

Non-indigenous fishes and their role in freshwater fish imperilment

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8.1 INTRODUCTION

The current state of freshwater biodiversity, and that of freshwater fishes in particular, can only be described as dismal (Dudgeon *et al.*, 2006; Burkhead, 2012; Chapters 1 and 2). Freshwater extinction rates have been estimated to be around 1000× above background extinction rates (Ricciardi & Rasmussen, 1999; Burkhead, 2012). Using North America as an example, a recent American Fisheries Society assessment indicates that 39% of North American freshwater fish taxa are imperilled: 230 are vulnerable, 190 are threatened, 280 are endangered and 61 are extinct or extirpated (Jelks *et al.*, 2008). Global assessments paint the same general picture (www.iucn.org). What are the factors ultimately responsible for this situation? The objective of this chapter is to examine the role of non-indigenous fishes (hereafter NIF) in the decline and imperilment of native freshwater fishes. We provide a short primer to clarify a few key terms relating to invasion biology (Box 8.1).

A biological invasion should not be viewed as an event, but rather a process comprised of several successive stages (Figure 8.1). The non-indigenous species introduction process begins with uptake of individuals, transport to a new area (*transport outside of native range*), and subsequently release into the wild (*introduction to the wild*). These released individuals may then establish a self-sustaining population in the new area (*establishment*), and an established population may increase in abundance and expand its geographic range (*spread*). Typically it is only when a species becomes abundant and/or widespread that it is

Box 8.1. Terminology relating to non-indigenous species

Studies tend to use a wide assortment of poorly defined and often confusing terms to represent the introduction and establishment of species outside of their presumed native or historical geographic range (Davis, 2009). While the terms invasive, non-native, non-indigenous and exotic are all commonly used, we adopt the term non-indigenous fishes (NIFs) in this chapter to refer to any fish species occurring in the wild outside of its natural range or potential natural range of dispersal, irrespective of the original country of origin or political jurisdiction. By using this general definition, we do not differentiate between species from another country/continent, transplants to new regions within a continent, or even translocations among watersheds. We also note that a wide variety of non-indigenous species that are not fish may have both direct and indirect impacts on native freshwater fishes and aquatic ecosystems, but that in this chapter we will limit our treatment to the effects of NIFs.

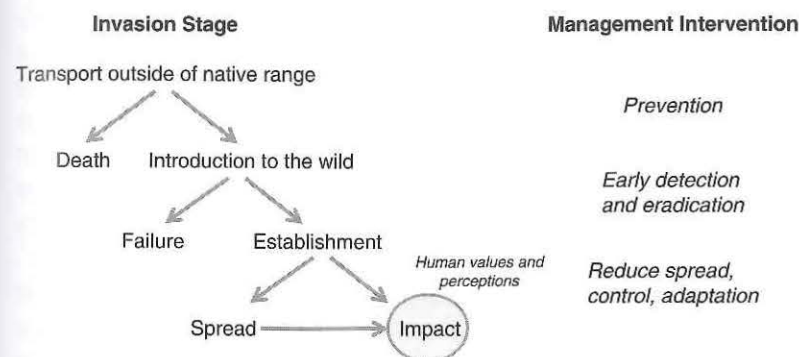


Figure 8.1 Successive stages of the biological invasion process, and the appropriate or relevant management responses along the successive stages. Our diagram highlights the fact that both occurrence and spread can contribute to invasive species impact, and that human values and perceptions also play a large role when judging impact.

perceived to cause ecological or economic harm (*impact*), such that the species is considered invasive (Lockwood *et al.*, 2013). Human values and perceptions greatly influence how and whether a non-indigenous species is viewed as having undesirable consequences. Alternatively, an introduced species population may remain small and localised in its distribution, with few or no tangible ecological or economic effects. To pass through the invasion stages shown in Figure 8.1, a species must

overcome a suite of barriers to advancement. At each stage, there are ecological, environmental and stochastic forces that can either facilitate or hinder transition to subsequent stages. These may include the characteristics of the species (e.g. reproductive rate, physiological tolerance), environmental conditions (e.g. temperature or salinity match) and the nature of the introduction event (e.g. timing of introduction, number of individuals moved). Identifying the stages and associated barriers of the invasion process allows for an explicit recognition that human beings can act as either inhibitors or facilitators at each stage.

Introduced species are widely recognised as an important component of global environmental change, and often have local consequences for populations, communities, food webs and ecosystems (Davis, 2009; Lockwood *et al.*, 2013). The key question from the conservation perspectives is, 'how often do they result in the imperilment and extinction of native fishes?' While there is relatively little debate surrounding the contributing role of NIF introductions in the decline of freshwater fishes (Lassuy, 1995; Richter *et al.*, 1997; Dudgeon *et al.*, 2006; Jelks *et al.*, 2008), it is often difficult or impossible to isolate the causal role of a single factor such as introduced fishes. This is because native species and ecosystems are often subject to multiple human impacts simultaneously, and the role of individual factors can be nearly impossible to tease apart. One approach has been to ask whether NIFs function as a 'passenger' or 'driver' of biodiversity loss (MacDougall & Turkington, 2005; Light & Marchetti, 2007). To illustrate the idea of 'passenger', habitat degradation may produce conditions that are no longer suitable for native species, but suitable for more tolerant non-natives. In such a case, a non-indigenous species could simply replace a native species due to changing habitat, even if there is no direct biotic interaction such as predation or competition. At the other extreme, non-natives can have direct predatory or competitive impacts on native species, such that the non-native is a causal 'driver' of native species declines. Differentiating between these two options is often challenging from correlational and observational data (typically what is available). In reality, the decline and extinction of native species typically involves multiple interacting drivers. For example, habitat degradation may simultaneously favour non-native species and produce declines in native species. Expansion of non-native species could further alter ecosystem properties, thereby causing additional declines in the native species, while also producing direct ecological impacts, such as predation on, or competition with, native species (Bauer, 2012).

While we acknowledge that NIFs typically interact with other human impacts on ecosystems and native fishes, the goal of this chapter is to systematically examine the role of NIFs as a driver of freshwater fish imperilment. To this end, we employ regional examples and case studies to illustrate key points.

