

# Biogeographic barriers, connectivity and homogenization of freshwater faunas: it's a small world after all

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## SUMMARY

1. Historically, biogeographic barriers to the movement of aquatic organisms existed at multiple spatial scales and contributed to the development of unique regional faunas. At increasing spatial scales, these barriers consisted of waterfalls and cascades; catchment divides; major mountain ranges and oceans. This hierarchy of movement barriers produced increasingly distinct aquatic biotas at larger drainage units.
2. Humans have provided a variety of pathways by which aquatic species can circumvent historical biogeographic barriers. These include both authorised and unauthorised stocking, construction of canals and water conveyance systems, transport in ship ballast water, fishing and angling gear (including boats) transferred among water bodies and intentional release of ornamental and other captive species.
3. One consequence of human-aided breaching of biogeographic barriers has been the spread of noxious species that have altered aquatic ecosystems and fisheries in ways that are undesirable to humans.
4. Another consequence of human-aided breaching of biogeographic barriers has been the homogenization of aquatic biotas. Homogenization occurs when a few cosmopolitan species come to dominate communities at the expense of unique native species. Among aquatic organisms this phenomenon is best documented for fish faunas where a small set of species introduced for sport fishing, aquaculture, or ornamental purposes have become widespread throughout the world.
5. Slowing biotic homogenization will require slowing the rate at which species breach biogeographic barriers. This will involve implementing regulations that limit stocking opportunities; increasing the public's awareness about the consequences of releasing non-native species and developing technological solutions that prevent movement of aquatic organisms or eliminate them before they become established.
6. River restoration can influence homogenization of aquatic biotas through two major mechanisms: by removing barriers to movement and by restoring natural habitat conditions. Removal of movement barriers may facilitate the spread of non-native species and thus contribute to biotic homogenization. Restoration of natural flow regimes and habitat conditions may reduce biotic homogenization by favouring regional native species over cosmopolitan, non-native species.

*Keywords:* aquatic organisms, biogeographic barriers, connectivity, homogenization, invasive species, rivers, United States

## Introduction

A host of factors that operate on different spatial and temporal scales determine which species are able to colonise and persist in local habitats. Among the most important factors for freshwater organisms are natural barriers such as oceans, mountain ranges, catchment divides and waterfalls that prevent the exchange of species among regions. These impediments to movement are referred to as biogeographic barriers. Historically, these barriers were a dominant factor in determining the composition of regional faunas and in promoting endemism (Cox & Moore, 1980; Ricklefs & Schluter, 1993). However, human actions have reduced the isolation formerly imposed by biogeographic barriers and the result has been an unprecedented mixing of the Earth's biological communities (Lockwood & McKinney, 2001; Rahel, 2002; McKinney, 2006).

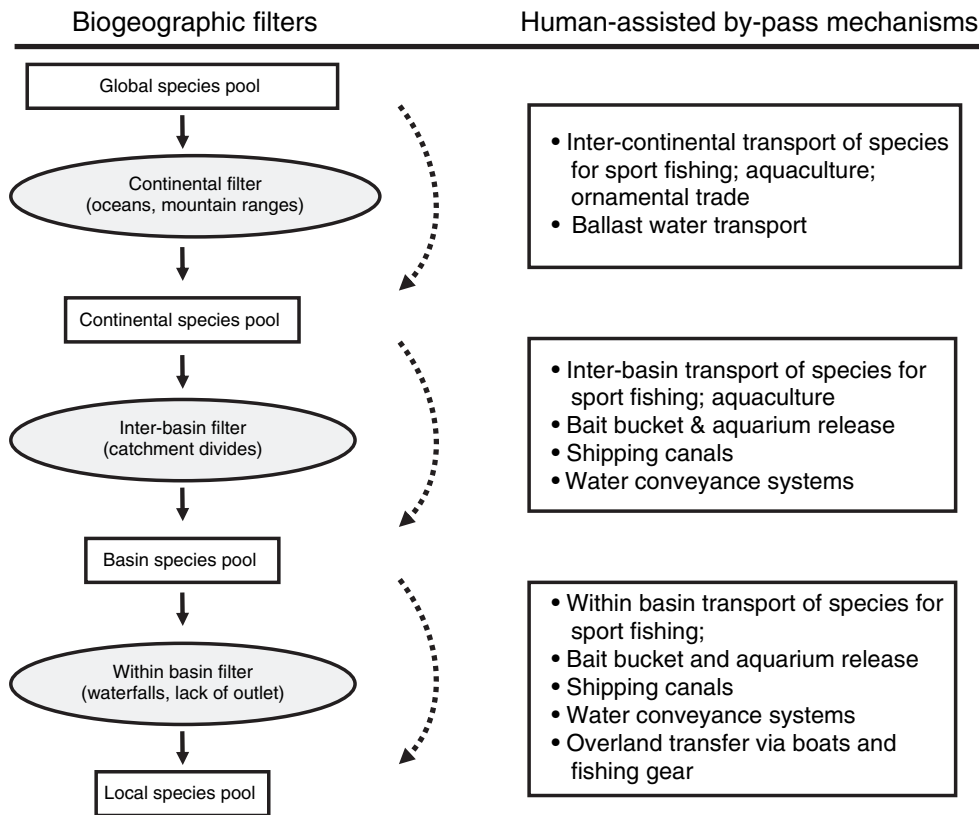
Much has been written about the loss of connectivity in aquatic ecosystems because of the construction of dams and levees (Pringle, 2003). Such a loss of connectivity can prevent seasonal migrations of aquatic organisms and reduce the diversity and productivity of aquatic habitats. Consequently, many stream restoration projects are directed at restoring connectivity within catchments (Hart *et al.*, 2002). However, at larger spatial scales, such as across catchment boundaries, humans can greatly increase the connectivity of formerly isolated biotas (Rahel, 2002; Crooks & Suarez, 2006). The purpose of this paper is to explore how human-aided circumvention of biogeographic barriers has increased the connectivity among aquatic ecosystems and fostered an unprecedented exchange among the world's zoogeographic regions. This paper also examines how this exchange has contributed to the increasing global homogenization of aquatic fauna.

