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# HYDROLOGIC CONNECTIVITY AND THE MANAGEMENT OF BIOLOGICAL RESERVES: A GLOBAL PERSPECTIVE

CATHERINE M. PRINGLE[1]

*Institute of Ecology, University of Georgia, Athens, Georgia 30602 USA*

*Abstract.* Increasingly, biological reserves throughout the world are threatened by cumulative alterations in hydrologic connectivity within the greater landscape. *Hydrologic connectivity* is used here in an ecological sense to refer to water-mediated transfer of matter, energy, and/or organisms within or between elements of the hydrologic cycle. Obvious human influences that alter this property include dams, associated flow regulation, groundwater extraction, and water diversion, all of which can result in a cascade of events in both aquatic and terrestrial ecosystems. Even disturbances well outside the boundaries of reserves can have profound effects on the biological integrity of these "protected" areas. Factors such as nutrient and toxic pollution and the spread of nonnative species are perpetuated by hydrologic connectivity, and their effects can be exacerbated by changes in this property. Hydrological alterations are now affecting reserves through increasingly broad feedback loops, ranging from overdrawn aquifers to atmospheric deposition and global climate change. Such alterations are often beyond the direct control of managers because they lie outside reserve boundaries, and data on hydrologic connection between reserves and surrounding landscapes are scant. The subject of water has also been typically excluded from the literature pertaining to both theoretical and practical aspects of reserve size, isolation, and design. This results, in part, from early management strategies developed when the landscape matrix outside of reserves was not excessively fragmented, and when awareness of hydrologic connectivity was in its infancy.

The location of a given reserve within a watershed, relative to regional aquifers and wind and precipitation patterns, can play a key role in its response to human disturbance transmitted through the hydrologic cycle. To illustrate this point, I discuss reserves of varying sizes from diverse regions throughout the world. Reserves located in middle and lower watersheds often suffer direct hydrologic alterations that cause severe habitat modification and exacerbate the effects of pollution. In contrast, reserves in upper watersheds may have intact physical habitat and contain important source populations of some native biota, yet hydrologic disturbances in lower watersheds may cause extirpation of migratory species, cascading trophic effects, and genetic isolation. Worldwide, <7% of land area is either strictly or partially protected, and many 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 hydrologic alterations that originate outside of their boundaries.

*Key words: aquifer; biological reserves; dams; flow regulation; groundwater; habitat fragmentation; hydrologic connectivity; landscape; management of human impact; parks; protected areas; rivers; streams; watersheds.*

## INTRODUCTION: LOCATION OF RESERVES WITHIN THE HYDROSCAPE, A NEGLECTED DIMENSION

As terrestrial landscapes become increasingly fragmented, so do hydrologic connections between landscape elements. *Hydrologic connectivity* is used here to refer to water-mediated transfer of matter, energy, or organisms within or between elements of the hydrologic cycle. The definition of this ecological property is stimulated by Ward's (1997) definition of riverine connectivity as energy transfer across the riverine landscape; rivers can be defined as having interactive pathways along three spatial dimensions (Ward and Stanford 1989*a*): longitudinal (headwater-estuarine), lateral (riverine-riparian/floodplain), and vertical (riverine-groundwater). When these dimensions are combined with climate (e.g., precipitation), the concept is expanded to *hydrologic connectivity* on landscape, regional, and even global scales. Human perturbations that alter hydrologic connectivity include dams, stream channelization, associated flow regulation, and water extraction (from both the stream channel and groundwater). Factors such as sediment transport, acid rain, and spread of pathogens and exotic plants along river

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[1] E-mail: pringle@sparc.ecology.uga.edu

and riparian corridors are not only perpetuated by hydrologic connectivity, but also their effects are often exacerbated by changes in this property (Pringle 2000*a*).

Hydrologic connectivity must be carefully managed, both within and beyond the boundaries of biological reserves. Much of the landscape's surface configuration can be attributed to its drainage network of rivers that form a predictable structural pattern affecting watershed geochemistry, topography, climate, and vegetation. However, protection and management of hydrologic connectivity have not been given the attention that they deserve by either conservation biologists or resource managers. There are three major reasons for this. First, hydrologic connectivity is typically not considered in the scientific literature dealing with management and conservation of fragmented landscapes (but see Page et al. 1997). Most of the theoretical underpinnings of the conservation biology of fragmented landscapes were developed under a conceptual model of landscapes that were not yet entirely fragmented, and when awareness of riverine connectivity was in its infancy. It has not been until the last decade that we have begun operating on the premise that groundwaters and surface waters are interconnected as a single resource (e.g., Winter et al. 1998). Although there are excellent books on the subject of habitat fragmentation, the words "stream" or "river" do not even appear in the indices of major books on this subject (e.g., see Shafer 1990, Schelhas and Greenberg 1996, Laurance and Bierregaard 1997, Soulé and Terborgh 1999). For example, the Biological Dynamics of Forest Fragments Project (also known as the Minimum Critical Size Ecosystem Project) involved the creation of forest fragments of different sizes and the monitoring of biodiversity in these fragments through time, yet the presence or absence of surface water was not a criterion in the experimental design (R. O. Bierregaard, *personal communication*). Secondly, hydrologic connectivity is often ignored until water quality and quantity problems reach problematic proportions, because of lack of data on how hydrology fits into the greater landscape. In many cases, information as basic as river discharge is not available. Finally, many alterations in hydrologic connectivity are outside reserve boundaries and beyond the immediate control of managers (Pringle 2000*b*).

Much emphasis has been placed on the size, shape, and configuration of reserves (summarized in Primack 1993), e.g., *Which is more optimal: one large vs. several small reserves? Are reserves connected by forested corridors or not connected?* However, these questions have not been asked within a hydrologic framework. For example: *How do the size, shape and configuration of a given reserve with respect to watersheds, regional aquifers, and precipitation patterns determine its response to disturbance?* In this paper, I discuss human effects on spatial and temporal dimensions of hydrologic connectivity and challenges of managing these effects. Examples are drawn from reserves throughout the world that vary in size, biome, and location within the hydroscape (i.e., with respect to watersheds, regional aquifers, and wind/precipitation patterns). Finally, a case study focuses on issues of hydrologic connectivity at La Selva Biological Station, Costa Rica, a relatively small (~15 $km^2$) biological reserve that is located in a hydrogeologically complex landscape undergoing rapid development.

## Human Effects on Spatial and Temporal Dimensions of Hydrologic Connectivity

There is a rich body of literature about connectivity in riverine ecosystems and how it is affected by human perturbations (DeCamps et al. 1988, Ward and Stanford 1989*b*, National Research Council [NRC] 1992*a*, 1999, Naiman et al. 1993, Bayley 1995, Poff et al. 1997, Pringle 1997, Michener and Haeuber 1998, Sparks et al. 1998). The magnitude and extent of human impacts (e.g., dams, water diversions, groundwater extraction, nutrient and toxic loading, and climate change) have altered the nature of hydrologic connectivity on local, regional, and now global spatial scales (e.g., Pringle et al. 2000, Rosenberg et al. 2000). Many impacts have complex and interrelated cumulative effects. Moreover, because of the continual transport that characterizes hydrologic systems, an effect originating in one part of the landscape may be expressed at a distant geographic location, often with a significant time lag.

Four global patterns emerging in human-dominated landscapes have important implications for the location and management of reserves (Pringle 2000*a*): (1) deterioration of lower watersheds, deltas, estuaries, and receiving coastal waters (e.g., NRC 1990, McCully 1996, Hinrichsen 1998); (2) deterioration and loss of riverine floodplains, connecting wetlands, and riparian ecosystems (e.g., NRC 1992*a*, Armantrout 1995, Abramovitz 1996); (3) deterioration of irrigated lands and connecting surface waters (e.g., NRC 1992*b*, Postel 1992, 1999, Lemly et al. 1993, Pringle and Triska 2000); and (4) isolation of upper watersheds (e.g., Pringle 1997). The first three patterns are usually clearly evident in the landscape, whereas the fourth is much more cryptic and often overlooked because habitat may remain intact and remnant populations of biota may be present.

