

Intentional Fragmentation as a Management Strategy in Aquatic Systems

FRANK J. RAHEL

Maintaining or restoring connectivity in aquatic systems can enhance migratory fish populations; maintain genetic diversity in small, isolated populations; allow organisms to access complementary habitats to meet life-history needs; and facilitate recolonization after local extirpations. However, intentional fragmentation may be beneficial when it prevents the spread of nonnative species or exotic diseases, eliminates hybridization between hatchery and wild stocks, or stops individuals from becoming entrapped in sink environments. Strategies for fragmenting aquatic systems include maintaining existing natural barriers, taking advantage of existing anthropogenic features that impede movement, severing artificial connectivity created by human actions, and intentionally creating new barriers. Future challenges for managing fragmentation include maintaining hydrologic connectivity while blocking biological connectivity in water development projects; identifying approaches for maintaining incompatible taxa, such as sport fishes and small nongame species; and developing selective barriers that prevent the passage of unwanted species while allowing normal life-history movements of other species.

Keywords: fragmented ecosystems, invasive species, dams, migration, connectivity

Restoring connectivity is a major theme in the management of aquatic systems. The benefits of maintaining or restoring connectivity are well documented and include the enhancement of migratory fish populations; increased genetic diversity and reduced extirpation risk in small, isolated populations; increased access to a range of complementary habitats needed at different life-history stages; and recolonization after local extirpations (Carlson and Rahel 2010, Fullerton et al. 2010, Liermann et al. 2012). Discussions of how biodiversity can be maintained in a changing climate often include recommendations to increase landscape connectivity, so that species can migrate to new habitats as current ones become unsuitable (Kostyack et al. 2011). As a result of the focus on connectivity, removing dams and improving fish passage at road culverts have become common activities in watershed restoration efforts (Kemp and O'Hanely 2010).

Nevertheless, connectivity can have a downside in some situations. Most biologists would agree that connecting waterways that were naturally isolated is not a good idea. Notorious examples of connections that resulted in biological invasions include the Welland Canal around Niagara Falls, which allowed sea lampreys (*Petromyzon marinus*) to invade the upper Great Lakes, and the

Rhine–Main–Danube Canal, which resulted in a massive biotic exchange between the Rhine and Danube drainages (Rahel 2007, Leuven et al. 2009). Less clear cut are situations that involve restoring connectivity in waterways that were historically connected or fragmenting currently connected systems (Fausch et al. 2009, Jackson and Pringle 2010). In fact, maintaining isolation or even intentionally fragmenting systems may be beneficial. The benefits fall into four main categories: preventing the spread of nonnative species, preventing the spread of exotic diseases, preventing hybridization between hatchery and wild populations, and preventing organisms from entering attractive human-created habitats that act as ecological traps. Therefore, natural resource managers face a tension in balancing the pros and cons of connectivity in aquatic systems (figure 1).

The benefits of fragmentation in aquatic systems

The invasion process can be viewed as a series of stages, involving colonization, establishment, and spread, that species must pass through before they cause widespread ecological or economic harm. At several points in this process, reducing connectivity becomes an important management objective.

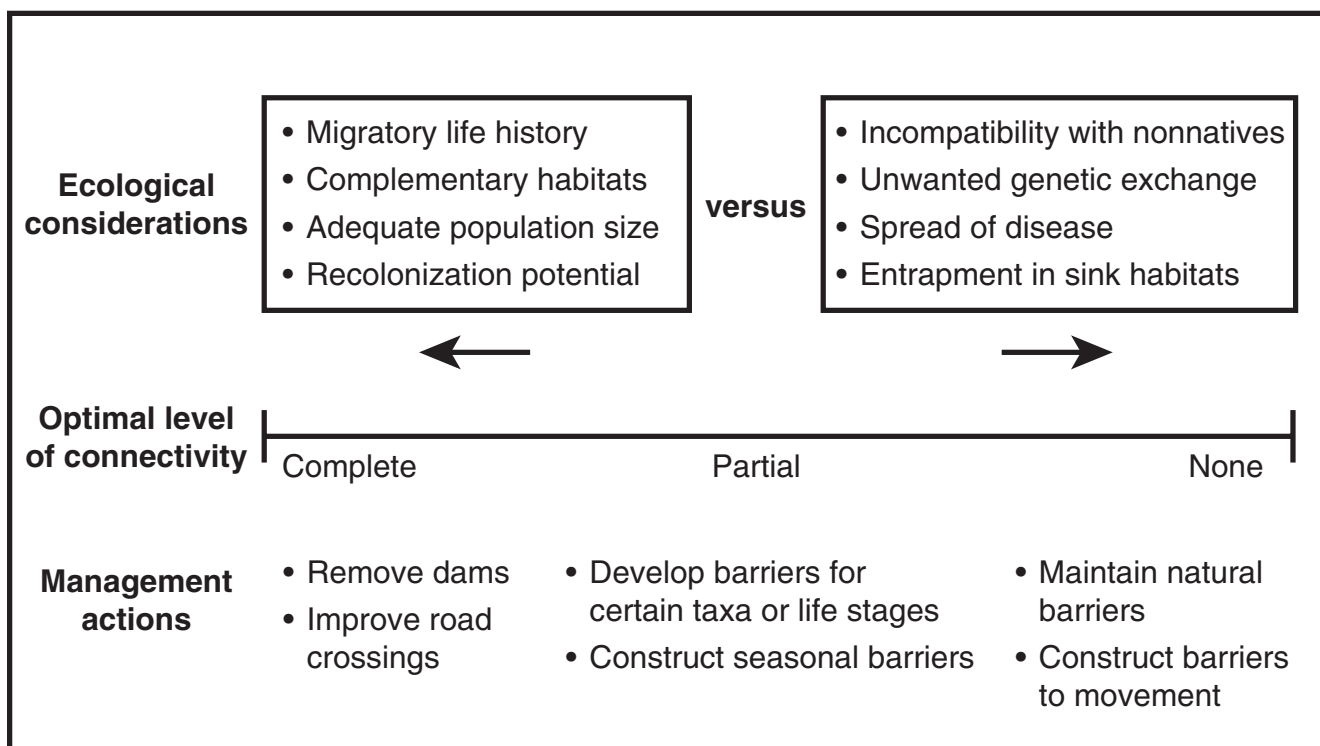


Figure 1. Tension between factors that support complete connectivity in aquatic systems (left) and factors that support no connectivity (right) in aquatic systems. When complete connectivity is warranted, appropriate management actions include removing dams and improving road crossings. When no connectivity is warranted, managers should retain natural barriers, such as waterfalls, or construct artificial barriers, such as dams, screens, or electric fields. A compromise is the development of selective barriers that provide at least partial blockage to movements by certain taxa or by species in certain life-history stages on the basis of differences in behavior, morphology, or the timing of spawning.

