

Role of Refugia in Recovery from Disturbances: Modern Fragmented and Disconnected River Systems

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ABSTRACT / Habitats or environmental factors that convey spatial and temporal resistance and/or resilience to biotic communities that have been impacted by biophysical disturbances may be called refugia. Most refugia in rivers are characterized by extensive coupling of the main channel with adjacent streamside forests, floodplain features, and groundwater. These habitats operate at different spatial scales, from localized particles, to channel units such as pools and riffles, to reaches and longer sections, and at the basin level. A spatial hierarchy of different physical components of a drainage network is proposed to provide a context for different refugia. Examples of refugia operating at different spatial scales, such as pools, large woody debris, floodplains, below dams, and catchment basins are discussed. We hope that the geomorphic context proposed for examining refugia habitats will assist in the conservation of pristine areas and attributes of river systems and also allow a better understanding of rehabilitation needs in rivers that have been extensively altered.

Habitats or environmental factors that convey spatial and temporal resistance and/or resilience to biotic communities impacted by biophysical disturbances may be called refugia. There are many kinds of refugia within a river system. These include localized microhabitats and/or zones within the channel, unique reaches, riparian vegetation, floodplains, and groundwaters. Such riverine refugia may exist as gradients or continua (as in the case of waters in the river channel connected hydraulically to adjacent waters) or may be fragmented by impoundments or by water isolated in an oxbox (i.e., a meander channel that has been disconnected from the main river system). They may also be a result of the juxtaposition within the basin of habitats or tributaries with special characteristics.

The diversity and complexity of river systems have been recognized only recently. Habitats in rivers are classically generalized to include pools, riffles, runs, and localized areas where easily observed species accumulate in numbers during some phase of their life

cycle (e.g., trout-spawning areas). In-channel woody debris, side- and extra-channel areas, floodplains, riparian vegetation, and groundwaters are now considered integral parts of the riverscape (Welcomme 1979, Pringle and others 1988). The latter group may appear isolated within the river or its valley and often have been treated as unimportant. However, they are hydrologically interconnected with the main river and are of paramount importance spatially and temporally in maintaining natural communities. It is the suite of habitats, both the traditionally recognized ones and the more recently identified ones, that we consider to be refugia.

Maintenance of the biotic diversity and natural community dynamics in streams and rivers is directly related to the preservation of natural habitats and associated processes within the basin. In many cases refugia may be inhabited by biota that are different or transient in comparison to the usual communities (e.g., macroinvertebrates and fish) that occur in the channel of natural rivers. However, they all function in various ways as source areas for natural recolonization of the river ecosystem following disturbances that reduce biomass or, in extreme cases, eliminate species.

Few reaches of large rivers remain pristine, thereby allowing refugia to function in a natural manner. Among large meandering rivers in the continental

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United States, only those contained within wilderness areas of national parks remain relatively intact ecologically, and those rivers tend to be concentrated within headwater reaches of the mountain West. Thus it is difficult to differentiate natural and anthropogenic disturbances with respect to natural refugia. We refer the reader to Resh and others (1988) for a useful synthesis of natural disturbances in regulating stream community dynamics and focus herein on the importance of refugia in relation to spatial scales within a basin and to human disturbances. Our main argument is that refugia are critical components of natural river ecosystems and that understanding their role in maintaining biodiversity may offer alternative insights into the conservation and management of rivers. Our objectives are to: (1) provide a context for examining refugia in streams at different spatial scales, ranging from small local to large basin scales; (2) give examples of refugia operating at these different scales; (3) discuss reversible and irreversible impacts of human disturbance and habitat alteration on natural refugia; and (4) discuss research and management needs.

Spatial Scales

Hierarchical Spatial Relationships and Catchment Geomorphology

A major problem for stream ecologists has been defining the boundaries of the system. This had led to problems associated with sampling, experimental design, and extrapolation of findings (Minshall 1988). Until recently stream biologists viewed the stream from the perspective of a benthos sampler and a habitat unit without including a geomorphic context. Factors responsible for the structure and function of stream ecosystems are multiple, and different factors dominate at different levels of resolution (Frissell and others 1986, Kellerhals and Church 1989, Grant and others 1990). Most discussions of refugia are placed in the context of a localized hydraulic unit, such as a pool, without giving consideration to larger-scale features. We feel that this localized spatial view does not adequately or fully address the range in which refugia operate in stream systems. We define a hierarchical scale of the linear river system and a four-dimensional system for viewing streams. Both are necessary in order to provide a context from which to define and discuss refugia in rivers.