## Biogeographic barriers in freshwater systems

The biogeographic barriers that determine which species are able to colonise local habitats can be viewed at three spatial scales: continental, interbasin and within basin (Fig. 1). At the largest spatial scale, freshwater faunas are isolated by their inability to cross oceans, high mountain ranges or expansive deserts, hence freshwater fish faunas are often considered in light of Wallace's six zoogeographic regions

that reflect continental-scale differences in faunal composition (Moyle & Cech, 2004). These are (i) the African region; (ii) the Neotropical region; (iii) the Oriental region; (iv) the Palearctic region; (v) the Nearctic region; and (vi) the Australian region. The distinctiveness of biota at this level reflects a long history of isolation during which speciation has resulted in unique fish faunas within these zoogeographic regions. Prior to human intervention, no species of freshwater fish occurred in all six of these zoogeographic regions and few species occurred in more than one region. Today, however, rainbow trout, brown trout, brook trout, mosquitofish, guppy, common carp and goldfish occur in all of the Earth's zoogeographic regions (Lever, 1996).

Within the six zoogeographic regions, major river basins constitute a second level of biographic barriers. At the scale of major drainage basins, freshwater fish would have to move across catchment divides or move through saltwater along coastlines in order to colonise adjacent basins. Such colonisation events are relatively rare and thus the six major zoogeographic regions are often divided into subregions and further into provinces based on major river systems. For example, within the Nearctic zoogeographic region (North America down to central Mexico), ichthyologists recognise three subregions that are further divided into a number of provinces based on differences in fish faunas among major river systems (Fig. 2). Although slightly different schemes exist for naming and subdividing regions (c.f. Burr & Mayden, 1992; Abell *et al.*, 2000; Taylor, 2004), there is general agreement that the major river systems in North America represent distinct fish assemblages that rarely exchanged species over ecological time periods (e.g. decades to centuries) prior to human intervention. Faunal exchanges over longer time periods (thousands of years and longer) occurred because of glaciation or stream capture events (Hocutt & Wiley, 1986). In general, northern river basins tend to consist of subsets of species that recolonised from glacial refugia. By contrast, southern basins in the Nearctic region that escaped glaciation tend to have more unique fish faunas than those whose drainage patterns were altered by extensive periods of ice cover. Particularly noteworthy is the Colorado River that forms the Colorado Province where 69% of the native fish species were endemic. The Colorado River basin has been isolated for millions of years and has



**Fig. 1** Barriers to the movement of aquatic species can be viewed as a series of nested filters. At the largest spatial scale, oceans and major mountain ranges prevent species movement among continents and result in the distinctive biotas recognised as zoogeographic regions. Within zoogeographic regions, catchment divides prevent movement among major basins. Within basins, waterfalls and high gradient reaches can prevent movement of organisms in streams, and lack of surface water connections can prevent movement of organisms among lakes. However, a variety of human activities provide mechanisms for aquatic species to bypass historic biogeographic barriers and colonise new areas.

seen the evolution of fishes adapted to large, fast-flowing rivers with high silt loads and large discharge fluctuations (Carlson & Muth, 1989). Despite sharing a long border with the species-rich Mississippi River Province, only five of the combined 400 native fish species historically occurred in both provinces. This indicates that the Rocky Mountains, which form the catchment divide between these basins, have been a formidable barrier to fish movement.

Within river basins, waterfalls and high gradient reaches function as a third level of biogeographic barriers to fish movement. In some cases, these barriers may be the result of large waterfalls. For example, Shoshone Falls (65-m high) on the Snake River, Idaho, has prevented upstream colonisation by 18 fish species, including anadromous salmonids (McPhail & Lindsey, 1986). Even when there is no single hydraulic feature distinguishable as a waterfall,

high gradient stream reaches that have extensive cascades also can prevent upstream colonisation by fishes. Kruse, Hubert & Rahel (1997) noted that gradients above 10% were associated with the upstream distribution limit of cutthroat trout in Wyoming. In the southeastern United States, the Fall Line, a 7- to 20-km-wide transition zone between upland areas and the coastal region, forms the upstream distribution limit for many fish species (Jenkins & Burkhead, 1993). At the Fall Line, streams increase their gradient and become a series of boulder-strewn cascades that effectively inhibit upstream movement by fish.