8.2 TRANSPORT AND INTRODUCTION OF NON-INDIGENOUS FRESHWATER FISHES

In this section, we address the first two stages of the invasion process (Figure 8.1): transport beyond the native range and introduction into the wild. Humans transport vast numbers of live organisms outside of their native range. Reasons for transport are varied and include the desire to create new fisheries, surround themselves with familiar organisms, accidental transport and simple negligence. Current estimates by the US Geological Survey document 697 unique fish introduced to both the fresh and brackish waters of the US (USGS, 2013). Of these, approximately 42% originate from other countries, and 54% are native to the USA but were introduced outside their native range (USGS, 2013). Freshwater fishes have been introduced to the USA from all continents except Antarctica. The rate of introduction of NIFs accelerated rapidly in the middle of the twentieth century (Allen & Flecker, 1993; Crivelli, 1995; Fuller *et al.*, 1999), but appears to have stabilised since 2000 (USGS, 2013).

While there are several ways to categorise the transport and introduction of NIFs, we classify NIF introductions according to the introduction pathway, which is the mode or reason by which the species was introduced. The broadest level classification is a simple dichotomy of intentional versus unintentional introductions. Intentional introduction refers to the import of organisms to a new area for an express purpose; these are often important to humans, and sometimes involve considerable effort and expenditure. Thus, we typically have relatively good records of intentional events. By contrast, unintentional introductions are an unintended consequence of the intentional transfer of some good or service, such that we typically have much poorer knowledge of these.

8.2.1 Intentional introductions

The intentional transport and introduction of organisms by humans has been occurring since ancient times (Wilson *et al.*, 2009). Here

we consider five general categories of intentional fish introductions: food-related releases, game and bait fishes, aquarium releases, biocontrol and scientific/conservation releases.

8.2.1.1 Food-related releases

Fishes are commonly introduced into new areas as a food source, both for aquaculture and to create or improve wild-capture fisheries. For example, tilapia (*Tilapia* spp. and *Oreochromis* spp.) have been introduced into over 90 countries for a wide variety of reasons, most recently to create new fisheries (Canonico *et al.*, 2005). Tilapia aquaculture has grown exponentially in the past few decades, and is valued at many billions of dollars (www.fao.org). While providing much-needed protein and employment to many developing areas, they are also highly invasive and exert major ecological impacts (Canonico *et al.*, 2005). One of the earliest known examples of fish translocation is that of common carp (*Cyprinus carpio*) (Balon, 1995). Native to the waters of the Ponto-Caspian in central Asia, common carp were transported to China and later Europe for pond aquaculture dating back 2000 years (Copp *et al.*, 2005). Common carp have since been widely introduced to inland waters throughout the world (Moyle, 2002; Koehn, 2004).

At present, the majority of global aquaculture production consists of NIFs, predominantly carps, tilapia, salmonids and catfishes. Unfortunately, aquaculture fishes often escape facility confines, or are intentionally released into nearby streams and waterways, and sometimes become successfully established (Canonico *et al.*, 2005; Kolar *et al.*, 2005; Weyl, 2008). An example of this is the farming of Atlantic salmon (*Salmo salar*), where the introduction and frequent escape of farmed fishes along the Atlantic and Pacific coastlines is an enormous problem (Naylor *et al.*, 2001). It has been estimated that up to 40% of 'wild-caught' Atlantic salmon fished in the North Atlantic and > 90% fished from the Baltic Sea are of farmed origin (Naylor *et al.*, 2001). In addition, more than half a million individual Atlantic salmon raised in aquaculture facilities on the west coast of North America escaped captivity between 1987 and 1997 (Naylor *et al.*, 2001). At the present time, Atlantic salmon have been found in 77 rivers and streams across British Columbia, and have been observed to spawn in some locations (Naylor *et al.*, 2001).

8.2.1.2 Game and bait fishes

Perhaps the largest category of NIFs are those introduced for game, noting that game and food fishes are sometimes one and the same. Until

recent decades, fisheries management in North America and elsewhere has been virtually synonymous with artificial propagation and translocation of fishes, which are often non-indigenous. Many NIF introductions in North America during the nineteenth and twentieth centuries involved intentional stocking by management agencies, and were aimed at 'improving' the native biota, expanding sportfishing, or providing forage for native or other introduced game fishes (Rahel, 1997). Settlers of the western US in the nineteenth and twentieth centuries preferred the familiar game species of the eastern US such as brook trout (*Salvelinus fontinalis*), black basses (*Micropterus* spp.) and catfishes (*Ictalurus* spp.) over the native fish fauna. NIFs were widely introduced throughout the western US, and many have successfully established (Moyle, 2002). Perhaps the best example of an introduced game fish is the virtually cosmopolitan rainbow trout (*Oncorhynchus mykiss*). This salmonid is native to streams and rivers of the western US, but as of 1996, has been introduced to every continent except Antarctica and more than 100 countries and oceanic islands worldwide (Lever, 1996; Cambray, 2003).

Coincident with the movement of game fishes is the importation of forage and bait fishes. Fishes used as bait are often released at the end of the day or fishing trip (Litvak & Mandrak, 1993). Species such as red shiner (*Cyprinella lutrensis*), golden shiner (*Notemigonus crysoleucas*) and fathead minnow (*Pimephales promelas*) now have broad distributions in the USA because of widespread transport and release due to their popularity as bait fishes (USGS, 2013). Ludwig and Leitch (1996) combined mail surveys, baitfish samples, interviews and literature data to quantify the role of bait bucket transfer in the dispersal of NIFs. They found bait bucket transfer to be a major vector for the dispersal of NIFs.

8.2.1.3 Aquarium pet releases

Many fishes have been introduced intentionally through the release of aquarium pets. The number of individuals and species involved in this pathway can be staggering. Radonski *et al.* (1984) estimate that up to 1500 species of freshwater fish were regularly imported into the USA for the aquarium trade in the early 1980s, although Fuller *et al.* (1999) suspect this to be a severe underestimate. Although aquarium fish release rates are not well known, Gertzen *et al.* (2008) estimated that approximately 10,000 fishes were released to the wild annually in areas surrounding Montréal, Canada, with most releases involving a handful of common aquarium species such as goldfish (*Carassius auratus*) and guppies (*Poecilia reticulata*). A similar result was reported for the Pacific

Northwest of North America by Strecker *et al.* (2011). Pet releases are an underestimated source of NIF introductions, and its importance as a pathway for NIFs is expected to grow in the future, especially as the global climate warms and the probability of establishment of aquarium fishes increases.

8.2.1.4 Biocontrol

Non-native fish introductions for biocontrol are often overlooked. Known natural enemies of pest species are introduced with an expectation that the enemy will reduce or control the population of the pest. In this case, pests have historically included native species considered harmful to humans, but also non-native species that cause economic or environmental harm. Some early biocontrol organisms were fishes. For example, the western mosquitofish (*Gambusia affinis*) has been widely introduced for mosquito control in the western US and around the world (Lever, 1996).

