## PROCESS DOMAINS AND THE RIVER CONTINUUM<sup>1</sup>

David R. Montgomery<sup>2</sup>

ABSTRACT: The concept of process domains is proposed as an alternative to the River Continuum Concept for the influence of geomorphic processes on aquatic ecosystems. Broadly defined, the Process Domain Concept is a multi-scale hypothesis that spatial variability in geomorphic processes governs temporal patterns of disturbances that influence ecosystem structure and dynamics. At a coarse scale, regional climate, geology, vegetation, and topography control the suite of geomorphic processes that are distributed over a landscape. Within the broad context so defined, stream channel classification can guide identification of functionally similar portions of a channel network, but the response of otherwise similar reaches can depend upon their geologic and geomorphic context. Within geomorphic provinces defined by differences in topography, climate history, and tectonic setting, areas with generally similar geology and topography define lithotopo units, which are useful for stratifying different suites of dominant geomorphic processes. Process domains are spatially identifiable areas characterized by distinct suites of geomorphic processes, and the Process Domain Concept implies that channel networks can be divided into discrete regions in which community structure and dynamics respond to distinctly different disturbance regimes. The concepts of process domains and lithotopo units provide both a framework for the application of patch dynamics concepts to complex landscapes and a context for addressing the effects of watershed processes on the ecology of mountain drainage basins.

(KEY TERMS: watershed management; aquatic ecosystems; erosion; sedimentation; hydrobiology; process domains; river continuum.)

#### INTRODUCTION

Understanding the role of spatial and temporal variability on links between geomorphic and ecological processes is central to achieving greater understanding of the consequences of land use change on the ecology of mountain drainage basins. A key challenge confronting efforts to better integrate an understanding of geomorphic processes into ecosystem management is how to compare such influences both

across and within physiographically diverse regions. Although the process of watershed analysis can provide a means for better understanding linkages between geomorphic processes and ecological systems (Montgomery et al., 1995), watershed-based approaches provide only a piece of a larger framework (Omernik and Griffith, 1991; Omernik and Bailey, 1997) and do not inherently provide guidance for how to interpret such linkages. This is particularly true for stream channel assessment and restoration efforts, as each channel reach has its own geomorphic context and associated history (Kondolf, 1995; Morris, 1995; Montgomery and Buffington, 1997).

General approaches to linking geomorphic processes and ecological systems incorporate conceptual frameworks that directly or indirectly guide sampling strategies. Perhaps the dominant framework for geomorphic influences on forest ecology is whether community structure tends toward an equilibrium condition or whether non-equilibrium communities are maintained by disturbances that occur frequently in respect to succession (Bormann and Likens, 1979). The dominant conceptual framework in aquatic ecology is the River Continuum Concept (RCC) proposed by Vannote et al. (1980), although the landscape mozaic concept also has been applied to river corridors (Forman, 1995). Many geomorphic schemes are available for classifying different types of stream channels (Church, 1992; Rosgen, 1994; Montgomery and Buffington, 1997). The power of such conceptual frameworks lies in the degree to which they guide sampling and interpretation of channel conditions or designing restoration activities. However, none of these approaches sets a channel reach into a context of watershed disturbance processes.

<sup>&</sup>lt;sup>1</sup>Paper No. 97133 of the Journal of the American Water Resources Association. Discussions are open until December 1, 1999. <sup>2</sup>Associate Professor, Department of Geological Sciences, Box 351310, University of Washington, Scattle, Washington 98195 (E-Mail: dave@bigdirt.geology.washington.edu).

The general lack of process-based context in the field of environmental management has resulted in great emphasis on sampling strategies based on the philosophy that environmental variability is primarily a statistical problem (e.g., EPA's EMAP program). Scientists and regulators also use characteristics of pristine areas as reference standards against which to evaluate the condition of other areas (Hughes et al., 1986). Although useful, these approaches can suffer from the problem that local geomorphic context and disturbance history profoundly influence ecological systems. Moreover, enough pristine sites may not exist in a region to build a comprehensive library of reference conditions for all channel types. Furthermore, both random sampling and pristine refugia approaches to assessing environmental variability can result in misleading comparisons when they ignore systematic patterns in the landscape processes that structure habitat and drive disturbances. As a means to overcome such shortcomings, the ecoregion and subecoregion approach to landscape stratification exemplifies how random sampling can be adapted to hierarchical variations in environmental conditions (Omernik, 1987; Bryce and Clarke, 1996). Nonetheless, the question of how to devise appropriate schemes for stratifying the assessment of landscape states and habitat condition remains a central challenge to integrating consideration of geomorphic processes into watershed management and restoration programs.

Watershed assessment and restoration efforts need to address local-scale impacts associated with particular land management actions. At the same time, the history of downstream routing, integration, and cumulative effect of upland impacts are ecologically relevant and yet difficult to interpret and assess without reference to a larger-scale spatial context and disturbance history. At present, such a framework for connecting disturbance history (and potential) to a spatial context generally is missing from conceptual models of geomorphic influences on ecological systems. This shortcoming is particularly true for current conceptual frameworks in aquatic ecology.

In this paper I discuss the importance of geomorphic context on physical habitat and introduce the concept of lithotopo units as a discrete hierarchical level for organizing analyses of geomorphic influences on ecosystems. I then discuss conceptual models for linking geomorphology and ecology and in particular whether the RCC is an adequate framework for assessing such linkages in mountain drainage basins. Based on these considerations I propose the concept of process domains for examining the influence of geomorphic processes on aquatic ecosystems. Finally, I present examples of how the concept of process domains provides an organizing framework for

linking the dynamics of watershed processes and aquatic ecosystems.

# GEOMORPHIC CONTEXT AND PHYSICAL HABITAT

Geomorphic processes affect ecosystems through their influence on physical habitat structure, although biological processes can, in turn, influence physical processes (Figure 1). At the broadest scale, climate, geology and topography dictate general runoff characteristics, substrate type, and slope (a primary control on both hillslope and channel processes). In mountain drainage basins, the type and distribution of geomorphic processes vary within the context imposed by such large-scale influences, and a hierarchical perspective (Frissell et al., 1986) helps to organize examination of geomorphic influences on ecological systems (Figure 2). Tectonic setting and climate history control the gross distribution of bedrock types, surficial deposits, and topography throughout a region, within which geomorphic provinces distinguish areas with different physiography, bedrock type and structure, climate and climate history. Lithotopo units define finer-scale areas with similar topography and geology and within which similar suites of geomorphic processes influence gross habitat characteristics and dynamics (Montgomery, 1996). Process domains define specific areas in which particular geomorphic processes govern habitat attributes and dynamics.

At the highest level of this hierarchy, tectonic setting defines the long-term rock uplift rates and boundary conditions that drive physiographic development, and also governs the suites of rock types present in a landscape. The eruption of Mt. St. Helens, for example, dramatically illustrated the effect of such macro-scale geomorphic influences on ecological processes at this scale (Bilderback, 1987).