Movement of aquatic organisms is also inhibited by a lack of surface water connections among lakes. Isolated lakes can be considered as aquatic islands surrounded by a sea of land, making it difficult for aquatic organisms to colonise these habitats (Rahel,

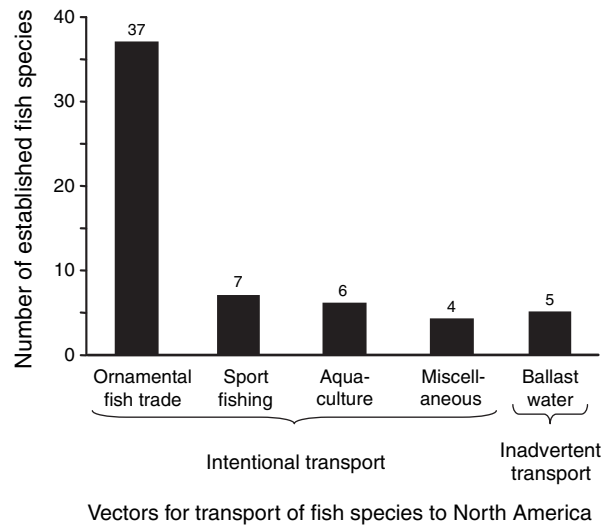


**Fig. 2** Zoogeographic divisions for fishes in the Nearctic zoogeographic region (North America to the southern edge of the Mexican plateau). There are three major subregions: (I) the Arctic-Atlantic subregion; (II) the Pacific subregion; and (III) the Mexican subregion, which can be further divided into ichthyological provinces as follows: IA, Rio Grande; IB, Mississippi; IC, Southeastern; ID, Central Appalachian; IE, Northern Appalachian; IF, Great Lakes-St Lawrence; IG, Hudson Bay; IH, Arctic; IIA, Alaska Coastal; IIB, Columbia; IIC, Great Basin; IID, Klamath; IIE, Sacramento; IIF, Colorado; IIG, South Coastal; IIIA, Sonoran-Sinaloa; IIIB, Central Mexico. Based on Moyle & Cech (2004) and Burr & Mayden (1992).

1984; Magnuson *et al.*, 1998). As a consequence, isolated water bodies often contain fewer fish species than water bodies with inlet and outlet streams (Tonn *et al.*, 1990; Snodgrass *et al.*, 1996).

### Circumvention of biogeographic barriers through human intervention

Human activities have provided a variety of ways for aquatic organisms to circumvent natural biogeographic barriers. At the largest spatial scale, intercontinental transport has resulted in many fish species becoming established outside of their native zoogeographic region (Lever, 1996). For example, 59 freshwater fish species whose native distribution is outside the Nearctic zoogeographic region have been introduced and become established in North America (Benson & Boydstun, 1999). Most of these (54 species) were

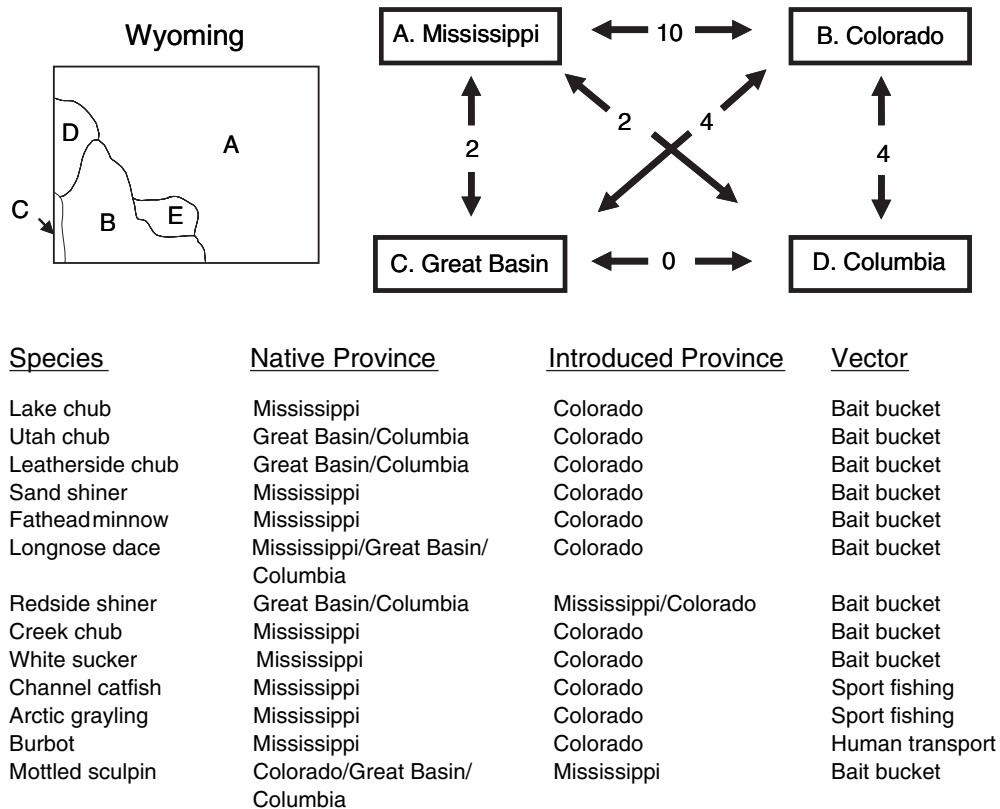


**Fig. 3** Summary of transport vectors for the 59 fish species whose native distribution is outside of the Nearctic region (i.e. outside of North America) and which have become established in the Nearctic region. Based on data from Benson & Boydstun (1999).

transported intentionally by humans across major land or oceanic biogeographic barriers and only five were inadvertently transported across an oceanic barrier in the ballast water of ships (Fig. 3). For those species intentionally transported, the majority were introduced in association with the ornamental fish industry. A similar situation exists for the Australian zoogeographic region where 22 of the 34 freshwater fish species introduced into Australia were intentionally transported across an oceanic barrier by the ornamental fish industry (Lintermans, 2004).

Within zoogeographic regions, there has been widespread transport of species across major basin divides into new faunal provinces. Consider, for example, the Colorado Province, which is part of the Nearctic zoogeographic region (Fig. 2). The native fish fauna consisted of only 32 fish species. However, 68 non-indigenous fish species are now established in the Colorado Province (USGS, 2004). Of these, 54 species are from other ichthyological provinces within the Nearctic zoogeographic region and 14 species are from other zoogeographic regions. In the Colorado Province, all of the non-indigenous fishes appear to have been the result of direct human transport across major catchment divides.

