Ecological Benefits of Reduced Hydrologic Connectivity in Intensively Developed Landscapes

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A broad perspective on hydrologic connectivity is necessary when managing stream ecosystems and establishing conservation priorities. Hydrologic connectivity refers to the water-mediated transport of matter, energy, or organisms within or between elements of the hydrologic cycle. The potential negative consequences of enhancing hydrologic connectivity warrant careful consideration in human-modified landscapes that are increasingly characterized by hydrologic alteration, exotic species, high levels of nutrients and toxins, and disturbed sediment regimes. While connectivity is integral to the structure and function of aquatic ecosystems, it can also promote the distribution of undesirable components. Here we provide examples illustrating how reduced hydrologic connectivity can provide greater ecological benefits than enhanced connectivity does in highly developed, human-modified ecosystems; for example, in urban landscapes, "restoration" efforts can sometimes create population sinks for endangered biota. We conclude by emphasizing the importance of adaptive management and balancing trade-offs associated with further alterations of hydrologic connectivity in human-modified landscapes.

Keywords: hydrologic connectivity, restoration, ecosystem management, hydrology, aquatic ecosystems

Connectivity regimes in intensively developed landscapes are characterized by disrupted hydrologic pathways and streamflows, and these disruptions occur within a matrix of pollutants and invasive species. Accordingly, management and restoration strategies require careful assessment of the environmental consequences of changes in hydrologic connectivity on landscape scales. Here we refer to hydrologic connectivity in a broad ecological sense as "water-mediated transport of matter, energy, or organisms within or between elements of the hydrologic cycle" (*sensu* Pringle 2001). Because of the intensity and magnitude of reductions in hydrologic connectivity by human activities (particularly alterations in river flows), recent river management and restoration efforts have focused on enhancing connectivity through a variety of mechanisms, including removing dams; altering reservoir management to provide more natural flow regimes; restoring natural morphology to streams disturbed by channelization, agriculture, or urbanization; removing tide gates; retrofitting fish passage to dams and locks; and eliminating interbasin transfers.

Enhancing hydrologic connectivity can provide valuable and extensive ecological benefits. However, when only partial restoration is possible in highly disturbed landscapes (which are increasingly characterized by exotic species and high levels of nutrients and toxins), restoration of flow regime may not achieve desirable ecological conditions. Accordingly, Poff and Allen (1998) stipulated that "ecological restoration of severely altered river ecosystems might not be achievable by flow management alone, irrespective of other limiting factors," and that "factors such as thermal and sediment regimes must be considered in developing any specific restoration plan for an individual river" (p. 247).

A broad framework is needed for evaluating potential ecological effects of enhanced hydrologic connectivity, particularly in landscapes that have been extensively altered by human activities. Management and restoration strategies require careful assessment of environmental consequences of changes in water-mediated transport of sediment, nutrients, toxins, invasive species, and energy under different water-management scenarios (Pringle 2003, 2006). Management options in highly modified systems are typically constrained, such that only some ecosystem drivers can be naturalized (figure 1). Kondolf and colleagues (2006) presented the idea of partial restoration in terms of longitudinal, lateral, and

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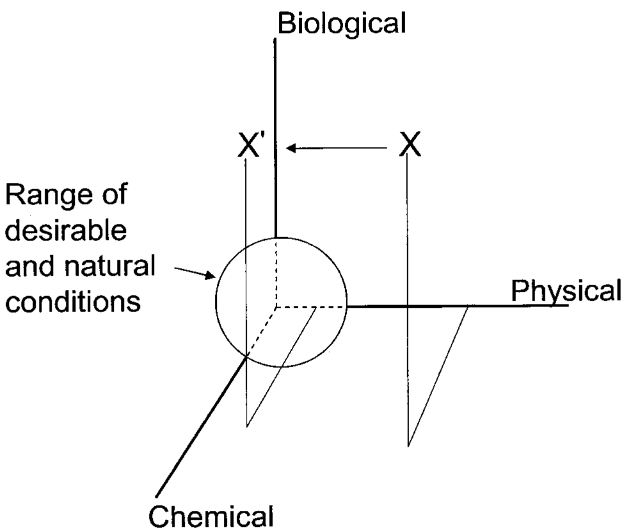