At the scale of geomorphic provinces, differences in regional climate, geology, and topography control the general geomorphic processes and ecosystems developed upon a landscape. Climate defines the temperature regime, general hydrologic characteristics (e.g., snowmelt-dominated versus rain-dominated hydrographs), and the variety of plants and animals capable of inhabiting a landscape (e.g., xeric versus temperate community associations). Regional geology influences both stream chemistry and the geomorphic processes occurring in a landscape. Karst topography, for example, reflects limestone bedrock, whereas earthflows typically occur in clay and tectonically shatterd or deeply weathered rocks.

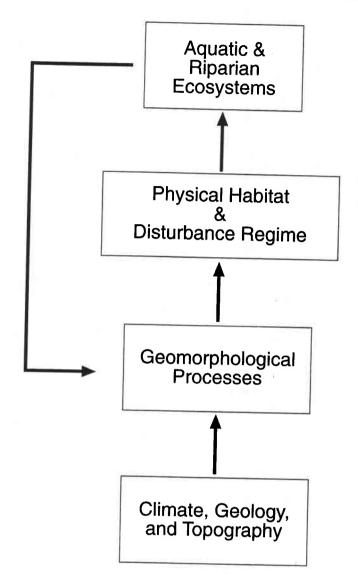


Figure 1. Schematic Representation of the Relations Among Geomorphological Processes, Habitat Structure, and Aquatic and Riparian Ecosystems.

The influence of regional topography on geomorphic processes is profound. For example, landsliding and debris-flow processes are important in steep terrain and relatively unimportant in low-relief watersheds. Moreover, topography governs channel slope, which strongly influences the structure and variability of in-channel habitat (Grant et al., 1990; Montgomery and Buffington, 1997). The combined influences of climate, geology, and topography determine the suite of landscape-forming processes that govern channel characteristics and processes (Leopold et al., 1964; Lotspeich, 1980; Brussock et al., 1985), as well as the type and relative abundance of specific habitat attributes that influence communities developed at finer spatial scales (Corkum, 1989).

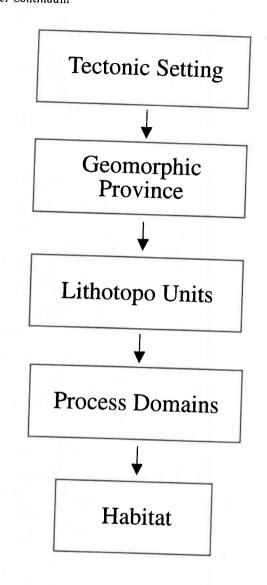


Figure 2. A Spatial Hierarchy for Examining Geological Controls on Ecological Systems.

Within a geomorphic province, systematic differences in rock type and relief strongly influence physical habitat type, abundance, and characteristics. On the Olympic Peninsula, for example, a set of five basic lithotopo units identifies areas within which we would expect similar suites of geomorphic influences on ecological processes: (1) low-relief areas underlain by glacial sediments and outwash, (2) moderate relief areas underlain by glacial sediments and tertiary marine rocks, (3) tertiary sedimentary rocks in either low coastal mountains, (4) the high relief core of the range, and (5) high relief areas of the basaltic crescent (Figure 3). All of the major rivers on the Olympic Peninsula flow across several of these lithotopo units. Habitat characteristics may be much more similar between locations within a single lithotopo unit, but

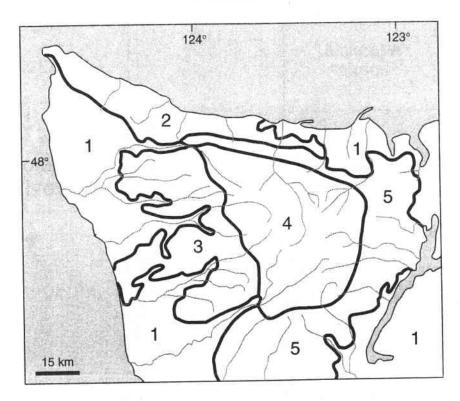


Figure 3. Lithotopo Units of the Olympic Peninsula; Numbers Correspond to Descriptions in the Text.

in different watersheds, than they may be between locations in two lithotopo units in the same watershed (Figure 4). Parallel to the ecoregion-level arguments advanced by Omernik and Bailey (1997), conditions in a similar lithotopo unit may provide insight into extrapolating assessments of environmental conditions across watersheds within a geomorphic province.

# GEOMORPHIC PROCESSES AND RIVER ECOLOGY

Physical processes influence species abundance and community structure in river systems through the variability of habitat characteristics in four dimensions: longitudinal (down valley), lateral (channel-floodplain), vertical (channel-groundwater), and temporal (Ward, 1989). While variability of the physical environment generally defines the habitat template to which organisms adapt (Southwood, 1977, 1988), the temporal and spatial variability of channel processes are particularly important controls on both local community composition and adaptive strategies for aquatic and riparian ecosystems (Minshall, 1988; Resh et al., 1988; Power et al., 1988; Ward, 1989; Poff, 1992). Two general conceptual models relate how

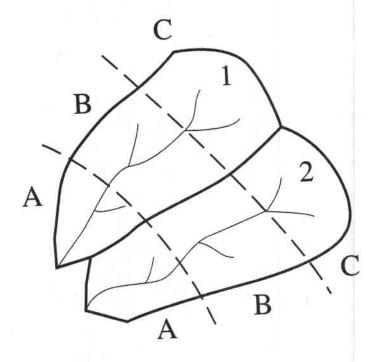


Figure 4. Relationship Among Lithotopo Units (A,B, C) and Watersheds (1,2). Stream channel properties in lithotopo unit C may be more comparable between the two watersheds than are stream channel properties within one of the watersheds, but in different lithotopo units.

biological communities and ecological processes respond to changes in the physical environment of river systems: the River Continuum Concept (Vannote et al., 1980) and ideas concerning patch dynamics (Pickett and White, 1985). While each of these models pertains to aspects of geomorphic influences on aquatic ecology, neither model provides a complete framework.

## River Continuum Concept

Vannote et al. (1980) proposed the River Continuum Concept (RCC) to relate longitudinal variations in aquatic communities to systematic downstream changes in river systems. The original RCC consisted of five propositions, but Statzner and Higler (1985) presented a compelling case for dismissing all but the primary tenet: that river systems are characterized by a gradational continuum of physical conditions that control aquatic community composition from small headwater streams to large floodplain rivers. Although proponents of the RCC recognize the influence of local processes that disrupt the continuum (Bruns et al., 1984; Cummins et al., 1984; Minshall et al., 1985), the RCC itself neglects discrete spatial differences in the effect of geomorphological processes on aquatic and riparian community structure. The interpretation of such spatial differences as local "exceptions" to the RCC (Bruns et al., 1984) provides no insight into how such exceptions may be organized across space and time.