8.2.1.5 Research and conservation

Fishes are sometimes transported to new areas to conserve or protect the species. This includes organisms brought to zoos, aquaria, or wildlife preserves, as well as endangered species moved to novel natural environments for their immediate protection and propagation. For example, the US Endangered Species Act (ESA) allows for the establishment of 'experimental' populations outside of the species range. The Devil's Hole pupfish (*Cyprinodon diabolis*) was introduced to the Amargosa Pupfish Station in 1983 (Sigler & Sigler, 1987) because the sole wild population was threatened by groundwater pumping (Soltz & Naiman, 1978). It was subsequently returned to its native habitat, although there now remain several additional non-native populations of the species.

The transport and introduction of species for conservation purposes has recently become an issue under the guise of assisted colonisation/migration. Assisted colonisation is a conservation strategy whereby a species is intentionally introduced to new locations, presumably because native populations are threatened by environmental change (Hoegh-Guldberg *et al.*, 2008; Ricciardi & Simberloff, 2009). While this may ultimately be a viable environmental management strategy in some cases, it should be recognised that assisted colonisation is essentially the purposeful transport and release of a non-native species, for which the ecological consequences will be unpredictable (Ricciardi & Simberloff, 2009; Olden *et al.*, 2011).

8.2.2 Unintentional introductions

Many fishes are transported unintentionally as a by-product of the movement of other goods or services; for example, fish are frequently transported as hitchhikers within cargo holds or ballast water. By their nature, unintentional introductions are difficult to evaluate in terms of their overall importance, although recent evidence suggests they are quite prevalent (Molnar *et al.*, 2008). The best-known example of unintentional transport involves movement of species in ship ballast tanks. Large transport ships often pump harbour water into ballast tanks to balance their cargo load. At the receiving port, much of this water and associated organisms (invertebrates, fishes, larvae) are unceremoniously dumped into the water. The significance of this pathway as a source of non-native fishes has grown with global trade and the size and speed of vessels (Carlton, 2000). It has been estimated that > 10,000 species may be transported within ship ballast water on any given day (Carlton, 1999). For example, round goby (*Neogobius melanostomus*) was transported to the Laurentian Great Lakes via ship ballast water, and subsequently spread throughout the Great Lakes and beyond via ballast water and by natural dispersal through connected waterways (Kornis *et al.*, 2012). In other situations, fishes are unintentionally transported within water diverted for human use. An example that combines both ballast water and water diversion pathways is the Shimofuri goby (*Tridentiger bifasciatus*), a small Japanese estuarine fish. The Shimofuri goby was initially introduced into the San Francisco Bay Estuary via ballast water during the mid-1980s (Matern, 2001; Moyle, 2002). It was then transported inland over 500 km, and then across a mountain range into the Los Angeles basin by water export through the California State Water Project (Matern, 2001).

We summarise the relative importance of different vectors of NIF transport for several regions around the world in Table 8.1. The two most important categories for NIFs are food-related and non-food-related, highlighting the utilitarian purpose of most NIF introductions. Unintentional transport was generally of moderate importance for freshwater NIFs across these diverse regions. In contrast, unintentional introductions tend to be the dominant vector for global marine organisms, indicating that the forces driving the proliferation of non-native species differs among biomes and ecosystems. While a relatively small fraction of NIFs are unintentional introductions (USGS, 2013), the relative importance of unintentional introductions has generally increased in recent decades (Ricciardi, 2006; Keller *et al.*, 2009). Recent recognition of the undesirable consequences of many species introductions in

Table 8.1 A summary of documented NIF introductions, according to the reason/pathway of introduction for different regions of the world. Values presented are numbers of NIFs for each region, while the percentage of the total pool for each region is shown in parentheses. The last column shows pathways for global marine organisms for comparison.

Reason/pathway for introduction	US freshwater fish ^a	California freshwater fish ^b	Great Britain ^c	Australia ^d	Spain ^e	Global marine organisms ^f
Food-related and game species	190 (31%)	49 (69%)	7 (39%)	30 (34%)	18 (72%)	141 (43%)
Non-food related	202 (33%)	5 (7%)	10 (56%)	29 (33%)	6 (24%)	20 (6%)
Biocontrol	35 (6%)	2 (3%)	0 (0%)	2 (2%)	1 (4%)	0 (0%)
Research and conservation	35 (6%)	2 (3%)	0 (0%)	15 (17%)	0 (0%)	0 (0%)
Transportation related (unintentional)	154 (25%)	13 (18%)	1 (6%)	10 (12%)	0 (0%)	282 (86%)
Unknown	0 (0%)	0 (0%)	0 (0%)	9 (10%)	0 (0%)	0 (0%)
Totals	616	71	18	87	25	329

Notes

^aBased on data from the US Geological survey, 2013. Nonindigenous Aquatic Species Database summary graphs. Available from: <http://nas.er.usgs.gov/xxxx>.

^bBased on data in Moyle (2002).

^cBased on data in Keller *et al.* (2009).

^dBased on data in Lintermans (2004) (note that some organisms are identified with multiple modes of transport so the percentages add up to greater than 100%).

^eBased on data in Elvira and Almodovar (2001).

^fBased on data from Molnar *et al.* (2008) (note that some organisms are identified with multiple modes of transport so the percentages add up to greater than 100%).

the developed world has led to policies that have curtailed intentional stocking of NIFs. Yet the rise of global trade and transport in recent decades has greatly increased opportunities for accidental introductions.

8.2.3 Many are called, few are chosen

Of the large number of NIF introductions, only a subset of the species ultimately establishes self-sustaining populations. For example, Courtenay and Williams (1992) noted that, of 99 exotic species occurrence records in the continental USA, 46 had self-sustaining populations. While the oft-cited 'tens rule' (Williamson, 1996) predicts that roughly 10% of introduced species establish and 10% of those spread, Jeschke and Strayer (2005) report much higher rates of establishment and spread (~50%) for vertebrates intentionally introduced between North America and Europe. Nevertheless, the point is that a species may be transported and introduced, but environmental conditions are often not suitable or favourable for maintaining a self-sustaining population. This is particularly the case at high latitudes, where cold winter temperatures limit survival for warm-water species. Even where conditions are potentially suitable, NIF colonists can face an uphill battle. The small numbers of individuals transported into a novel environment may have a difficult time finding food, habitat, or mates, while avoiding predators. Inbreeding can also be a concern. Not surprisingly, repeated introductions or introductions of a large number of individuals (i.e. increased propagule pressure) can increase the likelihood of establishment (Kolar & Lodge, 2001).