The drainage network of valley floor landforms within a drainage basin or catchment extends from headwaters downstream through a river channel of increasing size and into estuaries or freshwater wetlands (Figure 1). Segments of a drainage network are

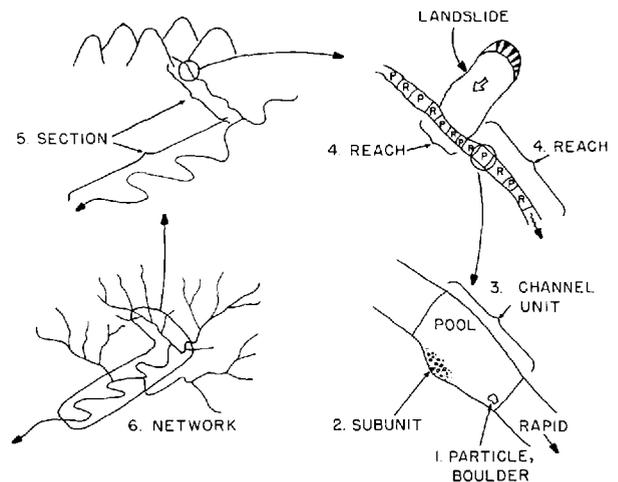


Figure 1. Spatial hierarchy of physical components (numbered from small to large) of a catchment (drainage network). The relative size of the six physical components vary from centimeters (component 1) to meters (2–4) and kilometers (5, 6). At the channel-unit (3) and reach (4) scales, P = pool and R = riffle. Scale 5 includes river sections in mountain and lowland valleys. (From: Gregory and others 1990).

delineated by major topographic discontinuities (scale of <1 to >100 km), such as high-gradient montane rivers, low-gradient lowland rivers in broad valleys, and broad rivers mouths influenced by sea-level changes. Drainage segments include continuous areas of the valley floor landscape that have different potentials for development of active channels and floodplains.

A drainage segment is composed of reach types, delineated by the type and degree of local constraint imposed by the valley wall at the channel margin. The degree of local constraint controls fluvial modification of geomorphic surfaces and therefore influences both terrestrial and aquatic communities through topographic, edaphic, and disturbance mechanisms (Gregory and others 1990).

Constrained reaches, in which the valley floor is narrower than two active stream channel widths, are formed where bedrock, landslides, alluvial fans, or other geologic or man-made features constrict the valley floor and thus limit lateral mobility of the channel (Gregory and others 1990). Streams within constrained reaches tend to be relatively straight, single channels with limited lateral heterogeneity. During spates, the position of constrained stream channels is relatively fixed within narrow floodplains and stream power increases rapidly with increasing discharge. Relative resistance to erosion affects the persistence of the constraint and the composition of the substrata in the active channel. Valley floors in

constrained reaches are characteristically narrow and include few geomorphic surfaces within the valley floor. Riparian vegetation in these areas is usually similar in composition to adjacent hillslope plant communities.

Unconstrained reaches, in which the valley floor is wider than two active channel widths, lack lateral constraint (Gregory and others 1990). Therefore broad floodplains are developed through erosional and sedimentation processes, and the active channel migrates across the valley floor. They are characterized by complex, often braided channels and extensive floodplains. At high flow the unconstrained stream spreads out across the broad valley floor, dissipating much of the energy of the current. Riparian zones in unconstrained reaches are broad and complex, with a diverse array of geomorphic surfaces and plant communities of different age. Riparian stands include components of hillslope communities but are composed largely of species adapted to fluvial environments. Evidence of natural, fluvial disturbance is widespread in these systems and is reflected by numerous small patches of early seral vegetation.

Reach types within the valley floor are composed of sequences of channel units whose distinct hydraulic and geomorphic structures reflect different formation processes (Grant and others 1990). In general, channel units are longer than one channel width and are distinguished on the basis of surface slope, degree of turbulence, and extent of supercritical flow. Channel units in low-gradient, gravel-bed streams have been classified into pools and riffles (Leopold and others 1964). In high-gradient streams with coarser bed material, the distinction between high- and low-gradient units is conspicuous, and the steeper units may be subdivided into several additional types (e.g., rapids, cascades, falls). Channel units are restricted to the active channel and include only a fraction of the riparian vegetation; however, they are major determinants of habitat for aquatic organisms.

Riffles, pools, rapids, and other features along the thalweg that are shorter than one channel width are categorized as subunits. Channel subunits are described by hydraulic and geomorphic features at scales less than the active channel width. Geomorphic features lateral to the thalweg such as backwaters, eddies, and side channels also are included as subunits and play distinctly different ecological roles than subunits along the main axis of the channel. Subunit features correspond to the habitat types employed in most aquatic ecological research. As flow increases and the active channel is completely inundated, channel units attain uniform surfaces and delineations between subunits become less distinct.

An important aspect of this hierarchical geomorphic system is that definitions of drainage scales are based on functional relationships between landforms and the processes that create or modify them. Processes operating at one scale can affect structures at other scales. For example, reach-scale landslide processes may deliver large boulders to a channel, thereby modifying adjacent reach types and the distribution of channel units, subunits, and particles. Within this hierarchical system, spatial scales are consistent with the physical mechanisms responsible for landform change. A disturbance can operate on all scales from watershed to particle, and the organisms affected may or may not use all of the spatial scales or temporal hydrologic scales within a basin.

Expansion and Contraction of River Ecosystems

Rivers must be viewed from four dimensions: (1) longitudinally from upstream reaches to downstream segments; (2) transversely away from the river channel through the floodplain to the valley walls; (3) vertically through interstices in the river bottom and into adjacent groundwater systems, especially in porous, gravel-bottom rivers; and, (4) temporally, such as seasonal, annual, and long-term (Ward 1989). These dimensions may be viewed as spatial gradients that may change gradually or abruptly, depending on the geomorphology and kinetic energy of the river system. Each of these spatial gradients is interactive with the others and is dynamic over variety of time scales (e.g., season to geologic).