### Patch Dynamics

Spatial and temporal variations in landscapeforming processes create habitat patches with distinctive sizes, persistence, and controlling mechanisms (Forman and Godron, 1978; Pringle et al., 1988). Many biological communities are influenced by the division of landscapes into patches maintained by either disturbance or spatial transitions in the processes creating and maintaining habitat (Wiens, 1976; Forman and Godron, 1978; Pickett and White, 1985). This view of the controls on community structure emphasizes the highly localized nature of many disturbance processes. Applied to river systems, patch dynamics concepts hold that temporally variable processes create distinct habitat patches that define an environmental template for aquatic and riparian ecosystems (Townsend, 1989). Such habitat patches can be created by a wide range of processes, and patch dynamics integrates inherently local effects. However, a key problem in applying patch dynamics concepts in mountain watershed is lack of ability to predict or identify areas characterized by different patch-forming processes.

## Routing Processes vs. Local Controls

The RCC and patch dynamics ideas respectively pertain to the influence of routing processes and local controls on aquatic ecosystems. Channels collect water, sediment, and organic debris and route these materials through and eventually off of a landscape. Channel form and function reflect both local controls that govern the supply of sediment, water, solutes, and large wood and the ability of the channel to transport these inputs (Montgomery and Buffington, 1997). Physical processes governing the delivery and transport of these materials thereby create spatial and temporal variability of in- and near-channel habitat. Within this context, the RCC and patch dynamics models can be viewed as end-member concepts for the influence of geomorphic processes on ecosystems at the scale of valley segments and channel reaches. While some physical phenomena that influence aquatic and riparian ecosystems are continuum driven, others are controlled primarily by local influences (Figure 5). Hence, geomorphic influences on aquatic and riparian communities reflect a combination of processes exhibiting either continuum-like or patchy characteristics, as recently argued by Townsend (1996).

Patch forming processes produce spatial environmental variability (Wiens, 1976), and spatial influences on stream and riparian habitat units are governed by discrete objects, conditions, or processes. Examples of spatially controlled patch-forming processes include pool formation by scour around woody debris, bank projections, and flow convergence through meander bends. Temporally-controlled patch-

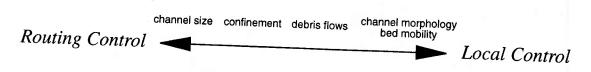


Figure 5. Continuum Between Local and Routing Controls on Certain Channel Processes.

forming processes involve a history of disturbance and recovery, such as side channel formation and abandonment, or variations in bed material due to fluctuating sediment supply (Reeves et al., 1995). Patch-forming events occur over many scales and can reflect either routing or local influences, but they nonetheless result in inherently local effects.

Both the RCC and patch dynamics models apply to some of the processes structuring aquatic and riparian ecosystems through river networks, but neither model addresses the underlying spatial structure of geomorphic processes; the RCC also does not address temporal variation. In this sense, patch dynamics ideas provide a mechanism in search of a context. The concept of process domains can provide both (1) a context for applying patch dynamics ideas across whole landscapes and (2) a complementary alternative to the RCC that integrates the effects of both temporal variability in disturbance processes and the effects of upland processes on river systems. In essence, the concept of process domains provides a way to explicitly link the consideration of spatial and temporal variability in geomorphic influences on aquatic ecosystems in mountain drainage basins.

## THE PROCESS DOMAIN CONCEPT

The Process Domain Concept (PDC) maintains that systematic, landscape-scale patterns to disturbance processes exert distinct influences on lotic and riparian ecosystems (Table 1), in effect extending long-standing ideas concerning relations between vegetation patterns and physiographic forms and processes (Cowles, 1901). The assumption underlying the PDC is that the influence of spatial and temporal variability in geomorphic processes on biological systems is controlled by the size, frequency, and duration of the associated habitat disturbance. In this context,

disturbance may be defined as "any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment" (White and Pickett, 1985, pg. 7). The disturbance regime describes the spatial pattern and statistical distribution of events in terms of frequency, magnitude, and duration of associated changes in the physical environment (Figure 6). Process domains are predictable areas of a landscape within which distinct suites of geomorphic processes govern physical habitat type, structure, and dynamics; the disturbance regimes associated with process domains dictate the disturbance template upon which ecosystems develop (Swanson et al., 1988). As such, process domains characterize systematic differences in the type and frequency of disturbance and habitat-forming events. In short, the concept of process domains provides a way to represent spatial differences in the disturbance regimes that structure habitat.

A key tenent of the PDC is that fundamental differences in landscape processes allow identification of landscape units that correlate with differences in ecosystem organization (for additional perspectives on this issue see the related discussions by Swanson et al., 1988; Takeuchi et al., 1995; and Parker and Bendix, 1996). Perhaps the most basic set of process domains includes: hillslopes, hollows, channels, and floodplains. Each of these, however, can be subdivided into finer scale distinctions (e.g., types of channels or floodplains). The PDC assumes that coarse differences in the distribution and/or community structure of aquatic and riparian flora and fauna parallel the distribution of these domains because of associated variations in disturbance processes. Simply put, the PDC holds that one can define and map domains within a watershed characterized by different geomorphic processes, disturbance regimes, response potential, and recovery time, and that the divisions so recognized have ecological significance.

TABLE 1. Effect of Spatial Scale on Geomorphological Influences on Ecosystems and the Biological Attributes Most Affected.

Spatial Scale	Geomorphological Influences	Biological Attributes
Regional/Physiographic Province	Climate, Topography, Geology	Types of Communities
Valley Segment/Channel Reach	Routing of Sediment, Water, and Organic Matter (RCC)	Community Composition and Species Abundance
	Process Domains and Disturbance Regimes (PDC)	
Channel Unit or Patch	Local Factors/Disturbance History	Habitat Use by Individuals

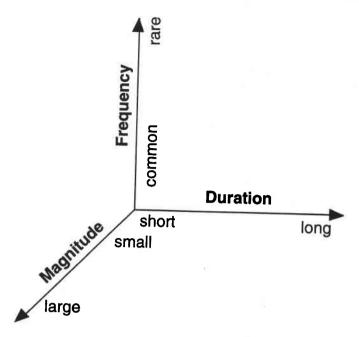


Figure 6. Disturbance Regimes for Geomorphological Processes Can be Defined in Terms of Frequency, Magnitude, and Duration of Associated Impacts.

The spatial extent of areas subject to different disturbance regimes are associated with areas subject to different geomorphic processes, such as fire, landsliding, channel migration, and flooding. Areas prone to shallow landsliding, for example, can be predicted using simple physics-based models (Dietrich et al., 1993, 1995; Montgomery and Dietrich, 1994). Mapping the relative potential for slope failure across entire watersheds reveals systematic patterns that can be interpreted to assess areas of a watershed in which debris flows are a dominant process. Extension of similar models to other processes enables prediction of process domains based on the predicted distribution of hillslopes, hollows, different types of channels, landslide-prone areas and bedrock outcrop (Dietrich et al., 1992, 1993). The process domains so identified predict areas with different habitat types, extent, and disturbance frequency in so much as they map disturbance regimes.

