

Ecological Impacts of Non-native Freshwater Fishes

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ABSTRACT: *There is a long history of introduction of non-native fishes in fresh waters and the introduction rate has accelerated greatly over time. Although not all introduced fishes have appreciable effects on their new ecosystems, many exert significant ecological, evolutionary, and economic impacts. For researchers, managers, and policy makers interested in conserving freshwater diversity, understanding the magnitude and array of potential impacts of non-native fish species is of utmost importance. The present study provides an illustrative conspectus of the most recent literature reporting ecological impacts of non-native freshwater fishes from a wide range of species and geographic locations and concludes with a prospectus of needed areas of scientific inquiry. Both directly and indirectly, invasive fishes affect a wide range of native organisms from zooplankton to mammals across multiple levels of biological organizations ranging from the genome to the ecosystem. Although a great deal of knowledge has been recently accumulated, this body of knowledge dwarfs in comparison to what we still need to learn. Specifically, we cite the need for additional scientific inquiry to fill knowledge gaps that are principally caused by taxonomically, geographically, disciplinarily, and methodologically unbalanced approaches.*

INTRODUCTION

Freshwater ecosystems touch nearly all aspects of human society, acting as centers of organization within the landscape, providing countless cultural and ecological services, and supporting a rich diversity of biological life. The escalating need to simultaneously meet the water demands of a growing human population and ensure ecological integrity is largely why freshwater organisms are among the most imperilled faunas worldwide (Leidy and Moyle 1998; Ricciardi and Rasmussen 1999; Jenkins 2003). Non-native invasive fish species are increasingly recognized as a significant contributor to extinction threat in fresh waters, one that joins and combines synergistically with habitat loss and fragmentation, hydrologic alteration, climate change, overexploitation, and pollution (Dudgeon et al. 2006). Although not all introduced fishes become established, and the fraction of those that do often have little appreciable effects on their new ecosystems, many others exert significant ecological, evolutionary, and economic impacts (Jeschke and Strayer 2005; Ricciardi and Kipp 2008). Ecological effects have

Impactos Ecológicos de Peces Foráneos de Agua Dulce

RESUMEN: Hay una larga historia de introducciones de especies de peces foráneos de agua dulce y la tasa de introducción se ha acelerado considerablemente a través del tiempo. Si bien no todos los peces introducidos tienen efectos notables en sus nuevos ecosistemas, muchos de ellos ejercen importantes impactos ecológicos, evolutivos y económicos. Para los investigadores, administradores y tomadores de decisiones que están interesados en la conservación de la diversidad dulceacuícola, es de suma importancia entender la magnitud y alcance de los potenciales impactos de especies foráneas de agua dulce. El presente estudio provee un panorama de la literatura más reciente sobre impactos ecológicos asociados a la introducción de peces foráneos de agua dulce, de una amplia gama de especies y zonas geográficas, y se ilustra mediante un folleto las áreas de interés para la investigación científica. Directa e indirectamente los peces invasores afectan a los organismos nativos, desde el zooplancton hasta los mamíferos, a través de diversos niveles de organización biológica, desde el genoma hasta el ecosistema. Pese a que recientemente se ha acumulado gran cantidad de conocimiento, esta información queda empuñada frente a lo que aún queda por aprender. De forma particular se hace notar la necesidad de investigación científica para cubrir huecos de conocimiento que son causados principalmente por un desbalance taxonómico, geográfico, disciplinario y metodológico en los enfoques de estudio.

been shown to be severe and range from behavioral shifts of native species in the presence of invaders to the complete restructuring of food webs and the extirpation of entire faunas. For researchers, managers, and policy makers interested in conserving fish species diversity in the future, understanding the magnitude and array of potential impacts of invasive species is of utmost importance.

The ecological consequences of freshwater fish invasions have been reviewed in the past, although these investigations have been narrowly focused either in terms of geographic location, species of interest, pathway of invasion, or level of biological organization (Moyle 1976; Moyle et al. 1986; Moyle and Light 1996; Simon and Townsend 2003; Dunham et al. 2004; Eby et al. 2006; Fausch 2007; Gozlan et al. 2010). In addition, several studies have been performed to determine the characteristics and identities of fish invaders (e.g., Ruesink 2003; García-Berthou 2007). In light of these informative

studies and the recent scientific literature, we argue that the time is now ripe for synthesizing our current knowledge of the ecological impacts of invasive fishes by providing a contemporary review that fully embraces the enormity of the subject relevant to freshwater conservation efforts. An evaluation of the broader body of literature that has accumulated in the last decade is needed to inform recent debates questioning whether fish species introduction in the past have been associated with negative ecological repercussions (Gozlan 2008; Leprieur et al. 2009; Vitule et al. 2009) and, more broadly, whether deliberate translocations of species in the future is a wise conservation strategy to mitigate the detrimental effects of climate change (Olden et al. 2011). Moreover, such an evaluation can help to provide a broader context of exploring how fish invasions have provided unique opportunities to test various ecological, evolutionary, and biogeographical concepts and theories in freshwater ecology (Strauss et al. 2006; Lockwood et al. 2007; Sax et al. 2007).

Herein, we provide an illustrative conspectus of the literature reporting ecological impacts of non-native freshwater fishes across multiple levels of biological organization (ranging from the genome to the ecosystem) and conclude with a prospectus of needed areas of scientific inquiry to advance this understanding. Our investigation focuses on the negative impacts of fish introductions, although we readily acknowledge that non-native fishes have also been associated with positive outcomes (see Rodriguez 2006; Gozlan 2008). The studies and topics selected for discussion are not intended to be exhaustive but representational of our current knowledge of the ecological impacts of invasive fishes in freshwater ecosystems. We provide a general synthesis of the most recent studies followed by a narrative of key examples in the text, while additionally summarizing the recent literature (1999–2009) in the Appendix. By design, we have included examples of species from a variety of groups and geographic locations, trying to select the most emblematic case studies from the literature. Despite this, any review of species invasions is inherently constrained by the observed taxonomic and geographic biases of past investigations (Pyšek et al. 2008). Notwithstanding these issues, the impacts of non-native fishes can be substantial even though there are still considerable gaps in our knowledge, and many species and geographic locations have yet to be examined. It is our hope that the present article will help reveal priority research needs that ultimately serve to advance our scientific knowledge and development of management strategies for conserving freshwater fish diversity in light of the continued spread of non-native fishes.

LITERATURE REVIEW AND PATTERNS IN PUBLICATION ACTIVITY

We used ISI Web of Knowledge to search for published papers reporting the ecological impacts of invasive freshwater fishes. As search terms, we included all potential combinations containing (1) “invasive species” or “exotic species” or “introduced species” or “nonnative species” or “non-native species”

or “alien species” or “non-indigenous species,” and (2) “fish*,” and iii) “impact*” or “effect*” or “consequence*” or “change*.” From this initial search, we selected those articles that quantified impacts; in addition, articles were acquired by examining references lists and conducting searches to obtain an extensive sample of the most recent studies. Studies that included manipulations or experimentations in situ were classified as “experimental,” whereas studies using a distribution database obtained from field surveys were classified as “observational.”

