

Editorial

The need for a more predictive understanding of hydrologic connectivity

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INTRODUCTION

Why do we continue to underestimate or overlook the key role of hydrologic connectivity in structuring ecosystems and determining ecological patterns in the landscape? All too often this property is acknowledged in hindsight, as new environmental problems emerge on regional and global scales. The ecological effects of many hydrologic alterations exhibit a time lag and manifest themselves at geographic locations far from the source of disturbance. Examples range from decreases in silicon delivered to coastal ecosystems by heavily dammed rivers (which may be an exacerbating factor in the process of coastal eutrophication: Turner *et al.*, 1998) to emergent patterns in the global distribution and ecological effects of harmful and persistent organic compounds within aquatic-based food chains (Colburn and Thayer, 2000).

'Hydrologic connectivity' is used here in a global ecological context to refer to the water-mediated transfer of matter, energy and/or organisms within or between elements of the hydrologic cycle (Pringle, 2001). Although this property is essential to maintaining the ecological integrity of ecosystems, it also serves to perpetuate the flow of human-derived nutrients, toxic wastes and exotic species. Dams, flow regulation, water diversion, and groundwater extraction are just a few of the many human activities that alter hydrologic connectivity. Environmental consequences range from obvious direct effects, such as the obstruction of fish migration by dams, to more elusive alterations in biogeochemical cycling such as methylmercury mobilization in reservoirs behind dams.

A major challenge in human-dominated landscapes is to manage hydrologic connectivity to minimize harmful effects. Yet, this property is often ignored until environmental issues become major crises, in part because of lack of data on how hydrology fits into the greater landscape. It has not been until the last decade that we have even begun operating on the premise that groundwaters and surface waters are interconnected as a single resource (e.g. Winter *et al.*, 1998). Also, human alterations have altered hydrologic connectivity before we have been able to understand completely how this property affects

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ecological patterns in the landscape (Pringle and Triska, 2000). Hydrologic connectivity is being altered at unprecedented rates and is contributing to losses in global aquatic biodiversity and ecosystem integrity (e.g. Master *et al.*, 1998; Rosenberg *et al.*, 2000). Of the 5.2 million kilometres (3.2 million miles) of streams in the USA (lower 48 states), 98% have been fragmented by dams and water diversion projects (Benke, 1990).

Although the term 'connectivity' is commonly used among conservation biologists, with respect to landscape corridors and landscape linkages between patches (Noss, 1991), hydrologic connectivity remains a largely neglected dimension within the field of conservation biology. The words 'stream' and 'river' do not even appear in the indexes of major books on the subject of habitat fragmentation (e.g. Shafer, 1990; Laurance and Bierregaard, 1997). Just one consequence of this omission is the lack of consideration of watershed (i.e. catchment) dynamics in the debate among conservation biologists regarding the importance of size, shape, and configuration of biological reserves. For example, the well-known *Biological Dynamics of Forest Fragments Project* in the Brazilian Amazon (also known as the *Minimum Critical Size Ecosystem Project* (Laurance and Bierregaard, 1997)) does not even use the presence or absence of surface water as a criterion in its experimental design — which involves the creation of tropical forest fragments of different sizes and the monitoring of biodiversity in these fragments through time.

HISTORICAL ROOTS OF HYDROLOGIC CONNECTIVITY

Although connectivity (or its inverse, isolation) has long been recognized as a fundamental factor in determining species distribution (e.g. MacArthur and Wilson, 1967), the concept of 'landscape connectivity' was first introduced by Merriam (1984) with respect to the interaction between species attributes and landscape structure in determining movements of biota among habitat patches.

Connectivity is a fundamental concept to both metapopulation biology and landscape ecology. In metapopulation ecology, which is concerned with gene flow between spatially distinct sub-populations of a larger metapopulation, connectivity is often considered as an attribute of a given habitat patch (Moilanen and Hanski, 2001). Whereas original metapopulation models were designed and tested on terrestrial biota, metapopulation theory has more recently been applied to riverine organisms such as fish and mussels (e.g. Stoeckel *et al.*, 1997; Gotelli and Taylor, 1999). From a general landscape ecology perspective, connectivity can be defined as the degree to which a landscape facilitates or impedes movement of organisms among resource patches (e.g. Tischendorf and Fahrig, 2000).

