

Hydrologic connectivity: a neglected dimension of conservation biology

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INTRODUCTION

Hydrologic connectivity refers to water-mediated transfer of matter, energy, and/or organisms within or between elements of the hydrologic cycle (*sensu* Pringle 2001). While this property is essential to maintaining the biological integrity of ecosystems, it also serves to perpetuate the flow of exotic species, human-derived nutrients, and toxic wastes in the landscape. All too often, we have acknowledged the importance of hydrologic connectivity in hindsight – as a result of environmental crises. Examples range from: the transport of exotic species that disrupt the food webs of rivers and lakes (e.g., Stokstad 2003); to the occurrence of extremely high levels of persistent organic pollutants (e.g., polychlorinated biphenyls PCBs) that bioaccumulate in global “hotspots” such as the Arctic (e.g., Aguilar *et al.* 2002); to effects of dams which impede riverine transport of essential elements such as silicon to coastal regions – which has been implicated in coastal eutrophication and the creation of coastal dead zones (e.g., Humborg *et al.* 2000).

Management and policy decisions regarding land-use activities are often made in the absence of adequate information on hydrologic connectivity in the landscape. An important area of research is to understand how human alterations of this property (e.g., dams, stream flow regulation, water diversion, inter-basin water transfers, water extraction) influence ecological patterns on local, regional, and global scales. Half of the accessible global freshwater runoff has already been appropriated

by humans and this could climb to 70% by 2025 (Postel *et al.* 1996). Freshwater ecosystems are being fragmented at a rate unprecedented in geologic history, contributing to dramatic losses in global aquatic biodiversity and associated ecosystem integrity (e.g., Dudgeon 2000; Pringle *et al.* 2000; Rosenberg *et al.* 2000). Fewer than 42 free-flowing rivers of over 200 km in length exist in the USA; the remaining 98% of US streams have been fragmented by dams and water diversion projects (Benke 1990). Wetlands across the USA and throughout the world have also suffered dramatic declines. Accordingly, the World Wildlife Fund's species population index, measuring the average change over time in populations of almost 200 species of freshwater birds, mammals, reptiles, amphibians, and fishes, has declined by 50% globally over the 30-year period from 1970 to 1999. Current rates of extinction of many freshwater taxa are more than 1000 times the normal "background" rate and, as a whole in the USA, freshwater species are more imperiled than terrestrial species (Master *et al.* 1998).

In this chapter I discuss: (1) a brief history of research on *river connectivity*; (2) the definition of *hydrologic connectivity* and the case for incorporating a better understanding of this property into the field of conservation biology, with emphasis on the vulnerability of "protected" areas to hydrologic disturbances within and outside of their boundaries; (3) a "protected" area case study on the Caribbean National Forest and downstream disruptions in hydrologic connectivity; (4) genetic- to ecosystem-level consequences of both reductions and enhancement of hydrologic connectivity; and (5) emerging environmental challenges involving hydrologic connectivity and the transport of contaminants on regional and global scales.

BRIEF HISTORY OF CONNECTIVITY RESEARCH IN RIVER ECOSYSTEMS

Longitudinal connections within riverine ecosystems have long been recognized by both aquatic and terrestrial ecologists, as illustrated by the widespread use of the term *river corridor* in the literature. However, the term *connectivity* did not really creep into the freshwater literature until the early 1990s (but see Amoros and Roux 1988). Following Crooks and Sanjayan's lead (Chapter 1), I conducted a review of 20 major journals in freshwater ecology and management from 1945 to 2003 (Fig. 10.1) which indicates that *connectivity* surpassed the use of the term *corridor* by the late 1990s – with the trend continuing into the 2000s. In contrast, the term *connectivity* was widely used a decade earlier in journals