A typical mountain watershed in the Pacific Northwest, for example, has a number of distinct landscape-scale process domains (Figure 7). Convex planform hillslopes define zones of sediment production where rock is turned into colluvial soil through processes such as tree throw, splintering by freezethaw cycles, or the burrowing of fossorial mammals. Soil profiles rapidly come into equilibrium with production rates (Dietrich et al., 1995), and hillslopes provide relatively stable, well-drained areas in which fire and wind are the dominant geomorphic

disturbance processes. Hollows are fine-scale, unchanneled valleys where topographic convergence concentrates sediment moved by soil creep, ravelling, and biogenic transport. Consequently, soil profiles thicken through time in hollows. Topographic convergence also focuses surface and subsurface runoff to hollows, which produces elevated soil moisture and leads to a cycle of gradual colluvial infilling followed by catastrophic evacuation by shallow landsliding (Dietrich and Dunne, 1978). Hollows have both greater seasonal saturation than neighboring hill-slopes and a natural debris flow recurrence interval on the order of thousands of years (Reneau and Dietrich, 1990, 1991).

Immediately downslope of hollows, fluvial processes are relatively ineffective in the ephemeral colluvial channels that form the tips of the channel network (Montgomery and Buffington, 1997). Here the dominant sediment transport process and disturbance agent is scour by debris flows originating in upslope hollows. Because of the numerous upslope debris-flow source areas, colluvial channels are subject to much more frequent disturbance than are hollows (Reneau and Dietrich, 1987). Steep alluvial channels tend to be confined by narrow valley walls, whereas lowgradient alluvial channels tend to build laterally extensive floodplains. Direct disturbance by floods is enhanced in confined channels in comparison to unconfined channels in which overbank flows spread across the floodplain. Channel migration and avulsions also give rise to a variety of habitat types over different time scales in floodplain channels. Avalanche chutes and bedrock outcrops are additional, distinct process domains that are common in high elevation catchments. Each of these topographic positions can be readily mapped in the field, and with appropriate methods can be predicted from digital topography (Dietrich et al., 1992). The PDC assumes that different physical processes and disturbance regimes in these distinct process domains impart spatial variability to the biological communities that develop upon a landscape.

## Landscapes as Mosaics of Process Domains

Landscape-specific arrangements and linkages among process domains impart unique spatial patterns to particular river systems. Hillslope/channel interactions, for example, differ dramatically between the wide u-shaped valleys of the northern Cascades and the narrow v-shaped valleys of the southern Cascades. Wide u-shaped valleys filled with glacial sediments tend to disconnect channels from hillslope processes, whereas channels in the narrow valleys of central Oregon are not buffered from disturbances

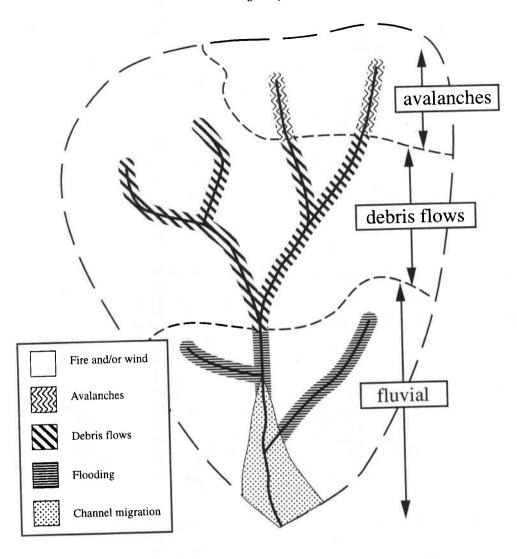


Figure 7. Typical Coarse-Scale Riverine Process Domains for Pacific Northwest Drainage Basins.

originating on hillslopes (Grant and Swanson, 1995). The particular mosaic of process domains arrayed across a landscape controls the types of physical habitat and their variability through time, which in turn, influence aquatic and riparian community composition and dynamics. Unfortunately, most land management approaches fail to recognize the highly structured nature of the process domains upon which human actions are superimposed.

Linking spatial and temporal variability in the controls on habitat to population, community, and ecosystem dynamics also requires consideration of scale. The disturbance regime of a single channel is an altogether different concept than the collective disturbance regime of channels in the headwater portions of a watershed. While local disturbance is important for an individual organism, temporal

patterns of disturbance over larger spatial scales control population and community response and stability (Reeves et al., 1995). Moreover, the relative influence of continuum versus local geomorphic influences on ecosystems to some extent reflects the scale under consideration. Local influences become progressively more important with decreasing spatial and temporal scales, whereas many geomorphic influences on aquatic and riparian ecosystems become more continuum-like over longer spatial and temporal scales. Although there are few data available against which to directly test the PDC, there are many examples that indicate the premise underlying the concept appears valid.

# EXAMPLES IN SUPPORT OF THE PROCESS DOMAIN CONCEPT

Hillslope processes strongly influence both community composition and patterns of hillslope vegetation. Recurrent disturbance of vegetation growing in landslide-prone areas, for example, can impart non-equilibrium conditions on forest development (Hupp, 1983). Moreover, the nature of post-disturbance succession differs for debris-flow source areas, runout paths, and deposits (Flaccus, 1959). In many alpine regions, recurrent avalanches are a dominant control on stand structure on steep convergent slopes and channels (Smith, 1974; Butler, 1979). Variations in soil moisture can also control community composition, and the presence of certain species can delineate seeps and springs (Meinzer, 1927; Dunne et al., 1975). As spatial patterns of soil moisture and landsliding are strongly controlled by topography (Beven and Kirkby, 1979; O'Loughlin, 1986; Montgomery and Dietrich, 1994), the distribution of landscape units associated with different disturbance regimes varies predictably across a landscape. Hack and Goodlett's (1960) classic study of Appalachian forests and hillslope processes demonstrated the strong spatial correspondence between landscape units and significant differences in vegetation community structure predicted by the PDC.

There is also strong correspondance between process domains and riparian or streamside vegetation. In some areas the association of riparian vegetation and process domains can be pronounced, as in semiarid areas where dramatic bands of riparian vegetation reflect differences in soil moisture (Meizner, 1927). Hupp's (1982) documentation of relations between differences in stream gradient, floodplain geometry and riparian forest diversity further illustrates relationships between identifiable landscape units and differences in riparian forests. Osterkamp and Hupp (1984) further showed that valley-bottom geomorphic surfaces that were characterized by different flow-driven disturbance frequency and intensity had distinct vegetation communities. In addition, riparian vegetation composition and structure differs in confined and unconfined valley segments (Gregory et al., 1991). In wide, unconfined valley bottoms with well-developed floodplains, disturbance associated with floods and lateral channel migration can lead to a complex riparian forest (Malanson, 1993; Forman, 1995). In contrast, confined alluvial channels that are not free to migrate across their valley bottom typically have only narrow riparian vegetation or terrestrial associations that extend to the channel banks, whereas confined channels recently disturbed by flooding or debris-flow processes can be lined by distinct riparian

or early successional communities, confined streams not recently disturbed may have close to full canopy closure of late successional associations (Malanson, 1993): Well-defined longitudinal corridors of riparian or early successional vegetation along such channels would indicate either synchronous catastrophic disturbance or a frequent disturbance regime. Hence, differences in the type of disturbance in confined and unconfined channels influence riparian community structure and dynamics, as expected by the PDC.

