

River Conservation Challenges and Opportunities

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Chapter 10 Offprint

Ecological Connectivity for River Conservation

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Ecological Connectivity for River Conservation

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Connectivity in river ecosystems can refer either to organisms and nonliving materials moving within and among river networks (*network connectivity*) or to nutrients and energy moving through food webs and linking aquatic with terrestrial or marine ecosystems (*web connectivity*). By nature, rivers are complex *networks of webs* in which multiple dimensions of connectivity interact. Many human endeavors disrupt these networks of webs, but thoughtful conservation management can help maintain sustainable levels of connectivity.

10.1. Fish and amphibians in the Necklace Lakes

The Necklace Lakes of Montana, USA are threaded like a string of pearls along a chain of small streams in a broad wilderness basin. In the lakes along this chain, trout have thrived for thousands of years (native cutthroat trout for most of that time, and introduced species like rainbow and brook trout more recently). Also present are several amphibians, including the long-toed salamander and various frogs. Interestingly, the necklace appears broken in some places, as a number of pearls strewn nearby are separated from the chain. These pearls are lakes without small stream outlets or inlets. A biologist out mucking around the Necklace Lakes basin will notice right away that, depending on the time of year, various stages of amphibians from egg to adult

thrive in much larger densities in the separated lakes than in those occupying the intact necklace chain.

A lack of *connectivity* to the main necklace chain renders these separated lakes fishless. Trout require aquatic habitat at all life stages, and because they cannot survive on land individual fish cannot make the move over even short distances to colonize neighboring separated lakes. Conversely, trout occupy all lakes along the intact necklace. The historically fishless state of the separated lakes has allowed amphibians to thrive in a state of release from both predation and indirect negative effects of fish. Adult amphibians, however, can move across land, so the concept of connectivity for these animals is not the same as that for fish. Hence, amphibians can be found in the sub-par habitat along the necklace chain, but it is likely that thriving populations in the fishless habitat of the separated lakes supplement the necklace populations regularly. At the landscape scale, fish and amphibians enjoy a stable coexistence in the Necklace Lakes basin, thanks in large part to contrasting definitions of connectivity for these two groups.

10.2. What is *connectivity*?

Network connectivity can be described both within and among independent river networks, encapsulates three spatial dimensions within networks, and typically increases with temporal flow pulses

If connectivity has different meanings for amphibians and fish, is there a general definition for the word? Typing *connectivity* into an internet search engine will give an idea of how the word is used most commonly – and what else do we find these days but references to computers and the internet (see Box 10.1). Ecologically speaking, connectivity has an analogous interpretation in terms of movement of cohesive *packets* from one place to another – only in the ecological realm, these packets are either organisms moving across a landscape (as the Necklace Lakes fish and amphibians) or materials of biological importance (e.g. nutrients and energy-containing molecules) moving either through a landscape or from one organism to another through a food web. Landscape connectivity is intuitive when we humans can see a physical pattern that might directly translate, for example, to an organism’s movement ability. Intuitive examples include the connected vs. separated lakes in the Necklace Lakes basin, large bridges over or passages under major roadways to allow movement of wildlife, or the lack of connectivity between oceanic islands or between stream segments upstream vs. downstream of a large waterfall. Colonization of the New World via the Bering Land Bridge between northeastern Asia and northwestern North America provides an intuitive human example. The land bridge was exposed during low sea levels of the last Ice Age, increasing connectivity for terrestrial organisms and allowing movement of human populations from what is now Asia into previously uninhabited continents.

Internet connectivity facilitates social connectivity

Box 10.1



There is a strong parallel between current widespread definitions of connectivity and the definition of “IP” (Internet Protocol), which refers to the transfer of packets of electronic information between two endpoints. Social networking sites like Facebook tout the benefits of facilitated connectivity of people around the world

via their internet-based service. Indeed, 845 million people (as of Feb 2012) enjoy the ease of globally communicating anything from their breakfast menu and baby photos to ideas seeding revolutionary uprising thanks to the increased international social connectivity that Facebook facilitates.

But landscape connectivity is not always intuitive. Sometimes, for example, connectivity for one organism relies on the presence and activity of another organism, as is the case for many freshwater mussels (Chapter 6). Adult mussels are sedentary filter-feeders but their larvae are capable of movement away from the natal site by temporarily parasitizing a fish’s fins or gills. This arrangement is typically species-specific, so the presence and movement behavior of particular fish species dictate how far mussels are able to move across the landscape (or “riverscape”, “riverine landscape”). Two riverscapes might look equally connected to the human eye, but one might have high connectivity for a mussel species owing to an abundance of its host fish species, and the other might have lost the host fish species resulting in extremely low connectivity for the mussel. So it is important to remember that connectivity is not solely a property of a landscape.

Rather, it is a property of the interaction of a landscape and an organism's movement-related traits (Taylor et al. 1993; Ricketts 2001).

Connectivity has a slightly different interpretation in the context of food webs, which are descriptions of which organisms eat which in an ecosystem. Food web connectivity should be equally intuitive, however: organisms still play the key roles, but it is their trophic interactions (who eats whom) that dictate connectivity of nutrients and energy (i.e. food) through a food web and, potentially, across ecosystem boundaries. Food web connectivity (as we apply the term in this chapter) increases when two or more ecosystems that are traditionally considered separately (e.g. aquatic and terrestrial) are linked via cross-system flows of energy and nutrients (Polis et al. 1997). Globally, about 1 billion people living in coastal communities depend on ocean fish and shellfish as a primary food source. Hence these terrestrial humans, via regular consumption of ocean-produced energy and nutrients, rely on original sources of primary food production in the ocean. In this example, ocean ecosystems are said to *subsidize* terrestrial ecosystems via the high degree of food web connectivity achieved by human fishing and eating behavior. In the Necklace Lakes basin, an adult frog may forage terrestrially and consume many flies that themselves consumed primarily the food produced by terrestrial plants. The frog's foraging success then allows her to lay 1,000 eggs, most of which get consumed within days by an introduced rainbow trout living in the lake along the edge of which the frog laid her eggs. Here, terrestrial production has subsidized the aquatic food web via trophic interactions among forest plants, flies, frogs, and fish.

10.3. Describing connectivity in river ecosystems

Rivers have a distinctive physical structure that has served to increase connectivity among human populations since pre-history. A glance at a regional map provides insight: a river's branching-linear appearance could lead one to mistake it for a series of roads (and the purpose of roads is to increase connectivity among human populations). The map also reveals that most cities lie on rivers, and rivers (like roads) typically link non-coastal cities (see Figure 10.1). This arrangement is of course no accident. Rivers not only provide essential consumable resources (food and water); they also greatly enhance trade and transport among human settlements.

The unique structural organization of river ecosystems into hierarchically branching networks is fundamentally the same worldwide wherever rivers occur, from rainforests to deserts and even in urbanized areas. The structure of smaller branches merging in pairs to form larger branches initiates with the tiniest up-

land streams and continues incrementally until a large river reaches an outlet. Hence, there is a physical continuity between a very large river and the multitude of smallest streams (“headwaters”) spidering across the uplands of the catchment feeding it. Conversely, small headwaters might be very near to one another on a landscape but not be connected hydrologically because they occur on opposite sides of a drainage divide (and therefore occupy different catchments). This unique structure of river ecosystems across landscapes has strong implications for connectivity via movement of organisms. Those organisms unable to leave the aquatic habitat (e.g. most fish) have no connectivity across catchment boundaries, while those organisms capable of terrestrial movement (e.g. amphibians) do not recognize such strict limitations on connectivity.

The branching network structure of river ecosystems is reminiscent of various biological transport systems within individual organisms (Lowe and Likens 2005). A common structural analogy is a tree, in which millions of tiny veins within thousands of leaves each are directly connected to a single large trunk. The circulatory and respiratory systems of humans are similarly arranged, with millions of tiny capillaries connected directly to one of the two largest veins feeding the heart (circulatory system) or millions of tiny alveoli within the lungs directly

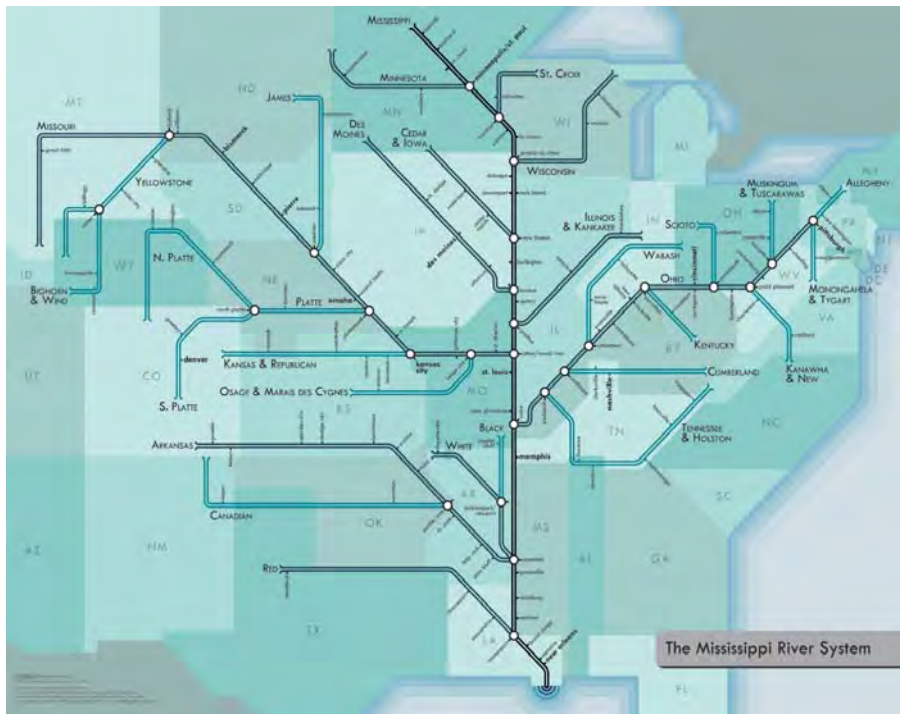


Figure 10.1: One of mapmaker Daniel Huffman’s “Rivermaps”, depicting the major drainages of the Mississippi River network. Huffman represents river networks as transportation corridors connecting cities, applying the style developed by Harry Beck in the 1930s for use in public transport maps (think London Underground). The style intentionally distorts the “true geography” to simplify and clarify connectivity