In total, 75 articles published between 1999 and 2009 were analyzed (Appendix). We found that publication activity was greater at the individual and population levels, representing 28.6% and 26.2% of papers, respectively (Figure 1A). In general, experimental studies were more prevalent at the individual and population levels, whereas observational studies dominated community- and ecosystem-level investigations. Studies that included both observational and experimental approaches were relatively rare, ranging from 0% to 9.1% for each level of biological organization (Figure 1A). In total, our survey included 15 families (Figure 1B) and, in agreement with the findings of Pyšek et al. (2008), we observed a taxonomic bias in publication activity whereby the greatest number of studies examined Salmonidae (35.8%) and Centrarchidae (17.9%).

By way of comparison, we also sought to determine whether research activities examining the impacts of non-native fishes has changed over the past decade. In relation to a review paper by I. M. Parker et al. (1999), we observed a significant difference in the number of studies quantifying impacts at different levels of biological organization (Figure 1A, chi-square test, $\chi^2 = 153.597$, $p = 0.004$, $df = 4$). This difference was caused by a decrease in the relative proportion of studies reporting impacts at the population level (43.9% to 26.2%) and an increase at the individual (21.1% to 28.6%) and ecosystems levels (7.0% to 14.3%) over the past decade.

ECOLOGICAL IMPACTS OF NON-NATIVE FRESHWATER FISHES

Several types of ecological impacts operating across multiple levels of biological organization have been associated with freshwater fish invasions (Figure 2). Herein, we review our current state of knowledge by providing a narrative of case studies using, in large part, articles published between 1999 and 2009. Some references published before 1999 were included when they provided what we considered a unique insight into an impact.

Genetic Level

Gene Transcription Patterns

Salmon and trout (Family: Salmonidae) are among the most widely introduced fish species, in part because of their high angling and aquaculture values. For this reason they are also among the most studied freshwater invasive organism. This is well illustrated by the rainbow trout (*Oncorhynchus mykiss*)—a species that originates from the Pacific coast and that has been introduced in many places worldwide. On the

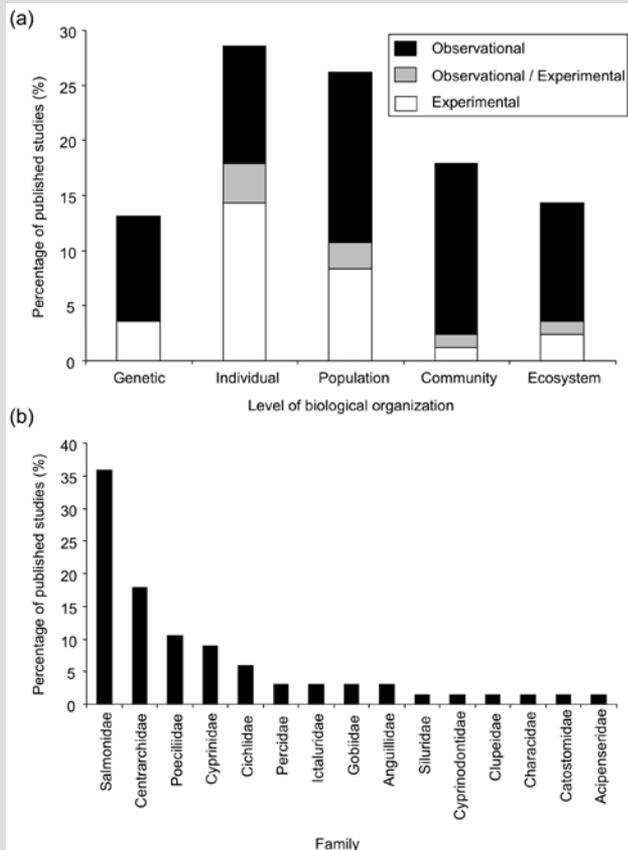


Figure 1. (a) Levels of biological organization at which the impacts of freshwater non-native fish species were reported using observational (black), observational/experimental (grey), and experimental (white) approaches. (b) Families of non-native fish species at which impacts were reported. Studies with several non-native fish species belonging to different families were not used in the taxonomic analysis. All calculations were based on 75 articles published between 1999 and 2009 (Table 1).

North American Atlantic coast, it now co-occurs with native Atlantic salmon (*Salmo salar*)—an anadromous species whose populations have strongly declined. Both species feed on drifting prey, and they are well known to compete for profitable territories in lotic habitats. In Canada, the competitive interactions of the rainbow trout have been found to disrupt the dominance hierarchies of the Atlantic salmon (Blanchet et al. 2007). Using microarray technology, Roberge et al. (2008) demonstrated that the presence of rainbow trout with Atlantic salmon led to a convergence in brain gene transcriptions between dominant and subordinate individuals of Atlantic salmon. In other words, an introduced competitor caused the suppression of gene differences between dominant and subordinate individuals. Notably, these genes are involved in oxygen transport, protein turnover, and neuronal structural change.

Hybridization and Introgression

Hybridization between native and non-native species has been reported in many fish families, leading to growing concerns of extinction risk (Rhymer and Simberloff 1996; Allen-

dorf et al. 2001). The main outcomes of hybridization between native and non-native species are threefold. First, hybridization can reduce reproduction efficiency by wasting native species gametes, which is particularly concerning when native populations are vulnerable, particularly if they are of high genetic value (e.g., isolated populations in headwater streams and lakes). A notable example can be found in many East African Lakes where isolated cichlids species (Family: Cichlidae) have evolved. In Lake Malawi, *Cynotilapia afra*, a species native to the northern shoreline, was introduced into the southern part of the lake in the 1960s by a fish exporter. There, hybridization between *C. afra* and the native *Metriaclima zebra* was observed (Streelman et al. 2004). Interestingly, the degree of hybridization was higher on the southern shoreline, which experienced greater wind exposure and low water clarity. This illustrates the potential context dependency of genetic interactions between native and non-native fish species. Second, hybridization can result in hybrid vigor that can ultimately replace the native parent population. For instance, in North America, hybrids of the native Pecos pupfish (*Cyprinodon pecosensis*) and the invasive sheephead minnow (*Cyprinodon variegatus*) were found to be ecologically superior in terms of higher growth and swimming endurance (Rosenfield et al. 2004). In Wyoming, the hybrids produced by the native flannelmouth sucker (*Catostomus latipinnis*) and the invasive white sucker (*Catostomus commersoni*) formed a “genetic bridge” between two native species by facilitating the introgression between the flannelmouth sucker and the native bluehead sucker (*Catostomus discobolus*), two populations that were initially isolated reproductively (McDonald et al. 2008). Third, hybridization can decrease genetic integrity in the native population through genetic pollution (i.e., hybrid swarms) from introgression. Muhlfield et al. (2009) demonstrated that introgression between native westslope cutthroat (*Oncorhynchus clarki lewisi*) and non-native rainbow trout in Montana decreased the fitness of the native species, a result inferred from a negative relationship between the mean number of offspring per female for westslope cutthroat trout and the degree of admixture with rainbow trout.