Preventing the spread of nonnative species. At the earliest stage, preventing a species from colonizing a region means reducing the likelihood that it will cross natural biogeographic barriers (figure 2a). This means avoiding actions that connect historically isolated waterways. In addition to directly connecting aquatic systems through canals, humans have indirectly connected aquatic systems through long-distance dispersal vectors, such as seawater ballast and the aquarium trade. Treating ballast water, not building canals, banning the importation of noxious species, and educating the public on the dangers of releasing unwanted aquarium specimens are the major approaches for preventing connectivity at the biogeographic scale. Once a nonnative species has become established in a system in which eradication is unfeasible, controlling the species' spread to nearby areas becomes a high priority (figure 2b). One way to slow the spread of nonnative species is by managing the human vectors responsible for transporting species to new areas. A prime example is the campaign to alert boaters that zebra mussels (*Dreissena polymorpha*) can be transferred among water bodies on boats and trailers. However, many aquatic invasive species are able to spread without human assistance (Rahel 2004, Fausch et al. 2009). Reducing the spread of these species

entails reducing the connectivity among habitats by implementing intentional fragmentation.

Intentional fragmentation is used when nonnative species are such strong competitors or predators that coexistence with the native species is unlikely (Clarkson et al. 2012, Marr et al. 2012). Typically, a barrier is constructed, nonnative species are removed, and native species are returned to upstream segments in a strategy known as *isolation management* (Novinger and Rahel 2003). This approach has been widely used in the conservation of native trout populations in the Rocky Mountain region of the United States and to protect small-bodied native fishes from larger, often piscivorous, nonnative species in warmwater streams of the desert Southwest of the United States (table 1). Most often, barriers function to prevent upstream migration by unwanted species. But barriers may also be used to keep nonnative fish from colonizing downstream habitats. For example, in Highline Lake, Colorado, a net placed across the outflow prevents nonnative sport fish such as the largemouth bass (*Micropterus salmoides*) from escaping over the spillway and preying on native fish of conservation concern in the Colorado River (Martinez 2003). The net is constructed of polyester and needs to be replaced about every 6 years but has proven to be effective in containing

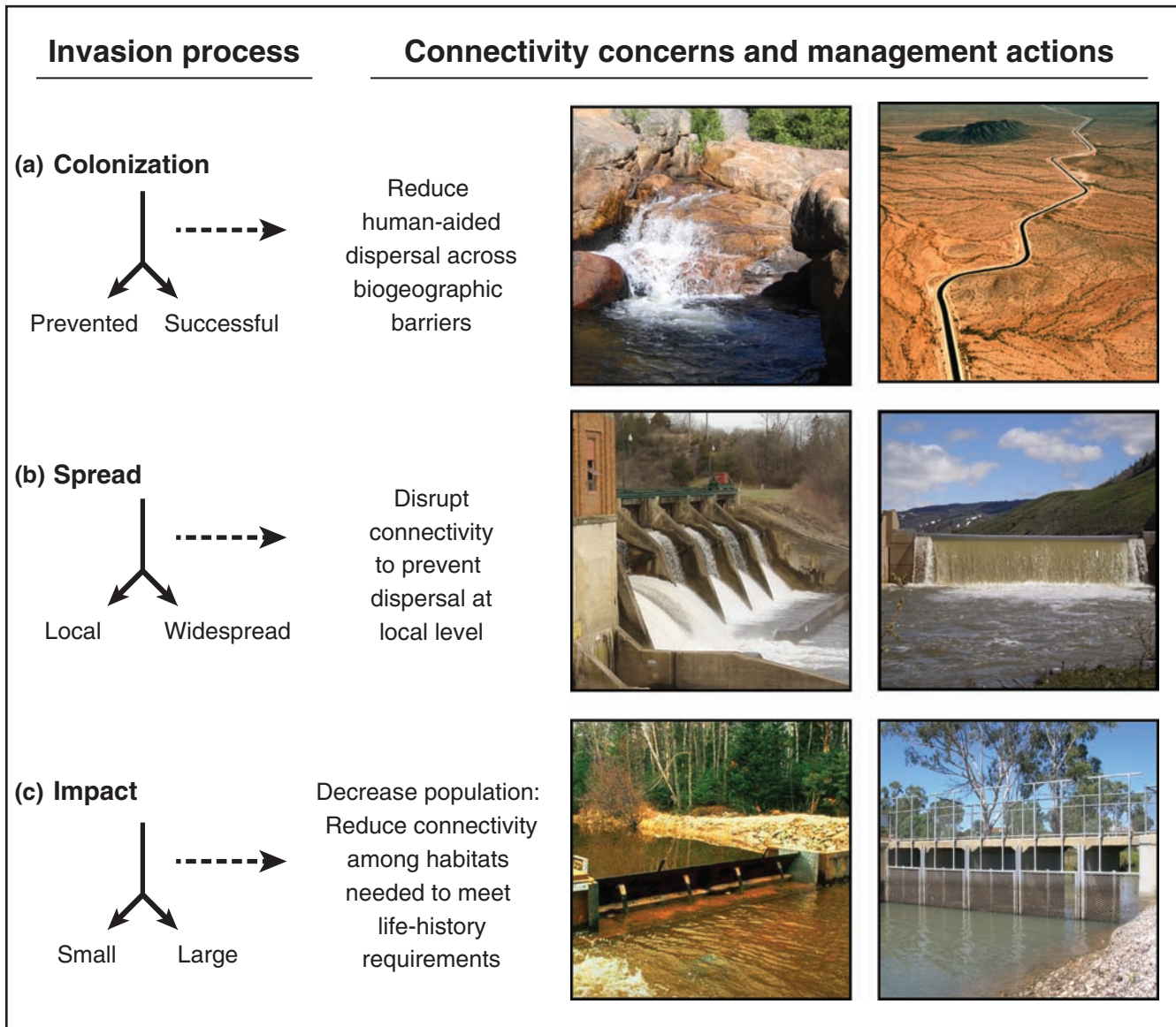


Figure 2. The influence of connectivity at various stages of the invasion process. (a) Maintaining the natural isolation among regions is important for preventing the initial colonization by nonnative species. Waterfalls such as the one in the left image, on the Rondegat River of South Africa, are barriers to colonization by unwanted species (photograph: Sean Marr, University of Cape Town). Canals such as the one for the Central Arizona Project, in the right image, can cross watershed boundaries (photograph: US Bureau of Reclamation). (b) Once a species is established, preventing its spread becomes important. Lakehurst Dam, on the Maquoketa River, Iowa (left image), prevents upstream colonization by Asian carp (photograph: the Iowa Department of Natural Resources). The right image shows an artificial barrier that prevents upstream colonization by nonnative trout species in LaBarge Creek, Wyoming (photograph: Hilda Sexauer, Wyoming Game and Fish Department). (c) Once a nonnative species is causing harm, reducing its population can be achieved by disrupting its movement among complementary habitats. The left image shows an adjustable barrier that prevents sea lampreys from accessing spawning areas (photograph: Great Lakes Fishery Commission). In the right image, screens prevent the common carp from accessing spawning wetlands in Australia (photograph: Karl Hillyard, University of Adelaide).

nonnative piscivores in the reservoir (figure 3). The net represents a compromise between the conflicting demands that fishery managers often face to protect native nongame species while also providing recreational opportunities for anglers seeking popular but nonnative sport fishes.