Figure 10.2:

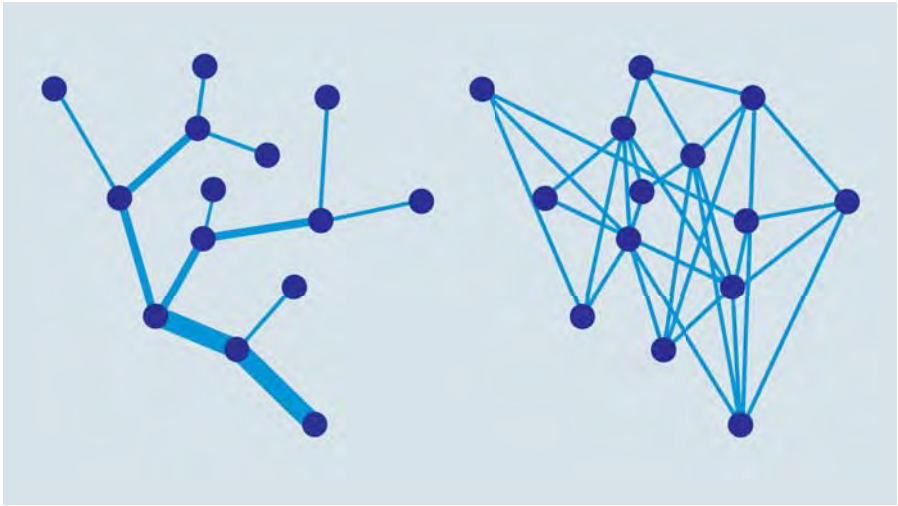
Conceptual diagrams to differentiate the terms “network” (left panel) and “web” (right panel), as they are used in this chapter.

Each panel contains the same number and orientation of nodes (dark blue circles).

Note two key differences:

1) Connectors linking nodes in a network are restricted to two upstream and one downstream, but the number of connectors linking nodes in a web are limited only by the abundance of other nodes.

2) For our purposes, sizes of connectors in a network are determined by their relative location, where those farthest upstream (e.g. headwaters in a river network) are smallest and have closest interaction with the surroundings. Sizes of connectors in a web follow no such restrictions



linked to the single, large trachea (respiratory system). In addition to the structural similarities among these network-like systems, there are functional analogies. Namely, in each of these examples, the most intimate interactions between the network and the surrounding environment occur within the smallest branches. Tiny veins in tree leaves drop off water molecules and pick up newly produced sugars from photosynthesis in the surrounding leaves. Tiny capillaries in the human circulatory system are the exchange sites for oxygen, carbon dioxide, and other nutrients and waste products with bodily organs and tissues. And the alveoli of the lungs are the sites of gas exchange (oxygen for carbon dioxide) with the blood. The small headwaters of river ecosystems also have a particularly intimate connection with the terrestrial landscape in which they are embedded, and strong terrestrial/aquatic interactions occur at these locations. Hence: connectivity between aquatic and terrestrial ecosystems is amplified in unimpacted headwaters.

For the remainder of this chapter, we will refer to the movement of organisms and nonliving materials of biological importance within and among river ecosystems as *network connectivity*, after the unique structural template of the river itself as a branching network strongly influencing the movement of organisms and materials. Food web connectivity in rivers we will shorten simply to “*web connectivity*”, to contrast structurally with network connectivity. A web structure, as in a food web, does not have the same branching, hierarchical restrictions as a network (Figure 10.2). One node in a food web, an invertebrate consumer in a small stream for example, can be connected to a multitude of other nodes in the web (e.g. it might be a generalist consumer connected to leaves, algae,

and moss, and it might be connected as prey to several large insects, a crayfish, three species of fish, and a few birds and bats). One node in a stream network, however, has a maximum of three connections: one downstream and two smaller upstream branches. We will see that both network and web connectivity are important to consider for river conservation.

10.4. Network connectivity

We must, in fact, not divorce the stream from its valley in our thoughts at any time. If we do, we lose touch with reality.

H.B. NOEL HYNES, 1975

10.4.1. MODELS OF ORGANISM MOVEMENT WITHIN AND AMONG RIVER NETWORKS

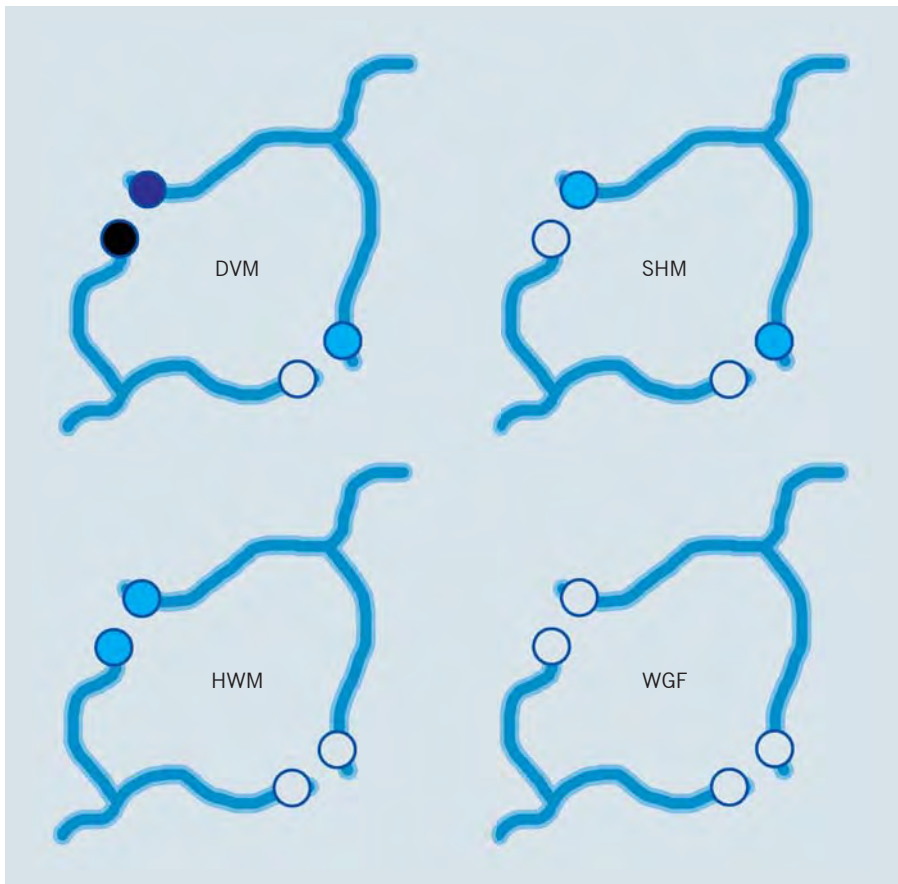
Recall that connectivity associated with organism movement is an interactive property of landscape structure and the movement-related traits of the organism in question. The Necklace Lakes example revealed different degrees of connectivity for amphibians *vs.* fish occupying the same structured landscape, because these two groups have different capacities for movement among lakes. When we move to consider connectivity across a much larger spatial extent, potentially including multiple independent river networks and a stream-size range from small upland headwaters to large outlet rivers, another factor to consider is the degree of habitat specialization of the focal organism.

Habitat specialization essentially describes the degree to which a species is restricted to a particular habitat type or, in rivers, a particular zone of a network. Suffice here to differentiate two major groups: *specialists* and *generalists*. The small headwaters at the myriad upper tips of networks harbor a great number of habitat specialists within river ecosystems. That is: many species are found only in headwater habitat. There could be multiple explanations for this pattern. One may be cold stenothermy (i.e. narrow temperature requirements on the low end of the thermometer). More generally: headwaters, tightly linked to the terrestrial ecology of the small basins they drain, provide unique habitat conditions that are also highly independent of one another, creating a mosaic of local habitat types even within a single river network. Examples include but are not limited to varying geological setting (e.g. granite *vs.* limestone), different water sources (e.g. groundwater *vs.* snowmelt), or different riparian conditions (forested *vs.* unforested) across headwaters in the same network. Streams occupying lower positions in the network blend the varied characteristics of the

multitude of smaller upstream segments and hence typically do not exhibit the degree of habitat uniqueness found in headwaters. It follows that a majority of habitat specialists in rivers are thought to occur in headwaters, and many of the species found in larger streams are more often habitat generalists.

Four models have been developed to describe connectivity within and among river networks according to an understanding of movement traits and habitat specialization of aquatic organisms (Figure 10.3) (Hughes et al. 2009; Meffe and Vrijenhoek 1988). Typically, a researcher makes a hypothesis about which of the four models might apply to a particular species, and the most common way to test the hypothesis is by collecting genetic samples from many individuals of the species, in several locations across multiple river networks. The genetic data represent some highly variable marker (or markers) in the genome, such that differences among individuals of the species are readily detectable. Sec-

Figure 10.3:
Conceptual diagrams of four different connectivity models, each applied to two simple networks that flow in opposite directions from headwaters originating in close proximity (e.g. same mountain range). Circles indicate locations of stream-dwelling animal populations; colors indicate similarity via presumed gene flow, such that populations of the same color experience the maximum connectivity. In order from left to right: Death Valley Model (DVM), stream hierarchy model (SHM), headwater model (HWM), widespread gene flow (WGF). See text for examples of each



tions of mitochondrial DNA have been probably the most commonly applied genetic markers to date for testing hypotheses about connectivity in rivers. Tests assess statistically how genetic differences are distributed across space, under the assumption that increased connectivity leads to increased genetic similarity among sampled locations – and vice-versa. *Gene flow* is a term analogous to connectivity indicating statistical evidence that genes are moving regularly from one location to another. Gene flow is a product of individuals physically moving and then successfully reproducing in the new location.