Individual Level

Behavior

Mounting evidence suggests that non-native fishes can modify the behavior of native species, principally when they are numerically dominant and/or more aggressive than native species in the recipient community. For example, the native Sacramento perch (*Archoplites interruptus*) was more likely to occupy closed canopy cover in the presence of the introduced bluegill (*Lepomis macrochirus*); a species displaying aggressive dominance (Marchetti 1999). This behavioral change was also associated with a decrease in growth rate due to interspecific competition. In South Africa, the native Cape galaxias (*Galaxias zebratus*) exhibited an increased use of—and abundance in—more complex microhabitats in the presence of the non-native largemouth bass (*Micropterus salmoides*; Shelton et al. 2008). Behavioral interactions between native and non-native

Ecological Impacts of Nonnative Freshwater Fishes

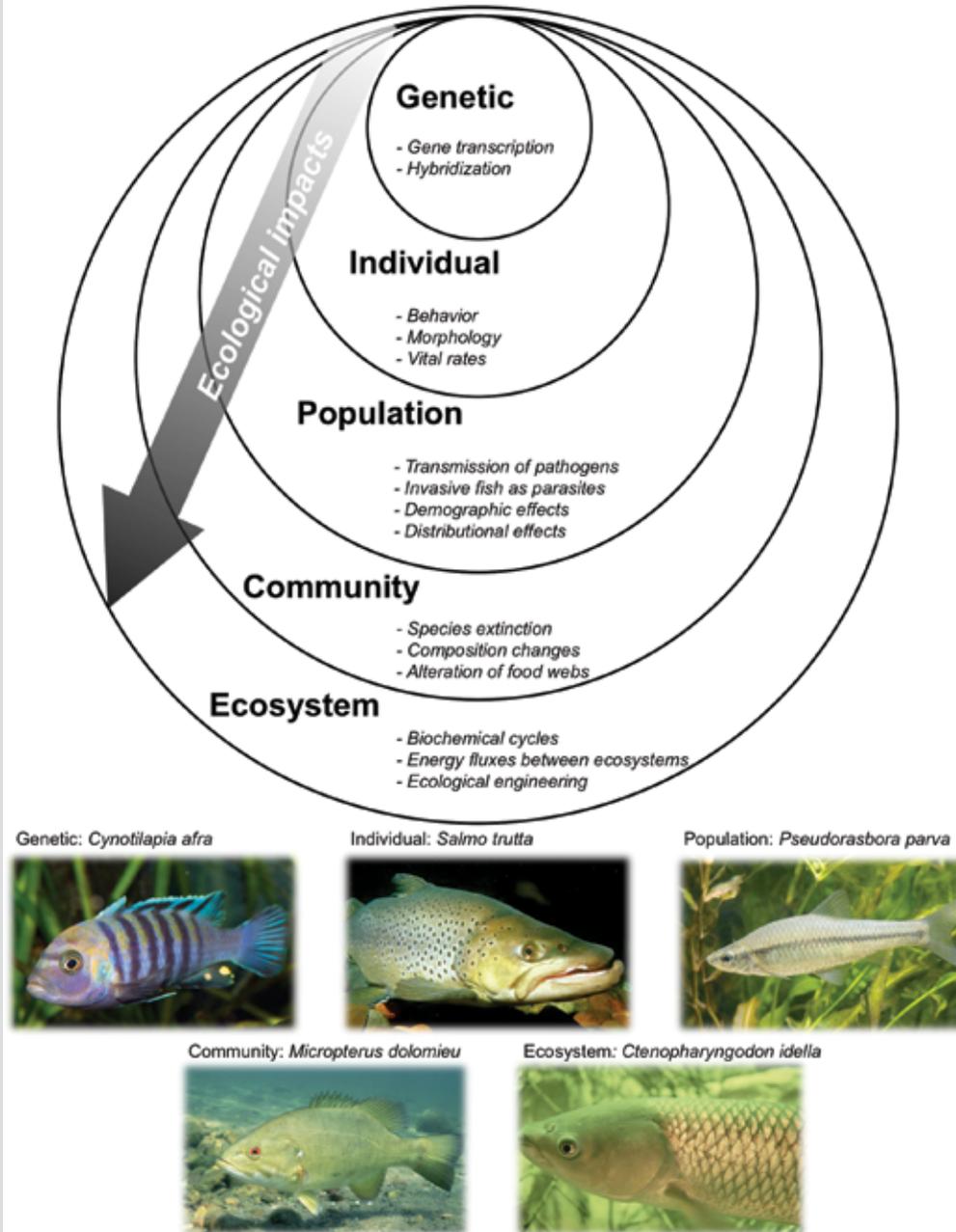


Figure 2. Schematic representation of the ecological impacts of non-native freshwater fishes at the five selected levels of biological organization (genetic, individual, population, community, and ecosystem). The black arrow indicates that the impacts of non-native fish species are often not restricted to one level but cascade across multiple hierarchical levels.

species can also induce change in diel activity of competitors and prey. A recent study by Blanchet et al. (2008) demonstrated that native Atlantic salmon fry were more active during daytime in the presence of introduced rainbow trout, a pattern hypothesized to be a result of interference competition for feeding territories. Although the modification of diel activity did not affect the rate of Atlantic salmon growth, it is thought to expose the fry to higher risk of predation. Brown trout (*Salmo*

trutta)—native to Europe and now widely introduced across the world—is considered one of the most ecologically successful salmonid species. The species success is likely due to its high degree of phenotypic plasticity and life history polymorphism, which include resident, landlocked, partially migrant, and anadromous populations. Outside of their native range, brown trout have been associated with strong ecological impacts; for example, in New Zealand streams the impacts of brown trout are well studied at different levels of biological organization (Townsend 2003), including genetic. For instance, McIntosh and Townsend (1996) experimentally demonstrated that the diel rhythm of habitat use by *Deleatidium* mayfly nymphs was affected by non-native brown trout. In the presence of native and non-native invasive fish, the number of mayfly nymphs on the upper surface of the substratum was lower than when no fishes were present, but this diminution was observed during the day in the presence of brown trout, whereas it occurred during the night in the presence of native galaxids. These behavioral changes were suggested to be caused by the different temporal patterns of predation between the two fish species.

