

Emerging concepts for management of river ecosystems and challenges to applied integration of physical and biological sciences in the Pacific Northwest, USA*

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ABSTRACT

Integration of biological and physical concepts is necessary to understand and conserve the ecological integrity of river systems. Past attempts at integration have often focused at relatively small scales and on mechanistic models that may not capture the complexity of natural systems leaving substantial uncertainty about ecological responses to management actions. Two solutions have been proposed to guide management in the face of that uncertainty: the use of “natural variability” in key environmental patterns, processes, or disturbance as a reference; and the retention of some areas as essentially unmanaged reserves to conserve and represent as much biological diversity as possible. Both concepts are scale dependent because dominant processes or patterns that might be referenced will change with scale. Context and linkages across scales may be as important in structuring biological systems as conditions within habitats used by individual organisms. Both ideas view the physical environment as a template for expression, maintenance, and evolution of ecological diversity. To conserve or restore a diverse physical template it will be important to recognize the ecologically important differences in physical characteristics and processes among streams or watersheds that we might attempt to mimic in management or represent in conservation or restoration reserves.

Keywords: Natural variability; template; diversity; integrity; scale.

1 Introduction

Biology has provided an important context for the study of physical processes in watersheds and river systems. “Ecology” implies an integrated understanding of biological and physical systems. Applied ecologists have long recognized the constraints imposed on natural systems by human disruption of physical processes. In application, natural resource managers in the Pacific Northwest region of North America have relied on biological and physical scientists to provide guidance for land-use and water management decisions. A principal goal has been to conserve biological diversity and the integrity of aquatic ecosystems, and to sustain production of the natural “goods and services” valued by society (e.g., Callicott and Mumford, 1997; Groves, 2003). This has not been a simple task.

Our understanding of aquatic ecosystems is confounded by their inherent complexity. Experience with complex, integrative, ecological models has engendered a growing sense that process based modeling of complex ecological systems may be fundamentally constrained in its usefulness (Scheffer and Beets, 1994; Root and Schneider, 1995). Uncertainty about key processes

is important. It seems likely, however, that even with detailed, mechanistic understanding it will be impossible to account for the large number of interactions that may strongly influence a system’s behavior. Often it has proved easier for applied biologists and physical scientists to work independently, focusing at relatively small and manageable scales, isolating a single process or site for intensive study. Although we have gained important basic knowledge, it has not been easily generalized or extended to larger systems (e.g., Root and Schneider, 1995).

Discussions of “sustainable” natural resource management (e.g., Christensen *et al.*, 1995; Dale *et al.*, 2000) highlight the uncertain and dynamic nature of ecosystems. The concepts of “ecological integrity” (Angermier and Karr, 1994; Angermeier, 1997; Callicott and Mumford, 1997) and “natural variability” (Landres *et al.*, 1999) suggest a framework for management faced with limited data and knowledge of complex systems. Bringing these ideas to application in the management of river ecosystems represents a challenge and an opportunity for a renewed integration of physical and biological sciences. Our intent in this paper is to outline several emerging concepts and consider the opportunities they represent for new work. We focus our discussion on

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fishes and their habitats as key elements of aquatic ecosystems associated with the rivers of the Columbia River basin because of our familiarity with those systems.

2 Applied integration

The case for an applied integration of biological and physical sciences has always been strong. In aquatic ecosystems the link between biological and physical elements is inextricable. The physical system influencing the supply and transport of materials (water, sediment, wood, nutrients) and heat/energy, directly constrains the structure, productivity, and the spatial and temporal variability of aquatic environments and habitat for aquatic organisms (Engstrom *et al.*, 2000; Naiman *et al.*, 2000). Ultimately these processes result in a spatially and temporally variable network of habitats, and a template for community and population dynamics, adaptation, and evolution (Southwood, 1977; Poff and Ward, 1990; Angermeier, 1997; Reeves *et al.*, 1998).