The first connectivity model, the *stream hierarchy model* (SHM) describes high connectivity internally within river networks from headwaters to large rivers and low connectivity from one network to the next. The SHM is the most intuitive of the movement models in rivers because the stream network itself is the major movement corridor, and organisms are presumed to be habitat generalists within the network. Hence, for species that follow the SHM, connectivity is higher within than among networks. The “hierarchy” in the SHM refers to the hierarchical structure the model can take, analogous to the hierarchical structure of stream networks: subnetworks within larger networks have increased internal connectivity. Animal species that typically follow the SHM are those having little or no ability to leave the aquatic environment – but also those that are not strict habitat specialists (e.g. in headwaters). These include many species of fish, as well as many invertebrates that have little possibility for terrestrial movement (e.g. mussels, aquatic insects lacking a terrestrial adult).

The second model is termed the *headwater model* (HWM). Fundamentally the inverse of the SHM, the HWM is expected for stream-dwelling species that are habitat specialists in headwaters and have some capacity for overland movement, typically by crawling or limited flying – e.g. amphibians, many crayfish, some aquatic insects. The HWM predicts that connectivity will be strongest among groups of nearby headwaters; i.e. those that are “crawling distance” apart, regardless of hydrologic connectivity. Such spatial clumping of headwater streams typically occurs in topographically complex landscapes, particularly when multiple island-like mountains, mountain ranges, or other uplifts in a region are separated by lower-elevation “seas” representing a different habitat type. The Madrean Sky Islands are a series of small mountain ranges rising above a sea of low desert in southern Arizona, USA and northern Sonora, Mexico that provide a compelling case of the HWM for both a stream insect predator, the giant water bug *Abedus herberti* (Finn et al. 2007), and the canyon treefrog *Hyla arenicolor* (Barber 1999). Headwaters and larger, lowland streams, exhibit strong habitat disparity in this region, as many headwaters have permanent surface water, and the lowland desert streams are intermittent. Although a group of headwaters originating on a single mountain range could occupy multiple independent

river networks (and headwaters from multiple mountains can occupy the same network), connectivity for both bug and frog is much stronger among headwaters sharing a mountain than among those sharing a network. To put this pattern in perspective: *A. herberti* mountain-range populations differ genetically from one another by up to 2% across this small region. The average genetic difference of two humans, randomly selected from the entire world, is approximately 0.4% (both estimated from mitochondrial DNA). Clearly, connectivity is quite low for *A. herberti* among mountain ranges. There are several other headwater specialists in the Madrean Sky Islands for which connectivity has yet to be assessed, but it is likely that the HWM holds for many of these as well.

The final two models represent opposite endpoints, between extremely low (the *Death Valley Model*, DVM) and extremely high connectivity (*widespread gene flow*, WGF). The DVM is an appropriate metaphor that implies aquatic habitats that are completely isolated from one another, no matter the landscape or river-network structure (e.g. headwater springs in Death Valley, USA). The DVM essentially represents an extreme of the HWM, suitable for cases when headwaters are isolated from one another to the extent that only very rare or zero among-site movement is possible. This situation could arise in one of two ways. First, the species in question, e.g. fish, have no ability to move from one aquatic habitat to another. This is the situation for the DVM's namesake, small fish occupying Death Valley springs with no surface water connection. Second, the focal species has a limited capacity to move among habitats, but the landscape surrounding the aquatic habitat is either too extensive or too inhospitable to allow successful overland movement. An example here is a rare, non-biting black fly (*Metacnephia coloradensis*) occupying the lake outlet streams of only very large, high-altitude lakes in the Rocky Mountains – the adult stage has limited capacity to fly, required habitats are rare, and the landscape separating them is treacherous, so connectivity among the few populations of this species is thought to be effectively zero.

Widespread gene flow occupies the opposite end of the connectivity spectrum and is expected for species having either a highly mobile terrestrial stage or traits allowing passive dispersal by either wind or temporary association with mobile animals such as water birds (Figuerola and Green 2002; Maguire 1963). Charles Darwin performed classic early studies demonstrating both the diversity of plant seeds embedded in the mud on a duck's legs and the association of some otherwise sedentary invertebrates (even as large as snails) with the legs of water birds. Such examples are more common than one might expect, and they often account for observed patterns of widespread gene flow in aquatic organisms that lack the ability to disperse among catchments under their own power. Conversely, many caddisflies (Trichoptera) are strong fliers that can

disperse long distances by themselves. An example is *Plectrocnemia conspersa*, a common caddisfly occupying upland streams in northern Europe (Wilcock et al. 2001). Although this species is a habitat specialist in small headwaters, connectivity is strong across most of its extensive range. As we hinted earlier, however, the structure of the intervening terrestrial landscape can strongly influence connectivity, even for flying aquatic insects. An eastern North American mayfly (*Ephemerella invaria*) is not a particularly picky habitat specialist, and given a forested terrestrial landscape (which provides an ideal environment for overland flight of many insects), widespread gene flow is expected. However, deforestation to the extent of leaving intact forest only along riparian buffer zones has reduced connectivity in recent years to the stream corridors, effectively changing the connectivity model for *E. invaria* to some combination of SHM + HWM (Alexander et al. 2011). Changing land use within drainage basins therefore is an important consideration regarding network connectivity in river ecosystems.

10.4.2. TEMPORAL “PULSES” AND THREE SPATIAL DIMENSIONS OF CONNECTIVITY WITHIN NETWORKS

Naturally, river habitat is defined by the spatial distribution of flowing water, the essential “ingredient” in river ecosystems. The presence of flowing water allows us to delineate where riverine and terrestrial habitats begin and end, and it strongly influences connectivity of both organisms and biologically important nonliving materials. But what if a river has no surface water? Or if flow has ceased, resulting in only a few separated pools of standing water along the streambed? Intermittent streams and rivers contain flowing surface water only during certain parts of the year, and some ephemeral streams flow only when it rains. A key to understanding such systems is to appreciate that nearly all river ecosystems undergo natural flow “pulses” similar to the pulsing of blood through the circulatory system (Junk et al. 1989; Poff et al. 1997).

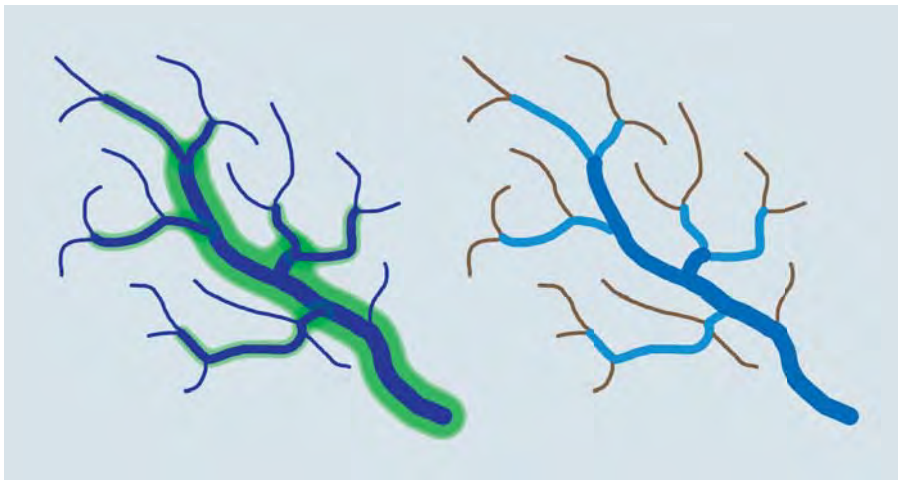
The “heart” controlling pulses in rivers is the annual cycle of precipitation and/or snow- or ice-melt characteristic of a region. Rivers and streams – whether perennial, intermittent or ephemeral – expand and contract in size with this temporal cycle (Chapter 2). Hence, streams that have temporarily lost surface flow (but nonetheless nearly always contain groundwater not far below the surface) are simply in-between pulses, when aquatic habitat is contracted to a minimum volume. The pulse in rivers (compared to our circulatory system) may or may not be highly predictable through time. Rivers fed by mountain snowmelt, for example, have predictable pulses in late spring when rapid melting occurs. Conversely, some desert and prairie streams are considered “flashy”, flooding unpredictably with chance rainstorms. Either way, pulses not only increase

the volume of liquid water, they also increase connectivity in three key spatial dimensions of river ecosystems: *longitudinal* (i.e. upstream-downstream), *vertical* (between groundwater and surface water), and *lateral* (between riparian/floodplain habitat and the main stream) (Figure 10.4) (Ward 1989). In the prior section, we focused on connectivity via organism movement patterns across large spatial extents, including multiple river networks and the landscapes that contain them. Here, we emphasize single networks and the importance of flow pulses to connectivity in the longitudinal, vertical, and lateral dimensions.

Longitudinal connectivity. When a pulse returns surface flow to an intermittent stream, hydrologic connectivity between headwaters and larger rivers is reestablished. Some stream-dwelling animals with a terrestrial stage (e.g. many insects) will disperse longitudinally along streams lacking permanent surface flow, and some very small organisms and dissolved materials can move longitudinally through groundwater under the streambed – but a surface water connection substantially amplifies longitudinal connectivity and is clearly necessary for movement of larger aquatic organisms (like fish) and nonliving materials (like leaves and other organic debris). The stream hierarchy model (above) also assumes the potential for relatively unrestricted movement through surface waters in both upstream-to-downstream and downstream-to-upstream directions. There is substantial evidence that several fish species move upstream to spawn in intermittent headwaters, where the porous cobble streambeds that provide ideal substrate for constructing nests ironically also are more likely to lose surface flow during dry periods. Coho salmon in the US Pacific Northwest often spawn in such streams. Juveniles remain and rear in isolated standing pools during periods when surface flow disappears, then they follow the network

Figure 10.4:

Two extremes of the flow pulse in a conceptual river network: a pulse of high flow (flood) on the left, and low-flow (drought) conditions in-between pulses on the right. Blue/brown shading in channel indicates degree of surface flow (maximum = darker blue; minimum = brown, no surface flow), and green indicates extent of lateral and vertical connectivity via inundation of floodplains and hyporheic zone



downstream to the sea during a subsequent flow pulse (Wigington et al. 2006). Coho, an anadromous species that spends most of its adult life in the ocean, illustrate clearly the importance of longitudinal connectivity in river networks. All salmon rely on connected waterways to move between the ocean and spawning habitats in small streams.