Figure 1. Condensing the many components of hydrologic connectivity into three generalized ecological components of physical, chemical, and biological conditions, the point X represents a highly developed aquatic system displaced from the range of natural variability along all axes. The point X' represents a new ecological state achieved by partial restoration focused on physical conditions alone.

vertical connectivity, and proposed that political and economic considerations made restoration easier and more likely on some axes than others. When constraints limit society's ability to restore some factors, it may be ecologically beneficial to balance the interplay among the drivers, and the most ecologically desirable conditions may not match precivilization conditions for any drivers. Analysis of the trade-offs of these multiple environmental effects in human-altered landscapes may sometimes suggest management strategies that by design reduce, rather than enhance, hydrologic connectivity.

Here we present examples that show how creating or maintaining reduced hydrologic connectivity can create ecological benefits. We provide local, species-level examples where protection of endangered native biota has been achieved by reducing peak flows, maintaining levees (reducing lateral river-floodplain connectivity), or by creating or maintaining dams or passage barriers (reducing longitudinal riverine connectivity). Examples at the regional ecosystem level include protection of regional biological integrity against invasion by keystone exotic species by creating artificial barriers, protection of streams against sediment "starvation" by reducing natural peak flows, and improvement of regional water quality through farm ponds. We then discuss the unique challenges of managing hydrologic connectivity in urban and irrigated landscapes where the environment has been so intensively modified by human activities that restoration efforts can result in the creation of population sinks for wildlife and endangered biota.

Protecting endangered species by maintaining levees and reducing peak flows

Reestablishing river-floodplain connectivity by removing levees and providing more natural flood pulses is a common restoration objective for regulated rivers (Sparks 1995, Postel and Richter 2003). This objective can have numerous environmental benefits, since lateral connections between rivers and their floodplains, created during natural flood pulses, drive key ecological processes that support system productivity and biological diversity (Stanford and Ward 1993). Many riverine species have evolved adaptations to the periodicity of flooding, using floodplains for reproduction and nursery areas, and using floodwaters for dispersal. Restoring lateral connectivity in river-floodplain systems can benefit river biota (e.g., recreating off-channel habitat for rheophilic species in the lower Rhine; Simons et al. 2001).

However, there may be negative consequences of reestablishing lateral connectivity in river systems where off-channel habitats have become refuges for native species eliminated elsewhere. Accordingly, Minckley and colleagues (2003) proposed a conservation plan for native fishes of the lower Colorado River that was based on isolating off-channel habitats protected from nonnative species. Scheerer (2002) made the case that restoring floods in the Willamette Valley in western Oregon could be strongly detrimental to the Oregon chub (*Oregonichthys crameri*), an endangered fish endemic to the system. The Willamette River system is highly modified by channelization and flood-control dams, and also by introductions of nonnative species. Nonnative fishes pose a primary threat to the survival of the Oregon chub, which persists in greatest abundances in off-channel habitats that are now isolated from the mainstem river. Isolation minimizes access to nonnative species; restoring more natural flood regimes and reconnecting these off-channel habitats to the main river could result in loss of the Oregon chub, even though this species evolved under the dynamic flood regime of the preregulation Willamette River (Scheerer 2002). Nonnative fishes also threaten native amphibians in the Willamette Valley, and this led Pearl and colleagues (2005) to recommend that mitigation wetlands are more valuable if isolated from other water bodies containing fish.