Among established NIFs, the majority have relatively limited geographic distributions, while a handful of species are geographically widespread (Fuller *et al.*, 1999; Gido & Brown, 1999; Rahel, 2000; Schade & Bonar, 2005). This highly right-skewed pattern is evident in Figure 8.2A, which shows that the vast majority of NIFs inhabiting the USA inhabit a small number of watersheds, while a very small number of species are widespread. The list of the most widespread North American species is dominated by intentionally stocked game fishes (Rahel, 2000). On other continents, a similar set of NIF species commonly occurs, with some variation as a result of climatic suitability. For example, an extensive basin-by-basin review of freshwater fishes in South America reports many of the usual suspects: tilapia (*Tilapia* spp., *Oreochromis* spp.), brown trout (*Salmo trutta*), brook trout (*Salvelinus fontinalis*), common carp and largemouth bass (*Micropterus salmoides*) (Barletta *et al.*, 2010). Even though large numbers of NIFs are transported and introduced, only a subset of these are capable of establishing self-sustaining populations.

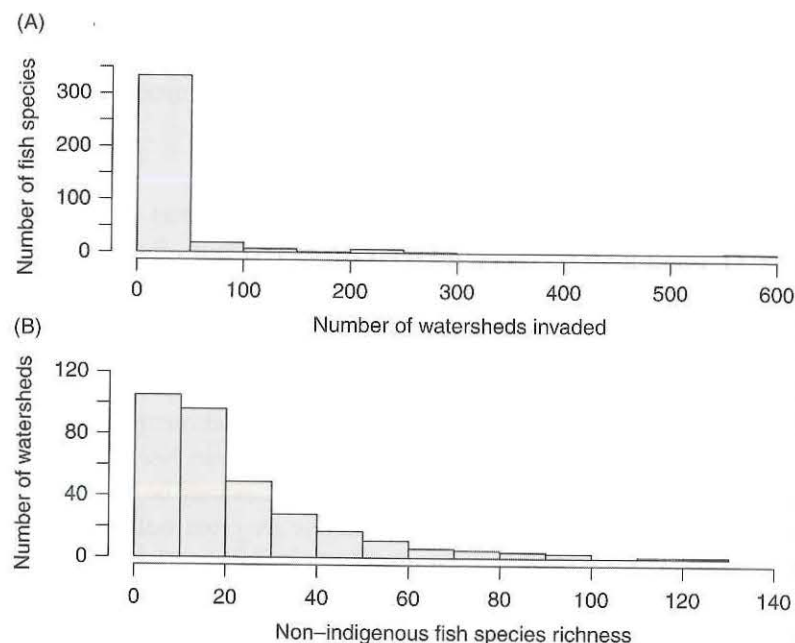


Figure 8.2 Frequency histograms showing NIF spatial distributions and species richness at the watershed level. (A) The number of watersheds in the US invaded by each individual NIF species known in the US. Most NIF species occur in a small number of watersheds, while a small number of NIFs are geographically widespread. (B) NIF species richness across these same watersheds. Most watersheds contain relatively few NIFs, while a small number of watersheds have high NIF species richness. Watersheds are USGS 6-digit HUCs (J.D. Olden, unpublished data).

A relatively small number of NIFs, predominantly game fishes, have become geographically widespread. Across US watersheds, NIF species richness is also right-skewed, with most watersheds containing relatively few NIF species and only a handful of watersheds containing large numbers of NIFs (Figure 8.2B). Despite this skewed distribution of species richness, NIFs dominate regional fish faunas in many human-dominated regions of the world, particularly in the Mediterranean and dryland habitats (Leprieur *et al.*, 2008; Marr *et al.*, 2010).

8.3 ECOLOGICAL IMPACTS AND RESPONSES

Established NIFs have the potential to affect native fishes, either directly or indirectly. In this section we consider only the ecological

impacts of NIFs and ignore socioeconomic considerations, given that our focus is the conservation of freshwater fishes. Although impacts of NIFs are at times considered dichotomous (i.e. benign versus high-impact), they are more accurately seen as a continuum (Lapointe *et al.*, 2012). In a practical sense, impacts of a NIF are often difficult to characterise. Although direct interactions with native species are sometimes quantified, indirect effects can be subtle and difficult to detect. It has been argued that a loss of biological or genetic diversity through species extirpations is required for large ecological impacts (Gozlan *et al.*, 2010), yet there are a suite of other effects that NIFs can have on aquatic species and ecosystems. Many freshwater systems are essentially habitat 'islands' because there is minimal connectivity among systems, and many species are adapted to localised conditions. This leaves freshwater communities vulnerable to the impacts of NIFs, particularly where the native taxa lack an evolutionary history of competition or predation with other species (Cox & Lima, 2006; Kuehne & Olden, 2012).

8.3.1 Mechanisms of NIF impacts on native fishes

There are a variety of potential mechanisms through which NIFs can impact native fishes. Although detailed elsewhere (Gozlan *et al.*, 2010; Leunda, 2010; Cucherousset & Olden, 2011; Ribeiro & Leunda, 2012), we briefly discuss mechanisms of impact here.

8.3.1.1 Predation and direct mortality

NIFs often prey directly on adults, juveniles and eggs of native species (Witte *et al.*, 1992b; Chaichana & Jongphadungkiet, 2012). For example, the introduction of Nile perch (*Lates niloticus*) into Lake Victoria is widely regarded as the direct cause of the decline or extinction of native cichlid species. There are many examples of direct predation as an important mechanism (Ross, 1991), particularly in the case of predator-naïve native prey species. Other forms of direct mortality can also have important population-level consequences. For example, parasitic NIFs such as sea lamprey (*Petromyzon marinus*) are known to kill some native fishes (Smith & Tibbles, 1980). In addition, the behaviour of some NIFs can lead to the destruction of native fish nests and eggs. For example, non-native rainbow trout are known to construct redds on top of native salmonid redds (i.e. superimposition), damaging and destroying native eggs in the process (Taniguchi *et al.*, 2000).