Although we have long-recognized the links between physical and biological systems (e.g., Forbes, 1887; Hynes, 1970) our ability to translate that to effective management has been limited. Human attempts to exploit and control aquatic and terrestrial resources have altered the key processes and largely changed, simplified, and often disconnected these habitat networks (Frissell and Bayles, 1996; Gregory and Bisson, 1997; Poff *et al.*, 1997). The results are globally apparent in the decline of species and the growing sense of impending crisis tied to accelerated extinctions and declining biodiversity (Purvis and Hector, 2000). The river systems of the western United States provide regional examples (Nehlsen *et al.*, 1991; Frissell, 1993; Lee *et al.*, 1997; Rieman *et al.*, 2003). Within the Columbia River basin (Figure 1), for example, there are 88 native taxa of fishes; at least 38 have been listed as threatened, endangered, or otherwise of special concern by the agencies responsible for their management (Lee *et al.*, 1997). Many are extinct from major portions of their historical ranges and others appear poised on the brink of extinction throughout the region. Disruption of habitat resulting from altered physical/hydrologic processes related to urbanization, agriculture, road construction and timber harvest, grazing, and storage and diversion of water, is a commonly cited cause (Lee *et al.*, 1997; Stouder *et al.*, 1997; Lichatowich, 1999; Williams *et al.*, 1999).

While biological and physical scientists have collaborated for some time, past attempts at bio-physical integration have focused generally at smaller scales, on single or few processes, and largely deterministic models. Much of the regulatory guidance (e.g., standards and criteria) for management of aquatic ecosystems reflects this influence (Poole *et al.*, 2004). Criteria or standards for management typically do not consider important interactions (e.g., criteria are based on a single or few thresholds), or larger-scale constraints (Frissell and Bayles, 1996) that lead to site-specific variation. Accordingly, resource managers have often based their decisions on guidelines that may belie the complex and dynamic nature of ecosystems (Ludwig *et al.*, 1993; Dale *et al.*, 2000; Ruckelshaus *et al.*, 2002). A focus on fine

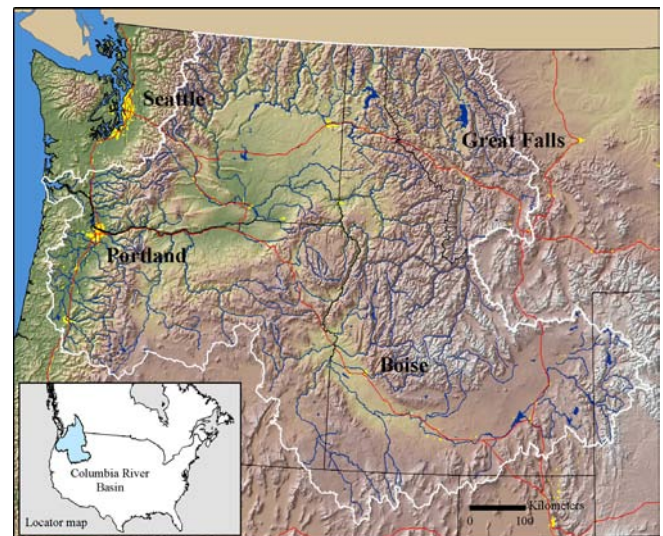


Figure 1 The Columbia River Basin within the United States is represented by a broad range of landscapes and watersheds, river and stream networks, and aquatic ecosystems that support a diversity of species and life history assemblages important from ecological, evolutionary, and socio-economic perspectives. The basin has been developed but the conservation and restoration of diverse, productive, and functional river-stream ecosystems is still possible and important.

sediment-fish incubation linkages, for example, has led biologists to evaluate management under the general model that erosion is bad, often failing to acknowledge that erosion is also the primary source of substrate for productive habitat (Reeves *et al.*, 1995). A focus on plot or small watershed studies has produced an understanding of erosional processes at that scale, but has provided little insight into the spatial and temporal dynamics that influence the conditions in larger and interacting networks of streams (Benda *et al.*, 1998, 2004). A focus on habitat conditions reflected in the correlation of fish abundance and stream channel structure, temperature, or flow has helped us understand the interaction of habitat and fine-scale fish distributions. It has also fostered an unrealistic view that structural standards for channels, or minimum temperatures or flows, should consistently produce productive populations (e.g., Bisson *et al.*, 1997; Poff *et al.*, 1997; Bilby *et al.*, 2003). A logical (though perhaps operationally impossible) goal in this latter case would be the homogenization of streams throughout managed systems with each stream or reach a static and isolated representation of optimal habitat (Reeves *et al.*, 1995; Bisson *et al.*, 1997; Poole *et al.*, 2004). In essence we have often focused on the “engineering” of stable, idealized (or more often in practice, minimally acceptable) habitat conditions in rivers and streams, rather than the processes that create and maintain those habitats (Bisson *et al.*, 1997; Beechie and Bolton, 1999) and the context in which they have evolved (Frissell *et al.*, 1997; Lytle and Poff, 2004).