In some cases, novel postdam riparian vegetation (i.e., vegetation that has become established in the absence of natural flood regimes) becomes important for expanding terrestrial animal populations such as Neotropical migrant songbirds, including the endangered southwestern willow flycatcher (*Empidonax trailii extimus*; Stevens et al. 2001). Other examples include the peregrine falcon (*Falco peregrinus anatum*) and the federally listed bald eagle (*Haliaeetus leucocephalus*), both of which use "unnatural" riparian habitats along the Colorado River for resting and foraging (Brown et al. 1989, 1992). Conserving species in unnatural conditions is always problematic, and restoring floods and floodplain connectivity in highly altered systems may have multiple unintended consequences that should be considered.

Protecting endangered species by maintaining or creating dams and barriers

Increasingly, drainages throughout the world contain non-native species assemblages that thrive in reservoirs and dam tailwaters—many with generalized habitat requirements and tolerance for low dissolved oxygen or altered water quality. Native fish faunas in these drainages have been displaced. Cold-water fishes such as trout have been introduced widely beyond their native ranges to support sports fisheries in tailwaters below dams (e.g., see reviews provided by Dudgeon 2000, Pringle et al. 2000). Because of fish introductions, the Colorado River basin in western North America now contains more than twice the number of fish species that were present 100 years ago (Starnes 1995). Facultative riverine species and lake-adapted species can also spread downstream past dams and upstream into unimpounded rivers, displacing or hybridizing with native species (e.g., Courtenay and Moyle 1992).

How can managers manipulate hydrologic connectivity to protect native species from invasive species in river drainages? One such effort involves protection of the endangered native greenback cutthroat trout (*Oncorhynchus clarki stomias*). Strategic placement of small dams in stream headwaters allows this fish species to persist. The greenback cutthroat trout 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 United States. 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 (Middleton and Liittschwager 1994). Barriers prohibit upstream passage of nonnative species. Whether this strategy will be successful in the long term is unclear.

Similarly, westslope cutthroat trout (*Oncohynchus clarki lewisi*) populations in the Rocky Mountains are threatened by invasions of brook trout introduced from the Appalachian Mountains. However, westslope cutthroat are also threatened by habitat fragmentation. Peterson and colleagues (2008) found that management actions to ameliorate one of these threats could exacerbate the other, and that "trade-offs between isolation and invasion were strongly influenced by size and habitat quality of the stream network to be isolated and existing demographic linkages within and among populations." Novinger and Rahel (2003) found that artificial passage barriers provided benefits for protecting native cutthroat from hybridization with invasive brook trout, but benefits were limited in their study by the lack of deep pool habitat in the small streams that were isolated. They concluded: "Where nonnative species pose an immediate threat to the survival of native fishes, isolation in headwater streams may be the only conservation alternative. In such situations, isolated reaches should be as large and diverse as possible" (p. 772).

Another management example that involves maintaining reduced hydrologic connectivity is the decision to retain dams that are blocking the passage of exotic fishes that would otherwise transport bioaccumulated toxic chemicals into upstream habitats in tributaries of the Laurentian Great Lakes in the midwestern United States (Freeman et al. 2002). Consequent cascading ecological effects throughout the food chain (that are predicted to occur if certain dams are removed) include impaired reproduction of bald eagles feeding on fishes contaminated with PCBs (polychlorinated biphenyls) and other persistent organic chemicals (Giesy et al. 1995).

Protection of regional biotic integrity through creation of artificial barriers

Alterations of hydrologic connectivity that involve interbasin transfers have resulted in new pathways for the invasion of exotic species. The Laurentian Great Lakes in North America provide compelling examples: Construction of the Erie Canal and the St. Lawrence Seaway (for navigation by boats traveling from the Atlantic Ocean into the Great Lakes) played a major role in the introduction of more than 170 nonindigenous 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 (Ricciardi 2001, Grigorovich et al. 2003). 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. Parasitism by the sea lamprey has caused declines of lake trout (*Salvelinus namacush*), the top predator in the Great Lakes, and much of the ensuing ecological instability—in turn, paving the way for the invasion of other exotic species. 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 coevolved exotic species—an amphipod (*Echinogammarus ischnus*) and a predatory fish (the round goby, or *Neogobius melanostomus*)—that are further destabilizing the ecosystem and leading some scientists to suggest that the Great Lakes ecosystem has entered an "invasional meltdown" phase (Ricciardi 2001).