Once an invasive species is established and elimination is unfeasible, the management goal changes to reducing its effect through population control (figure 2c). One strategy is to disrupt the connectivity between habitats needed for the species to complete its life cycle. Examples of this strategy

Table 1. Examples in which natural waterways have been intentionally fragmented to prevent dispersal of nonnative taxa.

Nonnative species	Native species	Type of barrier	Reference
Lake trout (<i>Salvelinus namaycush</i>)	Bull trout (<i>Salvelinus confluentus</i>)	Rock-filled gabion barrier at outlet of Quartz Lake, Montana	D'Angelo et al. 2010
Mosquitofish (<i>Gambusia affinis</i>)	Red-finned blue-eye (<i>Scaturiginichthys vermeilipinnis</i>)	Plastic mesh around springs in Queensland, Australia, with endangered red-finned blue-eye fish to prevent immigration by mosquitofish	Bush Heritage Australia 2011
Signal crayfish (<i>Pacifastacus leniusculus</i>)	Noble crayfish (<i>Astacus astacus</i>)	Barrier on Buaa River, Norway, to prevent upstream migration of signal crayfish	Gherardi et al. 2011
Crayfish plague (<i>Aphanomyces astaci</i>)	Noble crayfish	Electric fences on Vrangselva River, Norway, to prevent infected noble crayfish from moving upstream and spreading disease; the fences were ineffective	Taugbøl et al. 1993
Signal crayfish	Atlantic salmon (<i>Salmo salar</i>)	Paired barriers on the headwaters of River Clyde to prevent crayfish from colonizing the neighboring River Annan drainage	Colin Bean, Scottish Natural Heritage, personal communication, 4 January 2013
Red shiner, fathead minnow (<i>Pimephales promelas</i>)	Seven native fishes	Paired barriers constructed on Aravaipa Creek, Arizona; a portion of the stream naturally flows underground except during floods	Rinne et al. 2004
Common carp	Native stream fishes	Concrete-capped gabion prevented upstream movement of carp and other reservoir fishes into the Roaring River, Tennessee	Bulow et al. 1988
Largemouth bass, smallmouth bass (<i>Micropterus dolomieu</i>)	Native fish assemblages	Net to prevent sport fish in Highline Lake, Colorado, from escaping over a spillway and harming native fishes in Salt Creek	Martinez 2003
Silver carp, bighead carp	Great Lakes fishes	Steel fence prevented fish migration from the Wabash River in the Mississippi River drainage to the Maumee River in the Lake Erie drainage when headwater marshes commingled during floods	Asian Carp Regional Coordinating Committee 2010 (2011)
Brook trout	Various subspecies of cutthroat trout	Rock-filled gabions or splash pads downstream of road crossings in Wyoming and Colorado	Novinger and Rahel 2003, Young et al. 2005
Smallmouth bass	Rainbow trout	Rock-filled gabions on five streams in the Beaver Creek drainage of British Columbia, Canada, to limit the upstream spread of bass	Avis and Wilkinson 2011
Brook trout	Bull trout	Two rock and log barriers built to prevent recolonization after the removal of brook trout	Buktenica 1997
Rainbow trout, brown trout	Westslope cutthroat trout	Various anthropogenic structures across the western United States	Shepard et al. 2005
Smallmouth bass, green sunfish (<i>Lepomis cyanellus</i>)	Six minnow and sucker species	Barrier with 2-meter drop, Fossil Creek, Arizona	Marks et al. 2010
Largemouth bass, common carp, mosquitofish	Owens pupfish (<i>Cyprinodon radiosus</i>), Gila topminnow (<i>Poeciliopsis occidentalis</i>)	Headwater springs dammed to create pools and exclude nonnative predators in the Owens River and the Gila River of the southwestern United States	Minckley et al. 1991
Brown trout	Golden trout (<i>Oncorhynchus mykiss aguabonita</i>)	Gabion barriers, Kern River drainage, California	Pister 2010
Brown trout, rainbow trout	Gila trout (<i>Oncorhynchus gilae</i>)	Artificial waterfall barriers, Gila River drainage, in New Mexico and Arizona	Propst et al. 1992
Rainbow trout, brown trout	Apache trout	Rock-filled gabions in Arizona	Avenetti et al. 2006
Green sunfish, mosquitofish	Gila topminnow, desert sucker (<i>Castostomus clarkii</i>), longfin dace (<i>Agosia chrysogaster</i>)	Artificial and natural barriers to protect endangered fishes in the desert streams of the southwestern United States	Clarkson et al. 2012
Rainbow trout	Mountain galaxias (<i>Galaxias olidus</i>)	1.75-meter-high stream-gauging weir in Lees Creek, southeastern Australia	Lintermans 2000

include the use of low-head dams to block access to spawning tributaries for sea lampreys in the Great lakes of North America (Lavis et al. 2003, Pratt et al. 2009) and the use of screens to prevent the common carp (*Cyprinus carpio*) from reaching wetland spawning areas in Australia (Hillyard et al. 2010).

Preventing the spread of diseases. The spread of some diseases can sometimes be halted by preventing infected individuals from moving to new areas. For example, a 2-meter-high pond dam was a barrier to the upstream spread of an exotic pathogen of crayfish in a Czech stream (Kozubiková et al. 2008). Native crayfish were eliminated downstream of the



Figure 3. Net barrier in Highline Lake, Colorado, used to prevent the escape of nonnative sport fishes into an outlet stream that contains native fishes of conservation concern. Photograph: Danielle Tremblay and Jessica Hogue, Colorado Parks and Wildlife.

dam but no evidence of infection was seen upstream of the dam. In Norway, electric fences were tested as a means of preventing the upstream spread of crayfish plague through the Vrangselva Watershed. The fences failed to prevent the movement of infected crayfish, and the upstream spread of the disease was halted only by a large concrete weir that was a total barrier to crayfish movement (Taugbøl et al. 1993).

Reducing hydrological connectivity can also play a role in limiting the spread of diseases affecting fishes. Whirling disease, which is caused by a myxosporean parasite, can be lethal to young salmon and trout. Preventing the movement of infected fish to areas free of the disease is one strategy for limiting its spread. This was the rationale for constructing a rock gabion barrier on the West Fork of the Duchesne River in Utah. Because whirling disease occurred downstream, the hope was that the barrier would prevent infected fish from transporting the parasite into upstream reaches in which a transbasin water diversion would further allow the disease to spread into uninfected waters (Utah's Watershed Restoration Initiative 2010). Likewise, in-stream barriers were considered an important factor in limiting the spread of the virus causing viral hemorrhagic septicemia in fish in the Great Lakes Basin of North America (Amos et al. 2010).