8.3.1.2 Competition

Species introductions may cause a shift or decline in a prey community that negatively affects native species as a result of resource competition (Post & Cucin, 1984; Ross, 1991). Additionally, NIFs can compete with native species for space, shelter, or mates (Marchetti, 1999; Fleming *et al.*, 2000). In response, native species may alter their behaviour, including aggression, food consumption, dominance hierarchies, habitat use, diel activity patterns and emigration (Ross, 1991; Fraser & Gilliam, 1992; Marchetti, 1999; Cucherousset *et al.*, 2007; Nasmith *et al.*, 2010). For example, native brown trout in France changed their diet in the presence of introduced brook trout (Cucherousset *et al.*, 2007), and dace (*Phoxinus* spp.) became more active at crepuscular periods and adopted a more benthic-oriented behaviour in lakes stocked with non-native trout in Alberta, Canada (Nasmith *et al.*, 2010). The fitness consequences of competition may include decreased growth and fecundity (Fraser & Gilliam, 1992; Marchetti, 1999; Irons *et al.*, 2007; Britton *et al.*, 2010). Overall, resource competition with NIFs is an important mechanism underlying native fish declines (Ross, 1991).

8.3.1.3 Parasites and disease

The introduction of novel parasites and diseases is often inexorably linked to the introduction of NIF hosts. Novel parasites and diseases can be directly detrimental to native fishes (Vitule *et al.*, 2009). For example, common carp in the Czech Republic were affected by *Bothriocephalus gowkongensis*, a tapeworm carried by introduced grass carp (*Ctenopharyngodon idella*) (Lusk *et al.*, 2010). It is also possible for NIFs to alter the population dynamics of existing native parasites by acting as an alternate host, although such effects may either exacerbate or alleviate their impact on native species (Poulin *et al.*, 2011).

8.3.1.4 Ecosystem alterations

Aquatic habitats can undergo ecosystem-level changes in response to NIFs. Species such as goldfish (*Carassius auratus*) that feed in soft substrates can uproot macrophytes and re-suspend sediments, leading to increases in turbidity (Richardson *et al.*, 1995). Grass carp feed directly on macrophytes (Bain, 1993) and thereby remove habitat for other aquatic species. Feeding and excretion by NIFs can alter nitrogen and phosphorus cycling and availability in aquatic systems (Schindler *et al.*, 1993; Vanni, 2002). The ecosystem-level changes that come with NIF introductions can have a range of secondary consequences. Due

to the complexity of interactions between many NIF and native species and ecosystems, many of the broader ecosystem-level implications of fish introductions and game-fish stocking remain poorly known (Eby *et al.*, 2006).

8.3.2 Responses of native fishes to NIF introductions

8.3.2.1 Genetic effects

The potential genetic effects of NIFs are a critical conservation concern, particularly the loss of genetic uniqueness via hybridisation (Hitt *et al.*, 2003). Similarly, genetic introgression can occur when a non-native strain is stocked where a native population of the same species exists (Ferguson, 1990; Garcia-Marin *et al.*, 1999), or if fish escape from a hatchery and breed with natives. Such losses are a concern for fish conservation, but are restricted to cases where introduced species or strains are closely related to native populations. Perhaps more pervasively, NIFs can affect genetic diversity by contributing to the local extirpation of populations, which reduces native genetic diversity. Additionally, NIFs can exert strong selective pressures on native fishes, leading to evolutionary responses (Roberge *et al.*, 2008). Such responses could lead to the development of novel traits and thus increase the genetic diversity of native species (Schlaepfer *et al.*, 2011), but the development of novel traits in response to NIFs is more realistically viewed as a case of 'one step forward, two steps back' from a conservation perspective.

8.3.2.2 Population and species effects

NIFs commonly contribute to population declines in native species, which may ultimately lead to population extirpations or extinction (Ross, 1991). For instance, declines in commercially important native species in the Gargalheiras Reservoir, Brazil were attributed to the establishment of Nile tilapia (Attayde *et al.*, 2011). Studies of biodiversity decline have generally focused on species-level declines, imperilment and extinction. With the exception of highly localised endemics, species declines are the by-product of the extirpation of many individual populations (Hughes *et al.*, 1997). Rates of population loss are not well known, but are estimated to be 1000× higher than species extinction rates (Hughes *et al.*, 1997). Studies that have examined long-term freshwater fish community change indicate high rates of local population loss. Using historical data for rivers in Mexico, Mercado-Silva *et al.* (2006a) reported native species population-level loss rates of 10–30% per decade and a

concomitant 10–20% increase per decade in non-native species. Other studies report similar patterns of local extirpation of native populations, and increasing incidence of non-native species (Gido *et al.*, 2010). Native species undergo a gradual range-wide decline as local populations blink out. This phenomenon is analogous to the concept of extinction debt (Tilman *et al.*, 1994), in that species declines may not be easily observed, and regional or global extinction occurs only after a prolonged period of individual population losses.

As populations are locally extirpated, the risk of species extinction increases. Introduced species were the second leading factor (after habitat alteration), contributing to 68% of North American fish extinctions (Miller *et al.*, 1989). Similarly, Lassuy (1995) found that of the 92 freshwater fish species listed under the US Endangered Species Act, species introductions were a contributing factor for 70% of the taxa. Of these, 73% of cases involved species related to sport fishing (game, forage or bait fish), with centrarchids, ictalurids and salmonids leading the list. This same general finding, that NIFs are a major contributor to fish imperilment and extinction, has been reported elsewhere (Richter *et al.*, 1997; Wilcove *et al.*, 1998; Harrison & Stiassny, 1999). In contrast, a study of endangered fishes in Canada found that invasive species were notably less important as they were implicated for only 27% of the imperilled taxa (Venter *et al.*, 2006). Similarly non-native species were suggested as a main factor in the decline of only 15% of rare species across the Laurentian Great Lakes (Mandrak & Cudmore, 2010). Equivalent figures are lacking for many regions, owing in part to limited research in developing nations (Fazey *et al.*, 2005); however, non-native species are implicated in the decline of 29% of threatened neotropical fishes in South America (Rodriguez, 2001).

8.3.2.3 Community, food web and ecosystem effects

NIFs can cause profound changes in freshwater fish communities. Introduced predators can eliminate native fish species and assemblages in lakes (Chapleau *et al.*, 1997; Findlay *et al.*, 2000; Trumpickas *et al.*, 2011; Aiken *et al.*, 2012). Examples of assemblage-level impacts include the Nile perch (*Lates niloticus*) impacts on the endemic cichlids in Lake Victoria (Witte *et al.*, 1992a, 1992b) or the peacock bass (*Cichla*) introductions into neotropical reservoirs (Pelicice & Agostinho, 2009). Additionally, introduced salmonids have caused declines in native galaxiids across their range (McDowall, 2006; Habit *et al.*, 2010). In many aquatic systems around the globe, entire food webs are increasingly

dominated by NIFs (Ricciardi, 2006; Leprieur *et al.*, 2008; Marr *et al.*, 2010). While this can often result in increased local species richness, their presence strongly contributes to biotic homogenisation, a process whereby disjunct communities or biota become more similar over time due to the combined effects of native species loss and NIF introductions (Rahel, 2000; Olden *et al.*, 2010).