Introductions of fish within the state of Wyoming provide a good example of how humans have enabled



**Fig. 4** Map showing the four ichthyological provinces that occur in Wyoming: A, Mississippi; B, Colorado; C, Great Basin; and D, Columbia. E is a closed basin that lacks perennial water bodies. The boxes and arrows depict the number of species exchanges among the four provinces involving thirteen species native to at least one province within Wyoming. The greatest number of exchanges (10) occurred between the Mississippi and Colorado provinces. All of the exchanges were the result of intentional transport of species across basin divides by humans, mainly because of bait bucket releases by anglers. Data are from Baxter & Stone (1995).

fish to bypass historic colonisation barriers. Wyoming encompasses four of the ichthyological provinces in the Nearctic region (Fig. 4). Thirteen fish species have been moved among the four provinces within Wyoming, with the most common exchange involving transfer of species from the Mississippi Province to the Colorado Province. All of the introductions were done by humans intentionally transporting species across major basin divides, usually in association with sport fishing (Fig. 4).

Canals have provided a mechanism for fish to bypass historic biogeographic barriers to movement within zoogeographic provinces. For example, the Chicago Sanitary and Shipping Canal was opened in 1900 and provided a linkage between Lake Michigan of the Great Lakes–St Lawrence Province and the Des Plaines River of the Mississippi Province. This canal breached a catchment divide that had been a biogeographic barrier to fish movement between these

provinces for thousands of years. After the canal was opened, a group of aquatic species that included the round goby and zebra mussel used this route to move between provinces (Kolar & Lodge, 2000). Likewise, the Erie Canal provided a linkage between Lake Erie in the Great Lakes–St Lawrence River Province and the Hudson River of the Northern Appalachian Province. Among the aquatic species that used the Erie Canal to breach the historic biogeographic barrier between these faunal provinces are the white perch and the alewife (Mills, Chrisman & Holeck, 1999).

The faunal provinces depicted in Fig. 2 represent large drainage basins that empty into the ocean or are self-contained inland systems (e.g. the Great Basin Province). These basins can be subdivided into increasingly smaller catchments in a hierarchical fashion. For example, the Colorado Province has been divided into three ecoregions and the Mississippi River into 15 ecoregions for purposes of conservation

planning (Abell *et al.*, 2000). Colonisation of new aquatic habitats becomes increasingly easier as the spatial extent of the catchments under consideration decreases. This is particularly evident for species that are new to a faunal province and which spread out from the original introduction site largely through their own mobility. An example of a species that is currently undergoing an explosive spread is the round goby in the North American Great Lakes. From its initial introduction via ballast water in the St Clair River, this fish has spread rapidly across the Great Lakes–St Lawrence River Province and is poised to begin spreading in the Mississippi Province following its migration through the Chicago Sanitary and Shipping Canal system mentioned above (USGS, 2004). The spread of the rusty crayfish is another example of the rapid colonisation of an aquatic species through interconnected waterways once it has been introduced into a new ecoregion (Lodge *et al.*, 2000). Non-indigenous salmonids stocked into headwater lakes can rapidly spread throughout a drainage system and cause a loss of native salmonid species (Adams, Frissell & Rieman, 2001). Particularly troublesome are species such as the zebra mussel or New Zealand mud snail that have limited mobility, but which are readily transported by boaters or anglers overland to new water bodies (Bossenbroek, Kraft & Nekola, 2001; Kerans *et al.*, 2005).

Once a species is within a drainage system, it may be prevented from colonizing upstream regions by waterfalls or high-gradient reaches. Humans help species circumvent such biogeographic barriers by constructing canals around the barriers or by intentionally stocking species upstream of the barriers. One of the best known examples of the former is the Welland Canal that was built in 1829 and allowed ships to bypass Niagara Falls (Mills *et al.*, 1999). Being 49-m high, Niagara Falls was a formidable barrier to movement of aquatic organisms from the St Lawrence River and Lake Ontario upstream into the upper Great Lakes. The Welland Canal provided a mechanism for fish such as the sea lamprey and the alewife to bypass this barrier and colonise the upper portions of the Great Lake–St Lawrence River province.

Humans also have directly stocked fish above natural migration barriers. Bahls (1992) estimated that 95% of the nearly 16 000 high-altitude lakes in the western U.S. were historically fishless. Today, however, 59% (9500) of these lakes contain fish popula-

tions as a result of stocking by humans. Although fish populations generally existed in downstream portions of these catchments, steep gradients often prevented upstream colonisation by fishes following the end of Pleistocene glaciation. Stream gradients above 10% appear to prevent upstream movement by salmonids, even in the absence of vertical waterfalls (Kruse *et al.*, 1997). In a similar vein, stocking of fishless lakes in the upper portions of catchments has been occurring in Scandinavia since the 12th century (Nilsson, 1972).

### Circumventing biogeographic barriers promotes biotic homogenization

The circumvention of biogeographic barriers promotes homogenization of aquatic biota. Homogenization refers to the increased similarity of biota over time and is typically the result of displacement of native species by a small set of non-indigenous species that have been widely introduced through human actions (Rahel, 2004). These cosmopolitan species bring sameness to faunas that were historically unique because of biogeographic isolation (McKinney & Lockwood, 1999). Data on worldwide introductions of aquatic species illustrate the fact that a relatively small number of species are being widely introduced throughout the world (Welcomme, 1988). Although 233 aquatic species are known to have been introduced outside of their native area, the eighteen most widely introduced species accounted for nearly half of all introduction events (49%) despite constituting only 8% of all introduced species (Table 1). These widely introduced species were transported across major biogeographic barriers by humans for sport fishing, aquaculture, or ornamental purposes.