Longitudinal connectivity is also important with regard to transport of food materials (i.e. energy in the form of suspended and dissolved organic material, and nutrients) downstream from headwaters to larger rivers. Headwaters, acting as the capillaries of river networks, readily interact with the terrestrial environment in which they are embedded, and these interactions can have far-reaching effects at significant distances downstream. In many headwaters, more organic material enters the stream from the surrounding catchment than is consumed. Conversely, in larger rivers little organic material enters directly from the terrestrial environment, but there are typically more consumers. Hence, organic material transported longitudinally in various forms can supply essential energy sources to downstream food webs. Headwaters also appear to play a significant role in moderating water quality throughout river networks (Naiman et al. 1987). A study of a number of prairie streams of different sizes in Kansas, USA revealed that the best predictor of water quality (particularly nutrient load in this highly agricultural region) was riparian land cover associated with the smallest headwaters – no matter their longitudinal distance upstream (Dodds and Oakes 2007). That is: the condition of the riparian zone adjacent to headwater streams has far-reaching downstream effects on water quality.

Vertical connectivity. Groundwater is often overlooked as part of freshwater ecosystems for the simple reason that we can't see it. However, the *hyporheic* zone (literally “below the flow”, but often extending laterally some distance away from the stream channel) of streams and rivers is essential both as habitat for organisms and as a location for processing nutrients and organic material exchanged with the surface-water environment. Hence, vertical connectivity plays a key role in river ecosystems. Aquatic animals that are small or resourceful enough to travel the “interstitial highway” of contiguous aquatic habitat surrounding cobbles, gravel, and even sand of the hyporheic zone do so for different reasons. Some animals that are typically members of the surface-water community may use the hyporheic zone as a temporary refuge, either during particularly strong flow pulses (floods) or during droughts in intermittent streams. In streams with predictable pulse timing, the development rates of some invertebrates are timed such that they are still at a small enough stage of development to occupy the groundwater habitat when it is useful as a refuge. Other hyporheic occupants may specialize on this habitat and spend all or the majority of their life cycles there. Crustacean *meiofauna* (loosely defined: larger than microscopic but small

enough to pass through a 1mm mesh), which lack a terrestrial phase, are common examples (e.g. amphipods, copepods). However, there are also remarkable examples of long-term hyporheic macrofauna, many of which are burrowers that make a living in sandy hyporheos. The caddisfly *Pedomoecus sierra* achieved some notoriety at desert springs of the Great Basin (US) because researchers commonly collected the terrestrial adults and yet could rarely find the larvae in collections from the springs themselves (Myers 2011). Finally the researchers discovered that *P. sierra*'s entire larval (and pupal) life is spent burrowed within hyporheic sand. It appears to specialize on eating microbial growth attached to the sand grains. Stiff hairs and spines on the larvae both assist burrowing and prevent sand grains from entering the rock case.

Microbial growth is ubiquitous in hyporheic and groundwater habitats. Microbes can thrive in the interstices and in the absence of sunlight given a reliable source of dissolved organic material, which typically is supplied by the surface water. Nutrients, conversely, tend to be more concentrated in groundwater than surface water, and in locations where "upwelling" (net flow from groundwater to stream channel) occurs, streambed algae often grow rather densely (Boulton et al. 1998). However, nutrient dynamics at the surface/groundwater boundary are complex and typically quite situation-specific. Colonies of nesting birds occupying small catchments, for example, can drastically inflate nutrient concentrations in the groundwater, and, ultimately, the stream. Alternatively, high densities of spawning salmon can result in nitrogen flow from streams, where the fish spawn and eventually die, to the connected groundwater. Nutrient flow in this direction can supplement primary production, including tree growth, in the adjacent riparian zone (Chapter 4).

Lateral connectivity. During a flow pulse, the increased volume of water often exceeds the bounds of the river channel and inundates riparian habitat. The extent of this lateral inundation of what is known as the *floodplain* depends on the magnitude of the pulse and the degree to which the river is constrained (e.g. canyon sections of rivers have little leeway for lateral expansion). Inundated floodplains in their natural state can be quite extensive and complex, typically comprising a mosaic of surface-water habitats, from small standing pools to large braided channels that only flow during floods. This complexity combined with the lateral connectivity achieved between main channel and floodplain during flow pulses greatly enhances biological diversity and productivity of river ecosystems.

Major biological implications of lateral connectivity vary according to timing with respect to the flow pulse (Junk et al. 1989). Much directed movement from river channel to floodplain occurs on the approach to and during the peak stages of the pulse, when river-borne nutrients get deposited on the flood-

plain, and many stream-dwelling animals move laterally to use the more benign aquatic conditions of the floodplain as a refuge from high flows. A variety of insects adapted to conditions in regularly flooding streams actually extend the concept of lateral connectivity beyond the floodplain and well into the terrestrial landscape when they use heavy rainfall as a cue to crawl away from the stream and into the uplands in anticipation of the flood pulse (Lytle and White 2007). Closely following the peak of the pulse, newly deposited nutrients stimulate production in wetted floodplain habitats, terrestrially derived organic materials on the floodplain become available as food resources to the aquatic ecosystem, and many animals remain to take advantage of the rich environment and use the aquatic habitat for spawning and rearing of young. The intense biological activity in the floodplain generates organic material and nutrients that can then be transferred laterally to the main river channel. In rivers with intact floodplains, lateral supplements of organic material to the stream channel following a flow pulse can substantially exceed longitudinal supplements from the headwaters. Like headwaters, the mosaic of smaller aquatic habitats on the floodplain interacts closely with the surrounding terrestrial environment, essentially playing the same “capillary”-like role as headwaters but in a location directly connected to potentially very large rivers. Lateral connectivity can therefore have a strong influence on river ecosystem functioning .

10.5. Web connectivity

Food is the continuum in the song of the [Río] Gavilán. I mean, of course, not only your food, but food for the oak which feeds the buck who feeds the cougar who dies under an oak and goes back into acorns for his erstwhile prey. This is one of many food cycles starting from and returning to oaks, for the oak also feeds the jay who feeds the goshawk who named your river; the bear whose grease made your gravy, the quail who taught you a lesson in botany, and the turkey who daily gives you the slip. And the common end of all is to help the headwater trickles of the Gavilán split one more grain of soil off the broad hulk of the Sierra Madre to make another oak.

ALDO LEOPOLD, 1949

“Song of Gavilan”, in Part II of *A Sand County Almanac*

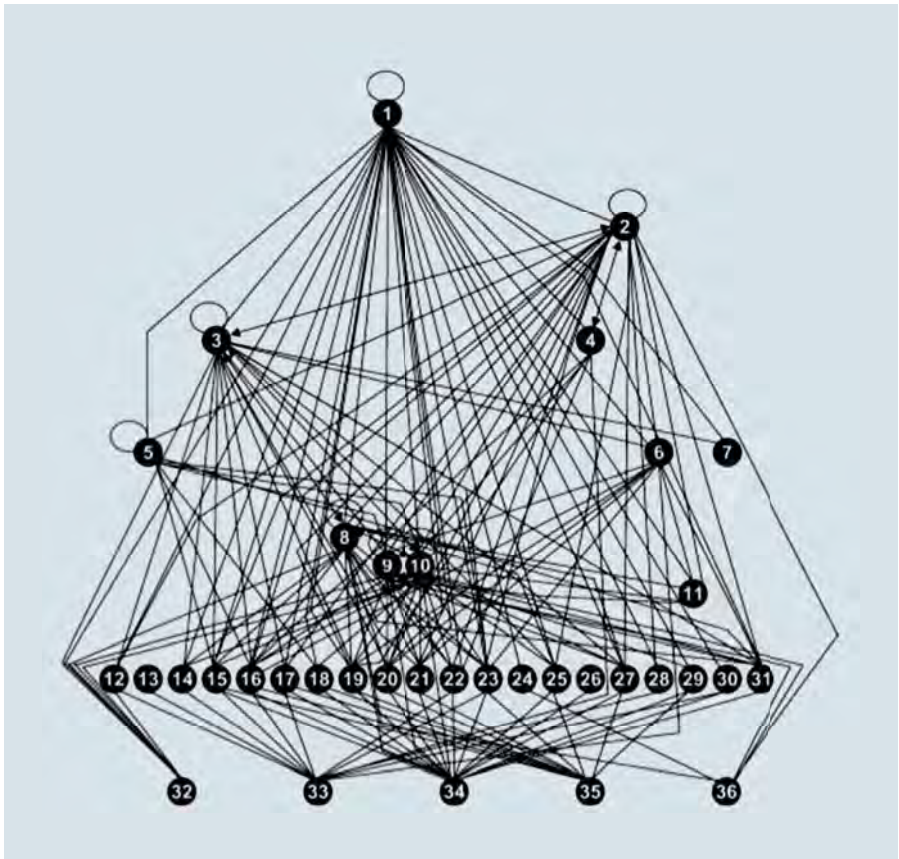
10.5.1. RIVER FOOD WEBS

The nutrients and organic material that move among river networks and within their three spatial dimensions form the basis of river food webs. Primary producers such as plants and algae take up essential nutrients like nitrogen and phosphorous in dissolved, molecular forms and “fix” inorganic carbon sources

(primarily carbon dioxide from the atmosphere or dissolved in the water) into energy-containing molecules. The combination of nutrients and energy-rich carbon-based molecules in aquatic primary producers and dead organic material then provide the basal food resources for all consumers in river food webs. When a consumer feeds on one of these basal resources or on another consumer (predation), nutrients and carbon effectively move from one node of the web to another. Even food webs in the smallest streams can be quite complex, with pathways connecting basal food resources to multiple levels of consumers and predators in myriad potential configurations (Figure 10.5).