## Reserve Location in a Watershed Context

Biological reserves throughout the world are affected by the aforementioned patterns. Effects often depend on a reserve's placement within a watershed. In turn, reserve location is often largely determined by trends in human settlement and socioeconomic development. Human populations generally settle in lowland coastal areas and fertile river valleys and then subsequently move inland and upland. Consequently, many reserves

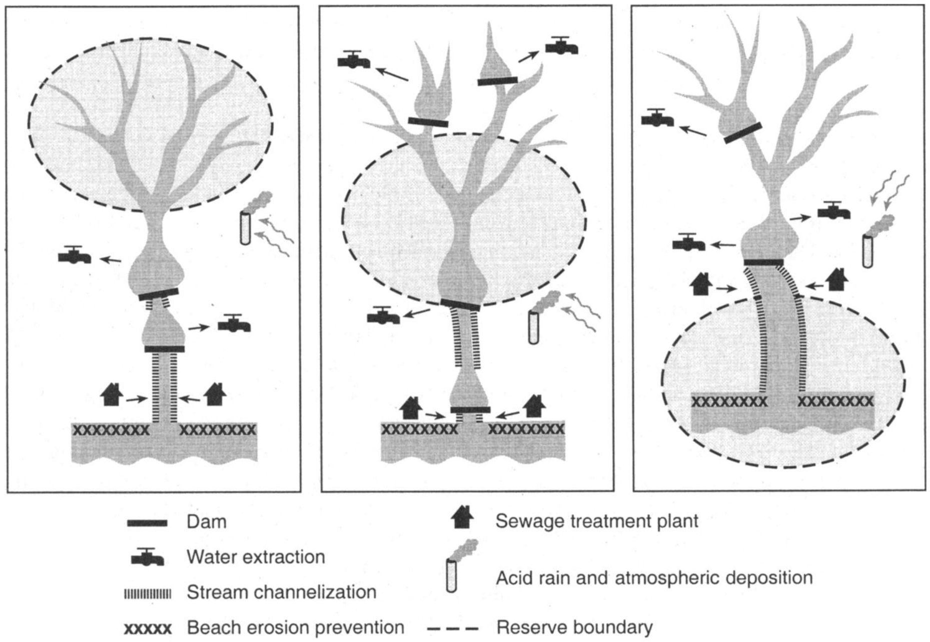


FIG. 1. Biological reserves in three stylized locations within a watershed: upper, middle, and lower. All are affected by alterations in hydrologic connectivity and pollution outside of their boundaries, regardless of their location in the watershed.

are located in highlands of "rock and ice"(World Conservation Monitoring Centre 1992). Here, I examine how biological reserves located in three "idealized" portions of the watershed (lower, middle, and upper; Fig. 1) respond to human disturbance transmitted through the hydrologic cycle. I use paired examples of reserves that span a range of different sizes and biomes throughout the world and discuss strategies for managing hydrologic connectivity to protect reserve *biointegrity* (Karr 1991).

### *Lower watershed*

Reserves that incorporate river deltas face extreme management challenges, given that rivers integrate watershed-level processes and the complexity of ocean–freshwater–land interactions. The mass movement of people to coastal urban areas is a dominant demographic trend of the late 20th century in both the developed and developing world (Hinrichsen 1998). The result is severely polluted terrestrial and aquatic ecosystems in lower watersheds and coastal areas (World Resources Institute 1996, Baer and Pringle 2000). In many countries, water diversion from rivers is so extreme that many rivers no longer flow into the sea for large parts of the year, thereby negatively affecting the biological integrity of lower river deltas, estuarine, and marine ecosystems. Such rivers include: the Colorado River in the United States (Glenn et al. 1996, China's Yellow or Huang He River, and India's Ganges River (Brown et al. 1998). Decreasing freshwater inputs increase the salinity of estuarine areas, driving concomitant biological change such as declines in mangrove forests and fisheries. The Indus River (Pakistan, India) has experienced discharge reductions of ~80%, resulting in salinity increases and massive mangrove dieoff (McCully 1996).

Sediments once carried by rivers to deltaic and coastal areas are now retained by upstream dams. Consequently, deltas and coastal areas are often "sediment-starved," leading to severe coastal erosion. Sediment once carried to the Mediterranean Sea by the Nile River is now deposited behind upstream dams (e.g., the Aswan High Dam), producing shore erosion in the Mediterranean (near Baltin, Egypt) of ~151 m/yr (McCully 1996). This pattern is repeated throughout the world, from the highly eroded Mississippi Delta on the Louisiana coast to the great mangrove forests in the Niger Delta. The latter are being eroded at a rate of tens of meters per year, as a result of a ~70% reduction in sediment transport by the Niger River following construction of upstream dams (Hinrichsen 1998). In the United States, many coastal parks suffer shore erosion: Cape Cod National Seashore, Cape Hatteras National Park, and Indiana Dunes National Lakeshore (NRC 1988, 1990). The submergence of existing wetland habitat in coastal areas is a long-term issue being examined by U.S. land management agencies (NRC 1990).

Such patterns of physical and biological deterioration create management challenges for those parks and reserves located in coastal areas and lower watersheds.

*How can healthy reserves in lower watersheds and deltas be maintained within a watershed that has been highly altered by human activities?* As an example, the Danube Delta Biosphere Reserve (Fig. 2A) drains a densely populated watershed containing 70% of the population of Central Europe. This large (~6792 km$^2$) reserve is a World Heritage Site, containing a rich variety of wetland habitats that serve as a critical buffer system between the Danube River watershed and the Black Sea. The biological integrity of the delta is threatened by intense eutrophication, toxicity from mercury and heavy metals, aquaculture, increasing salinities, and both stream channel and coastal erosion, which are caused by human disturbance upstream and within the delta itself (summarized by Pringle et al. 1993*b*). In addition, the biological integrity of the reserve is affected by deteriorating environmental conditions in the Black Sea, which is highly eutrophied by coastal communities and nutrient loads carried by the Danube and four other major rivers. The Black Sea is considered to be one of the largest anoxic marine basins in the world, and the depth of the upper layer of oxygenated surface water has declined dramatically over the last few decades (e.g., Murray et al. 1989), resulting in dramatic fishery declines. Salinities in the delta are increasing and the Danube annually carries 60 000 Mg of phosphorus and 340 000 Mg of inorganic nitrogen into the Black Sea (IUCN 1991). Degradation of water quality has shifted ecosystem primary production, whereby massive algal blooms have replaced rooted aquatic plants in many areas of the delta (Cristofor 1987).

Long-term management of the Danube Delta Biosphere Reserve depends on effective, integrated watershed management and international cooperation, not only among the 12 countries in the Danube's watershed, but also among those in the Black Sea watershed that encompasses the Danube drainage. The Bucharest Declaration, an agreement to cooperate on water management and pollution control, was signed by nine nations bordering the Danube. The recent Black Sea Action Plan and the Black Sea Transboundary Diagnostic Analysis (Global Environmental Facility 1996, 1997) provide a basis for further international cooperation, but socioeconomic and political problems are impeding progress.

Reserves located in lower watersheds within arid regions of the world are particularly vulnerable to alterations in hydrologic connectivity from irrigation projects. Water extracted from surface and groundwater for irrigation often reduces surface water flow; this problem is compounded by irrigation return flow, which can be toxic to wildlife (e.g., Presser 1994, Presser et al. 1994). Intensive irrigation in arid regions often leads to leaching of soil minerals (e.g., selenium, arsenic, boron, lithium, and molybdenum) that then become mobilized and enter the food chain. In arid regions of the United States, irrigation is considered to be the most widespread and biologically important source of contaminants to surface water (Lemly et al. 1993).

The Stillwater National Wildlife Refuge (Fig. 2B) in the western state of Nevada, USA, provides a case in point. This small (97 km$^2$) refuge is located in the arid desert at the terminus of the Carson River. Massive fish and bird mortality near the mouth of the Carson River in 1986 and 1987 (Rowe and Hoffman 1987) was attributed to bioaccumulation of elements within irrigation drainage (e.g., Dwyer et al. 1992, Lemly et al. 1993). As a result, inflow of agricultural drainage into Stillwater National Wildlife Refuge is now carefully regulated and existing water rights are being purchased to restore the refuge (NRC 1992*b*, Pringle 2000*b*). Stillwater is only one of many reserves in the arid west facing this problem. Deformities associated with selenium bioaccumulation in young birds have been found in over 11 locations in the western United States, including some national wildlife refuges (Lemly et al. 1993, Presser et al. 1994).

A disaster that indicates the potential magnitude of this problem occurred when the Kesterson Irrigation Drainage Reservoir, located in California's San Joaquin Valley, was incorporated into the U.S. National Wildlife Refuge System in 1970. This artificial wetland became an important habitat for breeding and migratory birds, in part because extensive water appropriation for agriculture had reduced or eliminated other suitable habitat. At least 90% of California's Central Valley wetlands are gone and >60% of the entire Pacific Flyway waterfowl population is now channeled into remaining wetlands during migration (Frayer et al. 1989). By the early 1980s, scientists and agencies reported deformities in birds and massive die-offs of waterfowl and fishes at Kesterson that were linked to application of irrigation water to soils naturally rich in elements such as selenium (e.g., Ohlendorf et al. 1986). Kesterson was removed from the national refuge system in 1985, with cleanup operations between 1985 and 1991 totaling about U.S. $24 million and current annual research/monitoring costs estimated at U.S. $1 million (USBR 1986*a*, *b*, Benson et al. 1993). The potential for bioaccumulation of toxic elements in other arid regions is very high (McCully 1996) and may emerge as a threat to reserves in developing countries with expanding irrigation development.