Morphology

When non-native species are introduced into a new environment, native species face new selection pressures in which they must show rapid adaptation to ensure continued persistence (Mooney and Cleland 2001; Strauss et al. 2006). These adaptive changes can lead to a modification in morphologi-

cal traits of native prey that reduces predation risk and niche overlap with the invasive species, and minimizes the potential for competitive exclusion. In Sierra Nevada, Fisk et al. (2007) compared the morphological and life history traits of zooplankton *Daphnia melanica* in lakes with and without introduced salmonids. The authors found that the presence of salmonids induced a rapid adaptive change by reducing the body size of *D. melanica*. This decrease in body size occurred through adaptive phenotypic plasticity as a response to fish chemical cues (Latta et al. 2007). In another example, Bourke et al. (1999) measured the effects of two introduced species, the creek chub (*Semotilus atromaculatus*) and the white sucker, on the feeding morphology of brook charr (*Salvelinus fontinalis*) in lakes of the Canadian Shield in Canada. In these ecosystems, brook charr displayed resource polymorphism; that is, diet-related forms using different trophic niches (e.g., “benthic specialists” and “pelagic specialists”). The presence of non-native competitors resulted in a marked decrease in the proportion of benthic form compared to the pelagic form in charr populations (from 41.3% without introduced competitors to 19.7% when coexisting with creek chub and 9.9% when coexisting with white sucker).

Vital Rates

The small-bodied mosquitofish (*Gambusia* spp.)—a globally ubiquitous species native to the United States and Mexico that has been intentionally introduced worldwide as both a mosquito control agent and unintentionally via the aquarium trade—is among the most invasive fish. It has been repeatedly reported to invoke strong impacts on vital traits (i.e., growth and reproduction) of native species of fishes and amphibians. In Israel, *G. affinis* was observed to physically damage the endangered fire salamander (*Salamandra infraimmaculata*) by nipping at the tailfin of the larvae, which ultimately reduced the growth and survival of the salamander. As a result, none of larvae that were exposed to mosquitofish survived to metamorphosis (Segev et al. 2009). In California, Lawler et al. (1999) experimentally tested the effects of *G. affinis* on the California red-legged frogs (*Rana aurora draytonii*). In the presence of *G. affinis*, the growth rate of red-legged frogs tadpoles decreased substantially (34% less weight at metamorphosis), a result of physical injuries and a decrease in foraging activity induced by the presence of the invader. In Australia, *G. holbrooki* was found to dramatically affect the breeding of the native Pacific blue eye (*Pseudomugil signifer*) by inhibiting its growth and reducing its ovarian weight and fecundity (Howe et al. 1997). Another interesting case study is the direct and indirect effects of the invasive round goby (*Neogobius melanostomus*) on the reproduction of native fishes. Round goby is native to the Ponto Caspian region and has been introduced into Western Europe and Laurentian Great Lakes (mainly via ballast water discharge from ships) to the detriment of many native species (Corkum et al. 2004). These declines are principally due to its aggressive behavior and ability to consume the eggs and embryos of fish, subsequently reducing native species recruitment. In the western basin of Lake Erie, Steinhart et al. (2004) stud-

ied the effects of round goby on the nest guarding smallmouth bass (*Micropterus dolomieu*), a species native to eastern North America. They observed that virtually no predation of round goby occurred when the nest was guarded by smallmouth bass males. However, when nest-guarding males were removed via angling (i.e., mimicking catch-and-release recreational fishing), round goby were able to consume large numbers of unhatched embryos (average of 2,000) before the males returned. After such an event, nest-guarding males chased round gobies nine times more frequently, subsequently increasing energy expenditure and the cost of parental care. Such interactions might affect the reproductive success of the native species if energy reserves are low (Steinhart et al. 2005).

Population Level

Transmission of Pathogens and/or Parasites

Non-native species can carry non-native parasites that can infect native populations (Prenter et al. 2004). One of the most well-known and dangerous fish parasites is the Asian tapeworm (*Bothriocephalus opsarichthydis*), a pseudophyllaeid cestode that is native to China and the Amur River basin and first discovered in the intestines of grass carp (*Ctenopharyngodon idella*). Following the introduction of grass carp from China to control aquatic vegetation in the 1970s, this species was found in several native North American fishes and has since become widespread through infestation of the common carp (*Cyprinus carpio*) and its translocation along with bait fishes and *Gambusia* spp. used for mosquito control (Hoffman and Schubert 1984). After infection, Asian tapeworms are potentially fatal to multiple age-classes of fishes either through direct mortality or creating diseased and weakened individuals. In the case of endangered desert fishes of the United States, it is believed that bait introductions of infected non-native red shiners (*Notropis lutrensis*) contributed to the infestation of many native populations (Heckmann et al. 1987). The rapid life cycle and non-host specificity of this parasite allow it to spread very quickly, making it difficult to control. Another non-host-specific fish parasite, the rosette agent (*Sphaerothecum destruens*), can cause high mortalities of European sunbleak (*Leucaspis delineatus*; Gozlan et al. 2005). This intracellular eukaryotic parasite has a broad temperature tolerance (Andreou et al. 2009) and, in Europe, it is believed to be carried by the invasive topmouth gudgeon (*Pseudorasbora parva*), a highly invasive cyprinid species. Under experimental conditions of cohabitation with topmouth gudgeon, sunbleak became infected with the rosette agent and experienced mortalities exceeding 60% (Gozlan et al. 2005).

Invasive Fishes as Parasites

The parasitic sea lamprey (*Petromyzon marinus*) occurs in the North Atlantic Ocean, spawning in rivers across Europe and in hundreds of coastal drainages in North America. Sea lampreys invaded Lake Erie (1921) and the upper Great Lakes (1936–1946) following major modifications to the Welland Canal (which bypasses Niagara Falls) between Lake Erie and Lake Ontario where a native landlocked population exists

(Bryan et al. 2005). Although there are several lampreys that are native to the Great Lakes, the invasive sea lamprey is far larger and more voracious than these species. The sea lamprey has a complex semelparous life cycle in which reproductively immature sea lampreys undergo a parasitic phase during which they consume large amounts of body fluids from host fishes, often resulting in host death. In the Great Lakes, parasitic-phase sea lampreys contributed to dramatic reductions and extirpations of populations of large predatory fish, such as lake trout (*Salvelinus namaycush*). This further resulted in cascading effects that caused drastic changes throughout the food web and also contributed to the collapse of regional and commercial fisheries and immense economic impact (Smith and Tibbles 1980). Mortality caused by sea lamprey parasitism is also believed to contribute to the extirpation of three endemic coregonids in the Great Lakes (Miller et al. 1989).

