marine Biology* **144**, 747–756.
- Ruiz, C.M., Fofonoff, P., Hines, A.H. and Grosholz, E.D. (1999) Nonindigenous species as stressors in estuarine and marine communities: assessing impacts and interactions. *Limnology and Oceanography* **44**, 950–972.
- Sala, O.E., Chapin, F.S. III, Armesto, J.J.E. *et al.* (2000) Biodiversity scenarios for the year 2100. *Science* **287**, 1770–1774.

- Sax, D.F. and Gaines, S.D. (2008) Species invasions and extinction: the future of native biodiversity on islands. *Proceedings of the National Academy of Sciences of the United States of America* **105**, 11490–11497.
- Sax, D.F., Gaines, S.D. and Brown, J.H. (2002) Species invasions exceed extinctions on islands worldwide: a comparative study of plants and birds. *American Naturalist* **160**, 766–783.
- Sharma, S., Jackson, D.A., Minns, C.K. and Shuter, B.J. (2007) Will northern fish populations be in hot water because of climate change? *Global Change Biology* **13**, 2052–2064.
- Simberloff, D. (2003) Confronting introduced species: a form of xenophobia? *Biological Invasions* **5**, 179–192.
- Simberloff, D. (2006) Invasional meltdown six years later: important phenomenon, unfortunate metaphor, or both? *Ecology Letters* **9**, 912–919.
- Smith, S.A., Bell, G. and Bermingham, E. (2004) Cross-Cordillera exchange mediated by the Panama Canal increased the species richness of local freshwater fish assemblages. *Proceedings of the Royal Society of London B* **271**, 1889–1896.
- Spens, J., Alanara, A. and Eriksson, L.O. (2007) Non-native brook trout (*Salvelinus fontinalis*) and the demise of native brown trout (*Salmo trutta*) in northern boreal lakes: stealthy, long-term patterns? *Canadian Journal of Fisheries and Aquatic Sciences* **64**, 654–664.
- Stachowicz, J.J. and Tilman, D. (2005) Species invasions and the relationships between species diversity, community saturation, and ecosystem functioning. In: *Species Invasions: Insights into Ecology, Evolution, and Biogeography* (eds D.F. Sax, J.J. Stachowicz and S.D. Gaines). Sinauer Associates Inc., Massachusetts, pp. 41–64.
- Strayer, D.L., Eviner, V.T., Jeschke, J.M. and Pace, M.L. (2006) Understanding the long-term effects of species invasions. *Trends in Ecology and Evolution* **21**, 645–651.
- Taylor, J. N., Courtenay, W. R. Jr and McCann, J. A. (1984) Known impacts of exotic fishes in the continental United States. In: *Distribution, Biology, and Management of Exotic Fishes* (eds W.R. Courtenay and J.R. Stauffer). The Johns Hopkins Univ. Press, Baltimore, pp. 322–373.
- Tedesco, P.A., Oberdorff, T., Lasso, C.A., Zapata, M. and Hugueny, B. (2005) Evidence of history in explaining diversity patterns in tropical riverine fish. *Journal of Biogeography* **32**, 1899–1907.
- Tilman, D. (2004) Niche tradeoffs, neutrality, and community structure: a stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Sciences of the United States of America* **101**, 10854–10861.
- Townsend, C.R. (2003) Individual, population, community and ecosystem consequences of a fish invader in New Zealand streams. *Conservation Biology* **17**, 38–47.
- Townsend, C.R. (2008) *Ecological Applications: Toward a Sustainable World*. Blackwell Publishing, Oxford, UK.
- Townsend, C.R. and Simon, K.S. (2006) Consequences of brown trout invasion for stream ecosystems. In: *Biological Invasions in New Zealand* (eds R.B. Allen and W.G. Lee). Springer Verlag, Berlin, pp. 213–225.
- Townsend, C.R. and Winterbourn, M.J. (1992) Assessment of the environmental risk posed by an exotic fish: the case of the proposed introduction of channel catfish (*Ictalurus punctatus*) to New Zealand. *Conservation Biology* **6**, 273–282.
- United Nations Environmental Programme (UNEP) (1992). *Rio Declaration on Environment and Development*. Made at the United Nations Conference on Environment and Development, Rio de Janeiro, Brazil. Available at: <http://www.unep.org/Documents/Default.asp?DocumentID=78&ArticleID=1163>. November, 2008.
- Vander Zanden, M.J. and Olden, J.D. (2008) A management framework for preventing the secondary spread of aquatic invasive species. *Canadian Journal of Fisheries and Aquatic Sciences* **65**, 1512–1522.
- Vitousek, P.M., Mooney, H.A., Lubchenco, J. and Melillo, J.M. (1997) Human domination of Earth's ecosystems. *Science* **278**, 494–499.
- Warren, C.R. (2007) Perspectives on the 'alien' versus 'native' species debate: a critique of concepts, language and practice. *Progress in Human Geography* **31**, 427–446.
- Williamson, M. (1996) *Biological Invasions*. Chapman & Hall, London.
- Yan, X., Zhenyu, L., Gregg, W.P. and Dianmo, L. (2001) Invasive species in China: an overview. *Biodiversity and Conservation* **10**, 1317–1341.