### *Middle watershed*

Reserves located in middle-watershed areas are vulnerable to cumulative effects of hydrologic alterations and pollution originating in both upper and lower watersheds (Fig. 3). Zion National Park (~593 km$^2$), located in arid Utah, USA, provides a temperate arid example. Threats to the park include: proposed dams on the Virgin River for expanding domestic and mu-

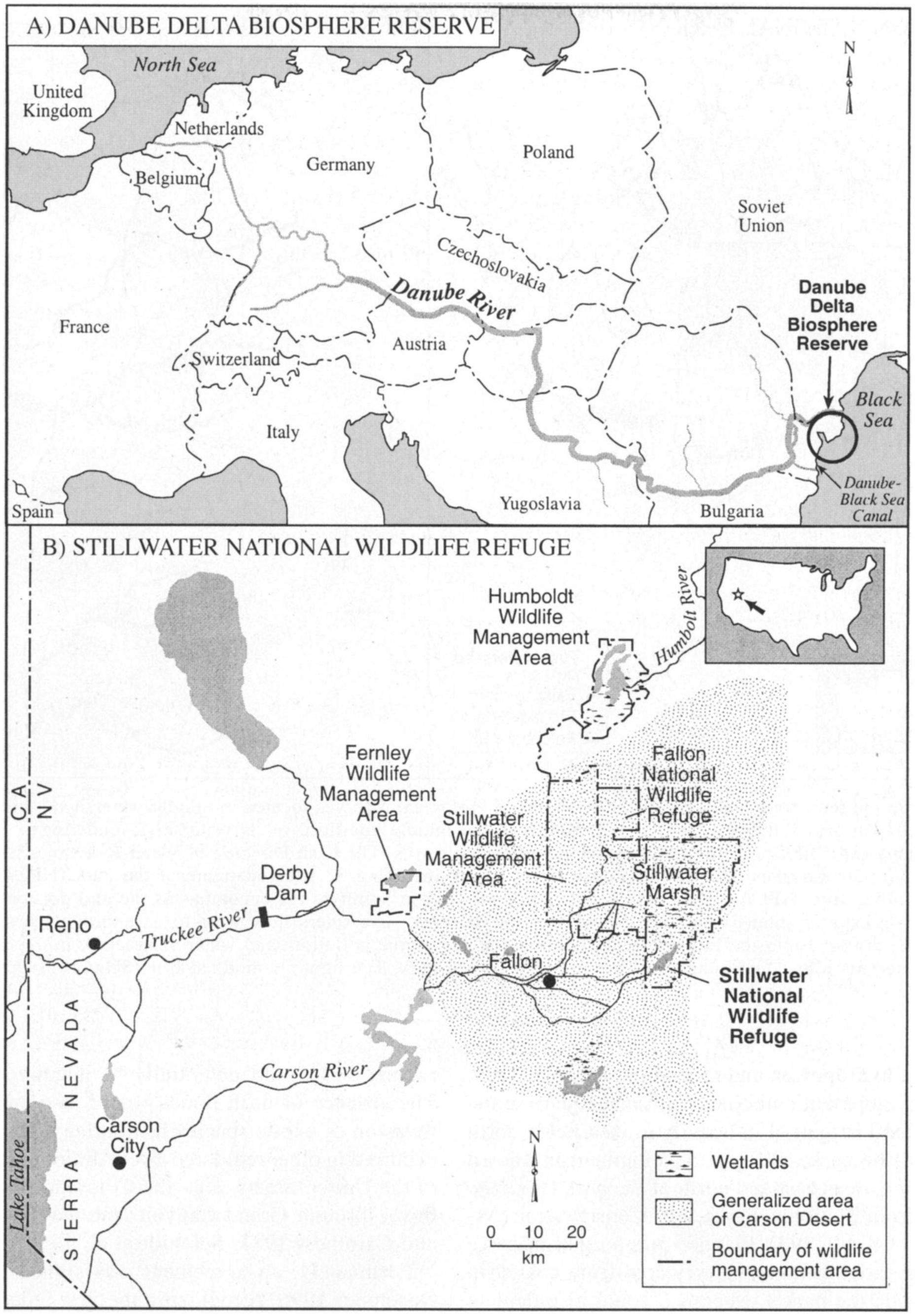


FIG. 2. Paired examples of reserves in lower watersheds encompassing wetlands of regional and global ecological importance. They provide critical habitat for breeding and migratory birds and are affected by upstream alterations in hydrologic connectivity and pollution. (A) The *Danube Delta Biosphere Reserve,* Romania, Europe's largest continuous marshland, lies where the Danube River enters the Black Sea. It is highly influenced by human activities in the Danube watershed, which falls within 12 countries. Many cities and towns dump untreated domestic and industrial wastes directly into the river and its tributaries, and >30 dams span the Danube. The figure is modified from Pringle et al. (1993*b*). (B) The *Stillwater National Wildlife Refuge,* at the terminus of the Carson River in western Nevada, USA (with headwaters in the Sierra Nevada Mountains), is part of a larger Wildlife Refuge Complex in the Carson Desert. Dams and river diversions (largely for agricultural uses) have resulted in reduced water flow into the refuge. Refuge wetlands are also threatened by accumulation of anthropogenic (e.g., pesticides) and natural contaminants (e.g., selenium, arsenic, and boron) from irrigation return flow. The figure is modified from Hoffman (1994).

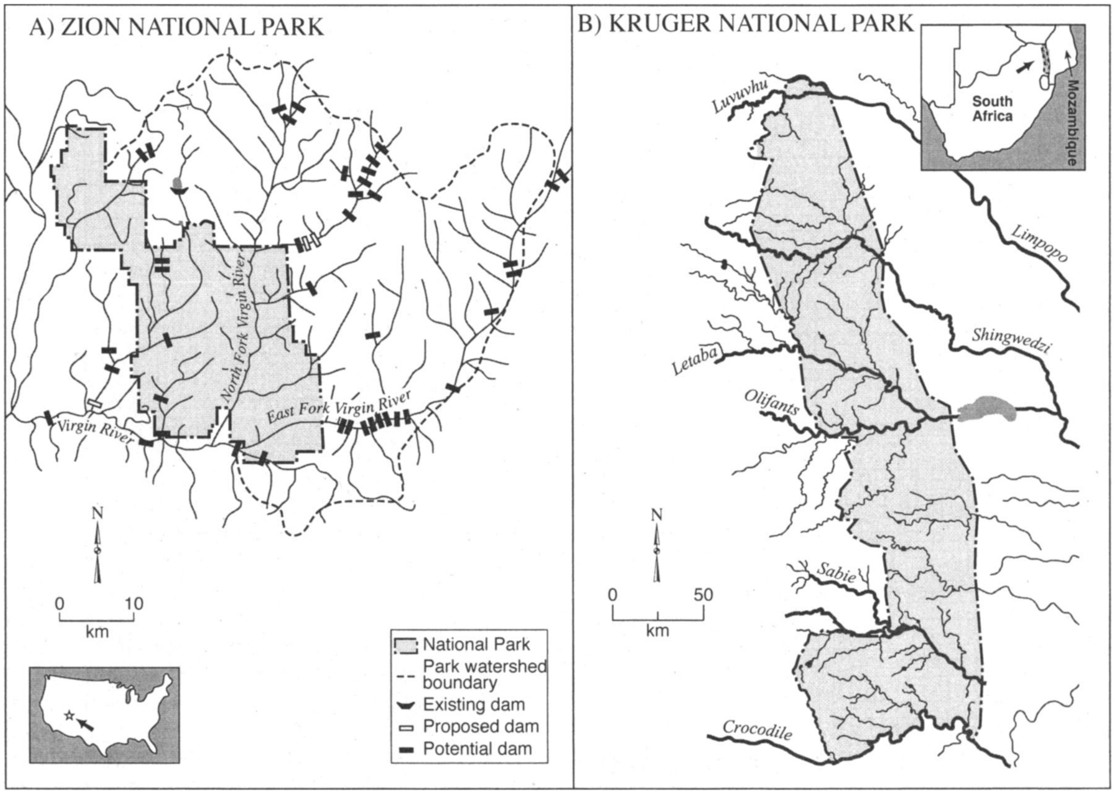


FIG. 3. Paired temperate and subtropical examples of biological reserves located in middle-watershed regions. (A) *Zion National Park,* in arid southwestern Utah, USA, lies in the middle one-third of its watershed, rendering it vulnerable to upstream dams and pollution from rapidly growing cities and towns. The Utah Division of Water Resources issued a report identifying 92 potential dam sites in the Virgin River Basin, including 33 sites upstream of the park (NPCA 1993). The figure is modified from NPCA (1993). (B) *Kruger National Park* in South Africa encompasses the mid-portion of six major rivers that originate in intensively settled land west of the park. The rivers flow west to east through Kruger and into Mozambique, draining into the Indian Ocean. Land use, point source pollution, and water abstraction in upper watersheds have led to serious water quality and quantity problems in the park. The figure is modfied from Scholes (1995).

nicipal use, hydropower, and recreation; urban and residential development combined with inadequate septic systems; flood irrigation in heavily grazed fields north and east of the park; and coal development in known coal resource areas east and north of the park (Fig. 3A, modified from National Parks and Conservation Association [NPCA] 1993). Planned pumping of massive amounts of groundwater to slurry coal from coal strip mines outside the park's watershed could also deplete groundwater recharge to the East Fork of the Virgin River (Fig. 3A), possibly affecting flows through the park.