This general view has progressively given way to the notion that physical and biological patterns and processes are inherently variable in space and time (Christensen *et al.*, 1995; Landres *et al.*, 1999). The concept of “natural variability” recognizes that variation is key to the resilience and productivity of ecosystems (Reeves *et al.*, 1995; Holling and Meffe, 1995) and the

persistence of the elements representing biological diversity. Deterministic and fine-scale models are being replaced by probabilistic models that represent larger landscapes as complex interacting systems (e.g., Benda *et al.*, 1998). In the larger view, however, many believe that we may never reduce any socio-ecological system or even a species population to models that provide the necessary understanding to adequately predict responses to our management or guide us to sustainable levels of exploitation (Ludwig *et al.*, 1993; Holling and Meffe, 1995; Beissinger and Westphal, 1998).

3 Emerging concepts for management

The task for river and watershed managers is to conserve or restore the natural patterns and processes that influence the structure, integrity, complexity, and resilience of aquatic ecosystems (Beechie and Bolton, 1999; Naiman *et al.*, 2000; Hilborn *et al.*, 2003; Palmer *et al.*, 2005). The challenge is to do that with limited ability to predict the behaviors of those systems (Poff, 1997). There are three ideas that have emerged repeatedly in recent discussions of natural resource management and may prove useful to this problem. The implications are that to be more successful, management should attempt to conserve *natural process and variability* and *natural elements of diversity*, and must acknowledge *the influence of scale*. Briefly these ideas can be characterized as follows:

Natural Process and Variability – Managers and biologists have often focused on describing and managing for what were perceived to be optimal structure or patterns in habitat and landscapes. Management more compatible with the natural processes that constrain or influence the structure and variability in landscapes should lead to more resilient, productive, and persistent systems.

Elements of Diversity – The natural variation or diversity in ecological systems is likely key to their resilience. It also represents an important evolutionary legacy. Conservation of remnant diversity and the underlying physical template is a foundation for both short and long-term conservation and any hope of restoration of more resilient and productive ecosystems.

Influence of Scale – Process and pattern are largely scale dependent. Identifying key processes and patterns for management will depend on understanding how those change across the systems of interest.

In the remainder of this paper we consider these concepts and examples of existing or potential work that highlight new directions and opportunities for applied integration of physical and biological sciences in aquatic ecosystem management.

3.1 Natural process and variability

Because of our limited understanding of the complexities of how ecosystems function, one proposed management goal is to maintain (or restore) the mix of historic ecological patterns, and

the processes that govern them, over time. In essence, management should be made more “natural” or compatible with natural processes and variation (Palmer *et al.*, 2005). Conceptually, ecological patterns emerge from the interplay of dynamic processes (climate, disturbances such as fire, or widespread disease) on a (temporally less dynamic) physical template, important elements of which include lithology, landform, and geologic history. Maintaining the mix of patterns and processes requires an assessment of the possible ranges of ecosystem attributes, often referred to as historic or natural “range of variability” (Landres *et al.*, 1999) natural “regimes” (Poff *et al.*, 1997) or “normative” conditions (Williams *et al.*, 1999). In addition to serving as a goal for management, this approach has been broadly proposed to evaluate management consequences, the basis being that past conditions provide a reference for understanding and predicting ecological impacts of natural and human disturbance (Swanson *et al.*, 1993; Cissel *et al.*, 1998; Landres *et al.*, 1999). The underlying logic behind natural management is that, from an evolutionary perspective, the spatial and temporal pattern of habitat dynamics influences the relative success of species (Poff *et al.*, 1997; Lytle and Poff, 2004). Accordingly, natural management should conserve a suite of conditions to which species are adapted. If ecosystems move outside the natural range, species respond, either by declining in abundance or moving; communities change, and extinctions may occur. The concept of natural variability suggests that there is no stable or ideal state for habitat, but that a range of conditions, influenced by the interplay of disturbance, landscape, and geomorphic constraints, produces a mosaic of habitat conditions that is dynamic in time and space. In this context, “disturbance” can have distinctly non-negative connotations, and should be viewed as an important channel structuring and habitat-forming phenomenon (Reeves *et al.*, 1995; Beechie and Bolton, 1999; Naiman *et al.*, 2000). Disturbance has also been defined as an environmental disruption that leads to a biological response (Pickett and White, 1985). Disturbance then may play a dual role as an important force structuring habitat (for example by providing wood and coarse sediment following floods or fire) and biological communities (Poff and Ward, 1990; Reice *et al.*, 1990).