Connectivity has been used extensively to describe spatial connections in riverine landscapes (e.g. Amoros and Roux, 1988; Ward and Stanford, 1989; Ward, 1997). Ward and Stanford (1989) define rivers as having interactive pathways along one temporal dimension (time scale) and three spatial dimensions (longitudinal (headwater–estuarine); lateral (riverine–riparian/floodplain); and vertical (riverine–groundwater)). Consideration of dynamic interactions along these four dimensions (i.e. as defined by Ward and Stanford (1989)) has proved to be an effective conceptual spatial framework to understand human impacts on river ecosystems (e.g. Boon *et al.*, 1992; Pringle, 1997, 2000; Pringle *et al.*, 2000).

Ward's (1997) definition of riverine connectivity (i.e. as energy transfer across the riverine landscape) stimulated me to consider the broader significance of hydrologic connectivity — which can be defined as water-mediated transfer of matter, energy, and/or organisms within or between elements of the hydrologic cycle (Pringle, 2001). In a recent paper, I discuss the vulnerability of biological reserves throughout the world to cumulative alterations in hydrologic connectivity outside of their boundaries (Pringle, 2001). The cumulative and interacting effects of altered hydrologic connectivity and pollutant loading are now threatening the ecological integrity of ecosystems worldwide (Pringle, 2003).

HYDROLOGIC CONNECTIVITY, SOLUTE TRANSPORT, AND EMERGING ENVIRONMENTAL PROBLEMS OF GLOBAL CONCERN

Contaminated irrigation drainage

Dramatic alterations in hydrologic connectivity in intensively developed agricultural areas have compromised the integrity of wetlands worldwide. Wetland drainage in arid regions, combined with contamination of many remaining wetlands with sub-surface irrigation drainage, has resulted in regional declines in migratory waterfowl and other wildlife (Lemly *et al.*, 2000). Although agricultural reductions in natural water supplies have caused wetland loss and deterioration for centuries, more recent threats are now beginning to be identified — such as the complexity of interactions between pesticides and naturally occurring trace metals in soils (Lemly *et al.*, 2000). Sub-surface irrigation drainage has caused massive mortality (and in some cases deformities) of migratory waterfowl and fish that has been linked to the application of irrigation water to soils naturally rich in elements such as selenium, boron and arsenic (e.g. Ohlendorf *et al.*, 1986; Whitworth *et al.*, 1991). These elements become mobilized in saturated soils and enter the food chain, thus causing toxic effects.

As just one example of many in the western USA, the Salton Sea is the largest body of water in the state of California (albeit artificially created) and it receives an influx of pesticides, fertilizers and salts from irrigation drainage from massive farming operations in the Imperial Valley. With no outlet and a high evaporation rate, contaminants are effectively trapped and accumulated. Because 95% of interior wetlands in California have been lost (primarily to irrigated agriculture), over 60% of the Pacific migratory flyway waterfowl population are channelled into available wetlands such as the Sonny Bono Salton Sea National Wildlife Refuge, which attracts more than 380 species of migratory birds. During the past decade, there have been massive bird and fish kills. For example, 14 000 birds (representing 66 species) perished in 1997 as a result of an outbreak of avian botulism.