Until recently, one of the most serious threats to the park's biological integrity was proposed dams (Fig. 3A; see NPCA 1993) upstream of the park that could potentially change the timing and quantity of water flows, altering water temperatures and disrupting transport and distribution of sediments and organic matter. The Virgin spine dace (*Lepidomeda mollispiris*), a fish endemic to the Virgin River, is adapted to a "flash flood" regime and would potentially be negatively affected. The absence of flash floods would also encourage the invasion of exotic species in riparian corridors, as has occurred in other regulated rivers draining federal lands in the United States, e.g., the Colorado River where it flows through Grand Canyon National Park (Johnson and Carothers 1987, Schmidt et al. 1998).

Fortunately, an agreement was signed for Zion in December 1996, recognizing the first federal reserved water right for a national park in Utah. This agreement secures water rights to protect instream flows and groundwater in the park, and provides a dependable water supply for local communities (McGlothlin and Hansen 1996). Construction of proposed dams on the main stem of the east and north forks of the Virgin River and a planned transbasin diversion are now prohibited. Limits and periods for water diversion are specified, along with bypass flows, and a ~3.2-km groundwater protection zone (on the northern, eastern, and southern boundaries of Zion) restricts development of high-capacity and high-volume wells.[2] Other solutions include widespread implementation of water conservation measures in towns and cities upstream of Zion, which would obviate the need for future proposed dams (NPCA 1993). Although the recent 1996 agreement limiting water development upstream of Zion is a "success" story, many biological reserves have not fared as well because legal and administrative tools (established to protect reserves) apply mainly within reserve boundaries.

Kruger National Park in South Africa (~20 000 km$^2$; Fig. 3B) is >30 times the size of Zion and provides a semiarid subtropical example of a reserve located in a "middle watershed." Similar to Zion, the upper watersheds of rivers transversing Kruger (Fig. 3B) are also characterized by burgeoning human populations that increasingly affect water quality and quantity. Rapid expansion of irrigation farming, tree farming (using exotic species), cattle grazing, mining, the establishment of large towns and cities, and associated industrial activity have occurred over the last two decades (Venter and Deacon 1995). As an example, the upper Olifants watershed (54 575 km$^2$), located upstream and to the west of the park, has 30 major dams and contains $\sim 2.5 \times 10^6$ people who largely live in rural Third World conditions. Also, coal burning (in large cities located southwest of the park) results in harmful acid deposition in Kruger. In addition to the water demands of the park and South African communities upstream, the country of Mozambique (located downstream and to the east of Kruger) also needs water for both human use and environmental values. Mozambique is not satisfied with the quantity of water that it is receiving, and the country has threatened to take its concerns to the World Court for resolution if South Africa does not more adequately address its needs (Arenstein 1996, Gleick 1998).

Intensive upstream water abstraction has made some perennial rivers ephemeral (e.g., Letaba and Luvuvhu) for prolonged periods (Moore and Chutter 1988, Russel and Rogers 1989). Although the Sabie River is the only river in Kruger National Park that has never stopped flowing, the flow has been reduced during recent years, and drops in the water table adjacent to the river channel have killed riparian vegetation in many reaches (Venter and Deacon 1995, Rogers and Naiman 1997). Aquatic vertebrates such as the crocodile (*Crocodylus niloticus*) and the hippo (*Hippopotamus amphibius*) are very vulnerable to reduced water flows and water pollution. Both play important roles in structuring riverine ecosystems (Naiman and Rogers 1997, Davies and Day 1998), and their loss can trigger a cascade of events throughout both aquatic and terrestrial foodwebs.

In addition to water quality and quantity problems originating upstream of the park, Kruger faces problems resulting from alterations of hydrologic connectivity within its borders. Most herbivorous mammals live within 6 km of surface water, and water dependence is a major factor limiting their abundance (Scholes 1995). To increase available habitat, park managers provided artificial watering holes in formerly waterless areas between major rivers. This altered the population dynamics of many species and resulted in catastrophic collapses of inflated herbivore populations (e.g., in 1966 and 1983), which became food limited. The result has been heavily damaged vegetation, especially near surface water (Thrash et al. 1991*a*, *b*). Temporary increases in carnivores and scavengers occur for a year or so after the herbivore population collapses, followed by subsequent collapse of carnivore and scavenger populations as their food disappears (Pienaar 1985, Scholes 1995). Thus, management alterations of hydrologic connectivity (i.e., the creation of groundwater-fed watering holes between major rivers) have altered the population dynamics of many animal species as well as vegetation.

Strategies being pursued to manage water quality and quantity within Kruger National Park include: reallocation of upstream waters; agreements with upstream communities to extract water during high and intermediate flows and to allow compensation flows to be maintained during dry months; development of instream flow needs and water management strategies for each of the park's rivers; simulation of historical flows to determine how dams should be managed; and, ironically, construction of new dams to store water for the park during dry periods. Emerging comprehensive strategies for watershed management of Kruger Park are described in detail elsewhere (e.g., Rogers and Bestbier 1997).

### *Upper watershed*

Many biological reserves occur within upper watersheds, especially in mountainous areas (World Conservation Monitoring Centre 1992). Governments often protect such areas because of a combination of poor agricultural potential, scenic value, or protection of human water supplies. Ecological and wildlife values are often a secondary benefit. Some of these areas contain the last vestiges of intact habitat, wildlife, and other natural features in human-dominated landscapes across the globe, yet they are increasingly vulnerable through progressive isolation from their lower watersheds (Pringle 2000*a*).

Effects of the isolation of upper watersheds on biological integrity are not well understood. Modifications of lower watersheds such as water extraction, channel modification, land-use changes, nutrient discharge, and toxic discharge can initiate a cascade of events upstream that are often not immediately associated with these original downstream sources of dis-

[2] W. R. Hansen and D. J. McGlothlin. 1998. Federal reserved water rights recognized at Zion National Park. URL: ⟨http://www1.nature.nps.gov/wrd/frwzion.htm⟩

turbance (Pringle 1997). The scale of effects of human disturbances in lower watersheds that are transmitted to upstream reaches varies from genes to ecosystems. Examples include: (1) genetic- and species-level changes, such as reduced genetic flow and variation in isolated upstream populations; (2) population- and community-level changes that occur when degraded downstream areas act as population "sinks" for source populations of native species upstream or, conversely, as "source" populations of exotic species that migrate upstream; and (3) ecosystem- and landscape-level changes in nutrient cycling, primary productivity, or regional patterns of biodiversity. There is a critical need to understand the impact of disturbance at all of these levels (Pringle 1997).

Olympic National Park (Fig. 4A; 373 km$^2$), located in Washington, USA, provides a temperate example of how the loss of connectivity in lower watersheds has upstream effects. Threats include: existing dams and numerous proposed hydropower projects on rivers that flow out of the park; proposed offshore oil leasing; existing oil barge and tanker traffic; logging of lower watersheds; water withdrawals from streams outside of the park; and acid precipitation (NPCA 1993).

Both the Elwha and Skokomish Rivers have been devoid of migratory fishes within Olympic National Park boundaries (Fig. 4A) since they were dammed. Dams block migration of several species of anadromous salmon and trout that, after maturing in the ocean, return to rivers in the park to lay their eggs or spawn. The dams modify downstream flow of nutrients, sediment, and woody debris necessary for successful spawning and rearing of juvenile fishes. Dams also inundate fish habitat and elevate downstream water temperatures (National Park Service 1995). Before Elwha and Glen Canyon dams (Fig. 4A) were built, the Elwha was used by 10 runs of salmon and trout. It was one of the few rivers in the contiguous United States that supported all of the anadromous salmonids native to the Pacific Northwest. Because of habitat loss, only a fraction of historical salmonids return to the Elwha to spawn (~3000 over a 8-km stretch of river below the first dam). The Elwha River sockeye salmon (*Oncorhynchus nerka*) has been listed as extinct, the spring chinook (*O. tshawytscha*) and chum (*O. keta*) salmon are possibly extinct, and summer steelhead (*O. mykiss*) runs are depressed (Wunderlich et al. 1994). Because salmonids are important food sources for >22 species of mammals and birds, there are potential cascading trophic effects in the ecosystem. Spawning salmon and their carcasses represent a major pathway that returns marine nutrients to freshwater and terrestrial ecosystems (Cedarholm et al. 1999). Decomposing carcasses are a critical source of energy for terrestrial vertebrates such as Bald Eagles (*Haliaeetus leucocephalus*), bobcats (*Felix rufus*), and river otters (*Lutra canadensis*, and can also provide nutrients for riparian vegetation along some spawning streams (e.g., Willson and Halupka 1995). Dams also obstruct elk (*Cervus canadensis*) migration's to winter range in the lowlands by flooding steep mountainous valleys (NPCA 1993).