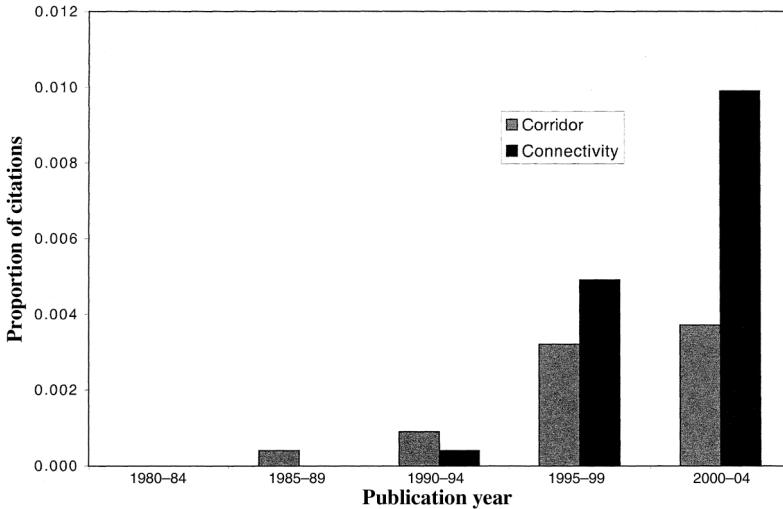


Fig. 10.1. Scientific papers published from 1980 to 2003 in 20 major journals in freshwater ecology and management, with the terms “connectivity” or “corridor” in their titles or keywords. The annual numbers of “connectivity” or “corridor” citations are standardized by the total number of citations in the 20 journals for each time period. The 20 journals examined were: *River Research and Applications*, *Regulated Rivers Research and Management*, *Lake and Reservoir Management*, *Freshwater Biology*, *Aquatic Conservation*, *Oikos*, *Aquatic Sciences*, *Journal of the North American Benthological Society*, *Transactions of the American Fisheries Society*, *Archives für Hydrobiologie*, *Journal of the American Water Resource Association*, *Aquatic Botany*, *Canadian Journal of Fisheries and Aquatic Sciences*, *Hydrobiologia*, *Environmental Biology of Fishes*, *Journal of Great Lakes Research*, *Copeia*, *Limnology and Oceanography*, *Aquatic Ecology*, and *Australian Journal of Marine and Freshwater Resources*.

in the fields of landscape ecology and conservation biology (Crooks and Sanjayan Chapter 1). Connectivity is also a fundamental concept of metapopulation ecology (Moilanen and Hanski Chapter 3). While original metapopulation models were designed and tested on terrestrial biota (typically insects and small mammals), metapopulation theory has been more recently applied to riverine biota such as fishes and mussels (e.g., Stoeckel *et al.* 1997; Policansky and Magnuson 1998; Gotelli and Taylor 1999; Fagan 2002; Neville *et al.* Chapter 13).

Freshwater ecologists frequently use the term connectivity to describe spatial connections within rivers (e.g., Stanford and Ward 1992, 1993; Ward 1997; Amoros and Bornette 1999; Wiens 2002). Ward (1997) defines *riverine* connectivity as energy transfer across the riverine

landscape. Ward and Stanford (1989a) define rivers as having interactive pathways along one temporal dimension (timescales) and three spatial dimensions, i.e., longitudinal (headwater–estuarine), lateral (riverine–riparian/floodplain), and vertical (riverine–groundwater). Consideration of dynamic interactions along these four dimensions has proven to be a very effective conceptual framework to understand human impacts on river ecosystems (e.g., Ward and Stanford 1989b; Boon *et al.* 1992; Pringle 1997, 2000; Tockner and Stanford 2002).

I will now move to a discussion of hydrologic connectivity. In contrast to riverine connectivity, it encompasses broader hydrologic connections beyond the watershed (or river basin) on regional and global scales.

HYDROLOGIC CONNECTIVITY AND ITS IMPORTANCE TO THE FIELD OF CONSERVATION BIOLOGY

Hydrologic connectivity (i.e., the water-mediated transfer of matter, energy, and/or organisms within or between elements of the hydrologic cycle) (Pringle 2001, 2003a, 2003b) (Fig. 10.2) plays an important role in maintaining the biological integrity of “natural” landscapes. As stressed earlier, this property also serves to perpetuate the flow of exotic species, human-derived nutrients, and toxic wastes in the landscape. Hydrologic connectivity is complex and often difficult to understand due to: (1) the inherent complexity of water movement within and between the atmosphere and surface–subsurface systems; and (2) the extent and magnitude of human alterations that alter this property (Pringle and Triska 2000). Cumulative effects of these alterations have resulted in regional and global environmental challenges.

Despite its importance, hydrologic connectivity remains a largely neglected dimension of conservation biology. The words “stream” and “river” do not even appear in the indices of major books on the subject of habitat fragmentation (e.g., Shafer 1990; Schelhas and Greenberg 1996; Laurance and Bierregaard 1997; Soulé and Terborgh 1999). Likewise, the field of conservation biology has placed much emphasis on the size, shape and configuration of biological reserves (e.g., the Single Large or Several Small (SLOSS) debate; see Frankham Chapter 4), without any consideration of reserve location with respect to watersheds, underlying regional aquifers, and atmospheric deposition patterns. As just one example, the Biological Dynamics of Forest Fragments Project (also known as the Minimum Critical Size Ecosystem Project) did not use the presence or absence of surface water as a criterion in its experimental