Researchers can trace the connectivity of nutrients and carbon between nodes in a food web with a number of different approaches. Most simply, one can observe the eating habits of animal consumers. This approach is most feasible for larger river-dwelling animals; particularly fish. Fish biologists often don a mask and snorkel to observe eating behavior, and fly-fishing can be a never-ending

Figure 10.5:
A diagram of the food web in Broadstone Stream, a small chalk stream in England. Each black circle is a species or group of similar species; vertical position of black circles indicates trophic position, with primary producers at the bottom, primary consumers second, and so on until the "top" predator; connector lines connect "who eats whom"



experiment testing which prey items different fish species are choosing to eat at particular times of the year. Another direct approach to evaluate diet is by looking at what consumers have already eaten (i.e. what is in the gut). For smaller consumers, like invertebrates, this typically involves completely removing and opening the gut cavity. For larger consumers, gut contents can be evaluated non-lethally, often by the process of “gastric lavage” (literally “stomach washing”), which forces water into and then out of the stomach to flush out its contents. However, because many of the nodes of a stream food web represent very small-bodied animals, and in some cases it is impossible to determine food items (e.g. the “true bugs”, Hemiptera, liquefy prey prior to sucking it through a straw-like mouth appendage), supplementary approaches are often necessary.

One common indirect approach to evaluating who is eating whom in a stream is by referring to a published list of known “functional feeding groups” (FFGs, e.g. Merritt and Cummins 1996) for stream-dwelling invertebrates. These FFG lists allow a researcher to assign to a consumer species the most probable of the important food resources available (e.g. algae growing on the streambed; large organic material, like leaves, from the terrestrial environment; fine bits of organic material suspended in the water column; living animal prey). Typically FFG lists are based on previous research, but they might also be inferred from other aspects of the species’ biology, such as the structure of its mouthparts, its behavior, or how closely related it is evolutionarily to another species for which the FFG is better understood. FFG lists are helpful in determining river food web structure, but a key drawback is that many aquatic invertebrates have a more generalist (i.e., omnivorous) diet than we often would like to admit. For example, it is clear that any animal that makes a living filtering small particles from the flow with either a constructed silk net (some caddisflies) or specialized appendages (black flies, many others) is eating fine bits of organic material. But this filter-feeder also could be undiscerning to the degree that it will eat small animals that have become detached from the streambed and drift into the filter apparatus, as is the case with some black fly larvae that have been observed to eat small, drifting midges. This example is one of many that reveals the truly omnivorous feeding nature of many stream-dwelling invertebrates.

Another indirect option for tracing the pathways of nutrients and carbon through river food webs is by evaluating chemical aspects of the elements themselves. An element’s isotopes vary in size (mass) by a minute degree that can be detected with an instrument called a mass spectrometer. Of particular relevance to river food webs are isotopes of nitrogen (N) and carbon (C). Proportions of heavier to lighter N isotopes in an organism provide a measure of how predatory that organism is. With each “step” in a food chain, from primary producer

Web connectivity links river ecosystems to other major ecosystem types (terrestrial, marine) via cross-boundary transfers of nutrients and energy through food webs

to consumer to potentially multiple predator levels, the ratio of heavy to light N isotopes increases at a predictable rate. Hence, ratios of N isotopes could allow us to separate filter-feeders, as above, that often consume animal prey from those that only consume fine organic material. Proportions of heavier to lighter C in an organism can give an idea of whether its basal food resources were mainly of terrestrial or aquatic origin, as primary production in these two environments results in different ratios of C isotopes. Evaluating C and N isotope ratios in concert therefore provides an opportunity to disentangle to some extent the diets of generalist consumers in river food webs. Carbon isotopes also can help evaluate web connectivity between terrestrial and aquatic food webs; i.e. to what extent one ecosystem subsidizes the other.

10.5.2. AQUATIC/TERRRESTRIAL WEB CONNECTIVITY

Ecologists have long recognized the importance of terrestrial subsidies to river food webs, and headwater streams embedded in forested basins are the prime archetype (Wallace et al. 1999). Especially during autumn leaf-fall, such streams become choked with leaves and other organic material, a massive food supply for primary consumers living in these streams and, sequentially, their predators. Many smaller bits of organic material move longitudinally from headwaters with downstream flow and can supplement food webs of larger streams that may have less local input of organic material (Vannote et al. 1980). Connectivity to floodplains along larger rivers of the network also can supply substantial amounts of terrestrially derived organic material to fuel aquatic food webs.

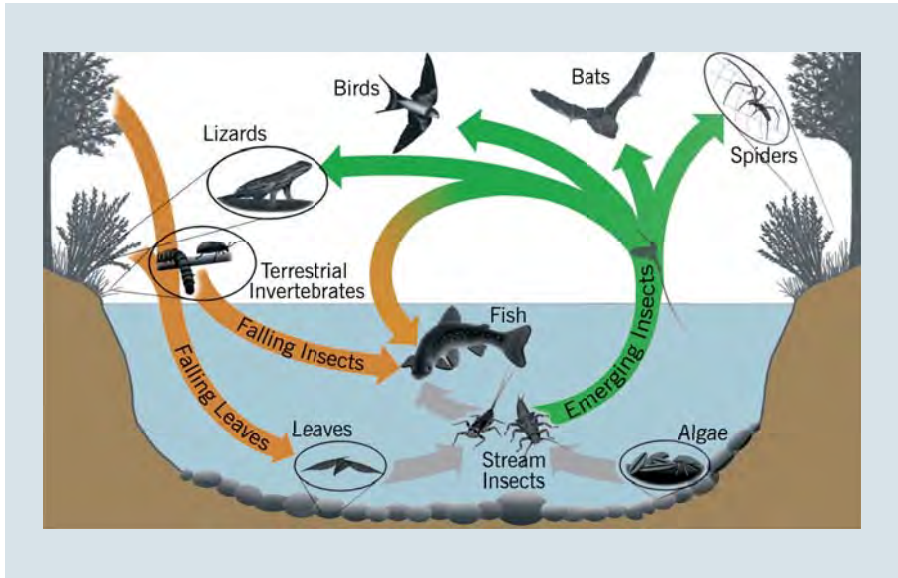
Although forested headwaters are the model of heavy terrestrial subsidization of river food webs, researchers now recognize a strong signal of terrestrial primary production even in many treeless headwaters (e.g. in arctic or alpine tundra). This terrestrial signal (determined by carbon isotope ratios in consumers) increases further in streams with proportionally more wetlands in their catchments. Wetlands contribute substantial dissolved organic material (primarily of terrestrial origin) to streams, so it is likely that these stream food webs are heavily reliant on microscopic fungi and bacteria (together: microbes) that decompose dissolved organic material, using it as a source of food energy (Dekar et al. 2012). With increasing rates of decomposition, microbes increase in biomass and grow in films attached to streambed rocks, leaves, and other substrates, creating a favored food item for many invertebrate primary consumers.

Beyond the major role that terrestrial production plays in subsidizing many river food webs, aquatic primary production is also an important and nutritious basal food resource. Given some light, carbon dioxide, and water, there will be algae – the main primary producers within stream ecosystems. One of the

key invertebrate FFGs is the *scraper*, which obtains the majority of food energy by scraping algal growth from the surfaces of rocks. Scrapers include several species of mayflies, caddisflies, and true flies. Snails and some fish species also specialize on eating algae. These are integral components of river food webs which are themselves food items for various aquatic predators. These and other stream-rearing insects eventually emerge as flying adults, and although some of these return their carbon and nutrients to the aquatic ecosystem (e.g. as prey for fish, or by laying eggs into and then returning as dead organic material to the stream), the preponderance of emerging insects never return. Instead, they help fuel the terrestrial ecosystem. A number of terrestrial predators – including spiders, ground beetles, lizards, birds, and bats – organize their lifestyles and particularly their feeding strategies to take full advantage of emerging aquatic insects, and some birds (e.g. dippers, herons) feed almost exclusively on prey derived directly from the aquatic habitat, including fish. A guild of terrestrial invertebrate predators occupies riparian zones and feeds primarily on newly emerged insects still crawling across the aquatic/terrestrial ecotone. Bats will time dusk flights to coincide with heightened aquatic insect flight activity over stream corridors. And perhaps most eloquently: web diameter of some sheet weaver spiders (Linyphiidae) increases substantially with distance from the streambank. These spiders require only a very small web to be efficient at trapping the easy and abundant prey closest to the stream, but must weave a very large web to be fruitful at a distance. These and many other examples of the reliance of terrestrial predators on stream-derived prey have helped ecologists make a strong case over the past decade for the importance of aquatic subsidies to terrestrial food webs (e.g. Sabo and Power 2002).

Clearly, web connectivity across the terrestrial/aquatic ecotone has the potential to provide subsidies not only from more expansive terrestrial ecosystems to stream food webs, but also in the opposite direction (Figure 10.6). These so-called *reciprocal subsidies* are the norm in relatively unimpacted river ecosystems. The late ecologist Shigeru Nakano and his colleagues performed a series of powerful, classic studies of reciprocal subsidies of invertebrate prey to predators across the aquatic/terrestrial ecosystem boundary at a stream in Hokkaido, Japan. In one study (Nakano and Murakami 2001), these researchers showed that peak aquatic vs. terrestrial insect abundance varied temporally such that prey of stream origin subsidized terrestrial predators (primarily birds) substantially in spring, when terrestrial prey was in low abundance, and terrestrial prey subsidized stream predators (fish) primarily in summer, when aquatic invertebrate abundance reached a minimum. This bidirectional web connectivity therefore annually supported greater abundance of both aquatic and terrestrial predators than either ecosystem could support alone. In other studies, Nakano and colleagues experimentally tested the effect of severing web connectivity by erecting

Figure 10.6:
Reciprocal subsidies.
 In streams, food web connectivity occurs in both directions: from terrestrial to aquatic ecosystems (trophic interactions shaded orange), and vice-versa (trophic interactions shaded green)



a lengthy greenhouse-like structure of fine mesh directly over the stream (Figure 10.7) (e.g. Nakano et al. 1999; Baxter et al. 2004). The structure prevented most of the prey flux between the two ecosystems, with significant ecological effects in both, including altered feeding behavior and decreased growth rates of predators. Reciprocal subsidies between terrestrial and river ecosystems likely play a key role in overall ecosystem functioning in many river basins of the world. Unfortunately, many human activities, including those as disparate as channelization for flood control and introducing non-native sport fishes, can effectively sever aquatic/terrestrial connectivity – almost acting as a metaphorical *greenhouse* preventing reciprocal subsidies. We discuss several anthropogenic effects on connectivity below.

