

River Conservation Challenges and Opportunities

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The Problem of Invasive Species in River Ecosystems

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The Problem of Invasive Species in River Ecosystems

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Invasive nonnative species are a major problem in river ecosystems, and have large ecological and economic costs. Few ecosystems can resist invasions. The species that tend to invade most readily are those that humans introduce the most, and the ecosystems they invade are those with the most human activity. Most invasions are irreversible, and control is expensive, so efforts should be focused on prevention of future invasions.

8.1. The problem of biological invasions in rivers

The number of new species invading ecosystems has exploded in the last 50 years, primarily because of the increase in human transportation and shipping. These forces have broken down natural barriers that previously prevented organisms from moving around the globe. Although humans have brought plants and animals of interest to new regions for thousands of years, the scale and speed of these introductions has recently increased exponentially, similar to the pace of human population growth and resource use.

Biological invasions have been especially rapid in freshwater ecosystems, where nonnative species now make up a substantial proportion of the fauna in many

regions (Moyle and Marchetti 2006). For example, across large regions like the Pacific Northwest of North America, southwestern Europe, central Eurasia, South Africa, and southern Australia, nonnative freshwater fish make up more than a quarter of all fish species in river basins and in some cases up to 95% (Leprieur et al. 2008). In contrast, in most continental regions of similar size the percentage of nonnative plants is < 25% (Vitousek et al. 1996).

Why are invasions so prevalent in freshwaters, including rivers and streams? First, most aquatic habitats have been highly modified by human actions, reducing native species and creating conditions suitable for tolerant nonnative fishes (Rahel 2003). Second, introductions of fishes and other freshwater organisms have been common and frequent, both intentionally for food or sport and inadvertently by creating canals or other connections between waterways. Larvae of most fish and invertebrates are tiny, and so are easily transported without notice when ships release ballast water, or when fish are stocked from hatcheries. In addition, anglers are now illegally introducing many species that they value highly for sport fishing.

But how important can these freshwater invasions be? After all, many people enjoy catching and eating fish, whether they are native or nonnative. Unfortunately, invasions in freshwater ecosystems can cause extensive problems for regional economies, human health, and the integrity of ecosystems. Many of the largest losses are caused by invertebrates that live in freshwaters for at least part of their life cycle. Asian tiger mosquitos (*Aedes albopictus*), which have invaded North America and Europe, are vectors for the viruses that cause dengue and yellow fever, among the most important human diseases in the tropics. The zebra mussel (*Dreissena polymorpha*), originally native to the Black, Caspian, and Azov seas, invaded North America via ballast water releases and Europe by a combination of pathways, including canals and shipping. These tiny mussels clog water intakes, and require hundreds of millions of US dollars to control (Strayer 2009). In addition, their filtering is altering river and lake ecosystems, by reducing phytoplankton and increasing macrophyte biomass, thereby altering entire food chains that support important commercial and sport fisheries. The introduction of Nile perch (*Lates niloticus*) in Lake Victoria is thought to have caused the greatest modern human-caused mass extinction of vertebrates by extirpating dozens of endemic cichlid fishes through predation. It is clear that invasions in freshwaters are major problems.

Ecologists now agree that nonnative species invasions are among the leading causes of biodiversity loss worldwide, falling not far behind direct habitat destruction (Vitousek et al. 1996). The world's freshwaters make up a tiny fraction of the water on earth, but support a large proportion of aquatic biodiversity, primarily



Figure 8.1:
Aquatic invaders can cause extensive damage to ecosystems, human health, and regional economies. Clockwise from upper left: Asian tiger mosquito, zebra mussels, rainbow trout, Nile perch

because their relative isolation allowed many more species to evolve (Dudgeon et al. 2006). Moreover, the loss of biodiversity is higher for organisms that inhabit freshwater ecosystems compared to terrestrial ones. For example, between a third and three-quarters of all fishes, crayfishes, and freshwater mussels in the U.S. are imperiled or extinct. Together, these two facts suggest that nonnative species invasions are a greater problem in freshwaters than terrestrial or marine ecosystems.

In this chapter we review this important issue in river conservation, focusing on the principles governing invasions in flowing-water ecosystems and how human-caused stressors change the causes and effects of invasions. We show that invaders can have important effects on many levels, from local extinction of native species to changes in ecosystem services. We compare the patterns of invasion in two highly-invaded regions, namely the Iberian Peninsula and the Colorado River Basin, and consider lessons learned. Finally, we summarize the implications of these lessons for river conservation, and discuss priorities

for management. We focus on inland fishes but also provide examples from of other groups of freshwater organisms.

8.2. Principles for invasions in river ecosystems

Ecologists have worked for many decades to answer two main questions about biological invasions of most interest to managers: 1) Which ecosystems are most likely to be invaded?; and 2) Which species are likely to invade next? The upshot of all this research is that invasions are not easy to predict, there are typically no simple answers, and some answers are paradoxical. Nevertheless, some general principles have emerged for aquatic ecosystems, including rivers, lakes, and reservoirs.