Because of this and other environmental damage, there is a movement underway to remove both the Elwha and Glines Canyon dams (Loomis 1996). Removing both dams would reestablish the year-round supply of food to the many species of birds and mammals that feed on salmonids. Almost 300 ha of terrestrial habitat would be restored, including riparian and wetland regions and 8.5 km of high-quality stream habitat that is currently inundated by the reservoirs. Although still controversial, dam removal has become a much more widely accepted solution to managing hydrologic connectivity to restore the biological integrity of the landscape (e.g., McCully 1997, Lovett 1999).

The Caribbean National Forest (Fig. 4B; 113 km$^2$) provides a neotropical island example of how downstream hydrologic alterations and pollution outside a biological reserve can potentially affect upstream ecosystem dynamics. In contrast to the anadromous salmonids of Olympic National Park, which spend most of their adult life at sea, most fishes and shrimps that inhabit the streams of the Caribbean National Forest are amphidromous (drifting to the estuary and/or ocean as larvae, where they spend a relatively short period of time, then returning upstream as juveniles to complete their adult life). Because all of the fishes and shrimps inhabiting the nine major streams draining the forest are migratory, water extraction associated with dams and pollution from sewage treatment plants (in rapidly developing coastal areas; Fig. 4B) can cause massive larval mortality (Benstead et al. 1999), potentially affecting upstream recruitment of adults and other ecosystem processes. For example, low vs. high shrimp abundance can cause interstream differences in algal and insect abundance, algal community composition, and total amounts of benthic organic matter (Pringle 1996, Pringle et al. 1999). 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), concomitant changes in ecosystem structure and function might occur. Although dams associated with water intakes within and outside the Caribbean National Forest are not large (usually <3 m) and they have spillways, the sheer number of intakes and volume of water withdrawn (Fig. 4B) are cause for major concern (Pringle and Scatena 1999). On an average day, >50% of riverine water draining the forest is diverted into municipal water supplies via water intakes before it reaches the ocean (Naumann 1994). There are also numerous proposals for additional water extraction. Several dams have no water below their intakes for much of the year, and all fish and shrimp larvae suffer direct mortality when sucked into water

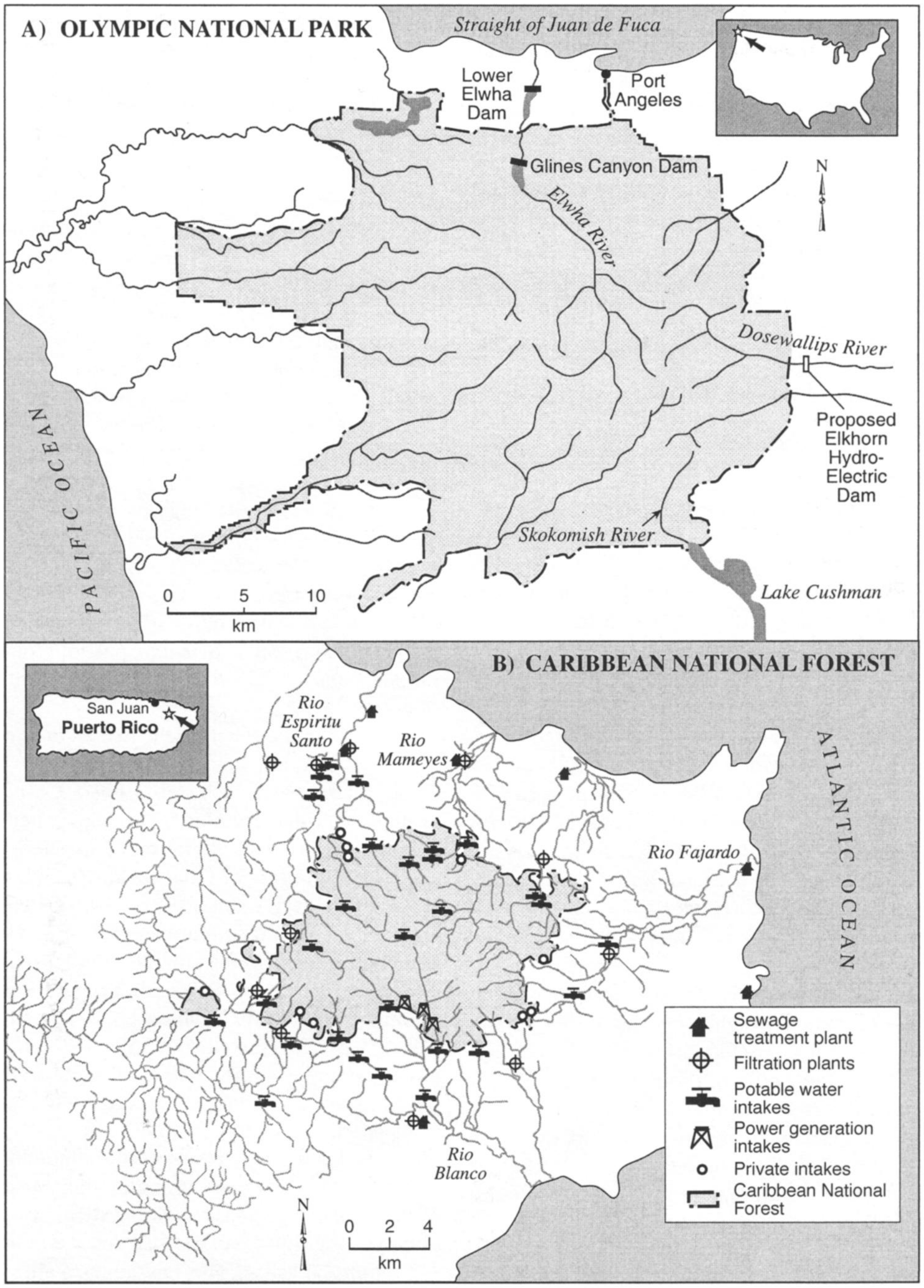


FIG. 4. Paired temperate and tropical rain forest reserves in upper watersheds that receive high annual precipitation and are affected by alterations in hydrologic connectivity within and outside their boundaries. (A) *Olympic National Park,* in the Olympic Peninsula of Washington, USA, is drained by 11 major rivers with ~200 tributaries. The largest watershed (Elwha) is fragmented by two dams: the Glines Canyon dam in the park and the Lower Elwha dam outside the park (~13 km downstream). On the Skokomish River, the Lake Cushman dam backs up water into the southeast corner of the park. The figure is modified from NPCA (1993). (B) The *Caribbean National Forest* in northeastern Puerto Rico is drained by nine rivers, all important sources of potable water for municipalities outside forest boundaries. The forest is intensively exploited for potable water by surrounding communities, as illustrated by numerous water intakes. Locations of sewage treatment and water filtration plants are also indicated. The Caribbean National Forest is near the San Juan metropolitan area (see inset), where about one-third of the island's inhabitants live. The figure is modified from Pringle (2000*b*).

intakes during migration. Recommendations for managing hydrologic connections between the Caribbean National Forest and downstream adjacent areas include: establishment of instream flow and habitat requirements of migratory biota (e.g., Scatena and Johnson 2000; N. Hemphill and E. Garcia, *unpublished data*); maintenance of minimum flows over dams (Benstead et al. 1999); installation and upkeep of fish/shrimp ladders (Benstead et al. 1999); and implementation of more environmentally sensitive water withdrawal systems (March et al. 1998, Benstead et al. 1999; J. G. March, *unpublished data*). Other downstream threats to the Caribbean National Forest include new proposals for water extraction, sewage disposal, and land-use changes.

The isolation of upper watersheds within reserves can sometimes be used as an opportunity to reintroduce and/or manage endangered species. For example, the greenback cutthroat trout (*Salmo clarki stomias*) is native to the South Platte and Arkansas River Basins in Colorado, USA. This subspecies was extirpated from much of its historic range by the 1930s through habitat degradation and the widespread introduction of nonnative trout species, which resulted in competition and/or hybridization. In the early 1980s, five genetically "pure" populations were located in four isolated headwater reaches of streams and alpine lakes (Stuber et al. 1988). *S. clarki stomias* is now being reintroduced into suitable habitat throughout its historic range by federal and state agencies. One criterion used in identifying reintroduction sites is the presence of a barrier (e.g., low-head dam) or potential barrier to prevent reinvasion by nonnative fishes. Artificial barriers have emerged as an important management tool for protecting populations of native fishes from encroaching non-native populations (Thompson and Rahel 1998). In the case of *S. clarki stomias,* this is necessary because most of the selected reintroduction sites have an existing nonnative trout population that must be removed (usually via fish toxicants). Most of the reintroductions have taken place in the Arapaho-Roosevelt and Pike-San Isabel National Forests and in Rocky Mountain National Park, western United States (Stuber et al. 1988).