10.5.3. MARINE/FRESHWATER WEB CONNECTIVITY

People commonly perceive rivers as one-way conduits moving materials from continents to oceans. An idea of streams as convenient sewage pipes of sorts led to a drastic increase in water pollution and associated environmental degradation during and following the industrial revolution. Currently, popular news stories about, for example, dead zones in near-shore marine ecosystems bolster the public's view of rivers as downstream conduits – and with good reason. Many marine dead zones are on the receiving end of rivers laden with excess nutrients (nitrogen and phosphorus in particular – often from agricultural activity in the catchments), and they reflect web connectivity between river and marine

ecosystems. Excess river-transported nutrients that become available to marine food webs feed massive algal growth. Although algae produce oxygen in the presence of sunlight, they must respire it at night; so excessive algal biomass can result in the severe oxygen depletion characteristic of dead zones.

However, despite common perception of upstream-to-downstream unidirectionality of movement in rivers, marine ecosystems can also subsidize freshwaters via web connectivity in the opposite direction. A diversity of fauna worldwide is diadromous – a general term that describes animals that migrate at some point in the life cycle between marine and freshwater environments. Diadromous species include both fish (e.g. salmon, sturgeon, eel) and invertebrates (e.g. some crabs, shrimps, and snails). Longitudinal connectivity in river networks is required for these species to migrate, and a successful migration from ocean to upstream habitat results in movement of marine-derived nutrients and carbon between the two ecosystems. This transport of materials is of particular relevance in streams when it arrives via large-bodied anadromous species, like salmon. Anadromous species (a subset of diadromous) spend



Figure 10.7:
Nakano's "greenhouse" that severed lateral connectivity between stream and riparian forest

most of their lives at sea where they feed and grow to maturity, then they return to fresh water to spawn. Spawning directly precedes death, which leaves carcasses – dense packages of nutrients and organic material, for all practical purposes – in and along stream channels and available to enter stream and terrestrial food webs via a number of pathways. In streams with strong spawning runs of salmon, researchers have shown that marine-derived nutrients can be found in nearly every node of stream and riparian food webs, from algae and microbes to predators and even to riparian plants and terrestrial consumers. Carbon and nutrients originating from the ocean and delivered in salmon carcasses subsidize stream food webs via direct consumption by animals, decomposition by fungal and bacterial microbes, and uptake of leached nutrients by primary producers. The additional nutrients and food energy that spawning salmon provide to stream food webs promote increased growth and reproduction of both producers and consumers compared to streams without spawning runs (Naiman et al. 2002).

10.6. Sustaining rivers as networks of webs: Conservation challenges

The term riverine landscape implies a holistic geomorphic perspective of the extensive interconnected series of biotopes and environmental gradients that, with their biotic communities, constitute fluvial systems.

J.V. WARD, 1998

The river is everywhere

HERMAN HESSE (SIDDHARTHA)

10.6.1. RIVERS AS NETWORKS OF WEBS

A synthesis that we have been converging upon is that river ecosystems in their natural state are fundamentally complex *networks of webs*. The example in the preceding section of salmon connecting marine and stream food webs via longitudinal connectivity in river networks reminds us that in fact these two concepts of connectivity are inextricably intertwined. *If there is no network connectivity, there can be no web connectivity.* In all river networks, dynamic webs of trophic connectivity take various forms in different localities along the longitudinal gradient from the myriad headwaters to main stem. Some webs (such as those linking marine and stream ecosystems through diadromous species) occupy a great deal of space and require extensive network connectivity in the

longitudinal dimension to achieve trophic [web] connectivity. Other webs may be localized to a particular region of the network or may primarily depend on network connectivity in lateral or vertical – rather than longitudinal – dimensions. For example, aquatic/terrestrial web connectivity might be focused along a very short stream reach where ground beetles and wolf spiders patrol a small gravel bar, feasting on newly emerged stream insects. Alternatively, web connectivity can span multiple drainage basins, as when strong-flying caddisflies emerge in large numbers and disperse laterally, providing prey for forest birds far from the stream. The “riverine landscape” of J.V. Ward (quote above) embodies the concept of rivers as complex networks of webs, relying on connectivity in multiple dimensions and directions. More simply, as we read in *Siddhartha*, “the river is everywhere”. A river is much more than a conduit from land to sea (Figure 10.8).

10.6.2. ANTHROPOGENIC IMPACTS ON CONNECTIVITY

Rivers are essential to commerce, agriculture, transportation, and most other human enterprises – which causes immense pressure on river ecosystems, in-

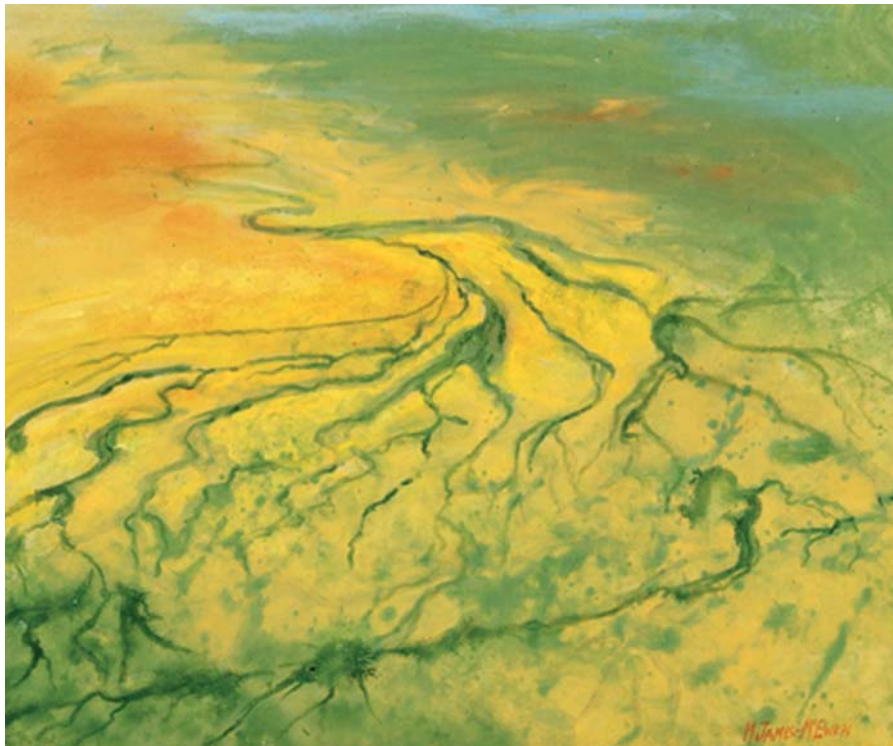


Figure 10.8: Green Fingers Across the Land, a painting by Helen McEwen captures the idea of a desert river as a network of webs: the visible network structure (green) is emphasized by the lateral and aquatic/terrestrial web connectivity that results in riparian trees and other vegetation thriving along the riparian corridor

cluding significant effects on network and web connectivity. Probably the most intuitive and frequently cited examples are dams. Even dams with fish ladders (which have variable success) or some other means to transport animals artificially around the structure disrupt longitudinal connectivity by altering the natural habitat gradient in a variety of ways; e.g. by creating a lengthy section of deep standing water (the reservoir) and impeding the downstream movement of nutrients and organic material (Ward and Stanford 1983). Dams also block the transport of sediments, resulting in profound effects on downstream habitat characteristics (Chapter 3). One function of many dams is to capture and store peak flows to avert downstream flooding. This thwarting of the annual flow pulse(s) decreases both lateral connectivity with floodplains and vertical connectivity with the hyporheic zone. Other dams act specifically to move water from the channel into ditches, canals, tunnels, or pipes for sometimes extensive transport to provide for irrigation or consumptive use in areas that do not themselves have a sufficient water supply for these purposes. These diversion dams often result in at least intermittent drying of downstream river sections, with clear negative impacts on connectivity in all three spatial dimensions. The assisted movement of water from one river network to the next, however, also creates an artificial *increase* in connectivity and can homogenize once-distinct populations and communities of strictly aquatic animals (Olden et al. 2004). This can result both from inter-basin transfers of water through canals and from long-distance transfer of water and organisms in the ballast water of ships, a major pathway for arrival of invasive aquatic colonists (Chapter 8).

Badly designed culverts under roads are another common disruption to longitudinal connectivity in smaller streams. Interestingly, stream sections upstream of perched culverts often contain fragments of native fish populations in regions where invasive species have been introduced in downstream reservoirs and larger rivers and spread throughout much of the network. The upstream-impassable culverts therefore represent the last bastions against invaders in many cases, leading to the perplexing management decision to leave the culverts unrestored in the interest of protecting these relict native populations.

Another pervasive engineering strategy in rivers is channelization, which typically involves straightening the course and installing riprap, levees, or even encasing the channel in concrete (e.g. the notorious Los Angeles River) in an attempt to prevent flooding in populated or agricultural areas (and sometimes to improve boat transport). Channelized rivers in general are almost completely disconnected in the lateral dimension, and concrete-lined rivers clearly also have zero vertical connectivity. The ecological effects of most channelized rivers can be anticipated from Nakano's *greenhouse* experiment that severed aquatic/terrestrial web connectivity, resulting in decreased productivity in both aquatic

and terrestrial ecosystems. Furthermore, channelized rivers are disconnected from their floodplains, which historically would have provided nursery habitat and refuge from fast flows for aquatic animals, and highly productive riparian zones. The effects are large declines in aquatic and riparian biodiversity.