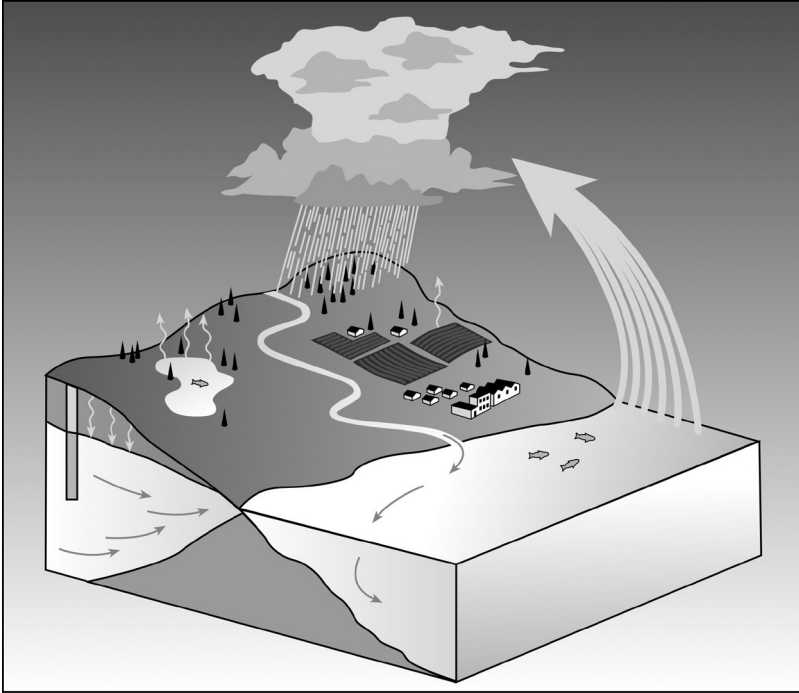


Fig. 10.2. Hydrologic connectivity is defined in a global ecological context as the water-mediated transfer of matter, energy, and organisms between or within elements of the hydrologic cycle (*sensu* Pringle 2001).

design – which involved the creation of forest fragments of different sizes and the monitoring of biodiversity in these fragments through time (R. O. Bierregaard, pers. comm.). This project would be strengthened by incorporation of a hydrologic perspective. The key question then becomes: How does the size, shape, and configuration of a given forest patch (or reserve), with respect to its location in the watershed, affect biota and overall biodiversity?

Worldwide, less than 7% of land area is either strictly or partially protected, yet many biological reserves are in danger of becoming population “sinks” for wildlife if we do not develop a more predictive understanding of how they are affected by alterations in hydrologic connectivity within the greater landscape (Pringle 2001). The location of a biological reserve, relative to watershed boundaries, regional aquifers, and wind and precipitation patterns, can play a key role in affecting biota and biodiversity and in determining the response of biota to disturbance transmitted through the hydrologic cycle. This is illustrated by an examination of the

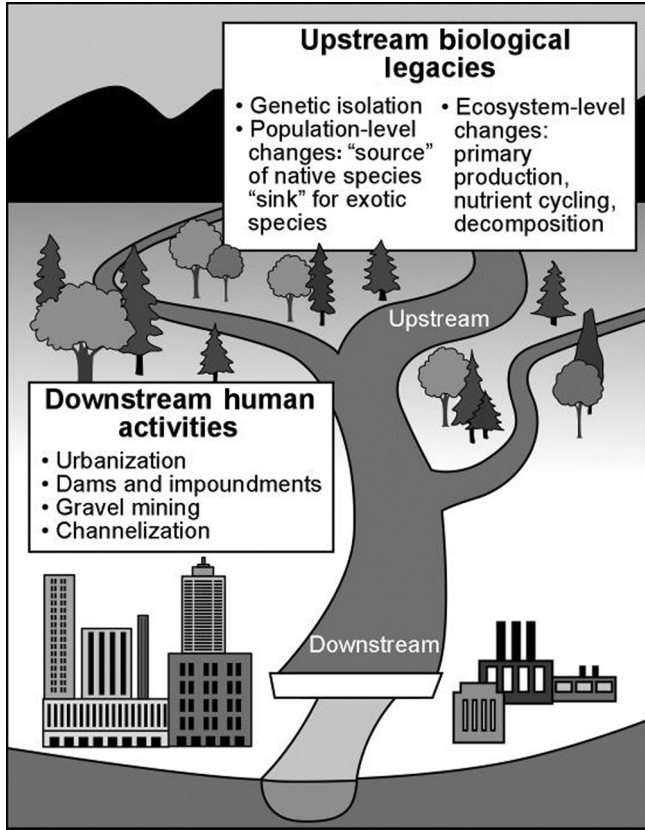


Fig. 10.3. Potential downstream influences on upstream communities. (Modified from Pringle 1997.)

vulnerability of biological reserves, in the USA (Pringle 2000) and throughout the world (Pringle 2001), to cumulative alterations in hydrologic connectivity within and outside of reserve boundaries. Reserves are vulnerable to different types of hydrologic alterations depending on where they are located within the watershed. In lower and middle watershed locations, reserves often experience direct effects of upstream alterations in hydrologic connectivity that cause habitat modifications and exacerbate effects of pollution (Fig. 10.3). In contrast, reserves in upper watersheds may have intact physical habitat and contain important source populations of some native biota, yet hydrologic alterations downstream may cause genetic isolation, extirpation of migratory species, invasion of exotic

species, and cascading ecological effects (Pringle 2001). Although many parks in the world that are located in headwater areas of “rock and ice” are esthetically quite pleasing, their biotic integrity has been compromised by hydrologic disturbances that have been transmitted upstream (Pringle 1997).