Longitudinal zonation of regional fish faunas and a universal upstream–downstream zonation scheme for rivers were among the earliest river classification attempts (Illies and Botosaneanu 1963). The river continuum concept (RCC) views downstream changes not as zones, but as resource gradients along which the biota are predictably structured (Vannote and others 1980). The RCC emphasizes that downstream communities are a function of both the adjacent riparian vegetation and upstream processes. Upstream–downstream linkages are important in streams, whether viewed as gradients or zones. For example, thermal loading, nutrient transport, and toxic dispersion are all strongly longitudinal. The quality and quantity of detritus in a given reach of stream is influenced by the allochthonous inputs, primary production, organizational processing, and retention characteristics of upstream areas. In this sense the upstream–downstream linkage is a type of refugium in that disturbed areas downstream may be rehabilitated by the simple process of materials being transported downstream into the disturbed zone. Pristine tributaries or side-flows from groundwater sources may function similarly.

The lateral dimension includes the form and dynamics of the channel itself, interactions between the channel and riparian vegetation, and the associated floodplain systems. Complex channel patterns provide numerous and important refugia for plants, invertebrates, fish, birds, and mammals (Welcomme 1979). Side arms provide thermal refugia. Backwater and side channels are often important nursery and spawning areas and provide corridors to floodplain refugia (Bouvert and others 1985). Studies conducted on small streams have demonstrated that vigorous and diverse riparian vegetation is required to maintain the integrity of land–water interactions (Karr and Schlosser 1978, Cummins and others 1984).

As streams go through the annual hydrologic cycle, there is an expansion and contraction of wetted area as well as periodic incorporation of active floodplains. Large floods and other high-magnitude, low-frequency events (e.g., volcanic eruptions) have shaped rivers and floodplains and created a vast array of side channels, oxbow lakes, side arms, and floodplain terrace streams that are connected to the main channel at different flow regimes. The greatest diversity and aerial extent of riverine refugia occur where there is a maximum interaction between floodplain and aquatic systems. In the great floodplain rivers of the world, the lateral interactions are highly developed in reaches that have predictable annual flooding and extensive floodplains (Welcomme 1979). Ward (1989) has illustrated a number of studies of biotic interactions with this dimension of the river.

The major vertical dimension is the contiguous groundwater level and a lateral hypogean component present on many streams and rivers (Stanford and Ward 1988). Alluvial aquifers are important in terms of the vegetation that can grow on the floodplain and the hydrologic connectedness of fluvial features in the floodplain (Amoros and others 1987).

Refugia at Different Spatial Scales

Habitat or refugia manifest at different spatial scales in response to the hierarchical scale of the geomorphic template (Table 1). Refugia function differently for different types and magnitudes of disturbance. As an example, deep pools in small streams may not be a refuge for organisms during a large flood, but are important as refugia during severe droughts. In general, the smaller the refugium, the less resistant it is to a particular disturbance. Refugia at the scale of reaches or larger tend to be both more resistant and resilient to a variety of disturbances.

Table 1. Kinds of refugia at different spatial scales

Spatial scale	Kind of refugium
Particles	Sand Cleaned gravels Wood
Channel Unit	Complex edge Cover Depths Large wood Groundwater inputs Streamside vegetation
Reach	Streamside vegetation Large wood Unconstrained areas, valley width: channel width >2 Tributary input Hyporheic and groundwater inputs Frequency of channel units per channel length
Section	Extent of frequency of well-vegetated unconstrained or wide floodplain areas Tributary junctions Lentic features (oxbow lakes, isolated side channels or arms) Streamside vegetation
Watershed	Extent and distribution of floodable vegetated floodplain Hydraulic transition areas Watershed condition Extent and distribution of streamside vegetation Location and frequency of connected lentic features Extent location and type of hyporeal or subsurface water

Particle, Channel Subunit, and Channel Unit Scale

The ability of channel units and subunits to function as refugia varies with stream size and the magnitude of the disturbance event. In both lower and higher order systems, channel units and subunits generally function as refugia in localized, low-magnitude disturbance events. However, they also may be important in more severe, less frequent events such as droughts. In larger systems, channel units and subunits are important refugia in higher magnitude events. Units in smaller stream systems may be obliterated or overwhelmed in larger or more intensive events. Refugia at this scale are more important in natural than in anthropogenic disturbances.

During floods, pools and backwaters function as refugia for fish. Matthews (1986) found that most abundant species of fish persisted in an Arkansas stream after severe flooding, but that there was a shift in order of abundance. The community recovered to pre-flood characteristics within eight months. Mat-

thews suggested that deep pools function as refugia in areas with stable substrate or permanent physical features. Ross and Baker (1983) found that fish moved to the margins of streams during spring floods.

Pools are also important refugia in droughts. In an intermittent stream in Iowa, fish survived in pools that persisted and remained inhabitable during drought conditions (Pauloumpis 1958). Fish that survived in these pools recolonized the stream when the system returned to higher flows Reeves (1979) observed a similar phenomenon in a small northern California stream.