How can managers effectively manipulate hydrologic connectivity to restrict the dispersal of exotic species and to protect native species? One example is the installation of powerful electric aquatic nuisance species dispersal barriers designed to prevent the upstream migration of exotic bighead carp (*Aristichthys nobilis*) and silver carp (*Hypophthalmichthys molitrix*), which are threatening to invade Lake Michigan through the Chicago Sanitary and Ship Canal. The canal was designed to reverse the flow of the Chicago River and to divert wastes from the city of Chicago into the Mississippi

River drainage (figure 2; Stokstad 2003). Scientists and managers believe that these large omnivorous invaders (aquaculture "escapees," which can reach up to 100 pounds and are considered by many fishermen to be unpalatable) will reach Lake Michigan within the next decade regardless of the barriers, with negative ecosystem-level effects and economic losses in fisheries. 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. An initial demonstration barrier has been in operation since 2002. The barrier consists of steel cables that are secured to the bottom of the canal, which transmit a low-voltage, pulsing direct current, creating an electric field in the water that is uncomfortable for fish, thus deterring them from swimming upstream. The Water Resources Development Act of 2007 authorized the US US Army Corps of Engineers (USACE) to upgrade this demonstration barrier to permanent status while a second more substantial and complex barrier is constructed and made fully operational.

This technological approach to restricting migrations of exotic fishes and regulating hydrologic connectivity has been costly: As of 2007, approximately $12.5 million had been spent on planning, design, construction, and ongoing operation and maintenance of the barriers. The estimated total

*Figure 2. Location of aquatic nuisance dispersal barriers with respect to Asian bighead carp (***Aristchthys nobilis***) distributions in the vicinity of the Chicago Sanitary and Ship Canal. Source: Figure modified from Stokstad (2003).*

project cost is $29.6 million. It has been suggested that the only viable long-term solution may be to permanently disconnect the Chicago Sanitary Canal. (For a more in-depth discussion and description, see the USACE Chicago District Fish Barrier Homepage at *www.lrc.usace.army.mil/projects/fish_barrier/index.html.*)

Protection of streams against sediment "starvation" by reducing peak flows

Undisturbed channels usually exist in a state of quasi-equilibrium between sediment supply and sediment transport capacity such that channels neither aggrade nor erode consistently over time. Alteration of bedload-transporting flows, without compensating changes to sediment supply or vice versa, will cause a disequilibrium and subsequent channel adjustment. Accordingly, reservoirs disturb both flow and sediment regimes downstream, and the downstream channel response depends on the relationship between the resulting sediment transport capacity and sediment supply. If natural peak flow regimes are maintained downstream of dams, the channels will erode because of the relative lack of sediment supply. Schmidt and Wilcock (2008) analyzed 4000 kilometers (km) of river channels below 18 dam systems and found that 60% of the downstream channel length was in sediment deficit, whereas sediment surplus was found in only a handful of reaches.

Since Lake Seminole (actually a reservoir) was constructed at the head of the Apalachicola River, Florida, the first 60 km of the river has downcut and widened its channel as a result of sediment starvation, channel straightening, and dredging (Light et al. 2006). The reservoir is operated to maintain fairly constant water levels, and no effort is made to reduce downstream peak flows. However, because the rivers feeding Lake Seminole were the principal sediment supply for the Apalachicola River, and because that sediment is now held in Lake Seminole and the five other major reservoirs upstream (figure 3), the resulting imbalance between unaltered transport capacity and greatly diminished sediment supply has resulted in downstream channel erosion. The river provides critical habitat for four endangered species, including Gulf sturgeon and three mussel species (Brim Box and Williams 2000, USFWS 2006), and connectivity between channel and floodplain habitats is considered important for these species.