First, analyses for several large areas in North America show that virtually all aquatic ecosystems, even those with many native species already, can be invaded (Moyle and Marchetti 2006). There is little evidence that those with more native species are somehow “saturated” and can resist invasions by nonnatives (Gido and Brown 1999). This is perhaps not surprising, because freshwaters worldwide support about 126,000 (9.5%) of the more than 1.3 million animal species described, including about 12,500 fish species. Many new species are available to enter every ecosystem.

Although all ecosystems are invulnerable, several factors tend to foster invasions in some more than others. Paradoxically, these have more to do with human factors than characteristics of the ecosystems or the species themselves. For example, lakes and reservoirs have been a main target of fish introductions, because anglers prefer to fish there, people enjoy them for recreation, and because reservoirs are wrongly seen as creating “empty ecological niches” that should be stocked with fish or invertebrates. However, reservoirs are nearly always fed or drained by rivers, as are many lakes, creating a perfect source for nonnative species invasions into flowing waters. Many fish invasions into reservoirs or headwater lakes have spread throughout entire river basins by connecting channels, especially in the downstream direction. And, because reservoirs are often the target for stocking, rivers and streams that are impounded by dams often have higher richness and abundance of invasive species (Marchetti et al. 2004). In contrast, some headwater streams have fewer nonnative species, either because they have received fewer introductions, or because natural or artificial barriers have prevented invaders from moving upstream into them (Fausch et al. 2009).

Ecologists have spent many years attempting to predict which fish and invertebrates will invade different aquatic ecosystems, the second main question of

interest. Many biological traits of nonnative species, such as temperature tolerance or body size, can be important determinants of their invasion success in particular water bodies. However, the best predictors for invasions are usually simply those species that are of interest to humans, and either are readily available or occur nearby. For example, rainbow trout (*Oncorhynchus mykiss*) have been introduced to nearly 100 countries worldwide for angling and are cultured in many for food. As a result, this species is much more likely to be introduced and invade in coldwater streams than many other small coldwater fishes which are restricted to certain regions and are never cultured or angled. In contrast, zebra mussels, New Zealand mudsnails (*Potamopyrgus antipodarum*), and the invasive algae *Didymosphenia geminata*, are more likely to be transported by humans on boats or gear to nearby waters than to those farther away, although long-distance transport is certainly possible.

One of the best predictors of which species will invade is simply those that are introduced most often (Simberloff 2009). Ecologists use the term “propagule pressure”, a combination of the number of organisms introduced and the number of times introductions are made. Propagule pressure is typically very high for introductions in aquatic systems compared to many terrestrial ones, for several reasons. First, large numbers of tiny fish and invertebrate larvae can be carried inadvertently when water is transferred among natural water bodies. Second, aquatic organisms like fish have many eggs and tend to be easy to raise in aquaculture, compared to birds or mammals, so many thousands can be produced for stocking. A third is that because freshwater ecosystems provide so many important ecological services to humans (recreation, transportation, irrigation), both water and fish are often transferred among them, increasing the frequency that nonnative organisms are introduced.

Human interest and activity often drive invasions (Marchetti et al. 2004). In general, humans introduce a very small percentage of the 12,500 freshwater fish species, focusing on those that are preferred or have been successful in the past, such as brown trout (*Salmo trutta*), common carp (*Cyprinus carpio*), and mosquitofishes (*Gambusia affinis* and *G. holbrooki*). These species are known to survive and reproduce in many waters, so they make up a small set of cosmopolitan species that are of interest to humans and become frequent invaders. In addition, because many introductions of fish to rivers are intentional, and nowadays often illegal, people that introduce them know well where certain species will be able to survive and reproduce. In particular, illegal stocking by anglers has recently become the most potent source of fish invasions (see Box 8.1). As a result, on a global scale human activity is a better explanation for where fish invasions occur than are either the number of native species that could resist invasions, or the characteristics of the environment that might resist or foster them (Leprieur et al. 2008).

Invading species not only drive native species locally extinct, but can also reduce the flow of nutrients and food resources in river food webs, and even into the riparian zone

Figure 8.2:
Illegal stocking by anglers of predators like the European catfish (Silurus glanis) is now a major source of fish invasions



A final principal common to all invasions is a key paradox. Although few of the species that are transported to new locations become established and cause damage, those few that do can be very costly. Most species that arrive in new regions are not introduced to the wild, most species that are introduced do not establish, and most that establish do not become pests. However, costs for damage and control of invasive species were already hundreds of billions of dollars for a small subset of developed countries a decade ago (Simberloff et al. 2005), and can only rise. In addition, because many introductions to freshwaters are intentional (e.g. fish and crayfish for food or angling), propagule pressure is high, and humans are able to match habitats closely for well-known invaders, invasions in aquatic ecosystems are becoming a major force in global ecological change.