NIFs can alter food webs and ecosystem processes across trophic levels and ecosystem boundaries. For example, the introduction of non-native smallmouth bass (*Micropterus dolomieu*) and rock bass (*Ambloplites rupestris*) into Ontario lakes caused dramatic declines in native littoral prey fishes via direct predation (Vander Zanden *et al.*, 1999). This had unexpected negative effects on the native top predator, lake trout (*Salvelinus namaycush*), which are highly dependent on littoral prey fish in the absence of their preferred pelagic forage fish prey (Vander Zanden *et al.*, 1999). The ecological effect of NIFs can propagate across several trophic levels, as demonstrated by studies in New Zealand streams, where brown trout introduction has altered insect communities and increased periphyton standing-stock (Flecker & Townsend, 1994; Simon & Townsend, 2003). In some cases, NIFs have been stocked to induce a system-wide trophic cascade for the purpose of improving water quality and clarity (Scharf, 2007). In addition, food web effects can sometimes cross ecosystem boundaries. In Japanese streams, introduced rainbow trout produced a suite of effects including reduced aquatic insect emergence, increased periphyton growth, and severed food web linkages between streams and the surrounding riparian ecosystem (Baxter *et al.*, 2004).

8.3.3 Generalities about impact

There is a great deal of uncertainty regarding the relative impacts of NIFs. It seems that a large percentage of impacts are caused by only a few species. However, it is unclear whether other NIFs are relatively benign or simply have poorly documented impacts. Such uncertainty can be ascribed to a number of factors including: differences in impact among regions, a lack of baseline data, the lack of impact assessments, and potential threshold, cumulative and synergistic effects. The impact of a non-native species depends on the distribution and abundance of both native and introduced species, and the response of the recipient biota and ecosystem. Impacts are likely to be heterogeneous across the introduced range (Ricciardi, 2003). For instance, species introduced to ecosystems near the limits of their physiological tolerances are unlikely

to have major impacts. Such variability leads to difficulties in broadly classifying NIFs as high- or low-impact invaders. Furthermore, pre-invasion data are generally unavailable (Cambray, 2003; Gherardi, 2007), and even when baseline data exist, impacts can be difficult to identify in the face of other environmental stressors and species introductions. These can involve cumulative or synergistic effects (Ricciardi, 2001), making it difficult to tease out the effects of a given species introduction.

Impacts also vary through time. There are often lag times between establishment and impact (Crooks, 2005; Richardson & Pysek, 2006). For instance, introduced predators with long generation times may not have significant impacts until some population threshold is breached (Schoen *et al.*, 2012). Impacts may only be realised after NIFs adapt to their new environment (Ricciardi *et al.*, 2013). Alternatively, NIFs can remain relatively benign until ecosystem conditions change (e.g. through climate change or the introduction of a new, facilitative species), leading Courtenay (1993) to describe non-indigenous species as potential ecological time bombs. Many introduced populations have not fully colonised the total extent of suitable habitat in their non-native range (Mercado-Silva *et al.*, 2006b; Papes *et al.*, 2011). Strayer (2010) described this situation as an 'invasion debt', likely to be paid over time as species spread. The period before the debt is 'paid' may be protracted for freshwater systems, as their spread at times requires secondary introductions. It is also possible that impacts may attenuate after reaching an initial peak if the NIF population eventually declines or because no further impacts on a native species are possible after the species has been extirpated (Strayer *et al.*, 2006).

8.3.3.1 Traits of high-impact species

Improved understanding of the traits of high-impact NIFs could lead to better predictability and inform risk assessments (Chapter 2); however, few generalities exist for NIFs because impacts depend in part on the characteristics of recipient ecosystems. Habitat suitability (e.g. on a latitudinal gradient) may not be equivalent across the introduced range of a NIF, and introduced piscivores may have a greater impact in systems lacking a top predator relative to communities with native piscivores. Interactions among NIFs and native ecosystems can be complex. Nevertheless, a few commonalities do exist in the traits of high-impact NIFs. Some of the most notable impacts of NIFs are the result of introduced piscivores. Introductions of predatory sport fishes are the main

threat to endemic fishes in the western USA (Minckley & Deacon, 1991). Primary consumers may also have strong impacts, whereas omnivores are often relatively benign (Moyle & Light, 1996; Ribeiro *et al.*, 2008). Broad physiological tolerance is also often associated with impact (Kolar & Lodge, 2002; Marchetti *et al.*, 2004; Ribeiro *et al.*, 2008), and studies have found large maximum body size and small egg size to be important (Kolar & Lodge, 2002; Marchetti *et al.*, 2004). Aside from species traits, taxonomic uniqueness relative to recipient communities, prior invasion success, and association with humans also correspond with impacts for NIFs (Marchetti *et al.*, 2004; Ricciardi & Atkinson, 2004; Ribeiro *et al.*, 2008). Species risk assessments provide a useful tool for prioritising and identifying potentially harmful NIFs (Ricciardi & Rasmussen, 1998; Lodge *et al.*, 2006).

8.4 NIFS AND INTERACTIONS WITH OTHER DRIVERS

Although this chapter is meant to examine the role of NIFs in the decline of native fishes, it is important to consider species interactions within the broader context of habitat and environmental change, which brings us back to the passenger versus driver dichotomy discussed earlier (Light & Marchetti, 2007). While often presented as a dichotomy, native species decline may commonly be the result of interactions among biotic and environmental drivers, such that NIF may simultaneously be both a driver of native species declines and a passenger of other environmental changes. This framework is analogous in many ways to biotic homogenisation, which emphasises the role of species introductions, native species loss, and habitat alterations in increasing the similarity of biotas over time (Rahel, 2002). At the landscape scale, the consequence is that initially distinctive fish faunas are replaced by a handful of tolerant and ubiquitous fish species (common carp, tilapia, rainbow trout, etc.). As a result, beta diversity, reflective of the uniqueness of local faunas, is reduced. Below, we highlight some of the well-known drivers that interact with NIFs.