The ability of a unit to be a refuge is a function of the characteristics of the unit itself and of the channel reach in which the unit or subunit is contained. In general, more complex units and channels are more likely to serve as refugia than less complex ones.

Wood is a primary factor in determining the complexity of channel units and subunits and may even serve as a refuge at the particle scale. Over the last 20 years, numerous investigations have documented the importance of woody debris as cover structure and the origin of habitat development for fish; useful reviews of many of these studies are given by Harmon and others (1986) and Bisson and others (1987). Wood, both in-stream and in the riparian zone, plays a critical role in modifying channel morphology, stabilizing stream banks, trapping eroding sediments from the land and from floodwaters providing fish cover, and regulating water temperature in the basin. Riparian vegetation also functions as a nutrient and energy source for stream invertebrates and habitat for terrestrial invertebrates (an important fish food source). Streamside vegetation is largely responsible for maintaining the physical integrity of small stream channels over a wide range of environmental conditions.

Large rivers had a historical frequency of snags in the same order of magnitude as the frequency of large woody debris and downed trees in intermediate-sized streams (Harmon and others 1986). Loss of large wood from the channel has had a significant impact on fish communities. The standing crop of fish in a snagged and straightened section of the Chariton River (Missouri) was 83% less than in an adjacent unmodified section 30 years after the channel was modified (Congdon 1971). The straightened reach also had eight fewer fish species. Snag removal also has contributed to a serious decline in catfish fisheries in the Missouri River (Funk and Robinson 1974). Fish samples from modified sections of the Olentangy River, Ohio (Griswold and others 1978) and the Luxapalila River, Alabama–Mississippi (Arner and others 1976), indicate that in addition to consistently supporting lower

fish standing crops, snagged and straightened sections of large rivers have markedly different fish community structures than unmodified sections. The decline in game fish populations is particularly striking. Moreover, many fish that are captured in straightened sections are actually transients enroute to more stable, unmodified habitats (Hansen 1971, Arner and others 1976).

In addition to the decline in physical habitat quality, snag removal also results in a severe reduction in fish food resources (Hansen 1971, Arner and others 1976, Benke and others 1985), since most of the aquatic invertebrate production in large, unstable-bottom rivers is associated with these structures. Benke and others (1985) estimated that snags represent only 4% of the area habitat of the Satilla River, Georgia, but contribute over 78% of the drifting invertebrates. Several species of game fishes obtain at least 60% of their food from the snag habitat in the Satilla River.

Many biologists and engineers are not aware of the historical frequency of snags in large rivers (Sedell and Froggatt 1984, Triska 1984). A conservative estimate of snag frequency and subsequent removal from several rivers in virtually every corner of the United States elucidates the extent of riverine habitat alteration (Table 2). Even the largest river in North America, the Mississippi, had over 600 snags per kilometer removed from its channel between St. Louis and New Orleans from 1866 to 1900. It may be inferred from these data the extent to which fish habitat in large rivers was dependent on large snags, and how lumbering and navigation concerns reduced riparian forests to brush and changed diverse and productive streams to navigable riverine highways. Individual snags not only were direct habitat but tended to aggregate at the outside bend of meanders and at channel cutoffs. These aggregations resulted in deep and complex scour pools (Wallace and Benke 1984).

Section or Reach Scale

Refugia at the section scale are best illustrated by mosaic habitats in a wide floodplain and low-gradient reach. Sections function as refugia in more extensive and higher magnitude events than do channel units and subunits. They may function as refugia in all types of natural and anthropogenic disturbances. The hyporheic zone is one such refugium. The hyporheic zone is defined as the area of interstitial space permeated by riverine water (Orghidan 1959). It serves as important refugia for river channel organisms, particularly invertebrates (Williams and Hynes 1974) during environmental stress in large gravel-bed rivers. It is also an area of energy and nutrient transformation.

Table 2. Summary of snags pulled from rivers in the United States for navigation improvement from 1867 to 1912 (Secretary of War 1915)^a

Rivers by region	Drainage area (km)	Snagged (km)	Snags (per km)
Southeast region			
Pamunkey R., VA	2,740	48	86
North Landing R., NC and VA	—	27	394
Pamlico and Tar R., NC	12,500	78	480
Contentnia Cr., NC	1,870	112	151
Black R., NC	3,960	112	172
Edisto R., SC	8,700	120	307
Savannah R. to Augusta, GA	27,100	397	123
Oconee R., GA	11,300	158	398
Noxubee R., AL and MS	3,070	110	1,306
Pearl R., MS	18,700	722	408
Tombigbee R., MS	26,900	770	372
Guyandot R., W VA	3,140	130	62
Cumberland R. above Nashville TN	45,800	573	135
Choctawhatchee R., FL and AL	11,200	339	524
Oklawaha R., FL	7,070	99	112
Caloosahatchee R., FL	—	35	452
Central region			
Grand R., MI	13,400	61	33
Minnesota R., MN	43,300	384	71
Red River, ND and MN	171,000	512	16
Red Lake R., ND and MN	13,500	240	6
Wabash R., IL and IN	83,900	77	102
Missouri R.	542,000	2800	9
Arkansas R.	411,000	1,920	100
White R., AR	71,700	480	124
Cache R., AR	2,660	157	217
St. Francis and L'Anguille R., AR	29,000	352	81
Southwest region			
Guadalupe R., TX	25,900	83	848
West Coast region			
Sacramento R., CA	60,200	368	91
Chehalis R., WA	4,600	24	202
Willamette R. above Albany, OR	11,500	88	61

^aMost rivers in the United States lost significant amounts of fish habitat by the year 1910 (adapted from: Harmon and others 1986).