Biotic homogenization is a relatively new term used to describe the spread and dominance by the relatively small set of cosmopolitan species that humans introduce to other ecosystems (Olden 2006). Loss of rare species found only in specific locations, called endemic species, also contributes to this pattern of the increasing similarity of the earth's biota. However, most of this increasing similarity among freshwater fishes is driven by the invasion and spread of nonnative species, rather than the local extinction of rare endemics (Gido and Brown 1999; Rahel 2003). For example, the 48 states in the conterminous U.S. now share 15.4 more species on average that they did originally (a 7%

Illegal fish stocking by anglers is the most important new source of intentional fish invasions

During 1850-1980, most of the purposeful introductions of fish to new waters throughout the world were conducted by government fisheries management agencies. However, given the burgeoning problems with invasive species, and better education and awareness, most fisheries management agencies have sharply curtailed introduction of nonnative species. An exception to this is the continued stocking of nonnative trout, especially rainbow trout, which in some regions are treated as a native or naturalized species.

However, a major new source of purposeful introductions is from illegal stocking by anglers. For example, unauthorized introductions in seven regions throughout the USA made up 90% of new fish introductions during 1981-1999, compared to only 15-43% during all previous periods. Similar trends are apparent in Europe and Australia (Johnson et al. 2009). Live fish wells in boats coupled with sophisticated knowledge and communication by anglers have made it easier than ever to move live game or bait fish to new bodies of water where anglers perceive that sport fisheries could be improved by introducing nonnative fishes.

Why do anglers stock illegally? One reason may be that anglers assume that stocking is not a problem, given that fisheries management agencies also have stocked nonnative fishes in the past, and sometimes do currently (Johnson et al. 2009). In addition, public education of the risks of stocking is often only rudimentary, and penalties are

modest, averaging less than US\$3,000 across 12 western states where problems are the greatest. Finally, agencies often fail to respond strongly to illegal stocking, in some cases even setting angling regulations to encourage sport fishing for the new species. This can also encourage angler groups that advocate for the new game fish, making future eradication politically impossible.

What problems does illegal stocking cause? Like other invasions by aquatic organisms, illegally stocked game or forage fish cause large losses to native fish assemblages, and to established sport fisheries based on managed or unmanaged nonnative fishes. When new nonnative species become established, they also provide sources for invasions elsewhere, and foster more illegal stocking. Costs for eradication or control of the nonnatives are huge. Eradication of nonnative northern pike (*Esox lucius*) twice from one California lake cost US\$33 million. Lake trout (*Salvelinus namaycush*) illegally stocked by anglers invaded Yellowstone Lake in Yellowstone National Park, and the lost revenue from fisheries for native trout alone will approach US\$1 billion over 30 years, not to mention the US\$300,000 per year for lake trout eradication. Likewise, the invasions themselves can invalidate recovery programs for threatened native fish species that cost tens of millions of US dollars (Johnson et al. 2009).

What can be done to reduce illegal stocking? Fisheries management agencies will need to set responsible policies for their

**Box 8.1 (cont.):
Illegal fish stocking
by anglers is the most
important new source
of intentional fish
invasions**

own stocking of nonnative fishes, and communicate the reasons for these to the public. They will also need to set uniformly strict regulations against illegal stocking, and holding or transporting live fish, as well as impose large fines that reflect the huge economic costs that illegal stocking causes. For example, Canada imposes a maximum fine of US\$100,000 for illegal stocking, which is still far short of the cost required

for eradication in most waters (Johnson et al. 2009). For anglers who are unaware of the risks, articulate and balanced messages that are widely distributed can help curb illegal stocking (see: <http://stopstocking.cowyafs.org/>). However, for those prone to vandalize waters, severe sanctions, large rewards for witnesses, and showcasing convictions will be needed to reduce the impetus for these acts.

increase in similarity), owing to introductions for sport fishing or aquaculture (Rahel 2003). Common carp, goldfish (*Carassius auratus*), brown trout, and rainbow trout are the species most widely introduced in this region. Similarly, fish assemblages in the Iberian Peninsula are 17% more similar now than originally, owing primarily to introductions from France of top predator fishes, like European catfish (Clavero and Garcia-Berthou 2006). Overall, these invasions by cosmopolitan species support the contention that few aquatic systems are “saturated” with species, and invaders that are pre-adapted for either natural or altered conditions are likely to invade if transported and released in sufficient numbers.

8.3. Human stressors that can change the outcome of invasions

The principles described above help ecologists understand and predict the general patterns of invasions in rivers, but other anthropogenic stressors can change the outcome of species introductions in specific locations. Ecologists are well aware that natural environmental factors can affect whether nonnative species become established, and how strongly they affect other species. For example, invasions of nonnative trout in North America are more common in regions where the seasonal flooding regime matches that in their native rivers than in regions where they do not match (Fausch 2008). Here we focus instead on how anthropogenic stressors can potentially change the outcome of invasions. English ecologist Charles Elton, who pioneered the field of invasion biology, gave the first example of this when he reported that invasions are common in habitats that have been degraded by humans, although many ecologists forget he also pointed out that species can invade pristine habitats. Nevertheless, various ecologists have inferred from Elton’s idea that restoring habitat quality

and natural processes may help reduce nonnative species abundance, or the risk of future invasions.