Preventing hybridization. Migration barriers can help maintain the genetic purity of fish populations that would

otherwise be subject to introgression with hatchery fish or closely related species. In Belgium, intensive stocking and exchange among hatcheries has resulted in the genetic homogenization of brown trout (*Salmo trutta*) populations in downstream reaches of the Meuse River, whereas movement barriers in the form of dams have preserved the indigenous genetic makeup of upstream populations (Van Houdt et al. 2005). Similarly, in Austria, genetically pure populations of the native Danubian lineage of brown trout occurred mainly upstream of natural or artificial barriers to movement by the widely stocked but nonnative Atlantic lineage of brown trout (Baric et al. 2010). Shepard and colleagues (2005) reported that fish migration barriers were important in preventing the hybridization of westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) with other salmonids in the western United States. Of the 172 conservation populations that showed no evidence of introgression, 56 (33%) were genetically "protected" by the presence of a fish migration barrier. Rubidge and Taylor (2005) found that hydroelectric dams in the Kootenay River drainage of British Columbia prevented hybridization between rainbow trout (*Oncorhynchus mykiss*) that had been introduced downstream and native westslope cutthroat trout located upstream of the dams.

Perhaps the most critical situation for preventing genetic exchange involves the isolation of genetically modified

organisms from their wild relatives. There has been considerable interest in raising fish for human consumption that have been genetically engineered to grow much faster than unmodified populations. But a major concern is ensuring that genetically modified fish will not escape and interbreed with wild fish, thus unleashing novel genes into the environment. Simply confining the genetically modified fish in pens, as is currently done for marine aquaculture, is not feasible, because of the high likelihood that the fish will escape the enclosure. The most promising method of confinement involves land-based systems of fish culture with facilities isolated from natural waterways by filtration apparatus or other forms of water treatment (Le Curieux-Belfond et al. 2009).

Preventing fish from entering ecological traps. Organisms can sometimes be attracted to habitats that are unsuitable for their long-term survival and that therefore function as ecological traps. In aquatic systems, irrigation canals can be ecological traps, because organisms that are attracted to the stream-like habitat subsequently die when water flows are terminated at the end of the irrigation season (Roberts and Rahel 2008). In fish populations, losses to irrigation canals can be substantial. For example, 23% of 40 adult cutthroat trout (*O. clarkii*) implanted with radio transmitters became entrained and subsequently died in an irrigation canal during a postspawning migration in a Wyoming stream (Schrank and Rahel 2004). To prevent the movement of aquatic organisms into such sink habitats, screens have been employed to sever the biological connectivity but retain the hydrological connectivity between rivers and canals. As an example, it was estimated that up to 25% of migrating steelhead trout in an Oregon stream would enter and subsequently die in irrigation canals if screens were not in place (Simpson and Ostrand 2012). In such situations, intentional fragmentation of river–canal systems is a desirable management objective.

Approaches to fragmentation

Once it becomes clear that isolation is an important goal, there are four major strategies for managing fragmentation in aquatic systems. The simplest strategy is to use existing natural barriers to prevent intrusion by unwanted taxa (figure 2a, left image). In South Africa, native fishes are heavily affected by nonnative predators (especially *Micropterus* basses and the African sharp-tooth catfish [*Clarias gariepinus*]), and populations thrive mainly in areas above waterfalls that serve as natural barriers to invasion by these predators (Ellender et al. 2011, Marr et al. 2012). In Australia and New Zealand, Crowl and colleagues (1992) noted that waterfalls appeared to be essential to the persistence of fish in the family Galaxiidae. Many species survived only above waterfalls that prevented upstream migration by nonnative brown trout or rainbow trout. A waterfall on the East Fork White River, in Arizona, prevented genetic introgression between native Apache trout (*Oncorhynchus apache*) and rainbow trout that had been introduced below

the falls (Rinne and Turner 1991). Stream reaches that have subsurface flow through boulder fields can serve as upstream colonization barriers for northern pike (*Esox lucius*; Spens et al. 2007). Construction of artificial boulder fields was suggested as a way to create long-term barriers to invasion by this highly piscivorous species that can have negative effects on native fish assemblages (Spens et al. 2007). In the Paraná River on the border between Brazil and Paraguay, the Sete Quedas Falls provided a natural migration barrier for fishes. When the falls were inundated by the creation of Itaipu Reservoir, 38 fish species colonized the upper reaches of the river, causing harm to some endemic species and homogenizing these formerly distinct fish faunas (Vitule et al. 2012).

A second strategy for managing fragmentation is to eliminate human-induced connectivity between formerly disconnected waterways. Humans have a long history of creating hydrological connections between naturally disjunct river systems. The earliest navigable canal linked the Tigris and Euphrates Rivers in Mesopotamia and was constructed in about 2200 BCE. Although canals facilitate economic development, they also dissolve natural barriers to the dispersal of aquatic organisms (Rahel 2007, Leuven et al. 2009). To prevent the dispersal of undesirable organisms, managers face the difficult challenge of disrupting biological connectivity while retaining hydrological connectivity. One method is to use electrical fields as a barrier to the movement of larger aquatic organisms, such as fish. An example of this approach involves the Chicago Sanitary and Ship Canal, which was built in 1910 to provide a connection between Lake Michigan and the Mississippi River (Moy et al. 2011). For much of its history, the canal was fishless because of low oxygen concentrations caused by sewage inputs from Chicago. But improvements in sewage treatment in the 1970s enhanced water quality to the point that a number of aquatic species used the canal as a migratory pathway between the Mississippi River and Great Lakes basins. To prevent future movements of nonnative organisms such as Asian carp (i.e., silver carp [*Hypophthalmichthys molitrix*] and bighead carp [*Hypophthalmichthys nobilis*]), an electrical grid system was constructed in 2002. The theory was that fish would avoid the electrical field, thereby stopping both upstream and downstream movement. Although the approach seems feasible, there is always the potential for power outages that would disrupt the electrical field. Some planktonic life forms also pass through the electric field unharmed. Therefore, fishery managers are now calling for a return to hydrologic separation between these two basins. Because a large amount of barge traffic uses the Chicago Sanitary and Ship Canal, there would need to be a cost-effective way to move goods across the land isthmus that would be re-created. Another effort to maintain biological isolation in the face of hydrologic connection involves the Central Arizona Project (CAP) canal in the southwestern United States (figure 2a, right image). This canal transports water from the Colorado River to the cities of Phoenix

and Tucson and is dominated by nonnative fishes. The CAP canal connects with the Gila River, which retains many native fish species. An electrical barrier was installed in an effort to prevent nonnative fishes, such as grass carp (*Ctenopharyngodon idella*) and red shiner (*Cyprinella lutrensis*), from migrating upstream into the Gila River drainage, where it is feared that they would have negative effects on many native species of conservation concern (Clarkson 2004).