Homogenization is also evident when fish faunas from around the world are compared. Consider the freshwater fish faunas in three widely separated countries that occur in different zoogeographic regions: Sweden in the Palaearctic region; the United States in the Nearctic region and New Zealand in the Australian region. Historically, Sweden and the United States had only six freshwater fish species in common, but now share an additional ten species (Table 2). Four of these ten species were native to Sweden, five were native to the United States and one was introduced to both countries. Sweden and New Zealand historically had no freshwater fish species in common but now share nine species; four of which

**Table 1** A summary of aquatic species that have been introduced outside of their native country

Species	Number of countries with introductions
Channel catfish	16
Redbelly tilapia	16
Blue tilapia	17
Bluegill	18
Bighead carp	24
Goldfish	24
Guppy	24
Redbreast tilapia	26
Brown trout	29
Mosquitofish	32
Silver carp	38
Nile tilapia	38
Brook trout	39
Grass carp	49
Largemouth bass	49
Common carp	59
Mozambique tilapia	66
Rainbow trout	82
26 species	6–10
12 species	11–15

Welcomme (1988) documented 1333 introduction events involving 233 species. Most species have been introduced into only a few countries. However, 18 species have been introduced in 16 or more countries throughout the world. Scientific names of species are given in Appendix 1.

were native to Sweden and five of which were introduced into both countries. Likewise, the United States and New Zealand historically had no freshwater fish species in common but now share 15 species; seven of which were native to the United States and eight of which were introduced from another country. As a group, the three countries had no species in common but now share eight species and thus their fish faunas have begun the process of homogenization.

Even within zoogeographic regions, movement of organisms across basin divides has contributed to the process of homogenization. Across the coterminous United States, for example, the average similarity of fish faunas among states has increased by 7.2%, and pairs of states now share 15.4% more species on average than they did prior to European colonisation of North America (Rahel, 2000). Most fish introductions in the United States involve species that are native to North America, but which have been moved into new catchments (e.g. the provinces shown in Fig. 2), primarily for sport fishing purposes. Of the 17

most widely introduced species, all but three were native to the Nearctic zoogeographic region of North America but have been moved to new catchments outside of their historical range (Table 3). A similar situation exists across Canada where fish faunas have undergone homogenization because of the widespread movement of relatively few species across historic ecoregion boundaries (Taylor, 2004). In California, there has been a large increase in the similarity of fish faunas among the state's zoogeographic provinces, a process driven largely by the stocking of species from other zoogeographic provinces within the Nearctic region (Marchetti *et al.*, 2001; Moyle, 2002).

Even within a catchment, circumvention of migration barriers such as waterfalls and rapids can contribute to the homogenization of aquatic faunas. In the Kanawha River in West Virginia and Virginia, U.S.A., the barrier is a section of river that includes the Kanawha Falls (7.3 m) along with extensive cascades having large boulder and bedrock substrates. Because of the barrier to fish movements posed by Kanawha Falls, the upper and lower sections of the river historically had only 36 fish species in common. Now, however, the upper and lower sections have 66 fish species in common as a result of humans moving 17 species from the lower to the upper section and stocking 13 new species into both sections (Stauffer, Boltz & White, 1995). As a result, the overlap in fish faunas between these two sections has increased from 29% to 46% based on Jaccard's Coefficient of Similarity, a commonly used measure of biotic homogenization (Rahel, 2002).

### Reducing the human-assisted breaching of biogeographic barriers

Human-assisted breaching of biogeographic barriers is largely responsible for the increased exchange of aquatic organisms among historically isolated zoogeographic regions, provinces and catchments. Three major mechanisms by which aquatic species bypass historical barriers to colonisation are through direct human stocking, entrainment in ballast water and by way of canals (Fig. 1). These pathways will have to be controlled if future homogenization of aquatic communities is to be minimised.

Direct stocking of species by humans can be considered in terms of two broad categories: author-

**Table 2** A comparison of the fish species in common among Sweden, U.S.A. and New Zealand (N.Z.)

Comparison	Species historically in common	Number of additional species in common	Additional species in common		
Sweden – U.S.A.	Sea lamprey Northern pike Atlantic salmon Burbot Threespine stickleback Ninespine stickleback	10	Sweden → U.S.A. Brown trout Ruffe Tench Rudd	U.S.A. → Sweden Cutthroat trout Brook trout Lake trout Rainbow trout Kokanee salmon	From another country Common carp
Sweden – N.Z.	None	9	Sweden → N.Z. Rudd Tench European perch Brown trout	N.Z. → Sweden None	From another country Common carp Rainbow trout Kokanee salmon Brook trout Lake trout
U.S.A. – N.Z.	None	15	U.S.A. → N.Z. Brown bullhead Mosquitofish Rainbow trout Kokanee salmon Chinook salmon Brook trout Lake trout	N.Z. → U.S.A. None	From another country Common carp Goldfish Rudd Tench Sailfin molly Guppy Green swordtail Brown trout
Sweden – U.S.A. – N.Z.	None	8	Sweden → U.S.A./N.Z. Rudd Tench Brown trout	U.S.A. → Sweden/N.Z. Rainbow trout Kokanee salmon Brook trout Lake trout	From another country Common carp

'Species historically in common' refers to species whose native range included the countries being compared. 'Additional species in common' refers to species that have become established outside of their native range with the arrow indicating movement from donor to recipient country. 'Another country' means that the species was introduced from outside of the countries being compared. Species scientific names are given in Appendix 1. Based on data from Lever (1996).