8.3.1. ALTERED FLOW REGIMES

Natural patterns of stream flow are expected to favor native species that are adapted to the natural “disturbance regime”, whereas nonnative species may be favored when hydrologic conditions are altered (Poff et al. 1997). For example, nonnative fishes are reduced by natural flash floods in southwestern USA desert streams, apparently because they lack appropriate capacity for seeking refuges. Mosquitofish are an aggressive predator that can extirpate native topminnows, and were favored in desert streams where floods were damped by hydrologic alteration. Similarly, nonnative fish were reduced in years of higher summer flows in a central California river with Mediterranean climate. However, years with lower flows and warmer temperatures favored nonnatives like largemouth bass (*Micropterus salmoides*) and common carp that spawned during summer. Nonnative crayfish were also reduced by natural floods in an eastern California mountain watershed.

Altered flows can also shift the balance for native and invading riparian plants, although the effects differ between them. Nonnative tamarisk (*Tamarix ramosissima*) has invaded many rivers of the southwestern USA, whereas native cottonwood (*Populus deltoides*) has simultaneously declined. Cottonwood seeds require moist bare sand created by natural floods to germinate, and high water tables caused by the floods to survive as seedlings. A wide-ranging comparative study showed that cottonwood seedlings are very sensitive to altered flows, and declined to low levels even with modest flow alteration (Merritt and Poff 2010). In contrast, tamarisk can invade under altered flows, because its seedlings can survive under more variable flow conditions than cottonwood. However, tamarisk can also invade under natural flow regimes, wherein the two species may achieve about equal abundance. Elton suggested that this scenario may be common, where natives may find at least partial refuge under natural conditions.

Paradoxically, natural droughts may also provide some protection for native species in arid climates. A native galaxiid fish, which is similar to trout, persisted better in the naturally intermittent flow regimes of headwater streams in south-central Australia. Nonnative trout died out under these conditions, but persisted better in downstream reaches with more constant flow. However, in southcentral USA streams, nonnative crayfish persisted better than native crayfish under drought, which experiments showed was owing to their greater tolerance to drying. Such drying may become more frequent with climate change.

These examples demonstrate that natural flow regimes may favor native species, but the effects are often complex. For example, nonnative species may be able to invade even under natural flows, as for tamarisk, or nonnatives may be more tolerant of periodic disturbances like drought, as for certain crayfish. Likewise, the ability of nonnative species to displace native species via competition, predation, or disease can interact in complex ways with changes in flow or temperature (Wenger et al. 2011). Therefore, predicting whether restoring natural flow regimes can favor native species over invaders, or how stressors like climate change will affect invasions, will require careful consideration and testing of such mechanisms (Rahel and Olden 2008).

8.3.2. HABITAT ALTERATION

Ecologists have consistently found that fish invasions are higher in areas with more human habitat degradation, such as from urbanization, transportation, and mining. This pattern is apparent in regions ranging from California, the lower Colorado River Basin USA, Australia, and across the world (e.g. Marchetti et al. 2004; Leprieur et al. 2008). However, these authors suggest that the actual mechanisms causing invasions are increased releases from unwanted aquarium fishes, bait buckets, ballast water, and intentional introductions, which are a by-product of higher urban and suburban development. Instead of habitat alteration itself promoting invasions, it may be simply that more species are introduced actively or passively in more disturbed habitats where more humans live.

8.3.3. CLIMATE CHANGE

Increased warming and variability of the climate is compounding other stressors like altered flow regimes and habitat degradation. Most studies of climate change have focused on the effects of increased temperature, especially for coldwater fishes, and large losses are projected for native trout and charr under typical warming scenarios. However, flow regimes are also predicted to change, often from snow to rain in mountain regions, and these may combine with temperature and species interactions to drive outcomes (Rahel and Olden 2008).

For example, cutthroat trout (*O. clarkii*), native to the western USA, are strongly depressed by nonnative brook trout (*Salvelinus fontinalis*), brown trout, and rainbow trout. However, these nonnative trout themselves are predicted to decline from increased water temperatures, and fall-spawning brook and brown trout are susceptible to increased winter floods that can wash away their spawning nests or newly-emerged fry (Fausch 2008). In contrast, rainbow trout and the native cutthroat trout spawn in early summer and so



Figure 8.3: *Habitat for trout in Rocky Mountain rivers of the western USA is predicted to decline by half by 2080 as the climate changes, but effects will be stronger for some nonnative trout than native species*

are little affected by winter floods. A detailed analysis throughout the Rocky Mountains using the latest climate and flow predictions showed that trout habitat will decline by nearly half in 70 years (2080) from a combination of these effects (Wenger et al. 2011). Paradoxically, habitat for nonnative brook trout will decline more than for cutthroat trout (77% vs. 58%), owing to warmer, rainier winters, making the situation for the native trout a bit better than it would have been otherwise. Nonnative rainbow trout are predicted to decline the least of all the trout (35%), because negative effects of increased temperature are partly offset by positive effects of more favorable flow regimes. Therefore, climate change will likely result in complicated interactions among several factors, all of which must be considered simultaneously to make accurate predictions.