Until recently, hyporheic zones have been thought to characterize a relatively small proportion of the riverine environment. Various studies have shown that the hyporheic zone of small streams frequently extends but a few centimeters, or at most, meters from the channel (Williams 1984). However, the hyporheic zone in gravel-bed rivers has been recognized recently to include extensive floodplain aquifers that are connected to the channel (Stanford and Ward 1988). As an example, riverine invertebrates have been collected up to 2 km from the main channel. In the Flathead River within Kalispell Valley, Montana, the volume of hyporheic habitat has been estimated at more than ten times that of the channel habitat (Stanford and Ward 1988).

Hyporheic zones may contain a very specialized fauna. Portions of the hyporheic fauna may reside permanently within the interconnected aquifers, while other species, particularly aquatic insects, may spend their larval stages deep within these interstices but return to the main channel to emerge and complete their life cycles (Stanford and Gauvin 1974, Stanford and Ward 1988).

The hyporheic zone may be extensively utilized by many stream invertebrates during intervals of disturbance. Floods and spates frequently result in bed load movement and the scouring of the stream channel, yet benthic organisms recolonize substrata quickly after flood subsidence. Hydropsychid caddisflies, which are known to require sufficient current velocities to main-

tain their passive filter-feeding and thus are usually located at the surface of the stream channel, migrate deep into the interstitial spaces of the cobble substrate of the Flathead River for pupation and escapement during spring runoff (Hauer and Stanford 1981, 1982). Other investigators have found similar patterns of zoobenthos migration into the substratum to avoid scour and the increased silt loading of spates and floods (Williams and Hynes 1974, Poole and Stewart 1976).

Hyporheic zones also may serve as important refuges from periodic drought or periods of unfavorable temperatures, which manifest as short-term disturbances to the stream ecosystem. Several studies have suggested that surface-dwelling macrozoobenthos may move into the substrata during severe drought (Hynes 1968, Imhof and Harrison 1981) in an attempt to remain within a wetted environment. Diapausing stonefly nymphs have been collected from as much as 25 cm below the substrate surface in a dry streambed (Williams and Hynes 1976).

Reeves and others (1987) have identified areas of upper Elk River in mountainous southwestern Oregon, which have characteristics of hyporheic zones, as important areas of fish spawning, rearing, and refugia from floods. They are low gradient (generally less than 2%) and have a wide valley floor. They are located at gradient breaks in the stream channel and are areas of sediment deposition. These reaches have extensive zones of active landslides and earthflows (McHugh 1986), which deliver large amounts of sediment and wood to the channel. Delivery of these materials to the channel and their storage in the channel is a major influence on the physical and biological characteristics and processes of the area, both in the short and long term. Ryan-Burkett (1989) found these areas to be very stable in character over time, even in the face of a 100-year flood.

Habitat composition in these reaches of Elk River is diverse. Pools are deep and morphometrically complex and have large amounts of wood associated with them. Multiple overflow channels are present and are important for rearing of recently emerged fish in the late winter and early spring, and as refugia from high winter flows. Researchers in other parts of the Northwest (Petersen 1982, Tschaplinski and Hartman 1983) have found similar habitats to be important overwintering areas for juvenile salmonids.

An important feature controlling the size of the hyporheic zone within any stream reach is the size and porosity of the substrata. Large cobble that has been sorted by fluvial processes usually has greater intersti-

tial space and flow rates than compacted gravels, sands, or bedrock. Typically, the volume of interstitial pore space is 25%–40% of the aggregate volume of substrata materials (Pennak 1940, Stocker and Williams 1972). In order to accommodate macrozoobenthic organisms, pore sizes need to be at least 50 μm in diameter.

The importance of the hyporheic zone in these rivers is just now being recognized and its role as a refuge should not be underestimated or overlooked. Hyporheic zones may be highly variable within and between stream systems, corresponding to the natural geomorphic variability. Thus, the size and localized importance of the hyporheic zone of any stream or river system expands and contracts laterally along the longitudinal gradient of the riverine corridor. This important added dimension in our understanding of the structure and function of stream ecosystems is merely in its infancy and needs considerable additional study to more fully realize its scope and interrelationship in stream ecology.

Segments of streams function as refugia during flood events and droughts. Matthews (1986) speculated that fish moved or were displaced to reaches of streams with deep pools, stable substrates, and other "permanent features" during floods in an Arkansas stream. Both Everest (1973) and Kralik and Sowerwine (1977) found that intermittent streams were important refugia for juvenile salmonids during winter high flows in streams of Oregon and California. Harrel and others (1967) thought that fish survived drought conditions in lower-order streams by moving to larger streams downstream. Smaller streams then were reinvaded after flows returned.