8.4.1 Impoundments and altered flow regimes

The creation of impoundments tends to favour NIFs at the expense of native species (Marchetti *et al.*, 2004; Havel *et al.*, 2005; Johnson *et al.*, 2008; Mims & Olden, 2013). The twentieth century has witnessed the construction of 40,000 large dams and untold millions of small dams

worldwide, transforming many river systems into series of impounded reservoirs (Chapter 4). In addition to creating slackwater conditions where water formerly flowed, dams block fish movements, eliminate floodplains and habitat complexity, disconnect fishes from spawning grounds, and alter downstream physical features, water temperatures, water quality and flow regimes (Baxter, 1977; Ligon *et al.*, 1995; Chapter 4). NIFs adapted to these novel, lacustrine conditions are often introduced or otherwise colonise impoundments. Downstream, flow regimes and habitats are also altered, including changes in the timing of peak- and low-flow events, water-level fluctuation patterns and thermal regimes (Poff *et al.*, 2007; Mims & Olden, 2013). Such changes tend to favour NIFs, often leading to severe declines in native fishes (Marchetti & Moyle, 2001), a well-known example being the declining endemic fishes of the Colorado River (Olden *et al.*, 2006).

8.4.2 Climate change

Climate change will have a suite of consequences for freshwater ecosystems, as well as human use and management of these systems (Rahel & Olden, 2008; Chapter 3). For example, increased surface water temperature is allowing a northward expansion of temperature-limited warm-water fishes such as smallmouth bass and other centrarchids (Sharma *et al.*, 2007). The northward expansion of warm-water fishes is already under way, with pronounced impacts on native fishes and lake food webs (Vander Zanden *et al.*, 1999). Using IPCC climate change scenarios, Sharma *et al.* (2009) identified thousands of lakes vulnerable to smallmouth bass invasion in response to projected climate change, serving as an example of how climate change might facilitate the spread of NIFs (Rahel & Olden, 2008).

8.4.3 Other drivers

A range of other drivers (e.g. pollution, sedimentation, stream channelisation, excessive surface and groundwater extraction, and over-harvest) can interact with NIFs to cause native species declines. As an example, the African Rift Lake, Lake Victoria, experienced the probable extinction of several hundred endemic cichlid fishes, and offers an illustrative case study. The lake experienced massive watershed erosion, shoreline development, and urbanisation during the twentieth century, eventually leading to cyanobacterial blooms, hypoxia, an approximately fivefold decline in water clarity, and infestation by introduced water hyacinth

(*Eichhornia crassipes*), a highly invasive macrophyte. Nile perch (*Lates niloticus*) was introduced into Lake Victoria in 1956, but it was more than 20 years before the population increased dramatically. Although predation by Nile perch undoubtedly played a central role in the loss of native cichlids from Lake Victoria, ultimately untangling the effects of interacting drivers of biodiversity loss may not be possible (Gurevitch & Padilla, 2004). This holds true for other complex case studies such as the Laurentian Great Lakes (Christie, 1974; Shuter & Mason, 2001; Madenjian *et al.*, 2002). In short, many aquatic ecosystems have been subject to a barrage of interacting stressors. In many cases, a single stressor is unlikely to cause the extirpation of a native species. It may be that when multiple stressors act in concert we tend to see NIF establishment, wholesale food web changes and native species extirpation. Examples involving multiple interacting ecological stressors may or may not involve non-native species, although in light of the expanding scope and magnitude of their spread and impact, they often do. There is a need to develop a better understanding of the interacting roles of introduced species, habitat alteration and other potential factors as drivers of native species decline (Light & Marchetti, 2007). It appears that at many spatial scales, anthropogenic impacts, NIFs and native species imperilment are inextricably linked (Leprieur *et al.*, 2008).

8.5 MANAGEMENT STRATEGIES

The main point of this chapter is that NIFs are often an important contributing factor in the decline and imperilment of native freshwater fish species and communities. NIFs are introduced for a variety of reasons, and can impact native species in multiple ways. In a general sense, the introduction of NIFs is inexorably tied to human activities (Leprieur *et al.*, 2008), and is part of a wider suite of environmental transformations that are associated with human-driven environmental change. While teasing apart the ultimate drivers of declining native species and communities is a challenge, managing and preventing impacts on native species and ecosystems is undoubtedly a far greater challenge. In this section, we examine management strategies in response to NIFs and their impacts. In reality, it is not only NIFs, but non-native species generally (i.e. both fishes and non-fishes), that may invoke environmental management responses aimed at reducing impacts on native fishes, as well as other environmental concerns (economic, aesthetic and broader ecosystem integrity impacts).

8.5.1 Prevention and containment

Perhaps it is self-evident that preventing undesired NIF introductions is likely to be the most cost-effective way of minimising their adverse impacts (Leung *et al.*, 2002). One key prevention strategy in many developed nations has been to limit or ban the import and introduction of presumed high-risk species (Ruesink *et al.*, 1995). This generally involves targeting potentially harmful species, as identified through risk assessments based on species traits as discussed above (Lodge *et al.*, 2006). Efforts to halt pest species at the border have the potential to be effective, although this approach is often not straightforward in light of the diverse pathways and reasons for NIF introductions, and the potential for conflicting values and demands. In considering an intentional introduction, one could simply weigh the expected costs and benefits, and act accordingly. For example, introducing tilapia into a newly built reservoir may be viewed as undesirable or high-risk from an ecological point of view (Canonico *et al.*, 2005). On the other hand, economic pressures to create new fisheries are likely to trump ecological concerns. Notably, if NIF introductions threaten the provisioning of ecosystem services such as water quality and recreation, economic and ecological concerns may align. Unfortunately, the value of ecosystem services remains poorly recognised.

There are many examples of where an undesirable species is in a region and spreading. In such cases, the management aim is to contain the species and prevent their further spread. As an example, rainbow smelt (*Osmerus mordax*) appeared in the Laurentian Great Lakes in the 1920s, and have subsequently appeared in hundreds of smaller inland lakes in the region as a result of illegal transport via bait-bucket spread and angler carelessness (Evans & Loftus, 1987). Rainbow smelt have documented strong negative impacts on native game species (Evans & Loftus, 1987; Hrabik *et al.*, 1998; Mercado-Silva *et al.*, 2007). Whether species such as rainbow smelt continue to spread will likely depend on whether anglers recognise and understand their adverse impacts, and alter their behaviour accordingly.

The issue of containment is at the core of the management debate surrounding Asian carp (primarily *Hypophthalmichthys nobilis* and *H. molitrix*) in North America. Asian carp escaped southern US aquaculture facilities in the 1970s, and subsequently dispersed throughout much of the Mississippi River basin (Kolar *et al.*, 2005). Asian carp eventually reached the Chicago Sanitary and Ship canal. This canal is an important shipping and navigational link between the Laurentian

Great Lakes and Mississippi River basins, and also represents an artificial breach of the biogeographic barrier that historically separated these basins. Although an electric barrier has been built in an attempt to halt fish movement through the Chicago Sanitary and Ship canal, Asian carp are now at the cusp of moving into and establishing in the Great Lakes drainage basin (Jerde *et al.*, 2011). While shipping canals have increased the connectivity of transportation networks, they have unfortunately also increased connectivity for aquatic biota (Rahel, 2007).