8.4. Invasions cause effects at multiple levels in ecosystems

In addition to predicting future invasions, ecologists have recently become more interested in determining the effects of invasions at multiple levels, from other species to whole ecosystems. Some invaders cause declines and even extinctions of other species through predation or competition. For example, mos-

Figure 8.4:
Nonnative brook trout (upper left) forage more on bottom-dwelling stream insects than native cutthroat trout (lower left) in streams of the western USA, ultimately reducing emerging adult insects that feed riparian spiders (right), as well as birds, bats, and lizards (see Box 8.2)



quitofish and two trout are listed among the 100 world's worst invasive species, and have caused many local extinctions of other fish species.

However, invaders may also affect communities and ecosystems in other ways. For example, species are often finely tuned to each other via natural selection, as predators and prey, or competitors. When an invader takes over, it can change these selective forces, and so cause native species to evolve different characteristics in response. In addition, the invaders themselves change genetically as they integrate into the new ecosystem and leave their natural enemies behind.

Invaders like zebra mussels can also alter ecosystem services, such as the way that nutrients like nitrogen and phosphorus are moved from river sediments into the water column and made available for plant growth (Strayer 2009). One of the most interesting cases is of nonnative trout, which can reduce the abundance of bottom-dwelling stream insects by their own foraging or by altering the foraging of native trout. This causes a cascading set of changes in the stream food web, which ultimately reduces the abundance of adult insects that emerge from the streams and become prey for streamside predators like birds, bats, lizards, and spiders (see Box 8.2).

8.5. An intercontinental comparison: The Colorado River and Iberian Peninsula

Case studies can be useful for comparing sources and patterns of invasions, and conservation challenges. Here we contrast the Colorado River Basin (CR)

Ecological surprises: Can nonnative fish in streams affect birds and spiders in the streamside forest?

Ecologists have long known that invertebrates that fall or blow into streams from streamside (riparian) forests or grasslands are valuable food for fish. However, they have only recently measured the emergence of adult aquatic insects like mayflies into the riparian zone, and discovered that many terrestrial animals there make a living on these insects that start life in the stream. For example, about half the food energy that fish in small streams need comes from insects that fall in from the land, and more than a quarter of the energy that riparian birds need can come from insects emerging from small streams. Emerging insects also provide much of the diet for riparian bats, lizards, and spiders, especially in early spring when most insects emerge from streams.

As it turns out, nonnative trout can strongly reduce this insect emergence. In turn, this can reduce spiders, and potentially other riparian animals like birds and bats, through a cascading series of changes in the stream-riparian food web. For example, adding nonnative rainbow trout to reaches with native Dolly Varden charr in a northern Japan stream caused the charr to switch their feeding to bottom-dwelling insect larvae. In turn, this reduced the abundance of the emerging adult insects by a third,

which reduced the abundance of spiders in the riparian zone by two thirds (Baxter et al. 2004). Cutting off the emergence entirely using a mesh greenhouse reduced spiders by about 85%, so the effect of rainbow trout was indeed strong by comparison.

Nonnative brook trout in Rocky Mountain streams of the western USA have similar effects when they replace native cutthroat trout (rather than being added to them as in the Japan study). Brook trout forage more on the bottom-dwelling insects, and two studies showed that they reduced the biomass of emerging insects by between a third to a half compared to the native trout (e.g. Benjamin et al. 2011). This reduction in emergence was projected to reduce riparian spider abundance by 6-20%.

These studies are part of a growing body of evidence that nonnative species can have strong, unexpected ecological effects, such as on emerging insects that form strong linkages between streams and riparian zones. More importantly, these effects can cross habitat boundaries to create ecological surprises in distant locations. Nonnative trout can indeed affect riparian birds, as well as other riparian animals that people care about.

in the southwestern USA with the Iberian Peninsula (IP; Spain and Portugal) in southwest Europe. Both are generally arid regions, which have been subject to many fish introductions and invasions. Our main goal is to seek common patterns between the regions, and differences, and to highlight the importance of the topics discussed previously. We focus on fish invasions because data and research are more complete, compared to invasions of plants or invertebrates.