## Beyond the Watershed

The global magnitude and extent of hydrological alterations (e.g., Benke 1990, NRC 1992*b*, Dynesius and Nilsson 1994, Young et al. 1994, Chao 1995, Postel et al. 1996, Rosenberg et al. 1997, 2000, Vorosmarty et al. 1997, Lundqvist 1998, Postel 1999, Pringle et al. 2000) is now affecting biological reserves through increasingly broad feedback loops. It is ironic that, just as we begin to understand the complexities of human effects on local watershed hydrology, reserves are threatened by regional and global processes such as overdrawn aquifers, atmospheric deposition, and global climate change.

### *Regional aquifers and/or hydrothermal systems*

Just as watersheds are the natural unit of management for surface waters, aquifers are the logical unit of management for groundwaters (e.g., Reetz 1998, NRC 1999). Because groundwater and surface water are usually integrally connected and aquifers do not always coincide with watersheds (e.g., Gibert et al. 1994*a*), both need to be managed and coordinated (e.g., Glennon and Maddock 1994). Management has generally underemphasized groundwater relative to surface water problems (NRC 1999), when, in fact, the landscape is a diverse and interconnected mosaic of geohydrologic units (Gibert et al. 1994*b*). In some regions of the world, aquifers and aquifer systems remain to be delineated. In other regions where aquifer systems have been thoroughly mapped, additional research is necessary to fully characterize groundwater quality conditions and groundwater–surface water interactions (Reetz 1998). The situation is also complicated by fragmented management of small portions of aquifers by jurisdictions with different management objectives (e.g., Reetz 1998).

Water deficit, defined as the excess of water pumping over recharge, has been estimated at $160 \times 10^9$ Mg/yr on a global basis (Postel 1999). Correspondingly, groundwater depletion and stream dewatering are contributing to loss and alteration of wetland and riparian ecosystems throughout the world (e.g., Gremmen et al. 1990, Stromberg et al. 1996), with particularly strong effects in arid and semiarid regions due to high water demand by burgeoning human populations.

For example, existing and proposed groundwater pumping outside the boundaries of Death Valley National Park, Nevada, USA (13 365 $km^2$; Fig. 5A) threaten to diminish aquifers that may be essential to the park's springs and water resources in other Nevada national park units (NPCA 1993). Threats to Death Valley's water-related resources include groundwater pumping to satisfy urban water demands in the Las Vegas Area, mining operations, irrigation, and development of a high-level radioactive waste dump (Yucca Mountain, Nevada). The Las Vegas Valley Water District has filed numerous applications to pump groundwater, proposing to withdraw $>228 \times 10^6$ $m^3$/yr (> 185 000 acre feet/yr) from proposed wells located in southern and east-central Nevada, including 74 wells that would pump water from the carbonate aquifer system feeding Death Valley's eastern springs (NPCA 1993). The National Park Service has formally challenged more than 74 groundwater pumping applications filed by the Las Vegas Valley Water District that could affect Death Valley, as well as 28 Las Vegas Valley applications that could affect Great Basin National Park. Similar situations have occurred at Organ

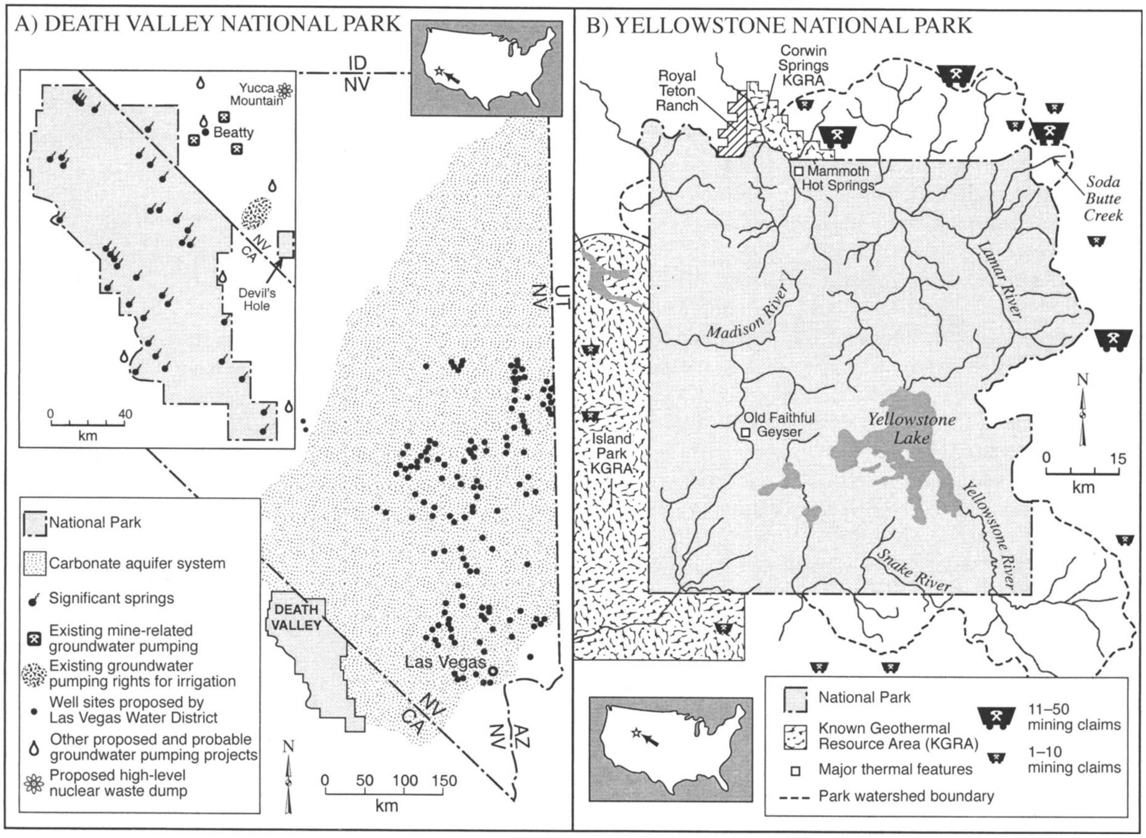


FIG. 5. Paired temperate biological reserves threatened by alterations in hydrologic connectivity from extraction of subsurface resources (e.g., water, oil, and gas) outside their boundaries. The figure is modified from NPCA (1993). (A) *Death Valley National Park* in Nevada and California, USA, lies on the southwestern edge of a regional carbonate aquifer system that extends far beyond the park boundary into east and central Nevada. Springs that arise on Death Valley's eastern escarpment are connected to the aquifer system and are threatened by groundwater overpumping outside the park's boundaries and, potentially, by a proposed high-level nuclear waste dump. (B) *Yellowstone National Park,* Wyoming, USA, has two known geothermal resource areas (KGRAs) just outside its northern (Corwin Springs KGRA) and western (Island Park KGRA) boundaries. Potential developments at these locations threaten park geysers and other geothermal features because of hydrological interconnections. Toxic mine drainage from abandoned, existing, and future mines is also a serious threat to the biological integrity of the park.

Pipe Cactus National Monument, where nearby groundwater pumping in Mexico appears to have diminished the aquifer that sustains important park springs. In the Chicksaw National Recreation Area, groundwater pumping near the park boundary is believed to be responsible for diminished flow of park springs (NPCA 1993). The San Pedro Riparian National Conservation Area in western Arizona has become a critical stopover for migratory birds because riparian forests on other rivers (e.g., Rio Grande, Colorado River) have largely disappeared as a result of hydrologic alteration (Stromberg et al. 1996). The San Pedro watershed contains the largest surviving expanse of broadleaf riparian forest in the southwest. The San Pedro Conservation Area is threatened by external groundwater pumping that vastly exceeds recharge rates. Stromberg et al. (1996) predict that future declines in alluvial groundwater levels will cause desertification of the riparian flora and net loss of local biodiversity. Solutions include groundwater recharge projects, restriction of groundwater pumping, and purchase of land and conservation easements that would further restrict groundwater pumping.

Yellowstone National Park (8998 km$^2$) in Montana, USA, is also threatened by development outside its boundaries (Fig. 5B). Until recently, potential damage to geothermal features within the park has been a serious concern. Drilling for hot water, oil, and gas can disrupt the flow of groundwater or release hydrostatic pressure critical to geyser eruption. Groundwater extraction can also deplete groundwater tables below levels necessary to maintain surface thermal features (NPCA 1993). For example, of the 10 major geyser areas in the world, all but three have been altered in recent years through nearby development (NPCA 1993). A well drilled on Royal Teton Ranch on the park's northern boundary (Fig. 5B) recently disrupted nearby flows to hot springs located just outside the park. Fortunately, recent water rights settlements for Yellowstone National Park have provided unprecedented protection for its hydrothermal systems. Thermal water developers now must prove beyond scientific doubt that proposed development activities will have no impact on the park's hydrothermal features (C. Pettee, *personal communication*).