Demographic Effects

There has been a rich history of salmonid introductions into high-elevation (and naturally fishless) lakes for the purpose of creating new recreational fishing opportunities. Unfortunately, these introductions have been associated with significant impacts on the receiving ecosystems, in particular some populations of amphibians (Knapp et al. 2001). Salmonid introductions have modified the structure of amphibian populations in two principal ways: directly by preying upon larvae (Orizaola and Brana 2006) and/or indirectly by facilitating a shared predator. For example, introduced trout was found to facilitate the expansion of the aquatic garter snake (*Thamnophis atratus*), which prey upon amphibians and cause additional decline (Pope et al. 2008). However, resilience of these demographic changes was observed when fishes have been removed. In an intriguing study, Vredenburg (2004) manually removed rainbow and brook trout from a series of five lakes of California and found a rapid recovery of mountain yellow-legged frog (*Rana muscosa*) populations. As a consequence of reduced predation on tadpoles, increases in the density of postmetamorphic and larval *R. muscosa* were measured within a few years after fish removal. In northern California, Pope (2008) similarly found increased young adult survival (from 59% to 94%) and recruitment and growth of Cascades frogs (*Rana cascadae*) when salmonids were removed from three lakes. Increased on-site recruitment from juvenile to adult life stages caused population resilience, and fish-removal lakes were indistinguishable from fish-free lakes within 3 years. Consequently, removal of invasive fishes in alpine lakes might contribute to the restoration of many amphibian populations and, subsequently, limit the decline.

Distributional Effects

Invasive fishes can affect the distribution of native species by decreasing their abundance through predation and by displacing them from optimal habitats through competitive exclusion. The largemouth bass originates from eastern North America and is a highly prized sport fish. As a consequence, this predatory species has been introduced in many continents,

including Europe, Asia, and Africa (Welcomme 1988). In South Korea, largemouth bass are ferocious predators of native fish species and display the highest level of piscivory (71%) reported in its native and introduced range (Jang et al. 2006). In streams located in central Zimbabwe, Gratwicke and Marshall (2001) found that largemouth bass selectively preyed upon five threatened species of small barbids (*Barbus spp.*) and strongly reduced their abundance (99%) and diversity in sites where bass were present. However, environmental conditions can mediate the competitive interactions induced by invasive fish species that create distributional changes of native species. In Spain, competition with *G. holbrooki* has been advocated as a contributor to distributional declines of the endangered Mediterranean toothcarp (*Aphanius fasciatus*) in waters with salinity >18‰. Alcaraz et al. (2008) experimentally demonstrated that increased salinity decreased the aggressiveness and food consumption of mosquitofish. These results indicate that waters with high salinity might serve as refuge for some physiologically tolerant native species against mosquitofish. Brown and brook trout are two species that have been reciprocally introduced in North America and Europe, respectively, and distributional changes with strong conservation implications have been reported in both continents. Indeed, brook trout partially replaced the native brown trout in small headwater tributaries of Northern Europe, and these habitats serve as a refuge for native brook trout when streams are invaded by brown trout in North America (Korsu et al. 2007).

Community Level

Species Extinction

Africa's Lake Victoria, the world's largest tropical lake, is the birthplace of nearly 400 native fish species, including around 350 haplochromine cichlids species considered as endemic. Traditional fisheries harvested many of these small-bodied species, although these harvests supported fisheries with only modest economic value. In an attempt to increase the economic value and use of fishes from the lake, the piscivorous Nile perch (*Lates niloticus*) was introduced into the Kenyan part of Lake Victoria in 1963. The purpose of introducing Nile perch was because the perch feeds on the small-sized haplochromine cichlids, which were at that time abundant, thereby converting the perch into a larger fish of greater commercial and recreational value (Kitchell et al. 1997). As intended, the Nile perch was a very successful predator, and populations boomed around 1980, increasing from 1% of the annual harvest in 1978 to 97% in 1987 (four times the maximum of previous fisheries for native species). Following the rapid increase in Nile perch populations, there was a severe reduction and, in some cases, total disappearance of many of the native species (Ogutu-Ohwayo 1990). Conservative estimates hold that 150–200 (or 60%) of the endemic fish species—most of which had not been fully described—are extinct (Witte et al. 1992). Many have claimed that the Nile Perch in Lake Victoria has caused the greatest vertebrate extinction known in recent times (Kaufman 1992).

Composition Change

By dissolving physical barriers to movement and connecting formerly isolated regions of the world, human-mediated species introductions have dramatically reshuffled the present-day biogeography of freshwater fishes. For example, numerous fish species of cyprinids, salmonids, cichlids, and centrachids have been introduced globally (Ruesink 2005), and highly endemic species are either threatened by or have already been driven to extinction (Harrison and Stiassny 1999). At the global scale, freshwater fish invasions have fundamentally changed the composition of major river basins (Leprieur et al. 2008a). On balance, a growing pattern is emerging, showing that the range expansion of ubiquitous nonindigenous species and the loss of endemic forms tend to be driving increasing similarity (i.e., homogenization) of fish faunas' species pools (i.e., decreasing beta-diversity) over time. In the first study of its kind, Rahel (2000) compared the species similarity of U.S. states between present-day and pre-European settlement times and found that pairs of states averaged 15.4 more species in common now than they did in the past. The high degree of biotic homogenization is best illustrated by the fact that the 89 pairs of states that historically had zero similarity (no species in common) now share an average of 25.2 species, resulting in an average present-day similarity of 12.2%. Similar broad-scale efforts have been conducted in other parts of the world. Olden et al. (2008) found that human-mediated species introductions have caused fish compositional similarity among major drainages of Australia to increase 3.0% from a historical similarity of 17.1% to a present-day similarity of 20.1%. In some cases the degree of faunal similarity between drainages doubled or even tripled with time. Patterns of homogenization were highly concordant with levels of disturbance associated with human settlement, infrastructure, and land use. A recent study in Europe has also shown that exotic and translocated native species generate distinct geographical patterns of biotic homogenization because of their contrasting effects on the changes in community similarity (Leprieur et al. 2008b). Although, species invasions have resulted in an overall increase in faunal similarity on the order of 2.2%, this study found that translocated native species (i.e., species introduced by humans into regions where they were not historically found) promoted homogenization among basins, whereas exotic species (i.e., species originating from outside Europe) tended to decrease their compositional similarity.

Alteration of Food Webs

Smallmouth bass and other centrachids species have been widely introduced to western and eastern North America and dozens of countries on nearly every continent (Welcomme 1988; Rahel 2000). The intentional introduction of bass (and other top predators) has traditionally been viewed as a form of fishery enhancement and, until recently, there has been little concern about their ecological consequences (Eby et al. 2006). In North America, adult bass are well known to be efficient piscivores that have substantial impacts on littoral prey fish diversity, abundance, and community structure (MacRae and

Jackson 2001). However, the interaction between smallmouth bass and other top piscivores, such as lake trout, were traditionally presumed to be minimal because bass inhabit nearshore, littoral areas, whereas trout inhabit offshore, pelagic areas. To address the broader food web consequences of bass introductions, Vander Zanden et al. (1999) used carbon and nitrogen stable isotopes to quantify differences in food web structure related to bass invasion. Corresponding with reduced littoral-zone prey fishes in invaded lakes (bass lakes = 2.4 species, without bass lakes = 8.2 species), lake trout (*Salvelinus namaycush*) trophic position based on $\delta^{15}\text{N}$ values was reduced, indicating a diet consisting of invertebrates rather than fish. In addition, the $\delta^{13}\text{C}$ values indicated that lake trout relied primarily on littoral prey fishes in lakes without bass (62% littoral-derived carbon) and depended on zooplankton where they are sympatric with bass (27% littoral-derived carbon), highlighting that lake trout often rely heavily on littoral prey fish. This example illustrates how the introduction of smallmouth bass has interrupted the trophic linkage of native prey fishes and lake trout (prompting lake trout to shift its trophic niche toward planktivory in the presence of bass), thus severely altering food web structure in lake ecosystems.