Unimpacted segments of streams and rivers serve as refugia during human-related disturbance. Krumholz and Minckley (1964) found that heavily polluted areas of streams in the upper Ohio rapidly recolonized when the pollution abated. They speculated that fish moved from unpolluted backwaters and tributaries to the previously uninhabitable areas. A similar scenario of recovery was observed by Olmstead and Cloutman (1974) in an Arkansas stream polluted with pesticides. There were differences in the types of fish that returned to the recovered areas over time. Earliest recolonizers were able to operate across a wide range of environmental conditions and had high rates of reproduction. Later-returning species had stricter environmental requirements and lower rates of reproduction. Hyporheic zones also may serve as refugia during anthropogenic disturbances. Rapid recolonization of benthic surfaces after poisoning of streams with insecticides

ticides or chemical spills has been attributed to population reserves within hyporheic refugia (Wallace and others 1973).

Zone or Watershed Scale

Recovery of aquatic biota from large-scale natural disturbance at the basin scale is dependent, at least in part, on the presence and juxtaposition of unimpacted reaches of stream. In the longitudinal dimension, streamside forests cannot directly impact flooding and water quality upstream of their occurrence, and their influence will diminish gradually in a downstream direction. Thus, streamside forests and wetlands in the lower reaches of the river ecosystems or directly upstream of critical habitat are more advantageous than similar size riparian forest or wetland elsewhere in the watershed.

In the transverse dimension, riparian forests adjacent to the riverbank or in areas of high probability of flooding will have the greatest impact on habitat structural diversity, water quality, and flooding, with a diminishing marginal return as the width of the forested corridor is increased beyond some measurable distance. Thus the placement of streamside forests is often dictated by areas humans want to maintain for critical habitats, recreation, or water-quality and sediment modification.

From a fish distribution and conservation view point, the geometry and geomorphology of rivers further complicates maintaining adequate refugia (Moyle and others 1982, Sheldon 1988). Rivers are open, directional systems, so protection of any segment requires control over the entire upstream network and surrounding landscape. There is little likelihood that such protection can be given to very many large streams, yet it is these streams that support the greatest diversity of fishes. It is hoped that strategically placed riparian controls and prevention of agricultural and industrial pollution, channelization, and impoundments may be sufficient to maintain diverse fish assemblages and maintain a diverse connected mosaic of habitats within a basin. Thus a whole-basin perspective is necessary for identifying, conserving, or restoring refugia within a basin.

The 1980 eruption of Mt. St. Helens eliminated the biotic communities in several surrounding basins or portions of those basins and serves as a good illustration of refugia operating throughout a basin. The eruption had two primary effects on the physical environment of these streams. First, massive quantities of ash and volcanic debris entered many stream channels. Second, the upslope forest and riparian communities were destroyed or dramatically altered. Stream hab-

itats changed in several ways as a consequence of these primary effects. Many channels became shallower and wider because of the increased sediment load. Mean particle size and substrate heterogeneity decreased, as did pool frequency and depth. Summer temperature increased because of decreased shading associated with the loss of riparian vegetation.

Biota have recolonized all of the disturbed streams in the Mt. St. Helens area to varying degrees. Invertebrate assemblages in streams with intact headwater forest had more taxa than basins in which all of the forest was destroyed (Hawkins 1988). Composition of these assemblages appeared to be a function of the character of streambed substrata, temperature, and random colonization. The most recognizable modes of dispersal over the undisturbed areas were passive downstream displacement of individuals into denuded reaches and active aerial flights by adults.

Densities of tailed frog tadpoles (*Ascaphus truei*) showed slightly different patterns among streams than those observed for invertebrate richness. Highest abundances were found in disturbed reaches below forested headwater areas (Hawkins and others 1988). Lowest densities were observed in basins with no remaining forest, and intermediate densities occurred in minimally disturbed basins. For this species the presence of heavy forest shade appears to be a critical habitat component. Tadpoles require cool water temperature and adults need the moist terrestrial conditions that heavy forest canopies provide. The high abundance in partially denuded basins appears to be due to the combination of abundant algal food in opened canopy reaches and suitable adult habitat in upstream forested areas. The eventual recolonization of heavily disturbed basins, in which this species is now locally extinct, may take several decades as the basin is reforested and sources of nearby colonists migrate. Although downstream dispersal by tadpoles can be rapid, movement across basins will probably be slow since adults are poor dispersers. For relatively isolated basins in the devastated area, very long recolonization periods may be realized (100+ years) because of the combination of distance to the nearest refuge and the slow dispersal rates.

Recovery of trout populations in this stream has been dependent on the existence of refugia within the basin, because a 30-m waterfall prevents upstream dispersion from areas lower in the drainage. For brook trout (*Salvelinus fontinalis*), the primary refuge sites were headwater lakes and side-channel springs. At the time of the eruption, these lakes were covered with an ice layer and thus insulated from the heat of the blast. Furthermore, unlike streams, they experienced little

scour, although they did receive substantial inputs of fine ash. Several spring sites that occur along Clearwater Creek also may have served as refuges. These springs are off of the main channel and would not have experienced the destructive scour or turbidity that characterized most of the stream channel.