As human populations grow in regions surrounding biological reserves, there is mounting pressure on water resources associated with these remnant areas as other sources of water are diminished (e.g., Pringle 2001; Dudley and Stolton 2003). Water development proposals focusing on diversion or withdrawal of water for human use have increasingly begun to focus on surface and groundwaters that flow into, under, adjacent to, or out of parks and other public lands (Pringle 2000). Of greatest concern are situations where hydrologic alterations outside of reserve boundaries end up controlling the biology of the reserve. For example, competition for water resources between national wildlife refuges and adjacent human populations is particularly acute in arid western states of the USA, where water supplies for many refuges are controlled by other agencies or organizations. Some refuges pay annual fees to irrigation companies for water delivery and/or pay pumping fees. Wildlife refuges in the USA were established specifically to protect wildlife (primarily migratory birds), yet many refuges report that their existing water rights are not adequate to support wildlife needs during an average year (Pringle 2000).

In the USA and other countries, rates of groundwater pumping and water withdrawals from rivers are so great that there is not enough surface water left in streams and wetlands to meet environmental needs. Groundwaters and surface waters are integrally connected (Winter *et al.* 1998) and in arid regions of the world it is not uncommon for groundwater pumping to proceed at maximum rates with decreases in river flow and, in some cases, the river drying up completely. In these cases, human water use ends up controlling river levels and ultimately fish, wildlife, and streamside ecosystems.

Cumulative effects of dams and other hydrologic modifications have increasingly altered the biotic integrity of public lands in the USA, from disruption of migratory fish passage and terrestrial wildlife that use riparian corridors (Nehlsen *et al.* 1991; Pringle *et al.* 2000), to alteration of riparian vegetation (e.g., Smith *et al.* 1991; Stromberg and Patten 1992) and the creation of conditions that allow for the proliferation of exotic species (e.g., Johnson and Carothers 1987).

**“PROTECTED” AREA CASE STUDY: THE CARIBBEAN
NATIONAL FOREST, PUERTO RICO, AND ITS
VULNERABILITY TO DOWNSTREAM DISRUPTIONS
IN HYDROLOGIC CONNECTIVITY**

The ecological consequences of river fragmentation downstream of a “protected” area are illustrated by the Caribbean National Forest of Puerto Rico. The forest (113 km²) is located in the highlands of northeastern Puerto Rico and is drained by nine major rivers that are characterized by a simple food chain (typical of oceanic islands), dominated by migratory freshwater shrimps and fishes which are food sources for both aquatic and terrestrial organisms, including humans. The migrations of fishes and shrimps form a dynamic link between stream headwaters and estuaries. In the case of shrimps, newly hatched larvae migrate downstream and complete their larval stage in the estuary. Upon metamorphosis, juveniles migrate upstream where they live as adults. When water is withdrawn from rivers for human use (drinking water, irrigation, etc.), this results in direct mortality of shrimp larvae migrating to the ocean. Water diversions for municipal water use at a typical low-head (2–3 m) dam cause direct mortality of drifting shrimp larvae. The concrete dam barrier, and low water flows behind the dam, can also negatively affect the upstream migration of juvenile shrimps (Benstead *et al.* 1999).

At present, all except one of the nine stream drainages within the Caribbean National Forest have low-head dams and associated water intakes on their main channels. The extent of water abstractions is so extreme that, on an average day, an estimated 70% of riverine water draining the forest is withdrawn into municipal water supplies before it reaches the ocean (Crook 2005). Massive larval mortality of shrimp resulting from these water withdrawals could potentially affect upstream recruitment of adults and other ecosystem processes. If migratory shrimps and fishes were to be extirpated above dams and water intakes, as has occurred above high dams without water spillways in other regions of Puerto Rico (e.g., Holmquist *et al.* 1998; Greathouse 2004; Greathouse *et al.* 2006), concomitant changes in ecosystem structure and function are predicted to occur (Pringle 1997).

Experimental studies provide evidence of the importance of these migratory species to the structure and function of stream communities. For example, shrimps: (1) significantly reduce algal standing crop and alter algal community composition (e.g., Pringle 1996); (2) reduce fine particulate organic matter and alter its nutritional value for other benthic

consumers (e.g., Pringle *et al.* 1999); and (3) increase leaf litter processing rates (e.g., March *et al.* 2002). Consequently, when shrimps are extirpated from above large dams, ecosystem processes such as primary production and nutrient cycling are altered. For example, the standing crop of algae increased by nine-fold, and the carbon and nitrogen content of depositional organic material increased by 27- and 14-fold, respectively, in the absence of shrimps upstream from dams in Puerto Rico (Greathouse 2004).