If disturbance is an essential element in the natural variation of aquatic ecosystems, it could be characterized by the frequency, spatial arrangement, and intensity of fluvial-geomorphic processes operating on the landscape (Swanson *et al.*, 1993). It is generally thought that a relatively small number of processes need to be described in order to understand the primary forces structuring ecosystems at any particular scale (Norton and Ulanowicz, 1992; Holling and Meffe, 1995). At the scales of biological relevance for river systems, variability in flow (Poff *et al.*, 1997), material delivery and transport (basically wood, sediment, and nutrients) (Swanson *et al.*, 1990), temperature (Beschta *et al.*, 1987; Poole and Berman, 2001), channel networks and connectivity (Reeves *et al.*, 1995; Rieman and Dunham, 2000; Dunham *et al.*, 2003), are key attributes that respond to disturbance. Cissel *et al.* (1998) and Benda *et al.* (2004) suggest that a small set of climatic and geomorphic processes, and forest fire, which is basically climate-forced, collectively comprise the disturbance

regime of many watersheds in the coastal region of the Pacific Northwest. We have a more limited understanding of the drivers in the interior region, but generally, in the Columbia River basin, fires and floods associated with rainstorms, rain-on-snow events, or snow melt trigger bank erosion, or surface and mass erosion on slopes, which in turn control the supply of wood and sediment to streams (Benda *et al.*, 2003). In similar fashion, runoff from storms transports and redistributes material in the channel, providing diversity in channel structure and aquatic habitats (Benda *et al.*, 2004). At the scale of small watersheds or stream segments, aquatic habitat response to single disturbance mechanisms (fire, logging, roads for example) has been well studied, particularly through paired watershed research (e.g., Clayton and Kennedy, 1985; King, 1994; Megahan *et al.*, 1995; Ketcheson *et al.*, 1999). In contrast, recognition of the link between pattern and process, and the diversity, range, and dynamics of larger interconnected systems and longer temporal scales as influenced by natural disturbance regime is an emerging field.

The links between disturbance and biology beyond that implied by the productivity and complexity of habitats has been explored in little more than a theoretical context (Ward and Tockner, 2001). We know that large natural disturbances can have dramatic and negative short-term consequences for aquatic organisms including local fish extirpations (Gresswell, 1999; Rieman *et al.*, 2003), but they may also have longer-term benefits by creating habitat (Reeves *et al.*, 1995), forcing dispersal (Rieman and Dunham, 2000), or maintaining diverse life history strategies (Quinn, 2005).

Ecological responses to altered patterns of variation and disturbance may be dramatic. Naiman and Turner (2000) suggest that human-induced changes such as fire suppression and flow regulation differ so radically from natural regimes that "all levels of system organization are affected". Poff *et al.* (1997) looked in detail at altered flow regimes below peaking power hydroelectric dams and dams that are managed to stabilize flow. Historically the natural patterns of extreme flows that were regular and predictable have changed such that the magnitude, frequency, rate of change and duration are markedly different. Organisms that time their feeding, migration, and reproduction to patterns in flow are not adapted, and must relocate or perish. Extreme daily variations in flow, that have no analogue in natural systems, lead, in particular, to mortality in shoreline bottom dwellers. When flows are stabilized, specialists are often replaced by generalists, leading to simplified faunal communities (Poff *et al.*, 1997).