Abandoned, existing, and future mines are also serious threats to Yellowstone Park. Toxic mine drainage can be transmitted throughout the park landscape via hydrologic connectivity. For example, large flood events on the park's eastern boundary could wash massive quantities of toxic mine tailings downstream into Soda Butte Creek (Fig. 5B; NPCA 1993). This specific problem remains unresolved. Also, several thousand mining claims currently exist in national forests encircling Yellowstone. Even though many claims do not lie directly within the park's watershed, pollutants from mining downstream of the park could also harm park resources (e.g., migrating trout).

### *Atmospheric pollution*

Emissions from fossil fuel-burning power plants and other industrial facilities have caused serious pollution problems (including acid deposition) in biological reserves throughout the world, from South Africa's Kruger National Park (Scholes 1995, Fig. 3B), to Poland's Tatra National Park (Kot 1992), to Acadia National Park in Maine, USA (NPCA 1993).

For example, Great Smoky Mountains National Park (2107 $km^2$) in North Carolina and Tennessee, USA, is downwind of many urban and industrial areas that generate millions of tons of air pollution annually (Shaver et al. 1994). Its regional nitrate deposition is the highest of any monitored site in North America. The park includes the largest remaining area of old-growth red spruce (*Pices rubens*) and Fraser fir (*Abies fraseri*) in the world. There is evidence in the park that acid deposition and associated pollutants are altering forest resistance to winter injury (Barnard and Lucier 1990), and are contributing to forest declines in the northern Appalachians. Vegetation injury in the park has also been linked to ozone exposure (Shaver et al. 1994), which can lead to ecosystem changes (Woodman 1987). Streams in the Great Smoky Mountain National Park region have the highest nitrate concentrations of any streams draining "protected" watersheds in the United States (Stoddard 1994). High stream water nitrate is associated with high N deposition and leaching from old-growth forests. High sulfate concentrations have been related to atmospheric deposition and sulfur-rich bedrock (Cook et al. 1994).

An emerging challenge for reserve managers is to address the interactive effects of atmospheric pollution and other hydrologic alterations on the biological integrity of reserves. *How will surface and subsurface water withdrawals, combined with stream nitrogen loading, interact with atmospheric N deposition and high ground levels of ozone to affect ecosystem functioning in a given reserve? How can these effects be mitigated?*

### *Global climate change*

Reserves are clearly being influenced by human activities through increasingly broad feedback loops in the hydrologic cycle that ultimately include alteration of climate. Although in-depth discussion of this topic is beyond the scope of this paper, predicted impacts of global change on water resources include: increases in global average precipitation and evaporation; changes in regional patterns of rainfall, snowfall, and snowmelt; changes in the intensity, severity, and timing of major storms; rising sea levels and saltwater intrusion into coastal aquifers (e.g., Firth and Fisher 1992, Everett 1995, Gleick 1998). These changes will have many complex, interrelated effects on landscape and regional scales that will affect biological reserves.

## CASE STUDY: ALTERATIONS IN HYDROLOGIC CONNECTIVITY AND LA SELVA BIOLOGICAL STATION, COSTA RICA

La Selva Biological Station/Reserve in lowland Costa Rica provides a case study that illustrates: (1) the complexity of hydrologic connections in a rapidly developing and hydrogeologically complex landscape; and (2) the challenges of proactively identifying and evaluating outside threats to reserve biointegrity. La Selva is a small (~15 $km^2$) reserve located in the Caribbean lowlands (Fig. 6A). It is owned and operated by the Organization for Tropical Studies, a nonprofit consortium of about 55 universities and other academic institutions dedicated to tropical education and research. La Selva borders Braulio Carrillo National Park (~488 $km^2$; Fig. 6A). The La Selva–Braulio Carrillo land corridor is the last intact gradient of rain forest spanning elevations from near sea level to ~2900 m a.s.l. on the Caribbean Slope of Central America. The land corridor protects a large portion of Costa Rica's biodiversity, including four life zones and two transition zones (Pringle et al. [1984], based on the classification of Holdridge et al. [1971]). La Selva's tropical wet forests are represented by relatively small areas (as are those life zones within the narrow panhandle of Braulio Carrillo National Park that extends northward down to La Selva), and are especially vulnerable to the effects of peninsularization.

The La Selva–Braulio Carrillo land corridor falls within the Rio Sarapiqui–San Juan drainage; La Selva lies at the junction of the Puerto Viejo and Sarapiqui Rivers (Fig. 6A). Most of the upper watersheds of these two rivers are currently protected within Braulio Carrillo National Park. However, their lower watersheds

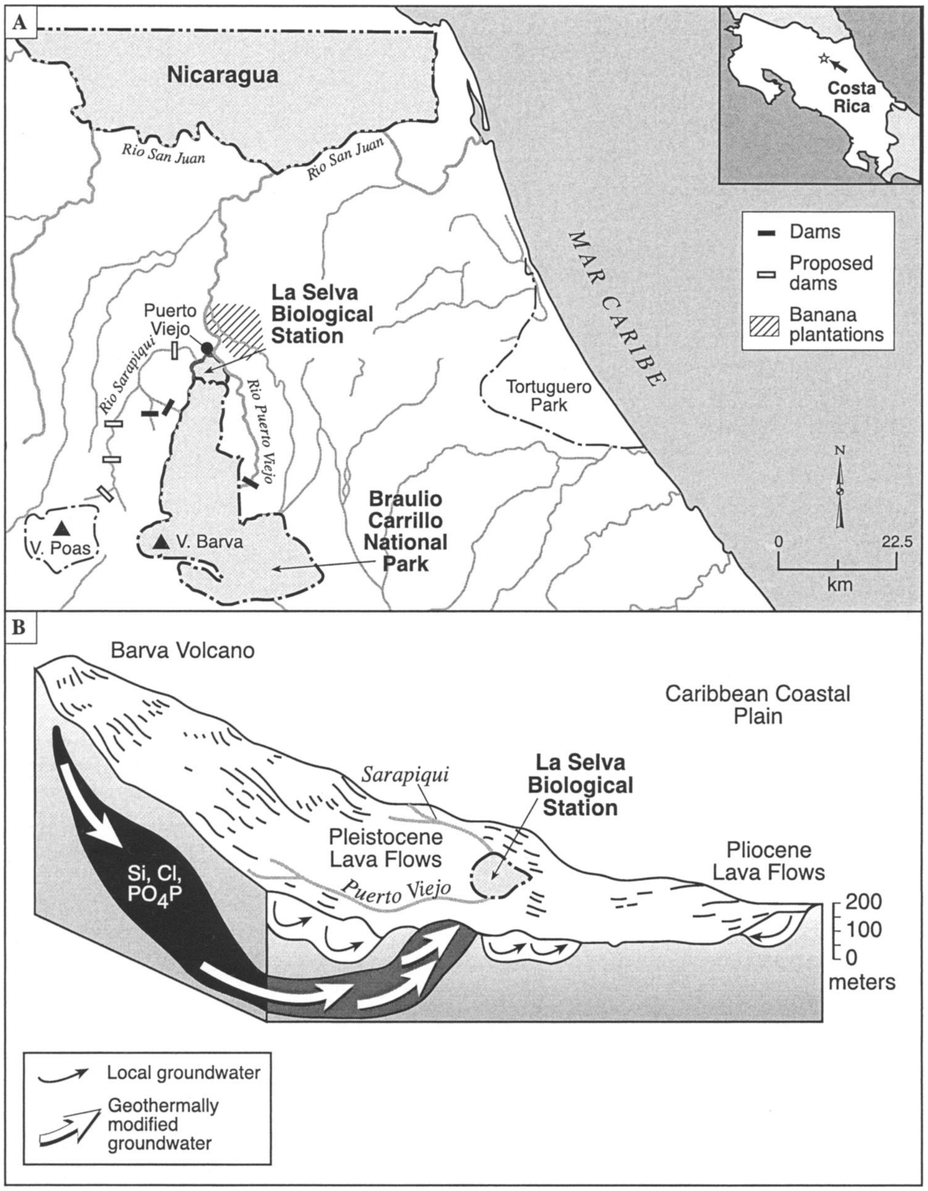


FIG. 6. (A) Watershed location of La Selva Biological Station and Braulio Carrillo National Park on Costa Rica's Caribbean slope. This reserve complex is vulnerable to disruptions in hydrologic connectivity from: proposed and existing dams or water diversions upstream or adjacent to the reserves (approximate locations of some projects are indicated); deforestation and changes in land use to the north, west, and east; and downstream pesticide contamination of the Rio Sarapiqui by banana plantations located downstream to the north. (B) Schematic diagram illustrating the location of La Selva Biological Station with respect to subsurface flow paths of geothermally modified groundwater rich in Si, Cl, $PO_4$-P, and trace elements. Geothermally modified ground waters emerge within La Selva, which is located at the break in landform where the foothills of the Central Mountain Range (e.g., Barva Volcano) merge with the Caribbean Coastal Plain.

have largely been cleared for agriculture or urbanization. Deforestation has resulted in greater runoff, decreased infiltration rate and aquifer recharge, and increased erosion and sedimentation in rivers (Pringle and Scatena 1999). The La Selva–Braulio Carrillo reserve complex receives rainfall of 4–5 m/yr, with highest levels occurring within the park. The high infiltration capacity of forested watersheds in the park helps to regulate surface water in the Sarapiqui and Puerto Viejo Rivers. Changes in land use in these protected areas could negatively affect lowland communities by causing increased flooding and decreased water quantity and quality.