Ecosystem level

Modification of Biochemical Cycles

The introduction of predatory and omnivorous fish species can lead to strong modifications of nutrient (e.g., nitrogen and phosphorus) cycles by shifting the relative proportion of each trophic level (Schindler et al. 2001; Eby et al. 2006). One such example is the introduction of tilapia species that broadly originate from Africa and are now established in many tropical and temperate ecosystems. In Brazil, Figueredo and Giani (2005) found that the Nile tilapia (*Oreochromis niloticus*) modified nutrient regimes by increasing nitrogen and phosphorus availability in a reservoir via excretion, promoting algae growth, and contributing to eutrophication. By capitalizing on a massive fish kill of predominantly two invasive tilapia species (*Oreochromis niloticus* and *Tilapia rendalli*), Starling et al. (2002) quantified the role of these species in nutrient cycling in a Brazilian reservoir. After the fish kill, water quality improved greatly, with a significant decrease of chlorophyll a and total phosphorus concentrations, demonstrating that the invasive species can indirectly contribute to the occurrence of cyanobacteria blooms and water eutrophication.

Modification of Energy Fluxes between Ecosystems

Ecosystems exchange nutrients, energy, and organisms, but invasive fish species can disrupt these fluxes, both longitudinally (marine–freshwater) and laterally (aquatic–riparian). Anadromous fish species return to freshwater to spawn after a growing period in the marine environment and usually die after spawning. Anadromous-derived nutrients represent an important source for many freshwater ecosystems (Schindler et al. 2003), but large-bodied introduced predators can interrupt these fluxes by intensively preying upon anadromous fish spe-

cies. In North America and Europe, the contribution of anadromous shad (*Alosa* sp.) to the diet of large-bodied introduced catfish (*Ictalurus furcatus* and *Silurus glanis*) has been quantified using stable isotope analyses ($\delta^{34}\text{S}$ and $\delta^{13}\text{C}$). In both continents, a significant contribution of anadromous species to the diet of invasive catfish was measured, averaging 42–43% in North America and 53–65% in Europe (MacAvoy et al. 2000; Syväranta et al. 2009). Such predation can ultimately lead to a decrease of anadromous species and, consequently, a modification of energy pathways between marine and freshwater systems. Stream and riparian ecosystems are also tightly linked through reciprocal flows of invertebrates that can also be disrupted by invasive fish species. In Japan, Baxter et al. (2004) demonstrated that the introduced rainbow trout seized terrestrial prey usually eaten by the native Dolly Varden charr (*Salvelinus malma*). Consequently, the native charr were forced to shift their diet toward benthic invertebrates that feed upon algae on the stream bottom, leading to a reduction of the emergent insects from the stream to the forest. This trophic cascade decreased the density of specialist riparian spider by 65% and led to a 31% reduction in growth of native charr in experimental streams and a 75% decrease in abundance when in sympatry with rainbow trout (Baxter et al. 2004, 2007).

Habitat Alteration by Engineering Species

A number of case studies have reported that non-native fish species can act as engineering species, profoundly affecting the environment outside of their native range. Perhaps the best example of this phenomenon comes from two species of cyprinids—the common carp and the grass carp (e.g., Koehn 2004; Pipalova 2006). The common carp modifies aquatic vegetation (submerged macrophytes) directly through uprooting or herbivory and indirectly through bioturbation and excretion, ultimately shifting the trophic status of water from clear to turbid (Roberts et al. 1995; Matsuzaki et al. 2009). Another example comes from salmonid species that dig large redds in river beds during spawning (Moore 2006). In New Zealand, redd construction by invasive Chinook salmon (*Oncorhynchus tshawytscha*) was found to decrease the abundance of mosses, algae, and macrophytes and of fines and detritus, leading to a geomorphic modification of pool-riffle sequences (Field-Dodgson 1987). This was ultimately associated with a strong decrease in the abundance (but not the structure) of benthic invertebrates.

PROSPECTUS

Recent investigations on non-native freshwater fishes have confirmed the existence of significant ecological impacts across multiple levels of biological organization from genes to ecosystems. Although it is clear from our synthesis that we know a reasonable amount about the impacts of fish invasions, it is safe to say that this body of knowledge dwarfs in comparison to what we still need to learn. Perhaps the greatest truism in invasion biology is that species invasions are generally irreversible and that once a new non-native species establishes,

it is almost impossible to eradicate without excessive collateral damage on native species (Myers et al. 2000). For this reason, it is clear that invasive species prevention must be the cornerstone of most management strategies (Vander Zanden and Olden 2008). With this in mind, there are two stark realities when dealing with invasive fish species. First, freshwater fishes have been introduced virtually to all ecosystems across the globe, and many (if not, most) of these populations will never be eradicated. Second, even with the best prevention strategies and management policies in place, introduction of new non-native fish species will inevitably occur. These inescapable certainties mean that the conservation of native species will necessarily involve the management of mixed assemblages of native and non-native species, and future research should aim at filling knowledge gaps that support the management actions of decision makers (Copp et al. 2009; Leprieur et al. 2009).

Given the current state of knowledge, we cite the need for additional scientific inquiry in the following core areas:

1. Increase our scientific understanding of the potential ecological impacts of non-native fishes for species of concern and in geographic regions that are poorly studied. Based on an extensive literature review, Pyšek et al. (2008) found that our current knowledge 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).
2. Obtain a more balanced perspective on the ecological impacts of fish invasions across levels of biological organization. Past research has focused unevenly on individual- and population-level responses, with less emphasis on the genetic and ecosystem consequences (this study; Parker et al. 1999).
3. Account for methodological bias and conscientiously interpret the results obtained from experimental and observational-based approaches. Experimental approaches promote mechanistic understanding but often fail at revealing the context dependency of impacts from invasive species. By contrast, observational-based approaches are often more realistic, but their conclusions can be blurred by other natural and human-induced perturbations. Well-designed studies that couple experimental and observational-based approaches are likely to return the greatest advancement.
4. Elucidate the adaptive and evolutionary responses of native species to the presence of invasive species and vice versa (Mooney and Cleland 2001; Strauss et al. 2006); we have little understanding in this area. Non-native species encounter a range of non-coevolved enemies and competitors in their introduced range, and evolutionary novelty is a key determinant of the ecological outcomes of these interactions. But who benefits from this novelty? Research into how evolutionary novelty enhances or suppresses non-native invasions and native resistance and the under-

lying genetic basis to these patterns is needed.