8.5.1. BASIN CHARACTERISTICS AND HUMAN STRESSORS

The two regions are of roughly similar area, and both drain from high mountains to the sea (Table 8.1). Climate is generally dry, although parts of the Iberian Peninsula are wetter or more arid than the rest. The Colorado River Basin generally has high flows during summer from melting snow, whereas most Ibe-

Table 8.1:
Intercontinental comparison of fish invasions in the Colorado River Basin in the southwestern USA, and the Iberian Peninsula in southwestern Europe

| Characteristic | Colorado River Basin, USA | Iberian Peninsula |
|---|--|---|
| Area (km ²) | 639,000 | 581,000 |
| Maximum elevation (m) | 3105 | 3479 |
| Climate; flow regime | Continental; summer snowmelt | Primarily Mediterranean; mostly autumn-winter rain |
| Primary/secondary habitat alterations | Dams and flow regulation/channelization | Dams and flow regulation/water abstraction |
| Number of native freshwater fishes (endemics; % of total) | 35 (24; 69%) | 51 ^a (41; 80%) |
| Imperiled ^b native species (% of total) | 20 (57%) | 49 (96%) |
| Number of established nonnative species (total; invasive) | 72; 29 | 26; 12 |
| Native region of most nonnative species (% of total) | Mississippi River Basin (67%) | Europe (42%) |
| Sources of most introductions | Stocking for fisheries management, bait minnow releases | Illegal stocking for angling, aquaculture |
| Prevention efforts | Eliminated stocking (except salmonids) | Black list of invasive species |
| | Restricted use of bait minnows | Restricted navigation in zebra mussel infested waters |
| | Boat inspections to prevent transporting invasive species | Outreach on the zebra mussel |
| Control and eradication efforts | Removal of nonnatives in trout streams and mainstem rivers | Control of the water hyacinth. |
| | Barriers to prevent trout invasions | Successful eradication of some fish populations in isolated lakes |
| | Flood releases to hamper nonnatives | Anglers directed to kill nonnative fishes captured |

^a Excludes 10 species that migrate to the ocean, like salmon and eel.

^b CR-includes Endangered and Threatened species under the ESA; IP-includes IUCN Threatened species.

rian rivers have high flows during the autumn-winter rainy season. Both regions suffer many human pressures and have many impoundments on rivers, which is the major source of habitat alteration. For example, on the Iberian Peninsula, >1,200 large reservoirs in Spain alone control about 40% of mean annual flow. Channelization, water abstraction, and water pollution are human stressors of the next greatest importance.

8.5.2. NATIVE AND NONNATIVE FISH SPECIES

The Iberian Peninsula has about 50% more native species than the Colorado River Basin (Table 8.1), and a high proportion in both regions evolved in these basins and are found only there (i.e. 69-80% are endemic). Both regions were long isolated and not covered by continental glaciers, allowing evolution of many endemic fish species. Unfortunately, most of these native species, between 57 and 96%, are imperiled and many have little legal protection. Protection is generally stronger in the Colorado River Basin, with most imperiled species having formal recovery plans under the U.S. Endangered Species Act (ESA), compared to the Iberian Peninsula where almost none have recovery plans yet.

In both regions nonnative species were introduced in the past mainly as sport fish, often by regional governments. Some were released as bait minnows by anglers, especially in the Colorado River Basin, and others were introduced inadvertently from aquaculture, especially in the Iberian Peninsula. A few in each region were unwanted aquarium fishes.

Large nonnative predators like largemouth bass (both regions), northern pike (CR), and European catfish (IP) are depleting native fishes in both regions. However, even small fishes such as mosquitofish (both regions) and small cyprinids like red shiner (*Cyprinella lutrensis*; CR) are capable of preying on larvae of native fishes and thereby depleting them or causing local extinctions. Some nonnatives hybridize with native species, like nonnative trout and suckers in the Colorado River Basin, and invasive cyprinids in the Iberian Peninsula.

Successful non-native species in both regions are well adapted to the newly created reservoir habitats, and the altered flow regimes downstream. The non-native species in the Colorado River Basin and the Iberian Peninsula fill many more ecological niches than the restricted set of niches filled by natives, many of which were well adapted to the fluctuating flow regime (e.g. Olden et al. 2006). In contrast, the successful nonnative species are generalist feeders adapted to warm, slow-moving water, and are weaker swimmers that do not require flowing water and coarse substratum for spawning. The abundance and rate of spread

of non-native species has been highest either in reservoirs, or among river fishes that overlap little in life-history traits with the natives.

8.5.3. PREVENTION AND CONTROL OF INVASIONS

There have been relatively few efforts to prevent invasions in either region, and these have occurred only recently. Fisheries management agencies in the Colorado River Basin are no longer stocking most nonnative fishes, although nonnative trout stocking continues in headwater tributaries and lakes of both regions. Some US states in the Colorado River Basin prevent or restrict the use of nonnative bait minnows for angling, but in both regions illegal introductions by anglers are a major source of new introductions (see Box 8.1). There are no policies in either region to prevent release of unwanted aquarium fish. In the Iberian Peninsula, legislation in December 2011 defined a “black list” of many plant and animal species which cannot be held, sold, or transported within Spain, which could reduce the number of new introductions.