Although the US Fish and Wildlife Service recognizes sediment starvation and channel manipulation as the root causes of channel disturbance, the agency's management strategies for endangered species in the Apalachicola River have focused on maintaining minimum flows in the river, and have so far ignored possible strategies for directly addressing the sediment problems (USFWS 2006). Reducing peak flows in the Apalachicola River, suspending dredging, reconstructing more natural sinuosity, or even dam removal may be more effective strategies for reconnecting channel and floodplain habitats, but strategies addressing imbalances in the sediment dynamics have not been publicly explored. It may also be possible to accelerate bank erosion and thus raise the

Figure 3. Sediment deposition at the top of West Point Lake, a reservoir on the Chattahoochee River draining to Lake Seminole and the Apalachicola River. Photograph: Google Earth™.

channel bed with local floodplain sediment by artificially creating bankfull flows followed by rapid flow reductions. When saturated streambanks do not have the counterweight of water in the channel, bank failure is common (e.g., Fox et al. 2007). In any case, the currently disturbed sediment regime of the Apalachicola requires a comparably disturbed hydrologic regime to achieve a more stable and desirable channel and floodplain condition. In this example, the best strategy for reconnecting the river with its floodplain is not obvious, and adaptive management principles are particularly relevant.

Improvement of regional water quality achieved through farm ponds

Small impoundments, principally farm ponds, are numerous in the American agricultural landscape. Smith and colleagues (2002) estimated there are at least 2.6 million small, man-made impoundments in the United States, mostly in agricultural areas of the Midwest and East. Fairchild and Velinsky (2006) identified 3183 ponds in Chester County, Pennsylvania, alone, and Merrill (2001) found 5467 impoundments—of which 99% were smaller than 10 hectares—in the upper Oconee River watershed in Georgia (figure 4). These small impoundments alter the hydrologic connectivity of the terrestrial and headwater landscape to the larger stream system in myriad ways: They sequester sediments and nutrients, promote denitrification, kill fecal bacteria, block or impede the longitudinal movements of aquatic organisms, fragment stream habitat, convert lotic stream habitats to lentic pond habitats, and alter flow time series.

For at least some period since European colonization, most of the forest land in the eastern United States has been converted to agriculture. Soil erosion, stream sedimentation, nutrient loads, and lentic and estuarine eutrophication have all increased as a consequence. At the extreme, historical

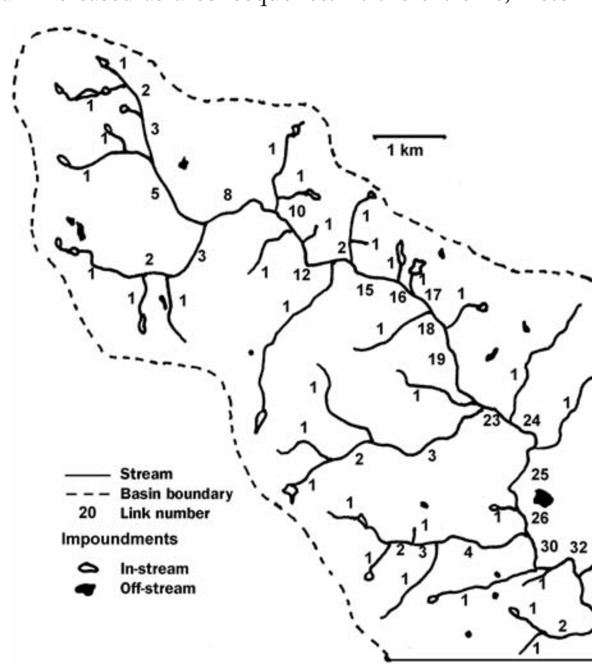

Figure 4. Typical distribution of small impoundments in a small watershed in the upper Oconee River basin, Georgia. Source: Merrill (2001).