Changes in Available Refugia

Human-disturbed river systems generally are characterized by landscape modifications within the watershed, such as destruction or removal of the mature vegetation of the region, channel modifications, dams and other stream regulation schemes, or major pollution (Hughes 1985). However, the most damaging anthropogenic impacts to stream biota usually result from changes in the basic structure and function of the stream ecosystem rather than as a result of pollution by toxic chemicals. Dynamic ecological characteristics of the riverine environment such as temperature, light, dissolved oxygen, nutrients, and organic matter sources are frequently modified permanently. Biotic community shifts caused by alteration of river ecosystems has resulted in extirpation or extinction of species in many areas of the globe (e.g., Davies and Walker 1986, Williams and others 1989). This will likely continue to be a significant problem, nationally as well as internationally. Some of these impacts are reversible, especially in reaches with low levees that allow water onto the floodplain. Sequences of dams and high levees are impacts that are socially and politically irreversible. However, floodplain restoration is possible, and some dam sequences on rivers provide refugia for headwater organisms, as we will outline below.

Reversible Changes

Between 1854 and 1967 the Willamette River, Oregon, became increasingly isolated from its floodplain as a result of channelization and agricultural modification of the riparian forests. In 1854, the riparian forest was in contact with >250 km of river edge on oxbow lakes and cutoff sloughs. By 1967 the length of river edge had been systematically decreased to 64 km, a reduction of 74%. Much of the change in riparian forest interaction was completed by 1910 owing to snag removal and "river navigation improvements" (i.e., revetments). The implications of these changes are that the ability of alluvial reaches to provide refugia, retain sediments and organic materials and to determine the quantity of organic inputs has been reduced severely.

Most wetlands and river floodplains slow the flow

of water from the land, store it for a period of time, and slowly release the stored waters downstream. In this way flood peaks of tributary streams are desynchronized, and flood waters do not reach the mainstream river at the same time. Increasingly during the past century on large rivers in both Europe and North America, the water table in river valleys below the rooting zones of the riparian forest has been lowered as a result of gravel mining, trapping of sediments by upstream dams, and channelization (De Camps and others 1988). The landscape processes of deforestation combined with floodplain levee systems isolate the river from the floodplain and accelerate storm runoff. However, where levee systems are not extensive, like the Willamette River, Oregon, or the Garrone River in France, we have the opportunity to reestablish floodplain forests and reconnect the river to its floodplain. River reaches with the greatest restoration potential must be identified with the objective of providing riverine refugia. The current greenway concepts along rivers for recreation purposes could be readily expanded, for biodiversity purposes, to adequately address the maintenance of refugia.

Irreversible Changes

Perhaps the most damage to the natural integrity of river systems has been wrought by stream regulation and the control of river flow for power generation, flood control, and water diversion. High dams have inundated major segments of most of the world's large rivers (Petts 1984, Davies and Walker 1986).

Four international symposia have been held to discuss the ecology of regulated streams. Many papers in the proceedings (Ward and Stanford 1979, Lillehammer and Saltveit 1984, Craig and Kemper 1987, Petts and others 1989) detail how stream communities have been altered by stream regulation and debate various methods for determining instream flows to protect biota. The principal impacts of stream regulation are the alteration (usually reduction) of the habitat mosaic by reducing the annual amplitude of the hydrograph (long-term flow stabilization) and alteration of temperature regimes by the differential heating and cooling effect of upstream reservoirs. Generally, communities are less diverse after regulation in relation to pristine conditions, although biomass and production may be much greater owing to increased nutrients from the bottom of the reservoir and discharges of clear water that reduce scour and maximize light penetration.

The ecology of rivers tends to be reset downstream from the confluence of tributaries (Vannote and others 1980) and below dams (Ward and Stanford

1983). Habitat attributes may be altered to reflect upstream conditions, allowing biota that would normally be found in upstream reaches to exist out of their typical sequence in the longitudinal gradient. For example, waters discharged from hypolimnial release dams are usually cool in the summer and warm in the winter, relative to preimpoundment conditions. For some distance downstream the thermal regime may mirror that of a far upstream segment of the unregulated river. Other variables may behave similarly, such as composition and relative embeddedness of the substrate, drift of organic matter, primary production, and other habitat characteristics that may determine community composition of macroinvertebrates, fish, and other species of economic importance. This phenomenon is flow dependent and may occur repeatedly in the longitudinal profile of a river, usually in response to serial sequence of dams. It has been referred to as the serial discontinuity concept (SDC) of river ecosystems (Ward and Stanford 1983). A number of case studies (Stanford and Ward 1984, Munn and Brusven 1987, Stanford and others 1988, Hauer and others 1989, Stanford and Ward 1989, Sabater and others 1990) demonstrate discontinuities in the longitudinal distribution of stream habitats and attendant biota, and in all cases cold-water invertebrates species have extended their range downstream. Cold-water biota tend to characterize areas that were dominated by warm-water organisms prior to impoundment. What has not been established are the colonization mechanisms and sources, because clearly the impoundments prevent downstream transport of most upstream biota.