Control of nonnative aquatic species is difficult in any region, and can be accomplished only at the local scale. Nonnative trout are removed from individual Colorado River headwater tributaries, and barriers are often used to prevent nonnative trout from invading upstream (Fausch et al. 2009). Com-

Figure 8.5:
The Colorado River has a high proportion of endemic native fish species, but now two thirds of fish species are nonnative



plete eradication of nonnative trout is possible only in some small streams, so in most, ongoing removal is required using electricity to capture the fish (Peterson et al. 2008). Releases from reservoirs to mimic natural floods are used in the upper Colorado River to hamper nonnative fish, but monitoring in a major tributary has shown that these floods benefit nonnative species as much as native ones. Large-scale removals of nonnative pike and bass are ongoing in another major upper Colorado River tributary, and do benefit native fish, but represent an expensive long-term management action to prevent their extinction. In the Iberian Peninsula, most funds are spent to control and prevent the further spread of zebra mussel and water hyacinth (*Eichhornia crassipes*) in specific basins. Zebra mussels, common carp, and brook trout have been eradicated in a few lakes, suggesting that other small closed ecosystems might be restored.

Overall, both regions have high proportions of endemic fish species, but are also highly invaded by nonnative species that threaten the native ones. Reservoirs, and the anglers who fish in them, are major sources of new invasions, and these habitats favor nonnative species. Prevention efforts have been too few and too late, and control efforts can generally be effective only at local scales. As for most regions, many more fishes are available worldwide to invade, so invasions will doubtless continue, although perhaps at a reduced pace given the distances involved.

8.6. Implications for conservation

The basic principles about aquatic invasions described above, and the more complex effects caused by other stressors, lead to important implications for conservation of aquatic biota in rivers. Here we describe seven important implications, as statements followed by an explanation.

Nonnative species are here to stay. Once nonnative fauna or flora species establish reproducing populations and spread, it is often impossible or very costly to remove them (Cucherousset and Olden 2011). For example, invasions by nonnative trout, even in streams only 3 m wide and 3 to 5 km long, are difficult and expensive to remove using fish toxicants like rotenone. Often, ponds created by beaver (*Castor canadensis*) or groundwater seeps provide refuges where a few nonnative fish survive. Carefully planned projects can be successful in small streams with relatively simple habitats, but virtually none could eradicate nonnative fishes or invertebrates in rivers at least 10 m wide. Moreover, it may be more cost effective to prevent further introductions into new waters, such as illegal introductions by anglers or aquarists (see below).

An ounce of prevention is worth a pound of cure. This old adage is especially true for invasions, and argues for much more focus on wise policies of preventing invasions than attempts to eradicate them after they establish and spread. Willful introductions by fisheries management agencies are less often a major vector of introduced species now than in the past, and many now prevent use of nonnative fishes as bait in specific watersheds. Likewise, recent research on the potential vectors of ballast water and aquarium fishes show that sharply reducing these vectors is technically possible. However, methods to reduce the growing trend of introductions of invasive piscivorous or forage fishes by anglers are in desperate need of attention by social scientists and fisheries biologists (Johnson et al. 2009; Box 8.1). In addition, early intervention using all means available to remove an invasion that is limited to a small area is far more effective than attempts to remove, control, or adapt to invasions after they have spread (Simberloff 2003).

It is worth closing the barn door after the first batch of horses is gone. Recent research and synthesis (Simberloff 2009) indicate that propagule pressure, the number and frequency of organisms introduced, is one of the most important factors driving invasion success. Managers may assume that once a species has arrived in a new location, there is little use in preventing future arrivals and introductions. However, many species may require multiple introductions, or a minimum number of propagules introduced at one time, to successfully overcome environmental or biotic limits and become established. Therefore, limiting further introductions can be highly effective at preventing invasions.

Protecting natural habitat and disturbance regimes may favor native species over nonnatives. Changing environmental factors is a powerful force that can shape groups of species in habitats. For example, the Natural Flow Regime Paradigm (Poff et al. 1997) holds that native species are strongly hampered when water abstraction alters natural flow and flood disturbance regimes, providing “niche opportunities” for nonnative species to exploit, thereby leading to invasions (see Olden et al. 2006). The converse has also been proposed, that restoring natural flow regimes may help reduce nonnative species abundance. There is some evidence to support this claim, but in other cases both natives and nonnatives can flourish under natural flow regimes (Merritt and Poff 2010). More work will be needed to test this important assertion, because many management schemes are based on this theory.

Dammed if you do, but perhaps damned either way. Managers often consider preventing upstream invasions into headwater streams using natural or artificial barriers to conserve native species. Many of these are simply road culverts or other human-made structures that have already prevented such invasions. However, isolating fish or invertebrate populations in short headwater fragments can also

hasten their extinction, either because the organisms lack all essential habitat needed to persist (especially after natural disturbances like fires, floods, freezing, or drying) or because populations are currently supplemented by immigrants from downstream. This tradeoff of using barriers to prevent invasions has been identified (Fausch et al. 2009), and methods have been developed to optimize it for native stream salmonids in the western USA. However, much more research will be needed for other species and regions to determine the lengths of stream fragments needed to support populations of native species into the future.