The lowland communities of Puerto Viejo and nearby barrios increasingly depend on potable water diverted from springs originating at the northern end of Braulio Carrillo National Park near La Selva's southern boundary (Fig. 6A). Local surface and ground water that once provided potable water is now contaminated with sewage, fecal coliforms, and other pathogens (Pringle and Scatena 1999). This is due, in part, to the rapid population increase. Sarapiqui County grew from 20 000 to > 46 000 people in about three years, largely because of the development of banana plantations (in the early 1990s) just northeast of La Selva. Socioeconomic changes and future increases in the human population over the next few decades will undoubtedly increase pressure on the relatively undisturbed watersheds of the La Selva–Braulio Carrillo reserve complex as a source of water for domestic and agricultural use (Vargas 1995).

Although potable water diverted from the foothills of Braulio Carrillo National Park is not anthropogenically contaminated, it has a very high mineral content from geothermal activity (e.g., Pringle 1991, Pringle and Triska 2000). Solute-rich waters emerging in the foothills of Volcan Barva are connected to a regional hydrothermal system associated with tectonic activity along the Central American Volcanic Arc (Fig. 6B; Pringle et al. 1993*b*). Our studies indicate that this water is geothermally modified and can be classified as sodium-chloride-bicarbonate water (Pringle 1991). These waters are biologically important within stream ecosystems because of high levels of soluble reactive phosphorus (up to 400 μg SRP/L). Rates of algal growth (Pringle and Triska 1991) and microbially mediated decomposition (A. D. Rosemond, *unpublished data*, A. Ramirez, *unpublished data*) are presumably phosphorus saturated in receiving streams. Our current studies are examining the extent to which higher trophic levels (e.g., benthic insects) are affected by elevated phosphorus levels.

Diversion of geothermally modified waters for potable water supplies may affect the structure and function of stream ecosystems at La Selva. Moreover, land use and other hydrological alterations in the landscape have the potential to alter interbasin transfers of geothermally modified groundwater to La Selva by affecting the quality and quantity of groundwater recharge (Genereux and Pringle 1997). These interbasin transfers are responsible for large fluxes of water and solutes to lowland streams, and can account for *over half* of the stream discharge and major cations at some times of year (Wood et al. 1998). La Selva is therefore very vulnerable to water quality and quantity alterations via regional hydrological connections that extend well beyond its boundaries and watershed.

In addition, as of July 2000, eight hydroelectric projects currently exist and as many as 13 are proposed for both the Sarapiqui and Puerto Viejo Rivers and their tributaries (ICE 1999; E. Anderson, *unpublished dissertation*). One proposed project on the Sarapiqui River, just west of La Selva (Fig. 6A), would remove ~ 90% of the river water over a distance of 4 km by diverting it into a large metal pipe. Cumulative effects of these projects may affect the biological integrity of La Selva Biological Station and Braulio Carrillo National Park. Alterations of river flow regimes as a result of this recent hydropower development could cause negative physical, chemical, and biological changes in stream ecosystems, riparian zones, and floodplain swamp forests (Pringle 2000*a*).

It remains to be seen how current and future alterations in hydrologic connectivity will affect La Selva Biological Station and Braulio Carrillo National Park. Human disturbances well outside the boundaries of these two reserves are not within the control of reserve management, yet they may negatively affect their biological integrity. To assess potential ecological impacts of hydrological alterations on La Selva Biological Station, we are currently: (1) identifying the nature and location of the proposed and existing hydropower projects in the region; (2) examining all existing environmental impact assessments for individual hydropower projects (along with historical discharge data of the Sarapiqui River) to make predictions about cumulative impacts of existing and proposed projects on the hydrologic regime of the river system (E. Anderson, *unpublished data*); (3) continuing our "long-term" (i.e., 1988 to present) monitoring of streams draining La Selva; and (4) expanding our environmental outreach program on water quantity and quality issues in local communities[3] (Pringle 1999) to include information about ecological effects of proposed hydropower projects.

## Conclusion

The field of conservation biology has focused much attention on the optimal size, shape, and configuration of reserves in the landscape without considering the hydrologic framework. The past decade has seen a tremendous advance in our knowledge of hydrologic connectivity that can be applied to the management of existing reserves and the location and design of new reserves. Of the world's land area, < 7% is either strictly or partially protected (World Resources Institute [WRI] 1994), yet many reserves are in danger of becoming population sinks (Pulliam 1988) for wildlife if we do not develop a more predictive understanding of how they are affected by changes in hydrologic connectivity outside their boundaries.

The following *basic tenets of hydrologic connectivity* should be carefully considered by conservation biologists concerned with reserve management, in the context of ecological issues in large-scale conservation biology.

[3] URL: ⟨http://www.arches.uga.edu/~cpringle/wflproducts.html⟩

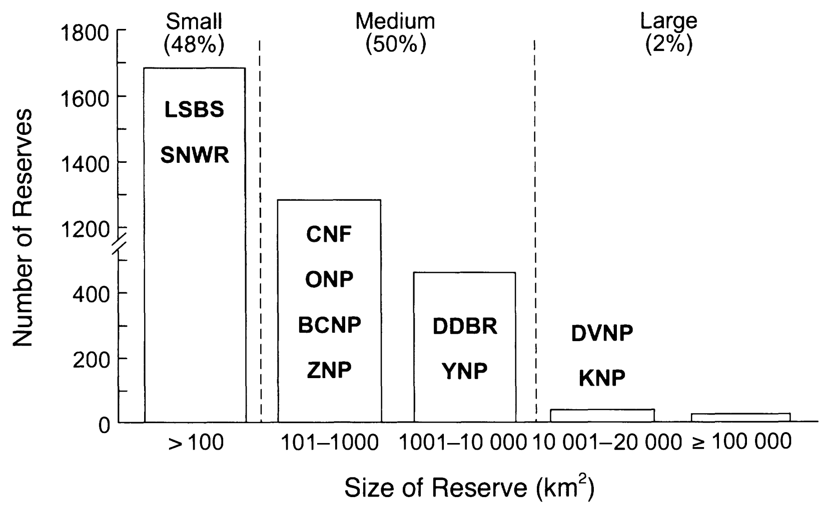


FIG. 7. Numbers of the world's parks and protected areas that fall into different size categories encompassing the different biological reserves discussed in this paper. Small reserves are La Selva Biological Station (LSBS, ~15 km$^2$) and Stillwater National Wildlife Refuge (SNWR, 97 km$^2$); reserves in the lower half of the medium-size category include the Caribbean National Forest (CNF, 113 km$^2$), Olympic National Park (ONP, 373 km$^2$), Braulio Carrillo National Park (BCNP, 488 km$^2$), and Zion National Park (ZNP, 593 km$^2$); the upper half of the medium-size category includes the Danube Delta Biosphere Reserve (DDBR, 6792 km,$^2$ with 1030 km$^2$ marine) and Yellowstone National Park (YNP, 8998 km$^2$); and the lower half of the large category includes Death Valley National Park (DVNP, 13 365 km$^2$) and Kruger National Park (KNP, ~20 000 km$^2$). The figure is modified from Primack (1993).

The biological integrity of a given reserve is affected by cumulative alterations of hydrologic connectivity and pollution both within and outside of its boundaries, from relatively local (e.g., single-dam effect) to regional (e.g., cumulative effects of dams, overdrawn aquifers, atmospheric deposition) and global (e.g., climate change) phenomena.

1) The location of a given reserve in the hydroscape (i.e., its juxtaposition with respect to watersheds, regional aquifers, and wind and precipitation patterns) plays a key role in determining how it will be affected by alterations in hydrologic connectivity and pollution transmitted through the hydrologic cycle.

2) Reserves in biomes ranging from arid deserts to tropical rain forests are vulnerable regardless of their size (Fig. 7) and watershed location (Figs. 2–6). An old adage of conservation biology is *"the larger the reserve the better,"* but the hydrologic connectivity of large reserves (e.g., the Danube Delta, Death Valley National Park, and Kruger National Park) must be managed on scales that often transcend cultural, political, national, and international boundaries.

3) There is an increasing 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.

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