In conclusion, the Caribbean National Forest in Puerto Rico provides just one example, among many “protected” areas throughout the world (Pringle 2001), where hydrologic alterations outside of its boundaries are affecting ecosystem integrity. This particular case study underlines the importance of understanding how hydrologic modifications occurring downstream are transmitted upstream (Fig. 10.3), resulting in cascading ecological effects. It illustrates the pressing need for innovative new strategies to manage hydrologic connectivity across the boundaries of biological reserves as they become remnant natural areas in human-dominated landscapes. Reserves in biomes ranging from arid deserts to tropical rainforests are vulnerable, regardless of their size and watershed location (e.g., Pringle 2001).

ECOLOGICAL CONSEQUENCES OF ALTERATIONS (i.e., REDUCTION AND ENHANCEMENT) IN HYDROLOGIC CONNECTIVITY

Here, I will briefly examine the ecological consequences of both reducing and enhancing the property of hydrologic connectivity on levels from genes to ecosystems. While some hydrologic alterations result in fragmentation of freshwater ecosystems, others result in enhanced connectivity. In landscapes exposed to increasing levels of fragmentation, consideration and management of hydrologic connectivity is becoming an important strategy.

Genetic and species-level changes

As rivers become increasingly fragmented, populations of aquatic organisms are subjected to reduced gene flow and loss of genetic variation. For obligate riverine species with large home ranges, impoundments may fragment the range of a species, causing losses in genetic diversity and local extinctions of populations. On genetic and species levels it is clearly important to locate and protect upstream areas and river tributaries

that are acting as source populations for native fishes (Howe *et al.* 1991) (Fig. 10.3). Isolated populations of native species need to be identified, genetically analyzed, and monitored (e.g., Meffe 1987).

Genetic and species-level effects of dams on economically important migratory fishes such as salmonids have received much attention (Pacific Rivers Council 1993; Neville *et al.* Chapter 13). Over 100 major salmon and steelhead populations or stocks have been extirpated on the west coast of the USA and Canada, while at least 214 more are at risk of extinction (Nehlsen *et al.* 1991). Less is known about the effects of stream fragmentation on North American biota of less economic importance (e.g., populations of freshwater shrimps, other invertebrates, and non-game fishes). Moreover, in tropical areas such as the Amazon basin, fish migratory patterns are so complex (covering huge drainage areas) that effects of stream fragmentation are unknown even for economically important fish species (e.g., Goulding *et al.* 1996).

Many fish species have been extirpated from river drainages throughout the world as a result of disruptions in hydrologic connectivity caused by dams. In a recent synthesis paper (Pringle *et al.* 2000), we summarized the regional effects of dams on fish and mollusk species in the New World. Effects include: (1) extirpation or imperilment of many migratory fish species; (2) faunal range fragmentation and population isolation; (3) extinction or imperilment of geographically restricted species dependent on uniquely riverine habitats; (4) reduction in abundances of flood-dependent species as well as species dependent on freshwater inflows to estuarine habitats; and (5) increases in lentic (i.e., lake/reservoir adapted) and exotic species.

Establishment of new hydrologic connections in the landscape (e.g., inter-basin transfers) can result in dispersal of exotic species into new habitats and hybridization with native species (see also Crooks and Suarez Chapter 18). For example, many exotic species have been introduced into the Laurentian Great Lakes of North America as a result of navigation canals constructed to connect the Great Lakes with the Atlantic Ocean. This complex network of canals has acted to dissolve barriers that had previously kept ships and animals from passing from one watershed to another (see review by Mills *et al.* 1994). Large-scale ballast water releases from ships using these canals have introduced organisms from around the world into the Great Lakes. For example, an allozyme survey showed that patterns of genetic variation in *Daphnia galeata* populations in the Great Lakes indicated hybridization with a previously undiscovered introduction of a European form of the species

in the late 1970s or early 1980s (Taylor and Hebert 1993). The introduction most probably occurred when the European form of *D. galeata* was introduced to the Great Lakes in the ballast water of ships.

Population- and community-level changes

Alterations of hydrologic connectivity have consequences that extend from single populations to multiple species within ecological communities. For example, many North American mussel species have been extirpated or are declining, in part because dams have resulted in the extirpation of their migratory fish host species which are necessary for their parasitic glochidial larval state. Just one example is the dwarf wedge mussel (*Alasmidonta heterodon*) of the US Atlantic coast. In the past 20 years, known populations of the mussel have dropped from 70 to 19 (Middleton and Liitschwager 1994). A leading theory for the cause of its demise is that the fish species that serves as its host during the critical glochidial stage of development may also be in decline. Although the identity of key host species for the mussel remains uncertain, it is suspected that the host fish is anadromous, and that dam construction has blocked its access to upstream mussel populations. The mussel is also extremely sensitive to the siltation that results from dams and riverbank erosion, and to toxic chemicals in agricultural and industrial effluents.