The influence of definable process domains on aquatic ecosystems has received less attention, but it is widely recognized that disturbance, such as that associated with high flows, may influence aquatic community composition through direct mortality or reduced recruitment and fry survival (Ross and Baker, 1983; Schlosser, 1985; Mathews, 1986; Erman et al., 1988; Freeman et al., 1988). Frequent disturbance may also prevent competitive exclusion, resulting in greater community diversity (Seegrist and Gard, 1972; Meffe, 1984). Hence, the predictability of high-flow events can influence the stability of stream fish assemblages (Moyle and Vondracek, 1985). The influence of discharge variability on community structure may be strongly influenced by the availability of refugia from high and low-flows (Schlosser, 1990). While the composition of many stream fish assemblages is correlated with stream order (Shelford, 1911; Sheldon, 1968; Horwitz, 1978; Platts, 1979; Li et al., 1987; Schlosser, 1990), such downstream patterns in fish community structure may reflect systematic changes in channel morphology and habitat characteristics. In addition, channel type, confinement, bed mobility, and the availability of off-channel refugia vary discontinuously through many channel networks. The utility of the PDC in this context lies in the ability to use such identifiable geomorphic characteristics to delineate areas with different community structure.

At a coarse scale, support for applying the PDC to aquatic ecosystems comes from evidence that stream community assesmblages differ consistently among physiographic provinces and ecoregions in Oregon (Hughes et al., 1987; Whittier et al., 1988). At a finerscale, channel-unit morphology is controlled by local processes, and the resulting character of the physical habitat controls both the type and amount of habitat available to fish communities. Gorman and Karr (1978) argue that most fish species are habitat specialists and that local geomorphic processes controlling habitat structure are a primary influence on the composition of fish communities. At different points in their life histories some species inhabit particular microhabitats defined by channel units with specific flow velocity and depth (Bisson et al., 1982). Changes in reach or unit-level channel morphology, therefore,

may influence community composition. For example, Angermeier and Karr (1984) report significant changes in the distribution and composition of fish species in response to removal of LWD in a small, low-gradient channel. Similarly, Gowan and Fausch (1996) report significant increases in trout abundance in response to habitat change resulting from installation of log weirs in Colorado streams.

In fine-scale applications to habitat-forming processes, the PDC also provides a framework for examining the distribution, abundance, and community structure of benthic fauna, which exhibit distinct habitat preferences based on bed surface texture and the type and distribution of channel units (Minshall,

1968; Cummins and Lauff, 1969; Minshall and Minshall, 1977; Huryn and Wallace, 1987). Channel-bed scouring may cause a drastic decline in benthic fauna (Boulton et al., 1992), and Gurtz and Wallace (1984) demonstrated that finer, and therefore more mobile, patches of channel substrate in a small headwater stream exhibited the greatest reduction in macroinvertebrate populations from sustained disturbance associated with logging. The influence of bed mobility on benthic fauna may be patchy at both the reach and channel unit scales (Downes et al., 1993), but streambeds in different channel types exhibit distinct styles of streambed mobility (Montgomery and Buffington, 1997). Hence, the PDC predicts that benthic

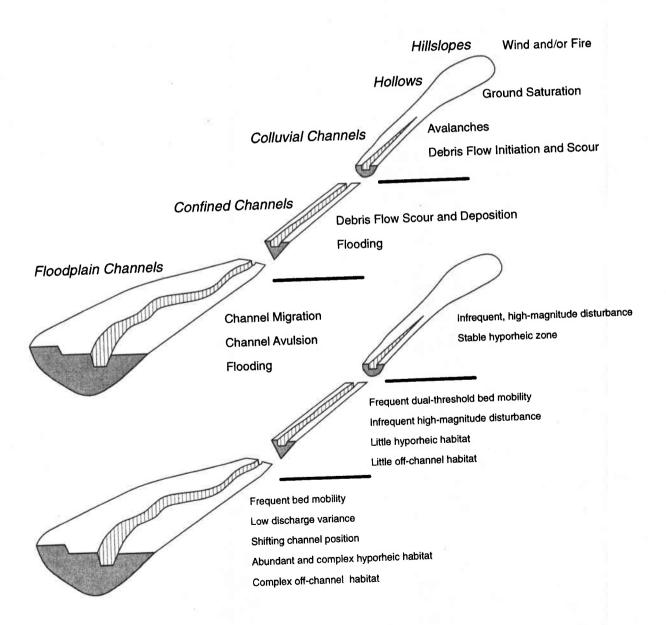


Figure 8. Schematic Illustration of a Mountain Channel Network Showing Valley Segments Characterized by Different Disturbance Processes (upper) and Associated Habitat Characteristics (lower).

communities should reflect local changes in channel reach and/or unit morphology. Similarly, Brussock and Brown (1991) found that reach-level variations in physical habitat both controlled macroinvertebrate distributions and obscured longitudinal patterns of community structure predicted by the RCC. Further support for the relevance of the PDC at fine spatial scales is found in Statzner and Higler's (1986) contention that changes in channel morphology and shear stress govern benthic community composition.

# PROCESS DOMAINS AND THE RIVER CONTINUUM

The spatial and temporal variability of geomorphic processes governing habitat quality, availability, disturbance, and recovery impart a patchy character to aquatic and riparian habitats. The resulting patterns of habitat availability define conditions within which community interactions develop. At the watershed scale, process domains identify distinct process zones that divide channel networks into channel reaches or valley segments dominated by different disturbance regimes and environmental characteristics (Figure 8). The RCC, however, does not account for these fundamental differences in channel processes and, therefore, provides an incomplete framework for examination of environmental influences on aquatic ecosystems. Similarly, the patch dynamics framework recognizes the form of habitat structure but does not address the underlying spatial structure to the processes governing the disturbance mosaic distributed across a landscape. The PDC provides a framework for viewing these processes in a watershed context, but it neither contradicts, nor is incompatible with the RCC. Some channel characteristics and processes, such as channel size and organic matter retention, may change gradationally downstream through a channel network and be well described as a continuum. Consequently, both the RCC and PDC prove useful for considering the full suite of channel characteristics and processes influencing aquatic and riparian ecosystems.

Regional differences in climate, geology, and topography strongly influence the relative importance of continuum and process domain processes. At the reach or valley segment scale, channels in areas with little relief, uniform climate, and simple geology should exhibit more continuum-like geomorphic influences on ecological systems. In contrast, channels in areas with significant relief, variable climate, and complex geology are likely to exhibit more process-domain-like controls (Figure 9). Consequently, channels in mountainous regions such as the Pacific

Northwest, southeast Alaska, and the Rocky Mountains are likely to exhibit a greater process domain character than low-relief watersheds in the mid-western United States. Neither approach, however, provides a universal model for the influence of geomorphic processes on aquatic and riparian ecosystems. Hence, a hybrid conceptual model that recognizes both routing processes and local controls on channel reach and valley segment characteristics provides a more general framework adaptable to any environment. Valley segment and reach-level controls may influence the habitat characteristics that ultimately drive community structure and distribution for species that are habitat specialists, but aquatic and riparian habitat is fundamentally patchy at the scale experienced by individual organisms. Perhaps the River Continuum and Process Domain Concepts are best viewed as end-member models for the largerscale template upon which finer-scale patch dynamics are superimposed. The concepts of process domains and lithotopo units provide a particularly robust framework for linking geomorphic processes and the ecology of mountain drainage basins.