Nonnative species can have far-reaching effects, even beyond the stream. Nonnative organisms may rapidly spread long distances, especially because flowing waters transport propagules and adults downstream. Paradoxically, effects of nonnatives can also be transferred to adjacent habitats across the terrestrial-aquatic boundary. For example, riparian invasions by nonnative tamarisk alter light and leaf inputs to streams, thereby altering organic matter dynamics and changing invertebrate and fish assemblages. Conversely, nonnative trout invasions can cause cascading effects within stream food webs that increase algae, and reduce the flux of emerging adults of aquatic insects that are major components of the energy budgets for riparian birds, bats, lizards, and spiders (Box 8.2; Baxter et al. 2004; Benjamin et al. 2011). Managers of either terrestrial or aquatic habitats often do not consider the effects of such invasions on the adjacent, tightly-linked ecosystem, which can confound efforts at restoration.

Preventing invasions in the first place is the most cost-effective management option, but control of invasions after they spread is often given the highest priority

Look before you leap, to control. When eradication is not possible, managers often consider long-term control measures to keep nonnative species from potentially replacing native species. After invasions have spread, such efforts are an expensive and ongoing cost. Long-term control may be an important option for species of high economic or conservation value, but such efforts are worth analyzing carefully, to optimize efforts. Peterson et al. (2008) linked population models for a native and invasive trout, including the effects of the nonnative on the native, to estimate the efficacy of different scenarios of frequency and magnitude of mechanical removal by electrofishing on persistence of the native trout population. Continuous annual control was not as cost-effective as successive 2-3 year periods of control. This pulsed control allowed survival of a cohort of juvenile native trout through the first two years of life, the only period when the relatively long-lived native trout were vulnerable to competition or predation from the nonnative.

8.7. What should be our priorities?

Managers often have limited time, expertise, and funding, and many consider that they have few options for addressing invasions by nonnative organisms

in stream and river ecosystems (Fausch et al. 2009). Many seek advice from scientists about where to start. In contrast, scientists often study questions that are interesting or personally rewarding, sometimes bypassing less interesting problems that, nevertheless, could be more effective at reducing or controlling invasions. Here, we seek to arrange management and research actions in order of importance for stemming the tide of invasions (Table 8.2).

The most important research involves profiling likely invaders at the arrival phase, to identify those that are likely to do the most damage. However, many

Table 8.2:
A list of potential management and research actions to reduce invasions of nonnative biota into river ecosystems, in order of priority from the most to least important

| Action | Explanation | Relevant references ^a |
|--|--|--|
| Profile and prevent | Estimate which species are most likely to arrive, by which vector and where. Assess which species are most likely to do damage if they spread | Kolar and Lodge 2002 Alcaraz et al. 2005 Vila-Gispert et al. 2005 Garcia-Berthou et al. 2005 |
| Educate public, and limit vectors | Educate the public about preventing arrival or spread of dangerous invaders, and develop methods to reduce risk of human or natural spread | Vander Zanden and Olden 2008 Strecker et al. 2011 |
| Reduce propagule pressure | Even after species have arrived, seek ways to reduce propagule pressure, a primary driver of nonnative species establishment and spread | Von Holle and Simberloff 2005 Simberloff 2009 |
| Manage habitat and flow regimes to favor native species | Habitat change is a powerful force that hampers native species survival and provides niche opportunities for invasions. The converse, that restoring natural flow or other disturbance regimes will reduce nonnative species invasions, is not always true but deserves more study | Poff et al. 1997 Lytle and Poff 2004 Marks et al. 2010 Merritt and Poff 2010 Hermoso et al. 2011 |
| Consider tradeoffs in social values and management options | The public may value some invaders while considering others noxious pests. This perception may change with more information, which deserves research | Fausch et al. 2006 |
| Understand establishment and spread | Once invaders have arrived, understanding what allows them to establish and spread may allow the development of management actions to limit these stages, or suggest stronger policies to reduce propagule pressure | Fausch 2007 Garcia-Berthou 2007 |
| Eradicate or control | Eradication may be possible at the early stages of invasion when the spatial extent is limited, and should be pursued with all means possible. Control is often difficult and entails large and long-term costs | Simberloff 2003 Peterson et al. 2008 Vander Zanden et al. 2010 |

^aSee Additional References for some references listed here.

ecologists may prefer to study what allows nonnatives to establish, which we place sixth in priority. Once dangerous invaders have been identified, the second most important work is to educate the public and to seek methods to limit vectors of these species. Both of these topics require interacting with social scientists and regulatory agencies, which many ecologists avoid. In contrast to these high priorities, the action least likely to be effective at preventing or eliminating invasions is direct control of nonnative species, even though this is often the first action considered by many ecologists and managers.

8.8. Conclusions

To conclude, two things are obvious. First, invasive species are a huge issue for river conservation. They deserve more resources, especially to prevent their introduction, but also to measure their ecological impacts and develop better methods of control. Second, many management options are technically possible, but need proper prioritization. Although managers often consider control of invaders their first priority, prevention would be more cost effective in the long run. Perhaps because invasive species are underwater and so not readily visible and particularly because they are living organisms, the public tends to appreciate this problem less than others affecting rivers. Therefore, the first step needed to improve management is effective communication and public awareness at many different levels.

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