5. Improve our understanding of how other facets of environmental change (e.g., habitat degradation, land-use change, climate warming) interact with invasive species and result in additive, synergistic, or antagonistic effects on native species and ecosystems (Rahel and Olden 2008; Ormerod et al. 2010). To date, these interactions have rarely been explored.

In conclusion, we believe that advancements in these areas of research will reduce current levels of uncertainty in the assessment of ecological risks posed by non-native freshwater fishes and optimize the conservation of imperilled freshwater ecosystems.

ACKNOWLEDGMENTS

J.C. was supported by the European Community's Seventh Framework Programme (FP7-PEOPLE-2007-2-1-IEF under grant agreement no. PIEF-GA-2008-219558) and acknowledges the Fisheries Society of the British Isles in supporting his travel to visit the laboratory of J.D.O. J.D.O. acknowledges funding support by the USGS Status and Trends Program, USGS National Gap Analysis Program, and the U.S. Environmental Protection Agency Science to Achieve Results (STAR) Program (Grant No. 833834).

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APPENDIX. Examples of ecological impacts of non-native freshwater fishes across different levels of biological organization (LBO)—genetic (G), individual (I), population (P), community (C), and ecosystem (E)—published between 1999 and 2009

Invasive Species	Native Species	Country	Effects on the native species and/or ecosystem	LBO	Reference
Acipenseridae					
<i>Acipenser baerii</i>	<i>Acipenser ruthenus</i>	Germany	Hybridization with non-native hatchery escapees	G	Ludwig et al. 2009
Anguillidae					
<i>Anguilla japonica</i>	<i>Anguilla anguilla</i>	UK Hungary	Swimbladder parasite <i>Anguillicola crassus</i> induces: More pronounced stress response to severe hypoxia Reduction of swimming performances	P	Gollock et al. (2005) Palstra et al. (2007)
Catostomidae					
<i>Catostomus commersoni</i>	<i>Catostomus latipinnis</i> <i>Catostomus discobolus</i>	United States	Hybridization that subsequently facilitated introgression between the two native species	G	McDonald et al. (2008)
Centrarchidae					
<i>Lepomis gibbosus</i>	Eight invertebrates taxa	The Netherlands	Decreased abundance	P	van Kleef et al. (2008)
<i>Lepomis macrochirus</i>	<i>Archoplites interruptus</i>	United States	Increased use of closed canopy and decreased growth	I	Marchetti (1999)
—	<i>Pseudacris regilla</i>	—	Shallower tail depth and lower activity	I	Benard (2006)
<i>Lepomis microlophus</i>	<i>Lepomis gibbosus</i> Multiple snail species	—	Decreased abundance and dietary change Decreased biomass	P & C	Huckins et al. (2001)
<i>Micropterus dolomieu</i>	<i>Culaea inconstans</i> <i>Pimephales promela</i> <i>Margariscus margarita</i>	Canada	Change of habitat use, reduced abundance and local extirpation	I & P	MacRae and Jackson (2001)
<i>Micropterus salmoides</i>	<i>Barbus spp</i>	Zimbabwe	Reduced abundance and diversity from predation	P	Gratwicke and Marshall (2001)
—	<i>Galaxias zebratus</i>	South Africa	Increased use of complex microhabitats	I	Shelton et al. (2008)
—	<i>Monodactylus falciformis</i> <i>Mugil cephalus</i> <i>Myxus capensis</i>	—	Predation during freshwater migration	E	Weyl and Lewis (2006)
—	Multiple species	South Korea	Decrease abundance of native piscivores	P	Jang et al. (2006)
<i>Micropterus dolomieu</i> <i>Ambloplites rupestris</i>	<i>Salvelinus namaycush</i>	Canada	Increased consumption of invertebrates (rather than fish) and reduced trophic position	C	Vander Zanden et al. (1999)
<i>Micropterus salmoides</i> <i>Lepomis macrochirus</i>	Multiple species	Japan	Decreased density of fish, crustaceans and odonates through trophic cascade	P & C	Maezono and Miyashita (2003)
Characidae					
<i>Astyanax fasciatus</i>	<i>Gambusia sexradiata</i> <i>Cyprinodon spp.</i>	Mexico	Decreased abundance, most likely from predation	P	Strecker (2006)
Cichlidae					
<i>Cynotilapia afra</i>	<i>Metriaclima zebra</i>	Malawi	Hybridization environmentally mediated	G	Streelman et al. (2004)

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APPENDIX. (continued)

Invasive Species	Native Species	Country	Effects on the native species and/or ecosystem	LBO	Reference
<i>Oreochromis</i> sp.	<i>Cyprinodon</i> spp.	Mexico	Increased infestation by a trematode and a nematode	P	Strecker (2006)
<i>Oreochromis niloticus</i>	Multiple species	Brazil	Eutrophication through increased N and P availability	E	Figueredo and Giani (2005)
<i>Oreochromis niloticus</i> <i>Tilapia rendalli</i>	Multiple species	—	Eutrophication and cyanobacteria blooms	E	Starling et al. (2002)
Clupeidae					
<i>Dorosoma petenense</i>	<i>Micropterus salmoides</i> <i>Lepomis macrochirus</i> <i>Menidia beryllina</i>	United States	Diet change and increased Hg concentration	C & E	Eagles-Smith et al. (2008)
Cyprinidae					
<i>Pseudorasbora parva</i>	<i>Leucaspis delineatus</i>	UK	High mortality induced by <i>Sphaerothecum destruens</i>	P	Gozlan et al. (2005)
<i>Cyprinus carpio</i>	Multiple species	Australia	Bioturbation: increased suspended solids and nutrients Decreased abundance of macroinvertebrates	E	Koehn (2004)
		Japan		P	Matsuzaki et al. (2009)
<i>Ctenopharyngodon idella</i>	Multiple species	N/A	Increased nutrient availability through excretion Decreased aquatic vegetation	E	Pipalova (2006)
<i>Carassius auratus</i>	<i>Carassius carassius</i>	UK	Some populations without pure individuals	G	Hanfing et al. (2005)
<i>Ptychocheilus grandis</i>	<i>Cottus aleuticus</i> , <i>C. asper</i>	United States	Increased mortality and decreased density	I & P	White and Harvey (2001)
Cyprinodontidae					
<i>Cyprinodon variegatus</i>	<i>Cyprinodon pecosensis</i>	United States	Hybrids with higher growth and swimming endurance	G	Rosenfield et al. (2004)
Gobiidae					
<i>Neogobius melanostomus</i>	<i>Micropterus dolomieu</i>	Canada	Predation of unhatched embryos Increased energy expenditure and cost of parental care	I	Steinhart et al. (2004) Steinhart et al. (2005)
Ictaluridae					
<i>Ictalurus furcatus</i>	<i>Alosa</i> sp.	United States	Predation of anadromous spawners	E	MacAvoy et al. (2000)
<i>Ameiurus melas</i>	<i>Esox lucius</i>	France	Reduced predatory success	I	Kreutzenberger et al. (2008)
Percidae					
<i>Etheostoma zonale</i>	<i>Etheostoma olmstedii</i>	United States	Increased buccal cavity length Habitat selection change from large to small substrate	I	Carlson (2008) Gray and Stauffer (2001)
Poeciliidae					
<i>Gambusia affinis</i>	<i>Rana aurora draytonii</i>	United States	Reduced growth due to injuries and reduced activity	I	Lawler et al. (1999)
—	<i>Linderiella occidentalis</i>	—	Reduced survival from predation	I	Leyse et al. (2004)
—	<i>lotichthys phlegethontis</i>	—	Differences in daytime and nighttime habitat use	I	Ayala et al. (2007)
—	<i>Salamandra infraimmaculata</i>	Israel	Reduced growth and survival due to physical damage	I	Segev et al. (2009)
<i>Gambusia holbrooki</i>	<i>Rhadinocentrus ornatus</i>	Australia	Increased activity and change in microhabitat use	I	Keller and Brown (2008)