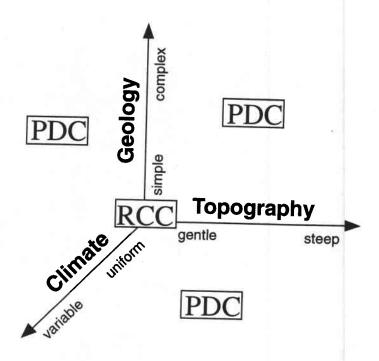


Figure 9. Hypothesized Effect of Climate, Geology, and Topography on the Degree to Which the Geomorphic Influences on Aquatic Ecosystems are Described by the River Continuum (RCC) and Process Domain (PDC) Concepts. Complex geology, steep topography, and a variable climate all enhance the ecological relevance of process domains, whereas simple geology, gentle topography, and a uniform climate enhance the ecological relevance of routing process.

#### ACKNOWLEDGMENTS

Preparation of this paper was supported by U.S.D.A. Forest Service co-operative agreement PNW 93-0441, U.S. Environmental Protection Agency through cooperative agreement CR824682, and gifts from the Washington Forest Protection Association and the Simpson Timber Company. The author thanks John Buffington, Pete Bisson and anonymous reviewers for helpful critiques and Jim Karr for his critique of a very early version of the manuscript.

#### LITERATURE CITED

- Angermeier, P. L. and J. R. Karr, 1984. Relationships Between Woody Debris and Fish Habitat in a Small Warmwater Stream. Transactions of the American Fisheries Society 113:716-726.
- Beven, K. and M. J. Kirkby, 1979. A Physically Based, Variable Contributing Area Model of Basin Hydrology. Hydrol. Sci. Bull. 2443.69
- Bilderback, D. E. (Editor), 1987. Mount St. Helens 1980: Botanical Consequences of the Explosive Eruptions. University of California Press, Berkeley, California, 360 pp.
- Bisson, P. A., J. L. Nielson, R. A. Palmason, and L. E. Gore, 1982. A System of Naming Habitat Types in Small Streams, With Examples of Habitat Utilization by Salmonids During Low Stream Flow. In: Acquisition and Utilization of Aquatic Habitat Information, N. B. Armantrout (Editor). Eastern Division, American Fisheries Society, Portland, Oregon, pp. 62-73.
- Bormann, F. H. and G. E. Likens, 1979. Catastrophic Disturbance and the Steady State in Northern Hardwood Forests. Am. Scientist 67:660-669.
- Boulton, A. J., C. G. Peterson, N. B. Grimm, and S. G. Fisher, 1992. Stability of an Aquatic Macroinvertebrate Community in a Multiyear Hydrologic Disturbance Regime. Ecology 73:2192-2207.
- Bruns, D. A., G. W. Minshall, C. E. Cushing, K. W. Cummins, J. T. Brock, and R. L. Vannote, 1984. Tributaries as Modifiers of the River Continuum Concept: Analysis by Polar Ordination and Regression Models. Arch. Hydrobiol. 99:208-220.
- Brussock, P. P. and A. V. Brown, 1991. Riffle-Pool Geomorphology Disrupts Longitudinal Patterns of Stream Benthos. Hydrobiologia 220:101-117.
- Brussock, P. P., A. V. Brown, and J. C. Dixon, 1985. Channel Form and Stream Ecosystem Models. Wat. Resour. Bull. 21:859-866.
- Bryce, S. A. and S. E. Clarke, 1996. Landscape-Level Ecological Regions: Linking State-Level Ecoregion Frameworks With Stream Habitat Classifications. Environ. Manag. 20:297-311.
- Butler, D. R. 1979. Snow Avalanche Path Terrain and Vegetation, Glacier National Park, Montana. Arct. Alpine Res. 11:17-32.
- Church, M., 1992. Channel Morphology and Typology. In: The Rivers Handbook, P. Carlow and G. E. Petts (Editors). Blackwell Scientific Publications, Oxford, pp. 126-143.
- Corkum, L. D., 1989. Patterns of Benthic Invertegrate Assemblages in Rivers of Northwestern North America. Freshwater Biology 21:191-205.
- Cowles, H. C., 1901. The Physiographic Ecology of Chicago and Vicinity. Bot. Gaz. 31:73-108; 145-182.
- Cummins, K. W. and G. H. Lauff, 1969. The Influence of Substrate Particle Size on the Microdistribution of Stream Macrobenthos. Hydrobiologia 34:145-181.
- Cummins, K. W., W. G. Minshall, J. R. Sedell, C. E. Cushing, and R. C. Petersen, 1984. Stream Ecosystem Theory. Verh. Int. Ver. Limnol. 22:1818-1827.
- Dietrich, W. E. and T. Dunne, 1978. Sediment Budget for a Small Catchment in Mountainous Terrain. Zeit. für Geomorph., Suppl. 29:191-206.