One management strategy to enhance longitudinal connectivity of rivers for fish communities is to employ passage devices that allow the upstream passage of fishes that would have been otherwise blocked by dams. Protection of instream flows (e.g., Gillilan and Brown 1997) is of key importance in enhancing hydrologic connectivity on longitudinal, lateral, and vertical dimensions – with benefits to populations of riverine fishes and the flora and fauna of wetlands and riparian areas. There is a growing awareness of the importance of modifying flow regimes beneath dams to be more reflective of natural flow regimes (e.g., Poff *et al.* 1997).

In some instances, managers have opted to purposely decrease hydrologic connectivity to protect populations of endangered species. The greenback cutthroat trout (*Oncorhynchus clarki stomias*) provides a case in point. It is one of four native species of cutthroat trout found in Colorado. It is vulnerable to displacement by exotic fishes, such as brook trout (*Salvelinus fontinalis*), which have been introduced into many river drainages of the western USA. Aggressive juvenile brook trout can displace juvenile greenback cutthroats from optimal habitat and make them vulnerable to predation, while other introduced trout species hybridize with them. In order to protect greenback cutthroat trout,

permanent physical barriers are maintained at the downstream end of headwater drainages where this endangered species has established populations. These barriers prohibit upstream passage of non-native exotic species. While this strategy has proven to be effective in the short term, the long-term success of this species recovery program is unclear.

Establishment of new hydrologic connections in the landscape, such as inter-basin transfers, can also have community-level effects. Tropical rivers are particularly vulnerable to inter-basin transfers, which can result in the diffusion of diverse faunal communities that were previously isolated. Hazards of these transfers include competition for resources, predation, and the spread of parasitic diseases among geographic isolates (Pringle *et al.* 2000).

Ecosystem- and landscape-level changes

When dominant faunal components of an ecosystem are excluded from upper portions of the watershed as a result of downstream human activities, a cascade of ecosystem-level effects may occur, particularly when the extirpated component was an important food source, predator, host species, or habitat modifier. We are just beginning to acknowledge the magnitude of ecosystem-level consequences of migratory faunal depletion caused by dams (see review by Freeman *et al.* 2003). As just one example, populations of bald eagles and grizzly bears that depend on salmonids as a food source in the Pacific northwest of North America may decrease if this food source is eliminated. It is also well documented that migratory salmonids can provide major inputs of nutrients and energy to freshwater systems when spawning adults return from the sea (Ben-David *et al.* 1998; Gresh *et al.* 2000). Consequently, when dams block salmonid migration routes, patterns of nutrient cycling in entire riverine ecosystems can be altered.

Ecosystem-level effects of the loss of mussel species from streams where they were once abundant provide yet another legacy of river fragmentation. Given that mussels filter an enormous amount of water, and that they were once plentiful across the landscape, consequences of their elimination likely include substantial losses in system productivity, decreased local retention of nutrients, and alterations in the structure and stability of the benthic stream environment (Strayer *et al.* 1999). Ninety percent of the world's freshwater mussel species are found in North America, and 73% of all mussel species in the USA are at risk of extinction or are already extinct. The prognosis is not good: in 1990, 90% of the listed mussels were still declining, and only 3% were increasing

(Master 1990). Declines have been linked to hydrologic connectivity including the loss of migratory hosts (as theorized for the dwarf wedge mussel above), susceptibility to water-transported contaminants, and stream-flow depletion (including groundwater pumping).

Groundwater exploitation in stream watersheds can sever lateral connections between stream channels and adjacent springs and wetlands, resulting in landscape-level changes in the drainage network and the distribution of biota (e.g., Winter *et al.* 1998; Pringle and Triska 2000). The increasing exploitation of groundwater reserves for municipal, industrial, and agricultural use is having profound effects on riverine ecosystems as groundwater tables are lowered. For example, populations of the anadromous striped bass (*Morone saxatilis*) are dependent upon coldwater refuges within riverine systems during hot summer periods because of their high oxygen requirement. In the southeastern USA, spring-fed stream systems are home to healthy and productive populations of striped bass. These streams have a high thermal diversity, and the fish can actively search out and use spring-fed areas as refuges (Van Den Avyle and Evans 1990). Extensive groundwater withdrawals threaten the springs, and thus the survival of biota such as striped bass dependent on coldwater refuges.

Restoration of hydrologic connectivity in highly modified human-dominated landscapes can also have ecosystem-level effects. For example, dam removal (or provision of fish passage devices around hydroelectric dams) in tributaries of the Laurentian Great Lakes can result in the transport of bioaccumulated toxic chemicals and also non-native species into upstream habitats (summarized by Freeman *et al.* 2002). Consequent cascading ecological effects throughout the food chain include impaired reproduction of bald eagles feeding on fishes contaminated with PCBs and other persistent organic chemicals (Giesy *et al.* 1995).