Implementation of management that seeks to conserve natural variability and the processes structuring aquatic habitats and communities may be relatively simple in wilderness lands, but will be more elusive elsewhere (Frissell and Bayles, 1996). In fact, returning to a natural disturbance regime (e.g., reestablishing natural fire patterns), which is likely to include large-scale events that can threaten human infrastructure and property, will often be impossible for obvious socio-political reasons (Reeves *et al.*, 1995). One alternative may be to substitute disturbances in an attempt to make the effects of our management more consistent with the effects of natural events. For example, Reeves *et al.* (1995) and Cissel *et al.* (1998) and others (e.g. Nitschke,

2005) have proposed that timber harvest might be substituted for large fires. By recognizing the key differences between natural disturbances and traditional management such as the disposition of wood left on-site, and the frequency, extent, and spatial distribution of the events, Reeves *et al.* (1995) suggest that management could be more compatible with the natural processes that create and maintain productive habitats. Poff *et al.* (1997) provided a similar consideration of natural flow regimes and the changes produced in regulated rivers. They concluded that protecting, or restoring a river's natural flow variability should be the single, most important goal of river management. Poff *et al.* (1997) identified five critical components of the flow regime that regulate ecological processes: magnitude of discharge, frequency of occurrence of flow, duration of specific flows, timing or predictability of flow, and rate of flow change or flashiness. They suggested paying particular attention to the magnitude and frequency of high and low flows. High flows and floods are necessary for sediment transport, delivery of wood, overbank flow connection to off-channel habitat etc., and low flows provide opportunities for riparian plant re-establishment. In recognizing that full flow restoration often is impossible, Poff *et al.* (1997) suggested that mimicking certain geomorphic processes could still provide important ecological benefits. Examples include artificial irrigation to recruit riparian vegetation, and clearing vegetation periodically to provide gravel to sediment-starved regulated rivers. Proposals to produce managed floods in the Colorado River (Poff *et al.*, 1997), to restore more natural flow regimes either by drawing down reservoirs or breaching dams on the Snake River (Williams *et al.*, 1999), and to mimic natural patterns of fire and upland disturbance through innovative harvest practices (Cissel *et al.*, 1999) are some examples of potential applications.

3.2 Elements of diversity

Conservation of biological diversity has become a cornerstone of public land management programs such as those of the US Forest Service (36 CFR 219.20). Implementation of management more consistent with natural variation has become an important element in the land management discussion focused on conservation of biological diversity (Christensen *et al.*, 1995; Dale *et al.*, 2000). Ultimately more natural management may be the only way to conserve biological diversity in human dominated landscapes (Franklin, 1993; Reeves *et al.*, 1995). The simple fact remains, however, that we have not demonstrated the capacity to do it (Frissell and Bayles, 1996; Rieman *et al.*, 2000; Poole *et al.*, 2004). Protection and restoration of key areas or "reserves" where management is essentially excluded has been argued as the only way to assure the maintenance of ecological diversity (Frissell and Bayles, 1996; Noss and Cooperider, 1994), at least in the short term. Such reserves might be viewed as a safety net bridging the gap until more enlightened management can actually be implemented (Reeves *et al.*, 1995), or conserving the last remnants of diversity if it is not.

In conservation biology and natural resource management, biological diversity is a central notion viewed as the representation of the variation among living organisms and the complexes

in which they occur (Angermeier, 1997; Groves, 2003). The richness of biological elements, which is key to the concept, has been represented most visibly in the global conservation discussion as the number and representation of distinct species. There is growing recognition and application, however, of the notion that diversity is multifaceted and includes not only the richness and frequency of species within and among habitats (e.g., Magurran, 1998), but also elements of intraspecific diversity (e.g., genetic and phenotypic), and the complexity of the structural and functional characteristics of species assemblages, populations and habitats networks (Noss, 1990; Angermeier, 1997; Reeves *et al.*, 1998; Ward and Tockner, 2001).