- Dietrich, W. E., C. J. Wilson, D. R. Montgomery, J. McKean, J., and R. Bauer, 1992. Channelization Thresholds and Land Surface Morphology. Geology 20:675-679.
- Dietrich, W. E., C. J. Wilson, D. R. Montgomery, and J. McKean, 1993. Analysis of Erosion Thresholds, Channel Networks and Landscape Morphology Using a Digital Terrain Model. J. Geol. 101:259-278.
- Dietrich, W. E., R. Reiss, M.-L. Hsu, and D. R. Montgomery, 1995. A Process-Based Model for Colluvial Soil Depth and Shallow Landsliding Using Digital Elevation Data, Hydrol. Proc. 9:383-400
- Downes, B. J., P. S. Lake, and E. S. G. Schreiber, 1993. Spatial Variation in the Distribution of Stream Invertebrates: Implications of Patchiness for Models of Community Organization. Freshwater Biology 30:119-132.
- Dunne, T., T. R. Moore, and C. H. Taylor, 1975. Recognition and Prediction of Runoff-Producing Zones in Humid Regions. Hydrol. Sci. Bull. 20:305-327.
- Erman, D. C., E. D. Andrews, and M. Yoder-Williams, 1988. Effects of Winter Floods on Fishes in the Sierra Nevada. Can. J. Fish. Aguat. Sci. 45:2195-2200.
- Flaccus, E., 1959. Revegetation of Landslides in the White Mountains of New Hampshire. Ecology 40:692-703.
- Forman, R. T. T., 1995. Land Mosaics: The Ecology of Landscapes and Regions. Cambridge University Press, Cambridge, Massachusetts, 632 pp.
- Forman, R. T. T. and M. Godron, 1978. Patches and Structural Components for a Landscape Ecology. BioScience 31:733-740.
- Freeman, M. C., M. K. Crawford, J. L. Barrett, D. E. Facey, M. G. Flood, J. Hill, D. J. Strouder, and D. G. Grossman, 1988. Fish Assemblage Stability in a Southern Appalacian Stream. Can. J. Fish. Aquat. Sci. 45:1949-1958.
- Frissell, C. A., W. J. Liss, C. E. Warren, and M. D. Hurley, 1986. A Hierarchical Framework for Stream Habitat Classification: Viewing Streams in a Watershed Context. Environ. Manag. 10: 199-214.
- Gorman, O. T. and J. R. Karr, 1978. Habitat Structure and Stream Fish Communities. Ecology 59:507-515.
- Gowan, C. and K. D. Fausch, 1996. Long-Term Demographic Responses of Trout Populations to Habitat Manipulation in Six Colorado Streams. Ecological Applications 6:931-946.
- Grant, G. E., F. J. Swanson, and M. G. Wolman, 1990. Pattern and Origin of Stepped-Bed Morphology in High-Gradient Streams, Western Cascades, Oregon. Geol. Soc. Am. Bull. 102:340-352.
- Grant, G. E. and F. J. Swanson, 1995. Morphology and Processes of Valley Floors in Mountain Streams, Western Cascades, Oregon. In: Natural and Anthropogenic Influences in Fluvial Geomorphology, J. E. Costa, A. J. Miller, K. W. Potter, and P. R. Wilcock (Editors). Am. Geoph. U. Geoph. Mono. 89, pp. 83-101.
- Gregory, S. V., F. J. Swanson, W. A. McKee and K. W. Cummins, 1991. An Ecosystem Perspective of Riparian Zones. BioScience 41:540-551.
- Gurtz, M. E. and J. B. Wallace, 1984. Substrate-Mediated Response of Stream Invertebrates to Disturbance. Ecology 65:1556-1569.
- Hack, J. T. and J. C. Goodlett, 1960. Geomorphology and Forest Ecology of a Mountain Region in the Central Appalachians. U.S. Geol. Surv. Prof. Paper 347, 66 pp.
- Horwitz, R. J., 1978. Temporal Variability Patterns and the Distributional Patterns of Stream Fishes. Ecological Monographs 48: 307-321.
- Hupp. C. R., 1982. Stream-Grade Variation and Riparian-Forest Ecology Along Passage Creek. Virginia. Bull. Torrey Bot. Club 109:488-499.
- Hupp, C. R., 1983. Geo-Botanical Evidence of Late Quaternary Mass Wasting in Block Field Areas of Virginia. Earth Surf. Proc. Landf. 8:439-450.

- Huryn, A. D. and J. B. Wallace, 1987. Local Geomorphology as a Determinant of Macrofaunal Production in a Mountain Stream. Ecology 68:1932-1942.
- Hughes, R. M., D. P. Larsen, and J. M. Omernik, 1986. Regional Reference Sites: A Method for Assessing Stream Potentials. Environ. Manag. 10:629-635.
- Hughes, R. M., E. Rexstad, and C. E. Bond, 1987. The Relationship of Aquatic Ecoregions, River Basins and Physiographic Provinces to the Ichthyogeographic Regions of Oregon. Copeia 1987(2):423-432.
- Kondolf, G. M., 1995. Geomorphological Stream Channel Classification in Aquatic Habitat Restoration: Uses and Limitations. Aquatic Conservation: Marine and Freshwater Ecosystems 5: 127-141.
- Leopold, L. B., M. G. Wolman, and J. P. Miller, 1964. Fluvial Processes in Geomorphology. W. H. Freeman and Co., San Francisco, California, 522 pp.
- Li, H. W., C. B. Schreck, C. E. Bond, and E. Rexstad, 1987. Factors Influencing Changes in Fish Assemblages of Pacific Northwest Streams. In: Community and Evolutionary Ecology of North American Stream Fishes, W. J. Mathews and D. C. Heins (Editors). University of Oklahoma Press, Norton, Oklahoma, pp. 193-202.
- Lotspeich, F. B., 1980. Watersheds as the Basic Ecosystem: This Conceptual Framework Provides a Basis for a Natural Classification System. Wat. Resour. Bull. 16:581-586.
- Malanson, G. P., 1993. Riparian Landscapes. Cambridge University Press, Cambridge, Massachusetts. 296 pp.
- Mathews, W. J., 1986. Fish Faunal Structure in an Ozark Stream: Stability, Persistence and a Catastrophic Flood. Copeia No. 2: 388-397.
- Meffe, G. K., 1984. Effects of Abiotic Disturbance on Coexistance of Preditor-Prey Fish Species. Ecology 65:1525-1534.
- Meinzer, O. E., 1927. Plants as Indicators of Ground Water. U.S. Geol. Survey Water-Supply Paper 577, 95 pp.
- Minshall, G. W., 1968. Community Dynamics of the Benthic Fauna in a Woodland Springbrook. Hydrobiologia 32:305-339.
- Minshall, G. W. and J. N. Minshall, 1977. Microdistribution of Benthic Invertebrates in a Rocky Mountain (U.S.A.) Stream. Hydrobiologia 55:231-249.
- Minshall, G. W., 1988. Stream Ecosystem Theory: A Global Perspective. J. North Am. Benth. Soc. 7:263-288.
- Minshall, G. W., K. W. Cummins, R. C. Petersen, C. E. Cushing, D. A. Bruns, J. R. Sedell, and R. L. Vannote, 1985. Developments in Stream Ecosystem Theory. Can. J. Fish. Aquat. Sci. 42: 1045-1055.
- Montgomery, D. R., 1996. Influence of Geological Processes on Ecological Systems. *In:* The Rain Forests of Home: Portrait of a North American Bioregion, P. K. Schoonmaker, B. von Hagen, and E. C. Wolf (Editors). Island Press, pp. 43-68.
- Montgomery, D. R. and J. M. Buffington, 1997. Channel Reach Morphology in Mountain Drainage Basins. Geol. Soc. Am. Bull. 109: 596-611.
- Montgomery, D. R. and W. E. Dietrich, 1994. A Physically-Based Model for the Topographic Control on Shallow Landsliding. Water Resour. Res. 30:1153-1171.
- Montgomery, D. R., G. E. Grant, and K. Sullivan, 1995. Watershed Analysis as a Framework for Implementing Ecosystem Management. Water Resour. Bull. 31:369-386.
- Morris, S. E., 1995. Geomorphic Aspects of Stream-Channel Restoration. Physical Geography 16:444-459.
- Moyle, P. B. and B. Vondracek, 1985. Persistence and Structure of the Fish Assemblage in a Small California Stream. Ecology 66: 1-13.
- O'Loughlin, E. M., 1986. Prediction of Surface Saturation Zones in Natural Catchments by Topographic Analysis. Wat. Resour. Res. 22:794-804.