A third strategy for managing fragmentation is to take advantage of existing anthropogenic features that already create isolation. For example, dams originally built for hydroelectric generation or water storage can be repurposed as colonization barriers for undesirable species. The Jemez Canyon Dam in the Santa Fe National Forest, in New Mexico, was constructed to store irrigation water but has also prevented upstream intrusion by the nonnative white sucker (*Catostomus commersonii*) into river reaches occupied by the Rio Grande sucker (*Catostomus plebeius*). The Rio Grande sucker is a species of conservation concern and is often displaced by the white sucker (Calamusso and Rinne 1999). The state of Iowa has identified a set of dams that could be retained as barriers to upstream colonization by Asian carp living in the Missouri and Mississippi Rivers (figure 2b, left image; Hoogeveen 2010). Lieb and colleagues (2011) noted that a rare species of crayfish in Pennsylvania exists almost exclusively above dams, which appear to prevent upstream colonization by nonnative crayfish species. Therefore, retaining these dams, even if they are no longer needed for hydropower, may be justified because these structures prevent encroachment by nonnative crayfish that can displace native species. In the Great Lakes region, dams block upstream movements of the round goby (*Neogobius melanostomus*) into tributary streams and are therefore important for controlling the spread of this invasive fish species (Kornis and Vander Zanden 2010).

Dams are not the only human-created features that can fragment systems. In California's Cosumnes River drainage, native fish assemblages persisted mainly above barriers that prevented colonization by introduced redeye bass (*Micropterus coosae*; Moyle et al. 2003). In some cases, these barriers to bass movement were provided by reaches with poor water quality or reaches that were dewatered because of agricultural water withdrawal. Rinne and Turner (1991) and Propst and colleagues (1992) also noted that dry stream reaches served as barriers to the upstream movement of undesired aquatic species in streams of the southwestern United States. In California, upstream colonization by the red swamp crayfish (*Procambarus clarkii*) was prevented by road culvert pipes that provided velocity barriers to crayfish movement (Kerby et al. 2005). This invasive crayfish has strong negative effects on native amphibian species. Kerby and colleagues (2005) suggested that concrete paved culverts with high water velocity and no natural substrates to provide velocity blocks would be especially effective migration barriers. But such efforts to reduce stream connectivity for

crayfish would conflict with efforts to create culverts that do not impede the upstream movement of small, native fishes.

Restoring lateral connectivity between main channels and floodplains is another focus of watershed restoration efforts, but restoring this connectivity may not always be beneficial for native species. Scheerer (2002) noted that an endangered fish, the Oregon chub (*Oregonichthys crameri*), persisted in greatest abundance in off-channel habitats that had become isolated by the channelization of the Willamette River. Reconnecting such habitats would likely be detrimental to the Oregon chub, because the species does not fare well in the presence of the introduced fishes that are now common in the Willamette River.

The fourth approach for managing fragmentation is to intentionally create movement barriers in waterways that are naturally connected (figure 2b, right image). Fishery biologists have referred to this as *isolation management* (Novinger and Rahel 2003), and it is a common approach when nonnative species are such voracious predators or superior competitors that coexistence with native species is not possible. Ideally, the barrier is installed prior to the arrival of the nonnative species (the first 11 studies in table 1). However, if the nonnative taxa are already present, construction of a barrier is followed by the removal of the unwanted taxa upstream of the barrier and restocking with native species (remaining studies in table 1). Intentional fragmentation may not be successful if barriers fail during floods or if members of the public sabotage removal efforts by reintroducing unwanted taxa above the barriers (Rinne and Turner 1991, Fausch et al. 2009). The benefits of migration barriers can also be negated if they create a novel habitat that encourages the introduction or establishment of nonnative fishes. For example, a dam on the Roaring River in Tennessee created standing-water habitat upstream that was colonized by several species that were probably introduced by anglers. These species were not present in the river prior to the dam's construction (Crummy et al. 1990). Despite these potential problems, intentional fragmentation is a major conservation strategy for situations in which native and nonnative taxa are considered immiscible (Rinne et al. 2004).

Challenges in managing fragmentation

Historically, isolation management was accomplished by constructing nonselective movement barriers, such as rock-filled gabions that mimic natural waterfalls (figure 2b, right image). Recently, there has been interest in developing selective barriers that inhibit movement by nonnative species but allow the passage of native species. Selective passage can be accomplished by exploiting differences in the swimming ability, jumping ability, morphology, or behavior among species. For example, sea lampreys have limited leaping ability, and therefore, even relatively small dams block their upstream spawning migrations while allowing the passage of most other species (Lavis et al. 2003). Another approach to selectively blocking migration is to employ low-head barriers during only the lamprey spawning season, thus

allowing free movement by native species during other times of the year (figure 2c, left image). In Norway, the introduced minnow *Phoxinus phoxinus* poses a serious threat to the native brown trout. The minnow is less adept at jumping over obstacles than is the brown trout. As a result, artificial barriers 35 centimeters in height would prevent upstream colonization by the minnow but would allow adult brown trout to disperse freely (Holthe et al. 2005). In Australia, the leaping behavior of the common carp has been used to separate this invasive species from native Australian fishes that do not show such a behavior (Stuart et al. 2006). Fish migrating upstream are blocked by a dam that directs them into a two-compartment fish trap. Native species remain in the first compartment, but up to 90% of the carp jump over a dividing wall into a secondary compartment. The trap has a mechanism to release fish in the first compartment and to allow them to continue moving upstream. Fish in the second compartment (almost exclusively carp) are removed from the system. Another approach to selectively prevent the movement of the common carp is through the use of screens that exclude large, deep-bodied fish, such as sexually mature carp, but allow slender native fish species to pass without restriction (figure 2c, right image; Hillyard et al. 2010). Hillyard and colleagues' (2010) monitoring indicated that the screens could prevent up to 90% of carp from reaching spawning grounds in wetlands in Australia. Such a reduction in spawning would help to reduce carp populations, but because some carp would pass through the screens, screening would need to be an ongoing activity.

An effective way to allow selective passage of species at dams is through a trap-and-sort operation at fishways. Fish that ascend the fishway are captured in traps and then manually sorted. Desirable species are allowed to continue their upstream migration, and undesirable species are removed from the system. This approach can be 100% selective but requires a lot of effort, because traps must usually be checked daily. The trap-and-sort method has been advocated as a way to mitigate the potentially harmful effects of low-head dams used to control sea lampreys (Lavis et al. 2003, Pratt et al. 2009). A similar approach is used at the fish passage facility of the Public Service Company of New Mexico on the San Juan River (Campbell et al. 2010). Fish move upstream through a side channel and are collected in a trap, where they are manually sorted daily. Native fish are allowed to proceed upstream, and non-natives are removed from the system. An advantage of this approach is that nonnative species can be salvaged and

stocked into systems in which they will not harm native species. In this case, channel catfish (*Ictalurus punctatus*) are moved to ponds in the Navajo Nation, where they provide sport-fishing opportunities.