This broader view is important in the Pacific Northwest US and the Columbia River basin in particular. The rivers of this region support relatively few species of fishes (88 native taxa in 10 families) in contrast to the remarkable richness found in regions such as the Mississippi basin (235 species in 33 families, Lee *et al.*, 1997; Reeves *et al.*, 1998). Many of the species in the Columbia River basin are found only in the larger mainstem rivers. Many of the moderate sized (10^3 – 10^4 sq. km) river basins associated with the Public lands of the region may support fewer than a dozen species. There is, however, a remarkable diversity within species. Genetic differentiation in several of the salmonids approaches species level distinctions across the region (Allendorf and Leary, 1988), and has been commonly recognized in distinct subspecies, races, or life-history types (Allendorf and Leary, 1988; Healey, 1991; Utter *et al.*, 1993). At finer scales (within moderate size basins) important variation is evident in genetic markers, and phenotypic characteristics represented by life history, morphology, and behavior (Healey, 1991; Wood, 1995; Willson, 1997; Taylor, 1999; Ruckelshaus *et al.*, 2002; Halupka *et al.*, 2003). Phenotypic diversity has genetic and environmental components (Adkison, 1995; Skúlason and Smith, 1995). A genetic basis for variable phenotypic expression is obviously critical, but variation in body form and size, habitat and forage utilization, and extent and timing of migration and spawning can also emerge as more plastic responses to variation in environment or habitat (Nikol'skiy, 1969; Taylor, 1990, 1999; Gross, 1991; Skúlason and Smith, 1995; Ruckelshaus *et al.*, 2002; Brannon *et al.*, 2004).

There is general consensus that much of biological variation reflects a response to differences in physical environments as a “template” for diversity (Southwood, 1977; Poff and Ward, 1990; Poff and Allan, 1995; Ward and Tockner, 2001). Whether that variation is the result of selection and adaptation or phenotypic plasticity may not be clear without detailed studies (Taylor, 1991; Adkison, 1995). Both cases occur, and in fact, a gradient of genetic divergence may develop as a result of selection and reproductive isolation associated with the existence of distinct phenotypes in common environments (Gross, 1991; Skúlason and Smith, 1995; Schaffer, 2004). Although phenotypic variation can emerge immediately as environments change, it also appears that some diversification may occur relatively quickly (e.g., in a matter of decades or 10's of generations) through adaptive (i.e., genetically based) radiation as distinct environments and opportunities for differential expression and selection are created or restored (Taylor, 1999; Quinn *et al.*, 2000; Quinn, 2005).

Regardless of the immediate cause, phenotypic diversity may be key to the stability, persistence, and productivity of populations in variable environments. Variation in the extent, timing, and location of spawning, rearing, and migration observed in many salmonids, for example, will place critical life stages in different environments or in the same environments at different times. As a result individuals and populations are not vulnerable to the same environmental disruptions (Healey, 1991; Wood, 1995; Rieman and Clayton, 1997). Variation in size, feeding morphology, and habitat use allows the exploitation of a variety of niches leading ultimately to higher overall abundance and production (Chandler and Bjornn, 1988; Healey, 1994; Healey and Prince, 1995; Skúlason and Smith, 1995). Phenotypic diversity may also be key to the long-term potential for adaptation in the face of environmental change (Ruckelshaus *et al.*, 2002) such as that associated with long-term climatic variation (e.g., Hilborn *et al.*, 2003). The maintenance of adaptive potential may depend on many things, but it is generally accepted that phenotypic variation, whether it is largely genetically or environmentally controlled, is the raw material for selection, adaptation, and radiation (West-Eberhard, 1989; Skúlason and Smith, 1995).

If phenotypic expression ultimately depends on the nature of the physical environment, failure to represent and maintain a broad range in the distinct types of environments may make effective conservation of diverse, resilient, and productive populations impossible (Healey and Prince, 1995). We may never fully understand the function of every organism and all the mechanisms structuring aquatic ecosystems. We can generally agree, however, that simplifying systems will at some point result in the loss of things we hold as important. If we can't predict that point, precautionary management should seek to conserve as much diversity and the processes that provide for its maintenance as possible.

3.3 Influence of scale

A key lesson from the emerging view of scaling in ecology is the need to consider both process and pattern, and how they may interact (Urban *et al.*, 1987; King, 1997). The concept of scaling in stream ecology has been developed primarily in reference to the hierarchical classification of physical processes that shape aquatic habitats (Frissell *et al.*, 1986; Hawkins *et al.*, 1993; Imhof *et al.*, 1996; Naiman, 1998). A general assumption in (or attributed to) many applications of these classifications to living systems is that the physical template directly constrains the scaling and organization of biological responses. While this may be true in many cases, when one considers the vast array of potentially important physical patterns and processes and biological responses, however, a single coherent view of scaling or landscape classification begins to cloud (Wiens, 2002).