used stockings done with some regulatory oversight and unauthorised stockings where there is no oversight (Rahel, 2004). Authorised stockings are usually done for sport fishing, biocontrol, aquaculture, or conservation purposes and are regulated by local and federal governmental agencies. The rate at which new species are being introduced for sport fishing by fisheries managers has declined in the U.S.A. (Rahel, 2004), in part because much of the demand for sport fishes in areas with few native game species has been satisfied and in part because of the greater awareness of the harm that introduced species can cause (Rahel, 1997). Use of fish such as grass carp for biocontrol of aquatic plants continues, but managers favour the use of sterile fish to minimise the likelihood that non-indigenous species will become established. Aqua-

culture remains an area where introductions will be likely to continue, in part because economic pressures may outweigh ecological prudence in decisions about which species should be imported (Naylor, Williams & Strong, 2001). For example, the U.S. aquaculture industry continues to favour use of black carp to control trematode parasites in catfish ponds despite the objections of fish biologists that black carp would harm native mollusk assemblages if it became established outside of aquaculture facilities (Ferber, 2001). Although the use of sterile fish for biocontrol and aquaculture applications would reduce the chance of new species becoming established, it would not eliminate that possibility because a small percentage of fish that undergo the sterilisation procedure remain capable of reproduction (Naylor *et al.*, 2001).



Species	No. of states	Zoogeographic origin	Reason for introduction
Common carp	48	Palaeartic region	Aquaculture
Goldfish	42	Palaeartic region	Ornamental trade
Brown trout	39	Palaeartic region	Sport fishing
Rainbow trout	35	Nearctic region	Sport fishing
Smallmouth bass	22	Nearctic region	Sport fishing
Northern pike	21	Palaeartic & Nearctic regions	Sport fishing
Black crappie	20	Nearctic region	Sport fishing
Yellow perch	20	Nearctic region	Sport fishing
Fathead minnow	19	Nearctic region	Sport fishing (baitfish)
Walleye	19	Nearctic region	Sport fishing
Largemouth bass	19	Nearctic region	Sport fishing
White crappie	18	Nearctic region	Sport fishing
Striped bass	17	Nearctic region	Sport fishing
Bluegill	16	Nearctic region	Sport fishing
Mosquitofish	15	Nearctic region	Mosquito control
Brook trout	15	Nearctic region	Sport fishing
Green sunfish	15	Nearctic region	Sport fishing

**Table 3** The most commonly introduced fish species in the coterminous United States

Shown are the number of states into which a species has been introduced, the zoogeographic origin of the species and the purpose of the introduction. Species scientific names are given in Appendix 1. Data are from Rahel (2000).

Despite the economic arguments and political pressures often brought to bear in support of species introductions, biologists can have an impact in preventing introductions by informing decision makers about potential harmful effects of non-indigenous species. Along these lines, biologists helped to prevent the introduction of channel catfish in New Zealand and zander in the U.S.A., by pointing out the negative consequences these fish could have on native species (Townsend & Winterbourn, 1992; Wingate, 1992).

Whereas authorised introductions are usually subject to some level of ecological scrutiny, this is not true for unauthorised introductions. Unauthorised introductions include the release of baitfish or aquarium pets; illegal stocking of sport fish by the public; and fish present as contaminants when other species are being stocked (Rahel, 2004; Rixon *et al.*, 2005). Release of unused baitfish and crayfish can be a significant source of introduced species in regions with a strong tradition of live bait use in sport fishing. Litvak & Mandrak (1999) listed 109 fish species thought to have been established outside of their native range as a result of bait bucket introductions in the United States. The spread of non-native crayfish in the United States and Canada also has been greatly facilitated by release of unused bait by anglers (Lodge *et al.*, 2000). As result of these unauthorised introductions, agencies that regulate sport fishing have implemented

increasingly strict regulations on the use of live bait, and have even outlawed its use in many areas (Meronek, Copes & Coble, 1995; Rahel, 2004).

The ornamental fish trade has been a major source of introduced fish species. Of the 59 fish species that have been introduced to the United States from outside of the Nearctic region (i.e. outside of North America), 37 were associated with the ornamental fish trade (Fig. 3). Worldwide, 150 species of vertebrates, invertebrates, plants and microbes have become established outside their native ecosystems as a result of aquarium releases or aquatic ornamental culture (Padilla & Williams, 2004). Because the aquarium trade industry has been able to lobby against regulations, ornamental fish trade will likely continue to be a major vector for introductions of non-indigenous species. This will be especially true for areas with mild climates since many of the species favoured by aquarists originate in warm climates. Importation bans may be implemented for particularly noxious species such as snakehead fish in the family Channidae (Federal Register, 2002), but public education about the dangers of releasing unwanted pets may be the best way to curb introductions of ornamental aquatic organisms for the foreseeable future (Padilla & Williams, 2004).

Unauthorised introductions also include the release of species that are present as contaminants in

authorised fish stockings. Crossman & Cudmore (1999) listed 28 fish species that have been introduced outside of their historic range in North America as contaminants during the authorised stocking of other species. Taxa that have been especially prone to this method of introduction include the brook stickleback, small sunfishes (Centrarchidae) and some catfishes (Ictaluridae). Rahel (2004) reported that 8% of unauthorised fish stockings in Wyoming involved species introduced as contaminants during authorised stocking events. Compared to the other vectors of introduction, reducing contaminants in fish stockings should be relatively easy. Eliminating this pathway for unauthorised introductions would involve obtaining fish for stocking from contamination-free sources; increased vigilance during the stocking process and a readiness to eliminate unwanted species as soon as they are detected in the receiving water (Rahel, 2004).