agricultural erosion in the southeastern Piedmont inundated streams and floodplains with sediments equivalent to 6000 to 10,000 years of natural fluvial sediment output (Jackson et al. 2005). Agricultural activities are the dominant source of enhanced nitrogen levels in aquatic ecosystems, and only 25% of anthropogenic nitrogen is exported from rivers as a result of denitrification in wetlands and aquatic ecosystems (Howarth et al. 1996). Starting in the 1950s, the US Department of Agriculture Soil Conservation Service (now the Natural Resources Conservation Service) began building small reservoirs and encouraging farmers to build small ponds for the purpose of sequestering soils and nutrients mobilized by past and current agricultural activities (Dendy 1974).

Until they fill with sediment, and until the phosphorus sorption capacity of the bed sediments is exceeded, small impoundments provide effective sequestration of excess sediment and nutrients from agricultural activities. Dendy (1974) found that small ponds sequestered 81% to 98% of incoming silts and clays, and that removal rates grew with residence time. Lowrance and colleagues (2007) found that farm ponds greatly reduced sediment and nutrient loads in streams draining row crop areas, and Fairchild and Velinsky (2006) showed substantial denitrification in small ponds. Fisher and colleagues (2000) discovered that a pond draining cattle pastures effectively removed enterococci and *Escherichia coli* bacteria from the creek. The available data and limnological theory indicate that farm ponds are very effective mitigation systems for the most problematic nonpoint pollutants from agricultural activities, and they enhance pollutant retention and cycling at rates greater than could be achieved with riparian buffers alone. In agricultural regions with downstream eutrophication problems, the system-wide benefits of small farm ponds are large, whereas the environmental problems they cause seem to be largely local.

The water-quality effects of small impoundments are partially analogous to the effects of beaver dams that were historically numerous in all humid regions of the United States (e.g., Rosell et al. 2005), the principal differences being that small impoundments completely prevent fish movement, whereas beaver dams only impede fish movement. Also, most beaver dams are built on streams larger than those usually impounded by farmers.

Unique challenges of managing hydrologic connectivity in urban landscapes

Urban restoration efforts are impeded by landscape-scale hydrologic alterations: Because urbanization imposes multiple collinear stressors on altered streams (e.g., hydrology, sediment dynamics, and water chemistry), urban streams pose special challenges for restoration activities. Urban stream restoration projects are commonly conducted to stabilize streambanks, facilitate fish passage, reconnect the channel with its hyporheic zone, diversify aquatic habitat, naturalize organic matter and nutrient dynamics (increasing leaf litter retention, for example), and improve aesthetics. In the US Pacific Northwest alone, millions of dollars are spent annually on both urban and rural stream restoration projects (Roni et al. 2002), and resource agencies spend more than $100 million annually on habitat restoration in the Sacramento-San Joaquin river system in California (Kondolf 2000). Often, the "morphologically based natural channel design method" (Rosgen 1996, Niezgoda and Johnson 2005) is used to estimate the natural geomorphic configuration for an urbanized stream, and this natural configuration becomes the design goal on the basis of the assumption that function will follow form. However, post hoc investigations have found that many stream restoration projects are geomorphically unstable (e.g., Downs and Kondolf 2002). Many naturalized channels cannot accommodate the flow and sediment regimes of urbanized watersheds and return to their prerestoration form (Kondolf et al. 1996). As a result of the low success rate of stream restoration projects, Palmer and colleagues (2005) proposed five basic standards for ecologically successful river restoration: (1) restoration design must be based on a guiding image of a feasible, dynamic, and healthy river; (2) ecological conditions must be measurably improved; (3) the resulting river should be more self-sustaining and resilient to external perturbations; (4) construction should cause no lasting ecosystem harm; and (5) pre- and postproject monitoring and assessment must be conducted.