Ecosystem-level consequences of interbasin transfers can be dramatic. Drawing again upon the Laurentian Great Lakes for an example: construction of the Erie Canal and the St. Lawrence Seaway (for navigation by boats traveling from the Atlantic Ocean into the Great Lakes) have played a major role in the introduction of over 170 non-indigenous species to the Great Lakes. Several of these exotic species have played key roles in destabilizing the native flora and fauna and contributing to cascading trophic changes and ecosystem-level effects through time (Mills *et al.* 1994; Ricciardi 2001; Grigorovich *et al.* 2003). For example, an early aquatic invader was the sea lamprey, *Petromyzon marinus*, which is believed to have invaded the Great Lakes by attaching to the hulls of ships or by migrating through newly constructed canals. Declines of lake

trout (*Salvelinus namacush*), the top predator in the Great Lakes, have been attributed to parasitism by the sea lamprey; in turn, reduction in lake trout populations have contributed to increases in other exotic species (e.g., the alewife, *Alosa pseudoharengus*) and further ecological instability. An early terrestrial invader in the Great Lakes region was purple loosestrife (*Lythrum salicaria*), which was introduced from Europe in solid ship ballast, dispersing along canals and other “corridors” to eventually displace the native cattail (*Typha* sp.) in wetlands throughout the eastern and midwestern USA, thus impacting wildlife that utilized cattail habitat. More recent invaders include the zebra mussel, *Dreissena polymorpha*, which has spread throughout the Great Lakes, resulting in dramatic ecosystem-level changes in nutrient cycling, primary production, and food-web structure and function. Moreover, the zebra mussel has facilitated the invasion of two co-evolved exotic species – an amphipod (*Echinogammarus ischnus*) and a predatory fish (the round goby, *Neogobius melanostomus*), which are further destabilizing the ecosystem and leading some scientists to suggest that the Great Lakes ecosystem has entered an “invasional meltdown” phase (Ricciardi 2001).

Future invaders of the Laurentian Great Lakes may include the bighead carp (*Aristichthys nobilis*) and the silver carp (*Hypophthalmichthys molitrix*), which are threatening to invade Lake Michigan through the Chicago Sanitary and Ship Canal, a canal constructed from a river that once naturally drained into Lake Michigan (Stokstad 2003). The canal was designed to reverse the flow of the river and to divert wastes from the city of Chicago into the Mississippi River drainage. Several million dollars have recently been implemented to construct two electric barriers on the Chicago Sanitary Canal to stop the upstream migration of bighead and silver carp into the Great Lakes. Scientists believe that these large omnivorous invaders (aquaculture “escapees,” which can reach up to 45 kg and are considered by many fisherman to be “trash” fish) will reach Lake Michigan within the next decade regardless of the barriers, with dramatic ecosystem-level effects and economic losses in fisheries.

EMERGING ENVIRONMENTAL CHALLENGES: HYDROLOGIC CONNECTIVITY AND THE TRANSPORT OF CONTAMINANTS IN THE LANDSCAPE

It is perhaps ironic that, just as we begin to understand how hydrologic connectivity works locally, cumulative anthropogenic alterations in hydrologic connectivity are now exerting effects on regional and global scales

(Rosenberg *et al.* 2000; Pringle 2003c). Perhaps the most compelling global example of how we have underestimated the role of hydrologic connectivity concerns the transport and distribution of persistent organic pollutants such as PCBs to “hotspots” such as the Arctic (e.g., Aguilar *et al.* 2002). The high concentrations found here are partly due to volatilization of PCBs in warmer climates and condensation and deposition in colder regions such as the Arctic. Ocean currents also transport PCBs, and biota that have sequestered PCBs, into the Arctic food web, where they undergo further biological magnification within long-lived animals such as seals and predatory polar bears, potentially affecting the long-term reproductive capacity of these animals and the native peoples that consume them (e.g., Skaare *et al.* 2002; Derocher *et al.* 2003). Atmospheric and hydrologic pathways by which PCBs enter the Arctic food chain were not immediately predicted; as pointed out by Colburn *et al.* (1997), one of the sad ironies is that researchers discovered the high levels of contamination among people in remote Inuit villages while looking for a less-exposed control group.

We also lack an understanding of the role of hydrologic connectivity in the transport of many pathogens (see also McCallum and Dobson Chapter 19). Again, pathways in the hydrologic cycle that play a key role in pathogen transport are often identified in hindsight. As just one example, a particular strain of cholera can live inside algal cells, resting encysted in a dormant state for long periods of time. The emergence of cholera in Peru in 1991 was traced to bilge water drawn from Asian seas by a freighter and discharged into the harbor on the coast of Peru. Cholera-contaminated shellfish subsequently ingested by the human population caused massive outbreaks of cholera (Anderson 1991; Colwell and Spira 1992). The water environment can also play a key role in transporting bacterial genes for antibiotic resistance, as well as providing pathways for resistant bacteria themselves to spread (e.g., McArthur and Tuckfield 2000; Iwane *et al.* 2001). A specific example of our lack of understanding of the role of hydrologic connectivity in pathogen transport concerns the spread of a chytrid fungus, which has been implicated in die-offs of stream-dwelling frogs in high-gradient streams throughout Central America and other regions of the world. It is not clear how this fungal pathogen is transported from river to river and what role, if any, that hydrologic connectivity plays. What is clear is that once the chytrid fungus begins infecting and killing stream-dwelling frogs in a given drainage, they are soon extirpated within that drainage. Accordingly, stream-dwelling frogs throughout Costa Rica (and much of Panama) have

been extirpated above 500 m above sea level. These extirpations appeared to occur as a “wave from north to south,” moving from valley to valley and leaving a wake of dying frogs infected with chytrid in its path (Young *et al.* 2001; Lips *et al.* 2003).