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APPENDIX. (continued)

Invasive Species	Native Species	Country	Effects on the native species and/or ecosystem	LBO	Reference
—	<i>Aphanius fasciatus</i>	Spain	Reduced distribution. Competition mediated by salinity	P	Alcaraz et al. (2008)
—	<i>Aphanius iberus</i>	—	Reduced offspring production	I	Rincón et al. (2002)
Salmonidae					
<i>Coregonus albula</i>	<i>Daphnia</i> spp. <i>Bosmina</i> spp.	Norway	Increased clutch size and decreased body size of females Elimination of <i>Daphnia longispina</i>	I & C	Amundsen et al. (2009)
<i>Salmo trutta</i>	<i>Salvelinus leucomaenis</i>	Japan	Hybridization	G	Kitano et al. (2009)
—	<i>Oncorhynchus clarkii</i>	United States	High degree of diet overlap	C	McHugh et al. (2008)
<i>Salvelinus fontinalis</i>	<i>Hesperodiaptomus arcticus</i> <i>Daphnia middendorffiana</i>	Canada	Species elimination (and recovery after fish removal)	C	B. R. Parker et al. (2001)
—	<i>Salmo trutta</i>	France Finland	Hybridization and redd superimposition Trophic niche shift Exclusion from tributaries and reduced reproduction	G C P	Cucherousset et al. (2008) Cucherousset et al. (2007) Korsu et al. (2007)
<i>Salvelinus namaycush</i>	<i>Oncorhynchus darki bouvier</i>	United States	Decreased migrating individuals and lower bear activity	E	Koel et al. (2005)
<i>Oncorhynchus mykiss</i>	<i>Salmo salar</i>	Canada	Modification of transcription patterns of genes Increase of daytime activity Disruption of hierarchical relationships	G I —	Roberge et al. (2008) Blanchet et al. (2008) Blanchet et al. (2007)
—	<i>Bufo boreas</i>	United States	Mortality induced by <i>Saprolegnia ferax</i>	P	Kiesecker et al. (2001)
—	<i>Salvelinus malma</i>	Japan	Reduced growth and abundance, diet shift Trophic cascade: reduced density of riparian spiders	P & C E	Baxter et al. (2007) Baxter et al. (2004)
—	<i>Oncorhynchus clarkii</i>	United States	Hybrids decreased juvenile growth	G & I	Seiler and Keeley (2009)
<i>Oncorhynchus mykiss</i>	<i>Oncorhynchus clarkii lewisi</i>	United States	Introgression related to elevation and stream width Decreased fitness with increased degree of admixture	G	Weigel et al. (2003)
<i>Oncorhynchus mykiss</i> <i>Salvelinus fontinalis</i>	<i>Rana muscosa</i>	—	Population decline and predation on juveniles	P	Muhlfeld et al. (2009)
<i>Oncorhynchus mykiss</i> <i>Salmo trutta</i> <i>Salvelinus fontinalis</i>	<i>Rana muscosa</i> Benthic macroinvertebrates Large crustacean zooplankton	—	Dramatic reduction of distribution and abundance but high resilience observed after fish removal	P	Knapp et al. (2001)

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APPENDIX. (continued)

Invasive Species	Native Species	Country	Effects on the native species and/or ecosystem	LBO	Reference
<i>Salvelinus fontinalis</i>	<i>Daphnia melanica</i>	—	Rapid adaptive reduction of body size as a response to fish chemical cues	I	Fisk et al. (2004) Latta et al. (2004)
—	<i>Triturus helveticus</i> <i>Triturus alpestris</i> <i>Triturus marmoratus</i>	Spain	Reduced distribution and abundance due to increased larval mortality	I & P	Orizaola and Brana (2006)
—	<i>Rana cascadae</i>	—	Additional decline due to predation by the snake (<i>Thamnophis atratus</i>) whose expansion is facilitated	P	Pope et al. (2008)
—	Multiple species	United States	Alteration of nutrient (P) cycles Stimulation of algal production	E	Schindler et al. (2001)
Multiple species	Multiple fish species	Chile	Decreased relative abundance	P	Arismendi et al. (2009)
Siluridae					
<i>Silurus glanis</i>	<i>Alosa alosa</i>	France	Predation of anadromous spawners	E	Syväranta et al. (2009)
Multiple Families					
Catostomidae <i>Catostomus commersoni</i>	<i>Salvelinus fontinalis</i>	Canada	Decreased proportion of benthic-specialist form	I	Bourke et al. (1999)
Cyprinidae <i>Semotilus atromaculatus</i>					
Characidae <i>Pygocentrus nattereri</i>	N/A	Brazil	Change in zooplankton community and species loss	C	Pinto-Coelho et al. (2008)
Cichlidae <i>Cichla cf. ocellaris</i>					
Characidae <i>Pygocentrus nattereri</i>	Multiple species	Brazil	Reduced species richness and diversity	C	Latini and Petrere (2004)
Cichlidae <i>Cichla cf. monoculus</i>					
Cichlidae <i>Astronotus ocellatus</i>					
Cyprinidae, Ictaluridae, Percidae	N/A	New Zealand	Reduced water clarity in lakes	E	Rowe (2007)
Multiple species	Multiple species	Spain Portugal	Mean increase in faunal similarity of 17.1%	C	Clavero and García-Berthou (2006)
Multiple species	Multiple species	Europe	Mean increase in faunal similarity of 2.2%	C	Leprieur et al. (2008b)
Multiple species	Multiple species	Australia	Mean increase in faunal similarity of 3.0%	C	Olden et al. (2008)
Multiple species	Multiple species	United States	Mean increase in faunal similarity of 7.2%	C	Rahel (2000)