Ballast water release from cargo ships has become a major way that freshwater species circumvent biogeographic barriers posed by oceans. The number of species introduced via ballast water has grown in recent years because of (i) increased global trade; (ii) increased access to new ports through completion of shipping pathways such as the St Lawrence Seaway in 1959; and (iii) faster ships that reduce the amount of time species must spend in transport before being released into new areas (Wiley & Claudi, 1999). Ways to prevent species from bypassing oceanic colonisation barriers are mainly centered on killing species that are entrained in ballast water to prevent them from being released alive into a new area. This is done by exchanging ballast water in mid-ocean, thus releasing entrained freshwater organisms into a marine environment where they have little chance of surviving. Other techniques that are being explored to prevent species introductions include filtration, sterilisation via ultraviolet light or chemicals, heat treatment and deoxygenation (Wiley & Claudi, 1999; Tamburri, Wasson & Matsuda, 2002).

Canals and water transport systems will continue to be a mechanism by which species can bypass historic barriers to colonisation (Mills *et al.*, 1999). Electrical barriers have been employed in such systems to block fish movement but such devices are expensive, subject to malfunction and are not 100% effective (Stokstad, 2003; Clarkson, 2004). Nevertheless, electric barriers and fish screens represent our current best efforts at

recreating colonisation barriers that have been breached by canals and water transport systems.

### River restoration and biotic homogenization

River restoration can influence biotic homogenization through two major mechanisms: by removing barriers to movement and by restoring natural habitat conditions. Barriers to movement can involve physical obstructions such as dams or highway culverts or river reaches with poor physical or chemical habitat conditions such as low oxygen or chemical contaminants. Removing such obstructions would allow native species to recolonise areas within their historic range, which most biologists would consider beneficial (Roni *et al.*, 2002). However, removal of barriers also may facilitate upstream expansion of non-native species, which would contribute to the homogenization of biotas (Freeman *et al.*, 2002). In fact, construction of barriers is a common approach for protecting isolated populations of native fishes when it is impractical to eliminate non-native fishes from an entire catchment. For example, barriers are important for the conservation of native trout in North America (Novinger & Rahel, 2003) and native galaxids in Australia (Jackson *et al.*, 2004). Barriers formed by low-head dams also prevent expansion of non-native sea lampreys into new spawning areas in tributary streams of the U.S. Great Lakes (Hunn & Youngs, 1980).

In some cases, stream reaches with poor water quality can serve as barriers to expansions by non-native species. A particular noteworthy example is the Chicago Sanitary and Shipping Canal that links the Great Lakes and Mississippi River basins (Kolar & Lodge, 2000). When the canal was opened in 1900, it was used as a repository for municipal sewage and water quality was so poor that fish could not survive in it. However, with improvements in sewage treatment, water quality conditions improved and the canal began to serve as a conduit for the exchange of organisms between the Great Lakes and Mississippi River basins. So far, ten fish species have moved through the canal, contributing to the homogenization of the fish faunas of these basins. Currently, there is concern that bighead carp and silver carp will use the canal as well to move from the Mississippi River into the Great Lakes, where they could have severe impacts on recreational and commercial fisheries. To prevent this exchange, a costly electrical barrier has

been constructed in an effort to re-isolate the basins (Stokstad, 2003).

Whereas enhancing biotic connectivity is likely to increase biotic homogenization, restoring natural habitat conditions, including natural flow regimes, may reduce biotic homogenization by favouring native regional species over widespread and often non-native species (Travnichek, Bain & Maceina, 1995; Marchetti & Moyle, 2001). This is especially true when impoundments are restored to free-flowing stream reaches and non-native lake fishes are replaced by native stream fishes (Kanehl, Lyons & Nelson, 1997). Restoration of natural habitat conditions can involve eliminating stressors such as low oxygen or high contaminant levels. Streams with degraded habitat and poor water quality typically have simplified fish assemblages dominated by a few tolerant species that are often non-native (Paul & Meyer, 2001). Restoring historic habitat conditions will often allow regionally distinctive native species to return to these areas and thus help to reduce biotic homogenization (Scoppetone *et al.*, 2005; Scott, 2006).

## Conclusions

Through a variety of mechanisms, humans have increased the connectance among aquatic systems that were historically isolated by biogeographic barriers to movement. This human-aided breaching of biogeographic barriers has led to significant homogenization of aquatic biotas. The degree to which aquatic biotas will continue to be homogenised will depend on the balance between factors that promote exchange among zoogeographic regions and factors that curb such exchanges. Factors that promote the breaching of biogeographic barriers include the increasingly global nature of commerce, the movement of water through canals and growth in the aquaculture and ornamental fish industries. To counter the spread of non-indigenous species, regulations need to be implemented that limit stocking opportunities, increase the public's awareness about the dangers of releasing non-native species and develop technological solutions that prevent movement of aquatic organisms or eliminate them before they can become established. Managers should consider the degree to which efforts at river restoration will facilitate the spread of non-native aquatic organisms, and thus contribute to the continued homogenization of the Earth's biota.