- Omernik, J. M., 1987. Ecoregions of the Coterminous United States. Ann. Assoc. Amer. Geogr. 77:118-125.
- Omernik, J. M. and R. G. Bailey, 1997. Distinguishing Between Watersheds and Ecoregions. J. Am. Wat. Resour. Assoc. 33:935-951.
- Omernik, J. M. and G. E. Griffith, 1991. Ecological Regions Versus Hydrologic Units: Frameworks for Managing Water Quality. J. Soil and Water Cons. 46:334-340.
- Osterkamp, W. R. and C. R. Hupp, 1984. Geomorphic and Vegetative Characteristics Along Three Northern Virginia Streams. Geol. Soc. Am. Bull. 95:1093-1101.
- Parker, K. C. and J. Bendix, 1996. Landscape-Scale Geomorphic Influences on Vegetation Patterns in Four Environments. Physical Geography 17:113-141.
- Pickett, S. T. A. and P. S. White, 1985. The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, New York, New York, 472 pp.
- Platts, W. S., 1979. Relationships Among Stream Order, Fish Populations, and Aquatic Geomorphology in an Idaho River Drainage. Fisheries 4:5-9.
- Poff, N. L., 1992. Why Disturbances Can Be Predictable: A Perspective on the Definition of Disturbance in Streams. J. North Am. Benth. Soc. 11:86-92.
- Power, M. E., R. J. Stout, C. E. Cushing, P. P. Harper, F. R. Hauer, W. J. Mathews, P. B. Moyle, B. Statzner, and I. R. Wais De Badgen, 1988. Biotic and Abiotic Controls in River and Stream Communities. J. North Am. Benth. Soc. 7:456-479.
- Pringle, C. M., R. J. Naiman, G. Bretschko, J. R. Karr, M. W. Oswood, J. R. Webster, R. L. Welcomme, and M. J. Winterbourn, 1988. Patch Dynamics in Lotic Systems: The Stream as a Mosaic. J. North Am. Benth. Soc. 7:503-524.
- Reeves, G. H., L. E. Benda, K. M. Burnett, P. A. Bisson, and J. R. Sedell, 1995. A Disturbance-Based Ecosystem Approach to Maintaining and Restoring Freshwater Habitats of Evolutionarily Significant Units of Anadromous Salmonids in the Pacific Northwest. In: Evolution and the Aquatic Ecosystem: Defining Unique Units in Population Conservation, J. L. Nielsen (Editor). American Fisheries Society Symposium 17:334-349.
- Reneau, S. L. and Dietrich, W. E., 1987. The Importance of Hollows in Debris Flow Studies; Examples from Marin County, California. *In:* Debris Flows/Avalanches: Process, Recognition, and Mitigation, J. E. Costa and G. F. Wieczorck (Editors). Geol. Soc. Am. Rev. Eng. Geol. 7:165-180.
- Reneau, S. L. and W. E. Dietrich, 1990. Depositional History of Hollows on Steep Hillslopes, Coastal Oregon and Washington, National Geogr. Res. 6:220-230.
- Reneau, S. L. and W. E. Dietrich, 1991. Erosion Rates in the Southern Oregon Coast Range: Evidence for an Equilibrium Between Hillslope Erosion and Sediment Yield. Earth Surf. Proc. Land. 16:307-322.
- Resh, V. H., A. V. Brown, A. P. Covich, M. E. Gurtz, H. W. Li, G. W. Minshall, S. R. Reice, A. L. Sheldon, J. B. Wallace, and R. C. Wissmar, 1988. The Role of Disturbance in Stream Ecology. J. North Am. Benth. Soc. 7:433-455.
- Rosgen, D. L., 1994. A Classification of Natural Rivers. Catena 22:169-199.
- Ross, S. T. and J. A. Baker, 1983. The Response of Fishes to Periodic Spring Floods in a Southeastern Stream. Am. Mid. Nat. 109:1-14.
- Schlosser, I. J., 1985. Flow Regime, Juvenile Abundance, and the Assemblage Structure of Steam Fishes. Ecology 66:1484-1490.
- Schlosser, I. J., 1990. Environmental Variation, Life History Attributes, and Community Structure in Stream Fishes: Implications for Environmental Management and Assessment. Envir. Man. 14:621-628.

- Seegrist, D. W. and R. Gard, 1972. Effects of Floods on Trout in Sagehen Creek, California. Trans. Am. Fish. Soc. 101:478-482.
- Sheldon., A. L., 1968. Species Diversity and Longitudinal Succession in Stream Fishes. Ecology 49:193-198.
- Shelford, V. E., 1911. Ecological Succession. Stream Fishes and the Method of Physiographic Analysis. Biological Bulletin 21:9-35.
- Smith, L., 1974. Indication of Snow Avalanche Periodicity Through Interpretation of Vegetation Patterns in the North Cascades, Washington. M.S. Thesis, University of Washington, Seattle, Washington, 279 pp.
- Southwood, T. R. E., 1977. Habitat, the Templet for Ecological Strategies? J. Animal Ecol. 46:337-365.
- Southwood, T. R. E., 1988. Tactics, Strategies and Templets. Oikos 52:3-18.
- Statzner, B. and B. Higler, 1985. Questions and Comments on the River Continuum Concept. Can. J. Fish. Aquat. Sci. 42:1038-1044.
- Statzner, B. and B. Higler, 1986. Stream Hydraulics as a Major Determinant of Benthic Invertegrate Zonation Patterns. Freshwat. Biol. 16:127-139.
- Swanson, F. J., T. K. Kratz, N. Caine, and R. G. Woodmansee, 1988. Landform Effects on Ecosystem Patterns and Processes. Bio-Science 38:92-98.
- Takeuchi, K., M. Ide, M. Yokohari, and R. D. Brown, 1995. Relationships of Landform and Biological Diversity in Landscape Ecology. Trans. Japanese Geomorph. Union 16:215-225.
- Townsend, C. R., 1989. The Patch Dynamics Concept of Stream Community Ecology. J. North Am. Benth. Soc. 8:36-50.
- Townsend, C. R., 1996. Concepts in River Ecology: Pattern and Processes in the Catchment Hierarchy. Arch. Hydrobiol. Suppl. 113 (1-4):3-21.
- Vannote, R. L., G. W. Minshall, K. W. Cummins, J. R. Sedell, and C. E. Cushing, 1980. The River Continuum Concept. Can. J. Fish. Aquat. Sci. 37:130-137.
- Ward, J. V., 1989. The Four-Dimensional Nature of Lotic Ecosystems. J. North Am. Benth. Soc.8: 2-8.
- White, P. S. and S. T. A. Pickett, 1985. Natural Disturbance and Patch Dynamics: An Introduction. *In:* The Ecology of Natural Disturbance and Patch Dynamics, S. T. A. Pickett and P. S. White (Editors). Academic Press, New York, New York, pp. 3-9.
- Whittier, T. R., R. M. Hughes, and D. P. Larsen, 1988. Correspondence Between Ecoregions and Spatial Patterns in Stream Ecosystems in Oregon. Can. J. Fish. Aquat. Sci. 45:1264-1278.
- Wiens, J. A., 1976. Population Responses to Patchy Environments. Ann. Rev. Ecol. Syst. 7:81-120.