Poorly understood riverine refugia exist that may allow some organisms to exist outside their normal ranges or may allow organisms to resist the wholesale disturbance of river regulation and become abundant as they adapt to the new habitats created by the regulation scheme. Probably in many of the case histories cited above, the invertebrate colonists were derived from refugia in unregulated tributaries downstream from the dams, rather than from refugia in the regulated river channel. From the most optimistic perspective, the discontinuity itself may be viewed as a refugium, at least for upstream invertebrate communities that may have been lost by impoundment. Therefore the impounded reaches may have a bearing on the objectives of conservation biology. This argument, of course, is not meant to provide justification for river regulation, because, in the cases cited above, warm-water native communities were lost or displaced downstream as consequence of the altered thermal regime and introduced exotic species.

Summary and Conclusions

Major self-regulatory ecosystem processes, in addition to spawning sites and other obviously important habitats, should be protected where they still exist or should be restored wherever they no longer function. Examples of such processes include lateral migration and hydrologic connectivity between the stream and its floodplain groundwater systems, organic matter production and utilization at different spatial scales (microbes to tree boles) in the channel, and structural dynamics of the floodplain vegetation. These processes often manifest or are controlled dynamically within geomorphically distinct segments, reaches, or channel units.

Most damaging to stream refugia is the isolation of a river from its watershed, primarily by uncoupling the biotic and hydrologic interaction between the stream and the riparian zone. Small streams uncouple differently from large rivers, although the principle remains the same.

Small streams are approximately ten times as numerous as rivers (Leopold and others 1964). They have a large surface area-to-volume ratio and are dependent on the riparian zone to regulate amounts of light energy, complex carbon sources (e.g., leaves and wood), and physical structures (e.g., downed trees, bankside root systems). Where the forest has been removed, the stream is decoupled from these regulatory mechanisms and becomes more hydrologically unstable.

Rivers are linked to the landscape through extensive floodplains and complex channel patterns. Frequently, degradation that causes landscape uncoupling occurs through channelization or flow regulation. As a result, the river is confined to a single channel and denied an annual or more frequent access to its floodplain. As with small streams, riparian vegetation is important structurally and as a source of carbon to the river.

The extent of coupling probably defines the ecological importance of a refuge and how it will affect resistance to or recovery from disturbance. Although no single habitat or site may be a refuge for all organisms from all disturbances, the more dynamic and self-regulatory the site is, the more biotically resistant and resilient it will be.

The refugia concept may be difficult to separate from the idea that stream organisms often require very specific habitats for completion of critical life history stages. Nonetheless, it is clear that natural biological diversity cannot be maintained in river ecosystems, nor can it recover after disturbances, unless these spe-

cialized habitats are available. It seems critically important to identify refugia in specific rivers that may be characteristic of areas of similar ecologies (i.e., ecoregions). Moreover, we must understand how these specialized habitats interrelate to the structure and function of river ecosystems.

Naturalists and ecologists have known for years the general habits of many popular or economically important fish and invertebrate species within river systems. Our understanding of the factors controlling stream communities has advanced dramatically in recent years (Stanford and Covich 1988). However, a more quantified and deterministic understanding is needed of key relationships between lotic communities and their life histories, habitat requirements, and relationships to specific watershed characteristics. For example, understanding the spacing of refugia within basins is both a practical and applied problem as well as a basic theoretical issue. What frequency of deep, perennial pools is required to drought-proof a system and protect biotic communities? What instream flows are needed for protection from winter ice scour or high summer temperatures, especially in regulated rivers? Should stream rehabilitation or enhancement projects for biota target specific habitats or stream reaches, or should they encompass the entire basin? These are examples of practical questions that managers struggle with every day. They do not have easy answers, especially in rivers for which there is little quantitative biophysical data. We suggest that a new and productive approach may be to assess the importance and frequency of refugia within river continua and to manage flows and lateral linkages accordingly. Obviously, new methodologies are needed if this approach is to be implemented in a practical way.

Very costly whole-system fish and wildlife rehabilitation efforts are underway in river systems that have been extensively altered by stream regulation, for example, the Columbia River (Northwest Power Planning Council 1987) and the Missouri River (Hesse and others 1989). Hopefully, a wider array of refugia protection and rehabilitation strategies and methods will evolve from these efforts.

We recommend that several research sites be established within ecoregions (see Hughes and others, this volume) of the United States. These demonstration sites would be dedicated to understanding processes, including spatial and temporal dynamics of refugia, that control biodiversity and the functional integrity river ecosystems (see also Meyer and others 1988). We feel this will be accomplished best by procuring and examining long-term data sets, following, for example, the lead of the Long Term Ecological Research Pro-

gram established by the Division of Biotic Systems of the National Science Foundation. The US Geological Survey is attempting a similar effort on what they call "benchmark" streams, and we encourage a logical expansion of the sites and incorporation of the refugia concept into the analyses.

If river refugia are to be protected in pristine systems and rehabilitated or enhanced in damaged environments, it is essential that management agencies at all levels of government work toward mutual goals that are achievable and based on the state-of-the-art science of river ecology. This necessitates more effective information exchange and, perhaps in some cases, new cooperative research initiatives between state and federal resource management specialists and university and agency scientists.

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