Barriers to movement based on structures, screens, nets, or electricity are subject to malfunctions, and therefore, redundancy in these systems needs to be considered when the cost of failure is high. Such is the situation for the electrical barrier designed to prevent Asian carp from moving through the Chicago Sanitary and Ship Canal and entering the Great Lakes. The potential detrimental effect of Asian carp on the Great Lakes ecosystem is considered to be so great that a second electrical barrier is being built adjacent to the existing one (Moy et al. 2011). In Scotland, biologists felt that there was a significant risk that an invasive crayfish species could pass from the headwaters of the River Clyde to a neighboring catchment, the River Annan, where it would be detrimental to salmonid populations. To prevent this, paired barriers, each consisting of a large apron, side walls, and overhang, were constructed (figure 4). Should the crayfish get past the first barrier, the stream reach between the barriers could be dewatered and treated with a biocide. A similar logic was behind the construction of paired gabion structures in an Idaho stream to prevent upstream colonization by the nonnative brook trout (*Salvelinus fontinalis*; Buktenica 1997).

Natural resource managers often face conflicting goals, such as the need to move water but not aquatic organisms across watershed divides. In essence, we need ways to facilitate hydrological but not biological connectivity when interbasin water transfers are planned. Screens, dams, or



Figure 4. Paired barriers to block upstream movement of the invasive North American signal crayfish in the River Clyde, Scotland. Left inset: The waterfall created by the barrier. Right inset: The signal crayfish. Photographs: Colin Bean, Scottish Natural Heritage.

electrical barriers have been employed to prevent the movement of aquatic organisms, as was discussed above. When multiple water transfer options are possible, managers can use information on the spatial patterns in riverine networks to choose canals that minimize the interbasin spread of unwanted species while maintaining the isolation of systems with high endemism (Grant et al. 2012). Managers must also balance the public's desire for sport fish, which are often nonnative species, with the need to conserve native nongame species. In some cases, both objectives can be met only by keeping the two groups isolated from each other. This conflict is especially prevalent in the Upper Colorado River Basin, where there is a high demand for nonnative sport fishes that often have negative effects on declining endemic fishes. As a compromise, several states have agreed to allow the stocking of nonnative fish, such as largemouth bass (*Micropterus salmoides*), only if the waters to be stocked are above the 100-year floodplain and have no direct connection to the floodplain. For lower elevations, the states required that the waters be bermed to the standards of the US Federal Emergency Management Agency from the 100-year floodplain and that the outlet be screened prior to stocking (USFWS 2009).

Isolation by barriers does have several drawbacks. First, it may result in small populations that are subject to the loss of genetic variation or to demographic fluctuations that can lead to extirpation (Fausch et al. 2009). These problems can be minimized if the amount of isolated habitat is as large as is possible. Young and colleagues (2005) postulated that stream fragments at least 10 kilometers long would sustain an effective population size of 500 cutthroat trout in the Rocky Mountain streams they studied. This threshold was considered sufficient to minimize the genetic and demographic risks associated with small population size. Second, barriers can prevent individuals from moving to refuges during periods of high temperature, low oxygen, or stream desiccation and then returning when conditions improve (Winston and Taylor 1991, Meyers et al. 1992). Therefore, managers would need to be vigilant in rescuing populations facing stressful conditions. Finally, intentional isolation might remove a population from the constellation of geographically separated but interacting populations that form a metapopulation. Such populations occasionally exchange individuals through long-distance dispersal, which allows for genetic exchange among populations and which can reestablish populations that have been extirpated by environmental catastrophes. With the loss of natural dispersal, managers may need to play a more active role in reestablishing populations through translocation (Olden et al. 2011).

Conclusions

Although it may seem paradoxical, removing artificial barriers in some systems and constructing barriers in others are both important tools for managing native freshwater organisms. Russell (2011) reviewed the conservation status of freshwater fishes in South Africa and noted that whereas

removal of fish migration barriers has been done to enhance native fishes in some parks, construction of barriers to prevent the spread of invasive species would be necessary to preserve native species in other parks. Schemes that evaluate the costs and benefits of dam removal may recommend keeping some dams if their removal would result in the expansion of habitat for aquatic invasive species (Lavis et al. 2003, Kemp and O'Hanley 2010, Kornis and Vander Zanden 2010, Lieb et al. 2011). With climate change, some aquatic species may need to be moved to new areas if they are unable to migrate on their own or to adapt fast enough to changing conditions. Plans for such assisted migrations emphasize the need to isolate these translocated populations above barriers to prevent their secondary spread through the landscape, where they might have unanticipated harmful effects on other species (Olden et al. 2011). Barriers to movement may be highly detrimental in coastal rivers with diadromous species (Liermann et al. 2012) but crucial to the survival of species restricted to headwater enclaves that lack predators or competitors (Fausch et al. 2009, Marr et al. 2012). Therefore, the relative value of the connectivity versus the fragmentation of aquatic habitats needs to be evaluated on a case-by-case basis, through which the beneficial effects of limiting the spread of invasive species or diseases, preventing hybridization with hatchery fish, or keeping organisms out of ecological traps are weighed against the potential detrimental effects on the movement patterns of native species.

Acknowledgments

The assistance of Jessica A. Dugan, Aimee H. Fullerton, Daniel K. Gibson-Reinemer, Annika A. Walters, and three anonymous reviewers is greatly appreciated. Elizabeth Ono Rahel created the figures.

References cited

- Amos KH, et al. 2010. Viral hemorrhagic septicemia virus (VHSV IVb) risk factors and association measures derived by expert panel. *Preventive Veterinary Medicine* 94: 128–139.
- Asian Carp Regional Coordinating Committee. 2010. 2011 Asian Carp Control Strategy Framework. Asian Carp Regional Coordinating Committee. (14 February 2013; www.asiancarp.us/documents/2011Framework.pdf)
- Avenetti LD, Robinson AT, Cantrell CJ. 2006. Short-term effectiveness of constructed barriers at protecting Apache trout. *North American Journal of Fisheries Management* 26: 213–216.
- Avis L, Wilkinson T. 2011. Invasive Smallmouth Bass Containment Structures in the Beaver Creek Watershed: 2010/2011. Habitat Conservation Trust Fund, British Columbia Conservation Foundation. Project File no. 5-211.
- Baric S, Riedl A, Meraner A, Medgyesy N, Lackner R, Pelster B, Dalla Via J. 2010. Alpine headwater streams as reservoirs of remnant populations of the Danubian clade of brown trout. *Freshwater Biology* 55: 866–880.
- Buktenica MW. 1997. Bull trout restoration and brook trout eradication at Crater Lake National Park, Oregon. Pages 127–135 in Mackay WC, Brewin MK, Monita M, eds. *Friends of the Bull Trout Conference Proceedings*. Bull Trout Task Force, Trout Unlimited.
- Bulow FJ, Webb MA, Crumby WD, Quisenberry SS. 1988. Effectiveness of a fish barrier dam in limiting movement of rough fishes from a reservoir into a tributary stream. *North American Journal of Fisheries Management* 8: 273–275.