In a recent synthesis book chapter (Pringle 2003c), I examine three emerging ecological problems that pertain to how alterations of hydrologic connectivity can change the way contaminants are transported and distributed in the landscape: (1) regional declines in migratory birds and wildlife resulting from wetland drainage and contaminated irrigation drainage; (2) bioaccumulation of methylmercury in fish and wildlife in newly created reservoirs; and (3) deterioration of estuarine and coastal ecosystems that receive the discharge of highly regulated (i.e., dammed), silicon-depleted, and nutrient-rich rivers. All three of the problems have surfaced within the last two decades and indicate the degree to which our ability to identify negative environmental impacts of technological change lags behind the application of those advances. They also illustrate the complexity of interactions between hydrologic change and biogeochemistry and the confounding effects of time lags between cause and environmental consequence.

To exemplify, I will briefly discuss the first of these three issues: effects of wetlands loss and contaminated irrigation drainage on wildlife. Wetland drainage and river dewatering for irrigation have resulted in migratory waterfowl and other wildlife being even more dependent on dwindling surface-water supplies. The biological integrity of many of the remaining surface water ecosystems in arid regions of the world has been seriously compromised because of reduced freshwater inflows and the accumulation of pesticides and contaminated subsurface irrigation drainage. Thus, cumulative impacts of wetlands destruction, and contamination of the remaining wetlands, are particularly severe, given that remaining wetlands often comprise only a small portion of historic wetlands and are important to fish and wildlife on regional scales (e.g., as stopovers for migratory waterfowl). California, in the western USA, provides a compelling example of this disturbing trend. Approximately 95% of the interior wetlands in California have been lost (primarily to irrigated agriculture), and this has resulted in over 60% of the Pacific migratory flyway waterfowl population being channeled into available wetlands (Frayer *et al.* 1989). One such wetland is the Sonny Bono Salton Sea National Wildlife Refuge – one of the few wetlands in southern California, attracting more than 380 species of migratory birds to its contaminated waters. Fish and bird die-offs are so common and massive that the US Fish

and Wildlife Service operates an incinerator to dispose of dead birds. The National Audubon Society uses the Sonny Bono National Wildlife Refuge as an example of the state of crisis of wildlife refuges in the USA. In 1997, over 14 000 birds (representing 66 species) perished as a result of an outbreak of avian botulism, including over 1400 endangered brown pelicans. The Sonny Bono Salton Sea National Wildlife Refuge is by no means an isolated example: several National Wildlife Refuges in the western USA have experienced die-offs of birds and fishes including Stillwater, Bowdoin, Kesterson, and Ourag National Wildlife Refuges, (Lemly *et al.* 1993). This phenomenon is not just confined to the western USA, but is occurring in other arid regions of the world, such as the Macquarie Marshes of Australia and the Aral Sea in central Asia (see reviews by Lemly *et al.* 1993, 2000). Solutions to the regional environmental problems caused by toxic irrigation drainage are not clear. Even when confined to toxic evaporation ponds, toxic irrigation drainage continues to attract wildlife, given the lack of remaining wetland habitat in many developed landscapes that have been drained for agriculture. It is clear that we need to proactively re-evaluate unsustainable agricultural practices.

CONCLUSION

In summary, it is critical that an understanding of hydrologic connectivity be incorporated into the field of conservation biology – into both theoretical constructs and practical applications. Hydrologic connectivity should be a basis of many cumulative effects and secondary impacts analyses as required under the US National Environmental Protection Act for federal actions, such as permitting for new reservoirs. We also must develop a more predictive understanding of how hydrologic connectivity, and alterations of this property, influence ecological patterns on regional and global scales – before environmental crises occur.

ACKNOWLEDGEMENTS

Many thanks to Mary Freeman and Sandra Tartowski for their suggestions which greatly improved this chapter. I would also like to thank my current graduate students who have provided feedback on material presented in this chapter: Elizabeth Anderson, Marcelo Ardon, Scott Connelly, Kelly Crook, Susan Dye, Effie Greathouse, John Kominoski, Chip Small, and Katherine Smith. I also acknowledge National Science Foundation (NSF)

Grant DEB-0234386 and NSF Grants DEB-0218039 and DEB-00805238 which support the Luquillo Long-term Ecological Research Program.

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