Changing terrestrial land use also affects both network and web connectivity in rivers. An extreme example is the practice of mountaintop removal coal mining, which literally removes mountain peaks or entire ridges to expose coal seams. The massive amounts of debris often get deposited in high valleys, resulting in burial of headwater streams and a total loss of connectivity of these important, capillary-like systems to terrestrial food webs and to the rest of the river network (Palmer et al. 2010). With any change in land use in a basin, even those less acute than mountaintop removal, it is important to consider both the impacts on cross-network connectivity via organism movement (e.g. the widespread mayflies now restricted to dispersal within riparian forest buffers, as above) and potential impacts of the changing terrestrial food web on local aquatic/terrestrial web connectivity (e.g. loss of riparian trees can lead to significant reductions in food web subsidies to the stream, both as leaves and prey items such as insects).

The burgeoning human population and our high demand for river-derived and other natural resources will continue to put pressure on river ecosystems and the connectivity necessary to sustain them. Reverting to near-pristine conditions is neither possible nor desirable. But there is hope for maintaining and/or restoring healthy levels of network and web connectivity hand-in-hand with river management for human needs. The final section of this chapter reflects on impacts, restoration, and continuing conservation goals in our home river network in western Oregon, USA, where we use various species of native fish as examples to illustrate connectivity issues in a densely populated river basin. Although a regional example, its real-world issues are representative of rivers everywhere, and we hope it will prompt readers to investigate connectivity in their own home networks.

10.6.3. CONNECTIVITY IN OUR RIVER: THE WILLAMETTE

*These tree trunks
These stream beds
Leave our bellies full*

PORTLAND, OREGON BAND THE DECEMBERISTS (*RISE TO ME*)

Dams and longitudinal connectivity

In the early days of human settlement in its fertile valley, the Willamette River provided the main north-south transportation corridor in western Oregon,

In anthropogenically modified river systems, restoration of web connectivity will often result indirectly from an emphasis on restoration of network connectivity

USA. The Willamette is a major tributary of the Columbia River, and their confluence is just downstream of Portland, the largest city both on the Willamette and in the state. The main stem of the river, extending 290 km from the city of Eugene (second largest in the state) north to the Columbia, is wide and low-gradient, with only a single natural barrier to longitudinal connectivity (for human transport as well as some migrating animals): Willamette falls in the lower river network (Figure 10.9). Although the largest waterfall in the Pacific Northwest (by volume), Willamette falls is only 12 meters in height, and its cascading nature historically allowed longitudinal connectivity for three key diadromous fish: winter-run steelhead (the sea-run form of rainbow trout, *Oncorhynchus mykiss*), spring-run Chinook salmon (*O. tshawytscha*), and Pacific lamprey (*Entosphenus tridentatus*). The steelhead and Chinook runs were limited to winter and spring because winter/spring rainfall and spring snowmelt feeding headwaters in the Cascade mountain range drives a predictable flow pulse in the Willamette during these seasons. The high-water pulse allowed the spring- and winter-run salmonids to leap upstream through the hydraulics of boulders associated with the falls. Populations and species of salmon with summer/fall run timing, such as coho (*O. kisutch*) could not access the upstream network because of the seasonal constriction of the flow pulse, which made the falls a barrier to upstream connectivity for salmon during these drier times of year. Pacific lamprey have a different approach to breaching the falls and could do so even during lower flows by using primitive, jawless, suckerlike mouths to climb up the steep rocks of the cascade. Although not well known in the fish market, these eel-shaped fish (often called *eels* colloquially) are an important staple and ceremonial food for local Native American tribes.

A hydropower plant was installed at Willamette falls in the late 1800s, including a low, weir-like dam just above the cascade and small reservoir (Figure 10.9) – to provide electricity for the growing city of Portland. In spite of the dam, fish ladders have allowed successful passage of salmon around the falls and dam for at least the full history of the power plant. Indeed, the fish ladders have been *successful* to the extent that summer- and fall-run species (e.g. coho) and populations that historically were not present in the upper Willamette are now able to bypass the falls (although still in fewer numbers than their spring/winter counterparts) (Figure 10.10). Lamprey, conversely, do not use the fish ladders successfully. Instead, they appear to *climb* the falls as per usual but then are stymied by the vertical concrete dam. Furthermore, in the years since the Willamette falls dam and fish ladder were installed, a series of large, impassable dams have been constructed on most major tributaries upstream in the network – rivers that mostly occupy higher-gradient basins in the mountains surrounding the Willamette valley. Hence, although salmon now can readily bypass Willamette falls in the lower network, a large

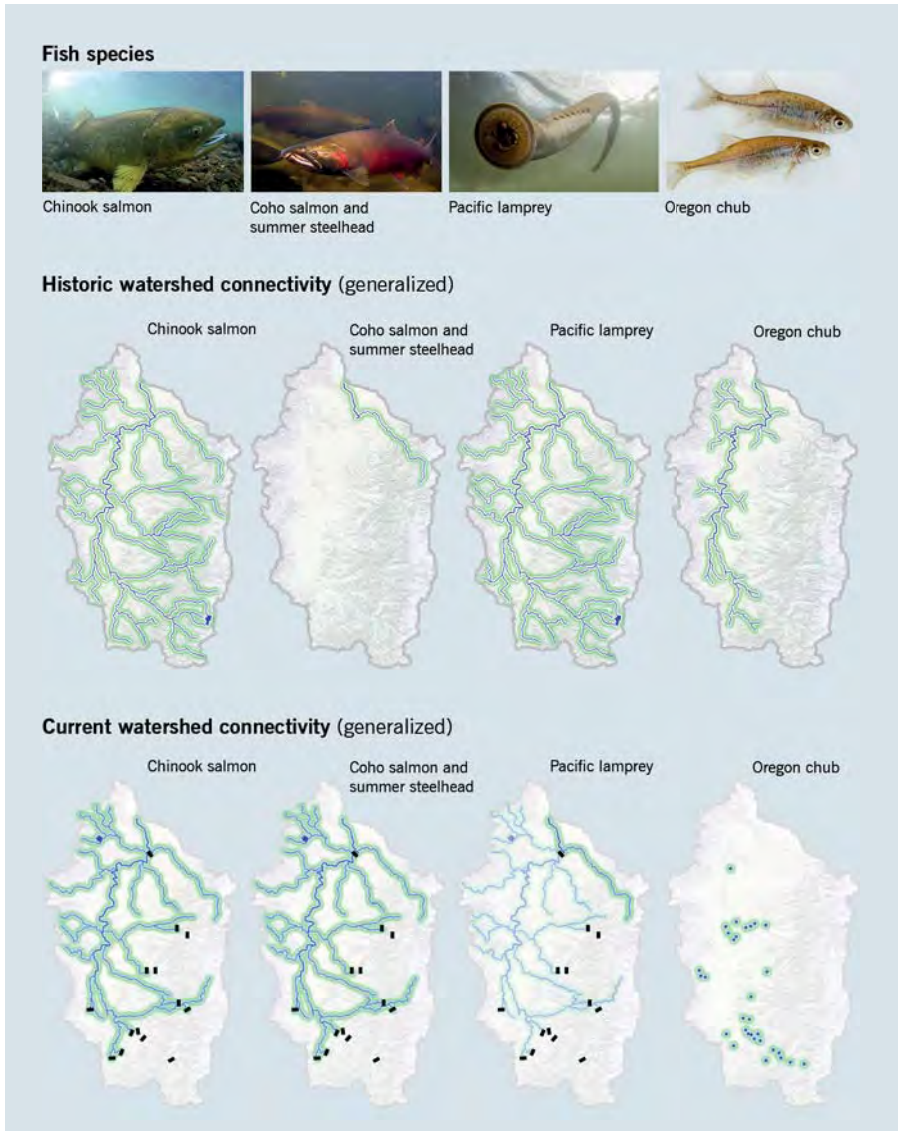


Figure 10.9:
*Willamette falls and dam in
the present day*

proportion of their spawning habitat further upstream is inaccessible. The combined result is that both lamprey and the two native salmon populations are seriously threatened.

The good news for conservation is that restoration of longitudinal connectivity on the Willamette River is progressing. First, lamprey passage at Willamette

Figure 10.10:
Four groups of fish discussed in the text, and their historic (prior to human settlement) and current distributions in the Willamette River network, Oregon, USA. Black bars show approximate locations of dams; streamflow is from bottom (south) to top (north). The Chinook salmon represents diadromous salmonids with upstream spawning runs in winter or spring, when the natural flow pulse occurs in the Willamette. The coho and summer steelhead represent diadromous salmonids with spawning runs in summer or fall, when flow is too low to breach Willamette falls (near the site of the downstream-most dam located in the figures of the bottom panels), but the current fish ladder allows passage that was not possible historically



Source: Hulse, Gregory and Baker (2002).

falls is a driving concern of state-level, tribal, and hydropower managers and is the topic of much ongoing research and monitoring. Installation of lamprey ramps (passage structures specific to the habits of lamprey) along the concrete lip of the weir, improvements to the fish ladder, and other efforts are underway and show promising results. Second, smaller dams obstructing tributaries and cutting off historic spawning reaches in the upper network are being removed, including recent removal of two dams on the Calapooia river. This Willamette tributary is now free-flowing, and longitudinal connectivity has been regained for spawning anadromous fish along its 99.7% of its length. Although larger dams on steeper tributaries in the Cascades are unlikely to be removed, there is a general consensus among stakeholders in the Willamette basin (unlike some other regions of the Western USA) that dams are a fundamental problem impeding recovery of threatened anadromous species, and concentrated efforts are underway involving diverse stakeholders to improve fish passage.