Methylmercury contamination

Alterations in hydrologic connectivity can have profound effects on biogeochemical cycling. The mobilization and bioaccumulation of mercury in food chains of newly created reservoirs and other hydrologically disturbed areas is a relatively recently acknowledged environmental problem. Many factors affect the biogeochemical cycling of mercury in the environment, and wetland disturbance and reservoir creation can lead to methylmercury formation and bioaccumulation by fish, with consequent toxic effects on fish-eating wildlife and humans. Conditions often exist in reservoirs (e.g. the hypolimnion of many stratified reservoirs) that stimulate the transformation of inorganic mercury into toxic methylmercury by sulphate-reducing bacteria. Mercury occurs naturally in rocks and soils, and all water bodies in the Northern Hemisphere are also contaminated with mercury as a result of long-range transport and deposition from human sources. An estimated 90% of the inorganic mercury, derived from human sources and released to the atmosphere in the last 100 years, is bound up in the terrestrial environment (Mason *et al.*, 1994), where it is released slowly to streams and rivers. Mercury contamination has now been documented throughout the temperate USA, where it is a national environmental concern (USA EPA, 1999).

Our understanding of the ecological implications of mercury is constrained by lack of data on concentration in the environment (e.g. in fish and wildlife tissue), sources, and effects of alterations in hydrologic connectivity on the biogeochemical cycling of mercury on regional and global scales.

Endocrine-disrupting chemicals

Knowledge of hydrologic connectivity on global scales is paramount in understanding how endocrine-disrupting chemicals (e.g. organochlorine pesticides, polychlorinated biphenyls (PCBs), dioxins) move

through the environment. Within just this last decade, the transport, bioaccumulation, and ecological effects of endocrine-disrupting chemicals have become major topics on the agendas of many experts groups, steering committees and panels of governmental organizations, industry and academia throughout the world (Lintelmann *et al.*, 2003).

Hydrologic connectivity plays a key role in determining geographic patterns in the global distribution of endocrine disruptors such as PCBs. As just one brief example, PCBs have become very highly concentrated within arctic food chains, in part due to volatilization in warmer climates and condensation and deposition in colder regions such as the Arctic. Ocean currents also transport biota that have sequestered PCBs into the arctic food web, where they undergo further biological magnification within long-lived animals. PCB levels in seals and predatory polar bears are, respectively, 384 million and 3 billion times the concentrations in ocean water — potentially affecting the long-term reproductive capacity of these animals and the humans that consume them (Colburn *et al.*, 1997).

As indicated by Colburn and Thayer (2000), it is imperative that ecologists now incorporate the movement of endocrine-disrupting chemicals through ecosystems in their models, just as they have with carbon and nitrogen. How do endocrine disruptors affect aquatic ecosystem functioning as they become biologically accumulated in aquatic food webs? What role does hydrologic connectivity play in the distribution of these chemicals in the environment? Recent studies indicate that even the transport of plastics in the environment are involved. Plastic particles absorb and concentrate toxins, such as PCB and dichlorodiphenylethylene (DDE), up to a million times their levels in ambient seawater. The plastic is essentially acting as a PCB/DDE magnet, and birds and fish that ingest the plastic are thus consuming massive doses of the endocrine disruptors (Mato *et al.*, 2001).

TOWARDS DEVELOPING A MORE PREDICTIVE UNDERSTANDING OF HYDROLOGIC CONNECTIVITY

In conclusion, we have grossly underestimated the power of the hydrologic cycle to transport human-generated wastes throughout the biosphere — just as we have often undervalued the positive aspects of hydrologic connectivity in providing essential ecosystem services and transporting essential elements. The environmental challenges described above have all emerged within the last few decades and illustrate the complexity of interactions between hydrologic connectivity and contaminant transport. Moreover, they suggest that the current extent and magnitude of global hydrologic alterations and pollutant loadings will result in additional problems emerging.

How can we develop a more predictive understanding of hydrologic connectivity so that we can identify these problems proactively? It is imperative that a consideration of hydrologic connectivity be incorporated into the field of conservation biology (both theoretical constructs and practical applications). An important area of collaborative study between hydrologists and ecologists is to understand how cumulative human alterations of hydrologic connectivity influence ecological patterns on regional and global scales. Such interdisciplinary research is fundamental for land-use decisions, which are often made in the absence of adequate information on how hydrological connections in the landscape structure ecosystems. The information can be used to consider carefully the ecological and socioeconomic trade-offs associated with altering hydrologic connectivity.

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