- Bush Heritage Australia. 2011. New hope at Edgbaston Reserve: A little fish inches back from the brink thanks to our supporters. Bush Heritage Australia. (14 February 2013; www.bushheritage.org.au/news/headlines/headlines_2011/new-hope-at-edgbaston.html)
- Calamusso B, Rinne JN. 1999. Native montane fishes of the Middle Rio Grande ecosystem: Status, threats, and conservation. Pages 231–237 in Finch DM, Whitney JC, Kelly JF, Loftin SR, eds. *Rio Grande Ecosystems: Linking Land, Water, and People*. US Department of Agriculture, Forest Service, Rocky Mountain Research Station.
- Campbell D, Durst S, Kantola AT, Kubly DM, Muth RT, Swett, J, Whitmore S. 2010. Overview of the Colorado River Basin Collaborative Management Programs. Pages 15–41 in Melis TS, Hamill JF, Bennett GE, Coggins LG Jr, Grams PE, Kennedy TA, Kubly DM, Ralston BE, eds. *Proceedings of the Colorado River Basin Science and Resource Management Symposium: November 18–20, 2008, Scottsdale, Arizona*. US Geological Survey. Scientific Investigations Report no. 2010–5135.
- Carlson AJ, Rahel FJ. 2010. Annual intrabasin movement and mortality of adult Bonneville cutthroat trout among complementary riverine habitats. *Transactions of the American Fisheries Society* 139: 1360–1371.
- Clarkson RW. 2004. Effectiveness of electrical fish barriers associated with the Central Arizona Project. *North American Journal of Fisheries Management* 24: 94–105.
- Clarkson RW, Marsh PC, Dowling TE. 2012. Population prioritization for conservation of imperiled warmwater fishes in an arid-region drainage. *Aquatic Conservation: Marine and Freshwater Ecosystems* 22: 498–510.
- Crowl TA, Townsend CR, McIntosh AR. 1992. The impact of introduced brown and rainbow trout on native fish: The case of Australasia. *Reviews in Fish Biology and Fisheries* 2: 217–241.
- Crumby WD, Webb MA, Bulow FJ, Cathey HJ. 1990. Changes in biotic integrity of a river in north-central Tennessee. *Transactions of the American Fisheries Society* 119: 885–893.
- D'Angelo VS, Muhlfeld CC, Miller BJ, Fredenberg CR. 2010. 2010 Summary Report: Preservation of Native Bull Trout in Glacier National Park: Continued Experimental Suppression of Nonnative Lake Trout in Quartz Lake, Glacier National Park. US Geological Survey, Rocky Mountain Science Center.
- Ellender BR, Weyl OLF, Swartz ER. 2011. Invasion of a headwater stream by non-native fishes in the Swartkops River system, South Africa. *African Zoology* 46: 39–46.
- Fausch KD, Rieman BE, Dunham JB, Young MK, Peterson DP. 2009. Invasion versus isolation: Trade-offs in managing native salmonids with barriers to upstream movement. *Conservation Biology* 23: 859–870.
- Fullerton AH, Burnett KM, Steel EA, Flitcroft RL, Pess GR, Feist BE, Torgensen CE, Miller DJ, Sanderson BL. 2010. Hydrological connectivity for riverine fish: Measurement challenges and research opportunities. *Freshwater Biology* 55: 2215–2237.
- Gherardi F, Aquiloni L, Diéguez-Urbeondo J, Tricarico E. 2011. Managing invasive crayfish: Is there a hope? *Aquatic Sciences* 73: 185–200.
- Grant EHC, Lynch HJ, Muneepeerakul R, Arunachalam M, Rodríguez-Iturbe I, Fagan WF. 2012. Interbasin water transfer, riverine connectivity, and spatial controls on fish biodiversity. *PLOS ONE* 7 (art. e34170). doi:10.1371/journal.pone.0034170
- Hillyard KA, Smith BB, Conallin AJ, Gillanders BM. 2010. Optimising exclusion screens to control exotic carp in an Australian lowland river. *Marine and Freshwater Research* 61: 418–429.
- Holthe E, Lund E, Finstad B, Thorstad EB, McKinley RS. 2005. A fish selective obstacle to prevent dispersion of an unwanted fish species, based on leaping capabilities. *Fisheries Management and Ecology* 12: 143–147.
- Hoogeveen N. 2010. Solving Dam Problems: Iowa's 2010 Plan for Dam Mitigation. Iowa Department of Natural Resources.
- Jackson CR, Pringle CM. 2010. Ecological benefits of reduced hydrologic connectivity in intensively developed landscapes. *BioScience* 60: 37–46.
- Kemp PS, O'Hanley JR. 2010. Procedures for evaluating and prioritising the removal of fish passage barriers: A synthesis. *Fisheries Management and Ecology* 17: 297–322.
- Kerby JL, Riley SPD, Kats LB, Wilson P. 2005. Barriers and flow as limiting factors in the spread of an invasive crayfish (*Procambarus clarkii*) in southern California streams. *Biological Conservation* 126: 402–409.
- Kornis MS, Vander Zanden MJ. 2010. Forecasting the distribution of the invasive round goby (*Neogobius melanostomus*) in Wisconsin tributaries to Lake Michigan. *Canadian Journal of Fisheries and Aquatic Sciences* 67: 553–562.
- Kostyack J, Lawler JJ, Goble DD, Olden JD, Scott JM. 2011. Beyond reserves and corridors: Policy solutions to facilitate the movement of plants and animals in a changing climate. *BioScience* 61: 713–719.
- Kozubíková E, Petrušek A, Ďuriš Z, Martín MP, Diéguez-Urbeondo J, Oidtmann B. 2008. The old menace is back: Recent crayfish plague outbreaks in the Czech Republic. *Aquaculture* 274: 208–217.
- Lavis DS, Hallett A, Koon EM, McAuley TC. 2003. History of and advances in barriers as an alternative method to suppress sea lampreys in the Great Lakes. *Journal of Great Lakes Research* 29 (suppl. 1): 362–372.
- Le Curieux-Belfond O, Vandael L, Caron J, Séralini G-E. 2009. Factors to consider before production and commercialization of aquatic genetically modified organisms: The case of transgenic salmon. *Environmental Science and Policy* 12: 170–189.
- Leuven RSEW, van der Velde G, Baijens I, Snijders J, van der Zwart C, Lenders HJR, bij de Vaate A. 2009. The river Rhine: A global highway for dispersal of aquatic invasive species. *Biological Invasions* 11: 1989–2008.
- Lieb DA, Bouchard RW, Carline RF, Nuttall TR, Wallace JR, Burkholder CL. 2011. Conservation and management of crayfishes: Lessons from Pennsylvania. *Fisheries* 36: 489–507.
- Liermann CR, Nilsson C, Robertson J, Ng RY. 2012. Implications of dam obstruction for global freshwater fish diversity. *BioScience* 62: 539–548.
- Lintermans M. 2000. Recolonization by the mountain galaxias *Galaxias olidus* of a montane stream after the eradication of rainbow trout *Oncorhynchus mykiss*. *Marine and Freshwater Research* 51: 799–804.
- Marks JC, Haden GA, O'Neill M, Pace C. 2010. Effects of flow restoration and exotics species removal on recovery of native fish: Lessons from a dam decommissioning. *Restoration Ecology* 18: 934–943.
- Marr SM, Impson ND, Tweddle D. 2012. An assessment of a proposal to eradicate non-native fish from priority river areas in the Cape Floristic region of South Africa. *African Journal of Aquatic Science* 37: 131–142.
- Martinez PJ. 2003. Westslope Warmwater Fisheries. Colorado Division of Wildlife.
- Meyers LS, Thuemler TF, Kornely GW. 1992. Seasonal movements of brown trout in northeast Wisconsin. *North American Journal of Fisheries Management* 12: 433–441.
- Minkley WL, Meffe GM, Soltz DL. 1991. Conservation and management of short-lived fishes: The Cyprinodontidae. Pages 247–282 in Minkley WL, Deacon JE, eds. *Battle Against Extinction: Native Fish Management in the American West*. University of Arizona Press.
- Moy PB, Polls I, Dettmers JM. 2011. The Chicago Sanitary and Ship Canal aquatic nuisance species dispersal barrier. Pages 121–1137 in Chapman DC, Hoff MH, eds. *Invasive Asian Carps in North America*. American Fisheries Society. Symposium no. 74.
- Moyle PB, Crain PK, Whitener K, Mount JF. 2003. Alien fishes in natural streams: Fish distribution, assemblage structure, and conservation in the Cosumnes River, California, U.S.A. *Environmental Biology of Fishes* 68: 143–162.
- Novinger DL, Rahel FJ. 2003. Is isolating cutthroat trout above artificial barriers in small headwater streams an effective long-term conservation strategy? *Conservation Biology* 17: 772–781.
- Olden JD, Kennard MJ, Lawler JJ, Poff NL. 2011. Challenges and opportunities in implementing managed relocation for conservation of freshwater species. *Conservation Biology* 25: 40–47.
- Pister EP. 2010. California golden trout: Perspectives on restoration and management. *Fisheries* 35: 550–553.
- Pratt TC, O'Connor LM, Hallett AG, McLaughlin RL, Katapodis C, Hayes DB, Bergstedt RA. 2009. Balancing aquatic habitat fragmentation and control of invasive species: Enhancing selective fish passage at