Even when geomorphically successful stream restoration is achieved, urban stream ecosystems may have undesirable consequences, such as water quality problems. Seattle Public Utilities (Seattle, Washington) has restored watersheds to improve salmon habitat in five streams, spending more than $26 million between 1999 and 2003 (Stiffler and McClure 2003). After restoration, these streams have been repeatedly stocked with salmon fry in efforts to restore wild fish runs. However, when adult coho salmon returned to these streams, almost all died before spawning. Annual prespawning mortality in these "restored" urban streams has ranged from 60% to 88% (Seattle Public Utilities 2002). Mortality was rapid; returning coho typically died within hours of entering these urban streams, and the culprit appeared to be toxic water chemistry (figure 5). The National Marine Fisheries Service has begun studying the issue, confirming that prespawning mortality in these restored urban streams greatly exceeds that found in rural pristine streams (Stiffler and McClure 2003). The mechanism for prespawning coho mortality is not known, although it may be relevant that short-term exposure to levels of copper typically found in street runoff (Greenstein et al. 2004) has significant neurological effects on coho salmon (Linbo et al. 2006, Sandahl et al. 2007). As stated by Nat Sholz, of the National Marine Fisheries Service: "Longfellow Creek looks beautiful. You'd think everything was healthy" (Stiffler and McClure 2003). It is possible that geomorphically restored streams act as population sinks that attract prespawning coho but preclude successful reproduction.

In a relatively small Texas stream, in which wastewater effluent comprised approximately 70% of baseflow discharge, large and frequent peak flows were vital to reducing nuisance accumulations of algal biomass (Murdock et al.

Figure 5. Gravid coho salmon killed by stormwater toxicity prior to spawning in Moxlie Creek, Olympia, Washington. Source: Wild Fish Conservancy (2008).

2004). Nuisance algal levels were a consequence of high nutrient and carbon loads and accumulated in as little as five days. However, because of the highly urbanized nature of the watershed, rainfall events as small as 1.3 centimeters produced floods capable of scouring all algae from the stream, and 47 such "resetting" events were observed in a 22-month study period. In this example, restoration of more natural watershed hydrology would actually degrade local water quality conditions. At larger scales, a relevant management question is how to manage the stream to promote nutrient cycling and denitrification to reduce downstream nutrient loads (Wenger et al. 2009).

Restoration efforts in arid areas when irrigation has mobilized natural contaminants and pesticides

Since naturally occurring toxic elements in arid soils can become mobilized by irrigation waters (extracted from surface or ground water supplies), it is problematic in many cases to allow irrigation return flows to enter riverine ecosystems. Toxic elements (e.g., selenium, boron, and arsenic in arid regions of the western United States) may bioaccumulate and be magnified within the food chain (e.g., Lemly et al. 1993a, 1993b), and subsurface irrigation drainage has caused massive mortality (and in some cases deformities) of migratory waterfowl and fishes that have been linked to these naturally occurring elements in many regions throughout the western United States (Presser et al. 1993, Presser 1994).

One example of this is the Stillwater National Wildlife Refuge (NWR) in the Nevada desert, a Western hemisphere shorebird reserve that is important to migratory shorebirds and waterfowl. The refuge is located at the terminus of a river that is intensively tapped for irrigation water supplies. It has been reduced from its former extent of 70,000 hectares by 84%, and the remaining marshland receives water that contains up to 100 times the levels of historic concentrations of dissolved solids (Lemly et al. 1993b). The refuge suffered massive mortality of fishes and birds in the mid-late 1980s (Rowe and Hoffman 1987), and, despite reductions in irrigation return flow drainage into the refuge, the number of nesting birds and the percentage of successfully fledged waterfowl have declined steadily (Lemly et al. 2000).