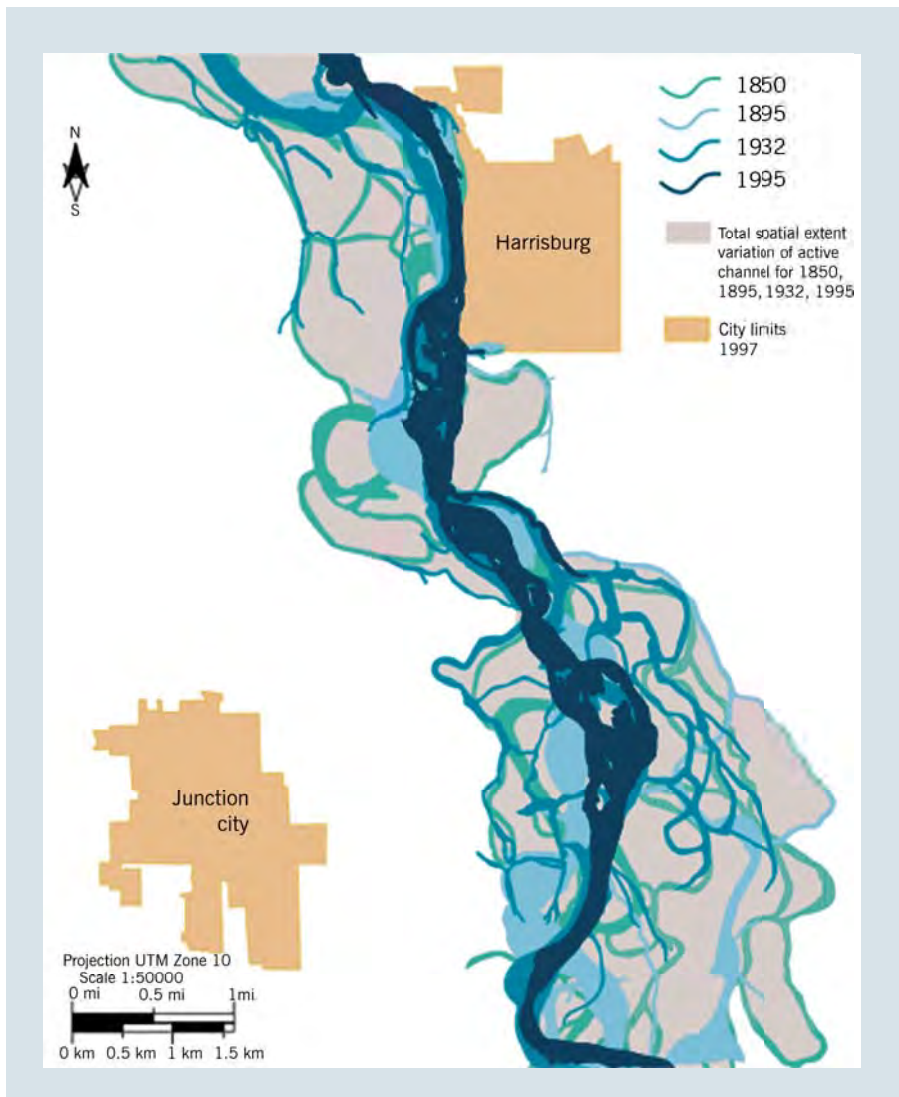
Channelization and lateral/vertical connectivity

Another pervasive impact on connectivity in the Willamette River has been channelization and loss of floodplain complexity in the period since settlement. As is typical of a natural river occupying a broad, low-gradient valley, the Willamette River mainstem until the mid-1850s boasted an extensive and complex floodplain comprised of many braiding side-channels of varying permanence, islands, wetland, and riparian forest. Although some degree of this structure remains in patchy fragments along the river, the mainstem has lost around 2/3 of its total channel length (Figure 10.11) – and with it a significant degree of floodplain complexity and riparian forest – as a result of works to improve navigation and agriculture and to prevent flooding.

These changes represent a significant reduction in both lateral and vertical connectivity, and with it we can predict some loss of ecosystem function and ultimately decreasing aquatic and terrestrial biodiversity. But fish diversity remains relatively high in the Willamette, all things considered; and although nearly half of the list of current species is non-native, the data still reflect reasonable native fish diversity. Indeed, in the mainstem river channel 90-95% of the fish sampled by biologists are native, although non-natives increase in downstream reaches and in off-channel sloughs. Presumably, the essential functions of the intact floodplain for native fish would have been in providing refuge from winter/spring flood pulses and nursery habitats for developing young; and it turns out that an unlikely “new” habitat may to some degree be taking the place of the historic floodplain in providing these functions. To cope with the rainy winter and spring, most farmers in the Willamette valley run ditches through their fields to serve as drains. These ditches, though ar-

tificial, function as intermittent streams directly connected to the mainstem river, similar to small headwaters or to side channels in a floodplain. A recent ecological study of multiple agricultural ditches made four key discoveries: 1) many fish species occupy these habitats during the flood season; 2) the majority of these are native species; 3) many juveniles are present, indicating spawning and rearing; and 4) a good predictor of fish species diversity in a ditch is forest cover in its local catchment (Colvin et al. 2009). So, these

Figure 10.11:
Changes in Willamette River channel complexity and lateral connectivity from 1850 to 1995 in the vicinity of the towns of Harrisburg and Junction City (in upper mainstem of the river). Decreasing braiding, side channels and meandering has resulted in a loss of ca. 2/3 of total channel length since 1850



Source: Hulse, Gregory and Baker (2002).

agricultural ditches are indeed acting as intermittent headwaters, and taking care of these ditches has become a new management directive. In the process, both farmers and native fish reap the benefits. These findings combined with a recent, multiple-stakeholder initiative to restore natural channel complexity and floodplain forest in promising locations along the mainstem Willamette allow cautious optimism for the future of lateral and vertical connectivity in our home river.

A connectivity vs. invasive species conundrum

The Oregon chub (*Oregonichthys crameri*) is a small minnow that loves pools found in murky, forested wetlands and is endemic to the Willamette River network. The chub probably once was distributed throughout the lowlands of the Willamette valley, associated with the complex floodplain aquatic habitat and riparian forests that have been so drastically reduced (Figure 10.10). It is now comprised of just a few isolated populations and is threatened with extinction. One of the key issues for the Oregon chub, aside from loss of its preferred habitat, is its inability to cope with invasive species. This situation leads to the conundrum (analogous to the case of relict native populations above dysfunctional road culverts) of how to manage this species concurrently with efforts to restore lateral connectivity. The problem is particularly perplexing because connectivity to the mainstem likely provides the key dispersal pathway for chub



Figure 10.12:
Agricultural ditch in the Willamette Valley draining productive cropland during the winter/spring rainy season (high-flow pulse)

movement from one wetland habitat to the next (in the absence of the historic connectivity within the floodplain itself).

Concurrent with the push to increase lateral connectivity in the Willamette then, a series of management actions have been prescribed for the chub. The main priority is to protect extant populations from additional stressors (such as water extraction or chemical impacts, e.g. pesticides or herbicides from agricultural activities). In cases where ecological connectivity to the mainstem might be regained, fish barriers to prevent the influx of invasive species may be necessary. These will provide interesting case studies for monitoring habitats with restored ecological connectivity for essentially all functions aside from fish movement. Unfortunately, invasive bullfrogs (*Rana catesbeiana*) also negatively impact the Oregon chub, and – as we saw in the Necklace Lakes early in the chapter – barriers to fish connectivity are not necessarily barriers to amphibians. Bullfrog reduction is therefore another priority in managing chub populations. Another key management strategy will be to manually relocate individuals to other potentially suitable sites disconnected from the river network. And finally, protection and restoration of floodplain forests in key locations should provide an essential component of the Oregon chub’s habitat requirements for the long term. Clearly, this problem, wryly nicknamed “chubs in tubs”, is representative of the complex issues of multiple anthropogenic impacts, combined with the naturally complex ecology of river systems. (For more on the problem of invasive species in river ecosystems, see Chapter 8.)

10.7. Emerging concepts

This chapter serves the dual objective of first conceptualizing the interesting, complex, and necessary role of network and web connectivity in natural river ecosystems; and second moving to the “real world” where a multitude of river resources are necessary for modern-day human populations, but extracting those resources alters (sometimes severely) the natural connectivity so important for river ecosystem functioning. We converge on the idea that we can perhaps “have our cake and eat it too” by managing resource-extraction activities thoughtfully to maintain a reasonable representation of the complex network of webs characteristic of fully functioning river ecosystems.

A key to thoughtful management for connectivity will be to emphasize vital individual elements from the complex tangle of interactions that scientists understand natural river ecosystems to be. One such element is that natural flow pulses are essential for maintaining connectivity in all three spatial dimensions of river ecosystems. A flurry of research activity has occurred over

the past ~15 years supporting the idea that what has been termed the “natural flow regime” (Poff et al. 1997) is a master driving variable in rivers. Maintaining components such as magnitude, timing, and frequency of flow pulses similar to what is expected naturally (e.g. given precipitation and snowmelt patterns) can preserve multidimensional ecological connectivity near natural levels even in highly regulated rivers.

Another vital element to emerge from the complexity is that *headwaters play a capillary-like role* in river networks by interacting intimately with the terrestrial environment and transmitting the effects of these interactions through the network. The same can be said for the small intermittent channels on floodplains. Taking care of these capillaries and their riparian areas should be a priority in holistic river conservation, likely resulting in a handsome return on investment as effects of healthy headwaters amplify through river networks.

Ultimately, it is important to remember that network connectivity in rivers must be maintained if we are interested in preserving web connectivity. The biotic interactions that drive web connectivity take place on the physical stage of network connectivity. Hence, what we might deem important and desirable outcomes of river ecosystem function (e.g. production of fish that we use for food, recreation, and ceremony) result *proximally* from web connectivity (e.g. the fish got enough to eat thanks to subsidies of terrestrial insects from the riparian forest) but *ultimately* from network connectivity (e.g. lateral connectivity between a river and an intact riparian zone). Analogously with the top Google definition of “connectivity”, Internet Protocol is the physical connectivity that merely sets the stage for the more visceral connectivity of human interaction. What if we were to decide that sustaining connectivity along river networks is as important as sustaining internet connectivity?

10.8. References (with comments)

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