- sea lamprey control barriers. *Transactions of the American Fisheries Society* 138: 652–665.
- Propst DL, Stefferud JA, Turner PR. 1992. Conservation and status of gila trout *Oncorhynchus gilae*. *Southwestern Naturalist* 37: 117–125.
- Rahel FJ. 2004. Unauthorized fish introductions: Fisheries management of the people, for the people, or by the people? Pages 431–444 in Nickum MJ, Mazik PM, Nickum JG, MacKinlay DD, eds. *Propagated Fishes in Resource Management*. American Fisheries Society.
- . 2007. Biogeographic barriers, connectivity, and biotic homogenization: It's a small world after all. *Freshwater Biology* 52: 696–710.
- Rinne JN, Turner PR. 1991. Reclamation and alteration as management techniques, and a review of methodology in stream renovation. Pages 219–244 in Minckley WL, Deacon JE, eds. *Battle against Extinction: Native Fish Management in the American West*. University of Arizona Press.
- Rinne JN, Riley L, Bettaso R, Sorenson R, Young K. 2004. Managing southwestern native and nonnative fishes: Can we mix oil and water and expect a favorable solution? *American Fisheries Society Symposium* 44: 445–466.
- Roberts JJ, Rahel FJ. 2008. Irrigation canals as sink habitat for trout and other fishes in a Wyoming drainage. *Transactions of the American Fisheries Society* 137: 951–961.
- Rubidge EM, Taylor EB. 2005. An analysis of spatial and environmental factors influencing hybridization between native westslope cutthroat trout (*Oncorhynchus clarkii lewisi*) and introduced rainbow trout (*O. mykiss*) in the upper Kootenay River drainage, British Columbia. *Conservation Genetics* 6: 369–384.
- Russell IA. 2011. Conservation status and distribution of freshwater fishes in South African national parks. *African Zoology* 46: 117–132.
- Scheerer PD. 2002. Implications of floodplain isolation and connectivity on the conservation of an endangered minnow, Oregon chub, in the Willamette River, Oregon. *Transactions of the American Fisheries Society* 131: 1070–1080.
- Schrank AJ, Rahel FJ. 2004. Movement patterns in inland cutthroat trout: Management and conservation implications. *Canadian Journal of Fisheries and Aquatic Sciences* 61: 1528–1537.
- Shepard BB, May BE, Urie W. 2005. Status and conservation of westslope cutthroat trout within the western United States. *North American Journal of Fisheries Management* 25: 1426–1440.
- Simpson WG, Ostrand KG. 2012. Effects of entrainment and bypass at screened irrigation canals on juvenile steelhead. *Transactions of the American Fisheries Society* 141: 599–609.
- Spens J, Englund G, Lundqvist H. 2007. Network connectivity and dispersal barriers: Using geographical information system (GIS) tools to predict landscape scale distribution of a key predator (*Esox lucius*) among lakes. *Journal of Applied Ecology* 44: 1127–1137.
- Stuart IG, Williams A, McKenzie J, Holt T. 2006. Managing a migratory pest species: A selective trap for common carp. *North American Journal of Fisheries Management* 26: 888–893.
- Taugbøl T, Skurdal J, Håstein T. 1993. Crayfish plague and management strategies in Norway. *Biological Conservation* 63: 75–82.
- [USFWS] US Fish and Wildlife Service. 2009. Procedures for Stocking Nonnative Fish Species in the Upper Colorado River Basin. Upper Colorado River Endangered Fish Recovery Program.
- Utah's Watershed Restoration Initiative. 2010. West Fork Duchesne River Fish Passage Barrier: Justification. Utah's Watershed Restoration Initiative. (14 February 2013; <http://wri.utah.gov/WRI/Proposal/Justification.aspx?id=1406>)
- Van Houdt JKJ, Pinceel J, Flamand M-C, Briquet M, Dupont E, Volckaert FAM, Baret PV. 2005. Migration barriers protect indigenous brown trout (*Salmo trutta*) populations from introgression with stocked hatchery fish. *Conservation Genetics* 6: 175–191.
- Vitule JRS, Skóra S, Abilhoa V. 2012. Homogenization of freshwater fish faunas after the elimination of a natural barrier by a dam in Neotropics. *Diversity and Distributions* 18: 111–120.
- Winston MR, Taylor CM. 1991. Upstream extirpation of four minnow species due to damming of a prairie stream. *Transactions of the American Fisheries Society* 120: 98–105.
- Young MK, Guenther-Gloss PM, Ficke AD. 2005. Predicting cutthroat trout (*Oncorhynchus clarkii*) abundance in high-elevation streams: Revisiting a model of translocation success. *Canadian Journal of Fisheries and Aquatic Sciences* 62: 2399–2408.

Frank J. Rahel (frahel@uwyo.edu) is a biologist in the Department of Zoology and Physiology at the University of Wyoming, in Laramie. He studies fish ecology, invasive species, and climate change.