8.5.2 Control and eradication

In many situations, NIFs have established and exert negative impacts on native species. Eradication is an attractive management option, particularly where recolonisation from surrounding populations is unlikely. Eradication has sometimes been achieved in small, self-contained ecosystems. For example, introduced brown trout and brook trout have been eradicated through over-harvest in numerous high elevation Sierra Nevada (USA) lakes, allowing rapid recovery of native community structure and the endangered mountain yellow-legged frogs (*Rana muscosa*) (Vredenburg, 2004; Knapp *et al.*, 2007). Rotenone has also been used to successfully eradicate unwanted NIFs (Britton *et al.*, 2011).

Often eradication is not practical, and management efforts aim to simply control NIF populations with the goal of minimising future spread, or reducing abundance and impacts. A well-known example is the multi-million dollar sea lamprey (*Petromyzon marinus*) control programme in the Laurentian Great Lakes aimed at protecting the current mix of native and non-native fisheries (Smith & Tibbles, 1980). Introduced lake trout (*Salvelinus namaycush*) in Yellowstone Lake, Wyoming are predators on native cutthroat trout (*Oncorhynchus clarki bowieri*). Intensive lake trout removal efforts have reduced their abundance and impact, allowing native salmonids to persist (Ruzycki *et al.*, 2003). Similarly, native Lahontan cutthroat trout (*Oncorhynchus clarki henshawi*) populations appear to have increased in response to removal of introduced brook trout at Independence Lake, California (Scopettone *et al.*, 2012).

8.5.3 Restoration

NIFs and habitat alteration are inextricably linked. A key question is whether habitat restoration or invasive species control is the best option to achieve native species and ecosystem recovery. In Ash Meadows, NV, efforts to restore spring habitats back to something resembling their

pre-disturbance condition shifted fish composition from non-native back to dominance by native species (Scoppettone *et al.*, 2005). In contrast, a replicated large-scale stream restoration experiment found that native fish species showed a greater recovery in response to exotic removal than to flow restoration (Marks *et al.*, 2010; Chapter 4, Box 4.2). Stream restoration efforts, including dam removals, allow restoration of natural flow regimes and habitats and tend to strongly favour native species (Kanehl *et al.*, 1997; Marchetti & Moyle, 2001). The flip side is that river restoration also tends to increase connectivity and thus may facilitate invasive species dispersal, highlighting the two counteracting sides of increasing connectivity (Rahel, 2007; Chapter 10).

8.5.4 Management targeting

In light of the magnitude and complexity of NIFs and their impacts, there is an urgent need to more effectively prioritise and target management activities, so as to minimise the spread and impacts of NIFs. Doing so requires that we ask questions such as the following. Which NIFs are of greatest concern? Which pathways or vectors are of greatest concern? Which sites or locations are most at risk or vulnerable to future spread and impact? Which management activities are most cost-effective in reducing impacts? Ecological and economic approaches such as species risk assessments (Kolar & Lodge, 2002), ecological niche modelling (Vander Zanden & Olden, 2008) and benefit-cost studies (Naylor, 2000) fall beyond the scope of this chapter, but are useful tools for improving the decision-making process and targeting and directing management actions more effectively.

8.5.5 Potential conservation value of NIFs

While the undesirable impacts of NIFs have been widely described, NIFs can also provide conservation benefits by facilitating or serving as prey for native species, or playing a substitute ecological role formerly played by an extinct species (Schlaepfer *et al.*, 2011). While few of the examples of conservation benefits noted by Schlaepfer *et al.* involved NIFs, the reality is that NIFs are increasingly widespread, and will only continue to expand their range and their ecological role in freshwater ecosystems. Freshwater food webs will increasingly include multiple interacting introduced species. This is the real-world context under which future ecosystem management decisions will need to be made. Decisions to control or eradicate NIFs will need to carefully consider their broader role in ecosystems (Zavaleta *et al.*, 2001).

8.6 SUMMARY

Although fishes have been translocated outside of their native range for millennia, the rate of fish introductions has rapidly accelerated in parallel with the globalisation of travel and trade. There are many ultimate causes for the transport and introduction of NIFs to new waters, and as such, efforts to address the problem need to be specific to the pathways and underlying reasons for their introduction. As a result, it is not likely that there will ever be a silver-bullet solution. Interestingly, the underlying reasons for fish introductions have changed over time in many areas. For example, in much of the developed world, sanctioned stocking of game fish to new waters has declined, while aquarium releases and illegal transport of game fish by anglers appears to be on the rise.

Perhaps the most troubling feature of NIFs is their permanence once they have established. In contrast with chemical pollutants, which often diminish over time, invasive species often exhibit secondary spread following their initial establishment in a region (Vander Zanden & Olden, 2008). For many NIFs, the outlook for continued spread and impact is high, in that there is much suitable but currently unoccupied habitat (Mercado-Silva *et al.*, 2006b). Preventing the introduction of new potentially harmful species and containing already established species is the key to minimising their adverse impacts. At the same time, some NIFs may be disfavoured in changing climates (Rahel & Olden, 2008). Furthermore, NIFs are the new reality, as ecosystems are increasingly compromised by multiple interacting NIFs. In light of this, we need to continue to find creative ways to manage ecosystems, and hopefully protect native species and ecosystems in spite of the presence, and occasional dominance, of NIFs (Rosenzweig, 2003). We must also recognise that NIFs interact with other anthropogenic drivers, and that factors such as habitat loss, water quality, flow regimes, climate and harvest mediate the interactions between native and non-native fishes. We can expect rapidly changing ecosystems in the coming decades, which will continue to pose novel challenges as we attempt to conserve native fishes, and the ecosystems that sustain them.

8.7 DISCUSSION QUESTIONS

1. How might researchers tease apart the impacts of NIFs on native freshwater fishes from other factors such as habitat loss and degradation?

2. How might researchers identify the indirect effects of NIFs on native freshwater fishes?
3. Should conservationists focus on conserving native freshwater fish species, or protecting ecosystem function and processes?
4. If biotic homogenisation continues for freshwater fishes around the world, what are some possible global consequences? Are there ways to forestall this end?
5. Because we are unlikely to rid freshwaters of NIFs, how might we best approach the management and conservation of native freshwater fishes?

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