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**Appendix 1** Common and scientific names of fish species and three other freshwater species referenced in the text

Fish family or other taxon	Common name	Scientific name
Petromyzontidae	Sea lamprey	<i>Petromyzon marinus</i> (Linnaeus, 1758)
Anguillidae	Atlantic eel	<i>Anguilla rostrata</i> (Lesueur, 1817)
Clupeidae	Alewife	<i>Alosa pseudoharengus</i> (Wilson, 1811)
Cyprinidae	Goldfish	<i>Carassius auratus</i> (Linnaeus, 1758)
	Lake chub	<i>Couesius plumbeus</i> (Agassiz, 1850)
	Common carp	<i>Cyprinus carpio</i> (Linnaeus, 1758)
	Grass carp	<i>Ctenopharyngodon idella</i> (Valenciennes, 1844)
	Utah chub	<i>Gila atraria</i> (Girard, 1856)
	Bighead carp	<i>Hypophthalmichthys nobilis</i> (Richardson, 1845)
	Silver carp	<i>Hypophthalmichthys molitrix</i> (Valenciennes, 1844)
	Black carp	<i>Mylopharyngodon piceus</i> (Richardson, 1846)
	Sand shiner	<i>Notropis stramineus</i> (Cope, 1865)
	Fathead minnow	<i>Pimephales promelas</i> (Rafinesque, 1820)
	Longnose dace	<i>Rhinichthys cataractae</i> (Valenciennes, 1842)
	Redside shiner	<i>Richardsonius balteatus</i> (Richardson, 1836)
	Creek chub	<i>Semotilus atromaculatus</i> (Mitchill, 1818)
	Rudd	<i>Scardinius erythrophthalmus</i> (Linnaeus, 1758)
	Leatherside chub	<i>Snyderichthys copei</i> (Jordan & Gilbert, 1881)
	Tench	<i>Tinca tinca</i> (Linnaeus, 1758)
Catostomidae	White sucker	<i>Catostomus commersoni</i> (Lacepede, 1803)
Ictaluridae	Brown bullhead	<i>Ameiurus nebulosus</i> (Lesueur, 1819)
	Channel catfish	<i>Ictalurus punctatus</i> (Rafinesque, 1818)
Esocidae	Northern pike	<i>Esox lucius</i> (Linnaeus, 1758)
Salmonidae	Cutthroat trout	<i>Oncorhynchus clarkii</i> (Richardson, 1836)
	Rainbow trout	<i>Oncorhynchus mykiss</i> (Walbaum, 1792)
	Kokanee salmon	<i>Oncorhynchus nerka</i> (Walbaum, 1792)
	Chinook salmon	<i>Oncorhynchus tshawytscha</i> (Walbaum, 1792)
	Atlantic salmon	<i>Salmo salar</i> (Linnaeus, 1758)
	Brown trout	<i>Salmo trutta</i> (Linnaeus, 1758)
	Brook trout	<i>Salvelinus fontinalis</i> (Mitchill, 1814)
	Lake trout	<i>Salvelinus namaycush</i> (Walbaum, 1792)
	Arctic grayling	<i>Thymallus arcticus</i> (Pallas, 1776)
	Gadidae	Burbot
Poeciliidae	Mosquitofish	<i>Gambusia affinis</i> (Baird and Girard 1853)
	Sailfin molly	<i>Poecilia latipinna</i> (Lesueur, 1821)
	Guppy	<i>Poecilia reticulata</i> (Peters, 1859)
	Green swordtail	<i>Xiphophorus hellerii</i> (Heckel, 1848)
Cottidae	Mottled sculpin	<i>Cottus bairdi</i> (Girard, 1850)
Gasterosteidae	Brook stickleback	<i>Culaea inconstans</i> (Kirtland, 1840)
	Threespine stickleback	<i>Gasterosteus aculeatus</i> (Linnaeus, 1758)
	Ninespine stickleback	<i>Pungitius pungitius</i> (Linnaeus, 1758)
Moronidae	White perch	<i>Morone americana</i> (Gmelin, 1789)
	Striped bass	<i>Morone saxatilis</i> (Walbaum, 1792)
Centrarchidae	Green sunfish	<i>Lepomis cyanellus</i> (Rafinesque, 1819)

## Appendix 1 (Continued)

Fish family or other taxon	Common name	Scientific name
	Bluegill	<i>Lepomis macrochirus</i> (Rafinesque, 1819)
	Smallmouth bass	<i>Micropterus dolomieu</i> (Lacepede, 1802)
	Largemouth bass	<i>Micropterus salmoides</i> (Lacepede, 1802)
	White crappie	<i>Pomoxis annularis</i> (Rafinesque, 1818)
	Black crappie	<i>Pomoxis nigromaculatus</i> (Lesueur, 1829)
Percidae	Ruffe	<i>Gymnocephalus cernuus</i> (Linnaeus, 1758)
	Yellow perch	<i>Perca flavescens</i> (Mitchill, 1814)
	European perch	<i>Perca fluviatilis</i> (Linnaeus, 1758)
	Zander	<i>Sander lucioperca</i> (Linnaeus, 1758)
	Walleye	<i>Sander vitreus</i> (Mitchill, 1818)
Cichlidae	Blue tilapia	<i>Oreochromis aureus</i> (Steindachner, 1864)
	Mozambique tilapia	<i>Oreochromis mossambicus</i> (Peters, 1852)
	Nile tilapia	<i>Oreochromis niloticus</i> (Linnaeus, 1758)
	Redbreast tilapia	<i>Tilapia rendalli</i> (Boulenger, 1896)
	Redbelly tilapia	<i>Tilapia zillii</i> (Gervais, 1848)
Gobiidae	Round goby	<i>Neogobius melanostomus</i> (Pallas, 1814)
Mollusca	Zebra mussel	<i>Dreissena polymorpha</i> (Pallas, 1771)
Gastropoda	New Zealand mud snail	<i>Potamopyrgus antipodarum</i> (Gray, 1843)
Decapoda	Rusty crayfish	<i>Orconectes rusticus</i> (Girard, 1852)