Several other NWRs in the western United States have experienced similar problems, including the Benton Lake NWR, Bowdoin NWR, Ouray NWR, and Malheur NWR (Lemly et al. 1993b). High incidence of aquatic bird deformities and deaths in the Kesterson NWR of central California ultimately led to the removal of Kesterson from the national refuge system, and it is now managed as a contaminated landfill (Lemly et al. 1993a, 1993b). Elsewhere, "solutions" have included scaring waterfowl away from toxic, selenium-laced evaporation ponds with continuous blasts from foghorns.

Similar environmental problems have emerged in arid regions of the world that have been intensively developed through irrigation for agricultural production, and where only a small portion of historic wetlands remains (Lemly et al. 2000). The area of irrigated land in the world is expanding, accompanied by wetland drainage and river dewatering.

Migratory waterfowl and other wildlife are even more dependent on remaining surface water supplies that are often contaminated by subsurface irrigation drainage.

How can hydrologic connectivity be better managed to avoid harmful environmental effects of irrigation drainage? As a society we need to reevaluate fundamentally unsustainable agricultural practices (Postel 1999), such as intensive irrigation of arid soils—particularly in areas that are geologically susceptible to contamination from irrigation drainage. Toxic and degraded farmland poses a major challenge, especially in arid regions that occur in closed basins with no outflows. To the authors' knowledge, there is currently no effective restoration or management solution to contaminated subsurface irrigation drainage.

Conclusions

The development of effective conservation and restoration strategies is critical, given the magnitude of land-use change and alterations to connectivity regimes (Crooks and Sanjayan 2006, Peters et al. 2008).

Poff and colleagues (1997) significantly altered the philosophy of river management when they proposed that streamflow is the master variable controlling stream health. Hydrograph characteristics exert strong influence over the dynamics, persistence, and reproductive success of in-stream biota (e.g., Bunn and Arthington 2002). Yet restoration of flow alone in intensively developed landscapes may have unintended consequences, such as the transport of pollutants and exotic species. As illustrated by the examples provided in this article, altered or reduced hydrologic connectivity regimes are sometimes more desirable than natural connectivity regimes in highly developed landscapes.

Restoration of hydrologic connectivity in a disturbed landscape moves an aquatic system toward a new ecological state, with which we often have little experience and which may have undesirable ecological attributes. The attributes of this new ecological state are difficult to predict, necessitating post-restoration monitoring and adaptive management. Per the objectives of the Endangered Species and Clean Water Acts, aquatic ecosystems ideally would be managed to (a) maintain viable populations of all native species, (b) increase habitat and numbers of individuals for threatened and endangered species, (c) prevent introduction or spread of nonnative invasives, (d) maintain spatial and temporal distributions of trophic states within the range of natural variability, and (e) maintain desirable ecosystem services including clean water, healthy aquatic organisms, and sustainable harvests of natural resources. These objectives may be unattainable, particularly given the uncertainties of ecosystem response in highly disturbed environments, further underlining the importance of adaptive management strategies (e.g., multimetric monitoring, ecosystem service accounting, revising of management activities).

Management and restoration efforts are most effective when placed in the context of previous management history and other watershed conditions. As stated by Saunders and Tyus (1998), when commenting on the work of Poff and colleagues (1997): "The potential for success of flow management strategies will depend on the extent to which target species or communities are limited by other factors, such as contaminants or the presence of nonnative species, that may not be responsive to changes in the flow regime" (p. 427).

Increasingly, management and restoration strategies are considering the trade-offs associated with further alterations of hydrologic connectivity in intensively developed landscapes. What are the environmental effects of different management scenarios on the water-mediated transport of sediments, nutrients, toxins, invasive species, and energy? What are the pros and cons (including environmental, social, and economic) of restoration of natural flow regimes in highly degraded landscapes? A major challenge is to develop a more predictive understanding of how hydrologic connectivity operates in intensively developed landscapes.

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