Physical processes and scale – Different physical processes may affect aquatic habitat at different spatial and/or temporal scales. For example, within a small (e.g., 10^2 ha) watershed, disturbances from landslides, floods, or fires may be manifested as infrequent, but high intensity events. Across a larger-scale (e.g., 10^4 ha), the probability of occurrence for these events increases

with basin area, but the overall intensity is lower because the disturbances are typically very localized (Benda *et al.*, 1998; Montgomery, 1999). The combination of localized disturbance and some degree of asynchrony in events should produce a spatially and temporally variable patchwork of habitat types and patterns of species occurrence (Reeves *et al.*, 1995; Rieman and Dunham, 2000). Alternatively, larger-scale sources of disturbance, such as regional climate cycles (e.g., Mantua *et al.*, 1997) or global change (e.g., Mote *et al.*, 1999) may be manifested simultaneously across very large areas. While ecosystems may be more resilient (e.g., recover more quickly or completely) or resistant to smaller-scale disturbances, larger-scale changes may be more pervasive and permanent. The intensity or magnitude of disturbance events are also important to ecosystem dynamics, and may be scale-dependent as well (e.g., Benda *et al.*, 1998).

Biological responses and scale – The physical template may have a significant influence on most, if not all, biological responses, but the connection will depend in part on the nature of the biological response, including evolutionary and ecological responses. The conventional view is that the physical template may effect important evolutionary changes (e.g., speciation, local adaptation) in species over long time scales (e.g., $>10^3$ years), but recent studies have indicated evolutionary responses can also occur on much shorter time scales (Quinn *et al.*, 2000; Quinn, 2005). Ecological responses include those of individuals (e.g., morphology, survival, growth, fitness), populations (e.g., productivity, distribution, viability), and species assemblages (e.g., species number, dominance, functional groups; Petchey and Gaston, 2002). The scale of these different responses will vary among species according to spatial requirements (e.g., home range, territory size, migratory patterns) and temporal constraints (e.g., generation time, migration timing) characteristic of each. For example, some stream insects may range only within a few meters of stream bottom during their lifetimes as juveniles, but their distribution may fluctuate dramatically among years due to numerous, small-scale disturbances and dispersal of eggs by winged adults (Cooper *et al.*, 1998). In contrast, longer-lived fishes may range very widely during their lifetimes (e.g., salmon that migrate thousands of kilometers to complete their life cycles), but consistently return to spawn in a small segment of stream, due to natal homing. Spawning distributions may be relatively constant on a year-to-year basis, but perhaps gradually fluctuate on a scale of decades to centuries (e.g., Hilborn *et al.*, 2003).

Given the diversity of physical process and biological responses, scaling therefore involves at least two essential steps. First, one must clearly define the relevant processes and how they may be structured to affect the responses of interest, whether physical or biological. Second, one must develop an effective sampling design to detect spatial or temporal patterning across the range of scales believed to be important (Duttillleul, 1998a, b). These steps should ideally be sequential in nature, but often patterns are first observed and then ascribed to some (often untested) process or mechanism. Ultimately, the process is often iterative. Effective scaling of natural landscapes or ecosystems should lead to spatially (or temporally) explicit (Conroy *et al.*, 1995) or

“distributed” (Seyfried and Wilcox, 1995) models and perspectives. The term “scale” must be used within a proper context to be meaningful.

Studies of habitat characteristics in aquatic ecosystems have been strongly influenced by scaling issues. Earlier work on habitat relationships for stream fishes emphasized smaller scales (e.g., Fausch *et al.*, 1988). Increasingly, the emphasis is on larger-scale analyses (e.g., Fausch *et al.*, 2002). There are several reasons for this, including lack of generality in finer-scale models (Fausch *et al.*, 1988), developments of new methods and approaches for larger-scale studies of aquatic ecosystems (Johnson and Gage, 1997). Some studies have been conducted at multiple spatial or temporal scales (e.g., Fausch *et al.*, 1994; Schlosser, 1995; Dunham and Vinyard, 1997; Wiley *et al.*, 1997; Dunham and Rieman, 1999; Montgomery *et al.*, 1999; Torgerson *et al.*, 1999; Baxter and Hauer, 2000; Labbe and Fausch, 2000). Results from these studies highlight the importance of scale and context; insights that would not be possible with a focus on a single spatial or temporal scale.

Changing scale is not a simple matter of changing the dimensions of a problem. The relevant variables, processes, and responses also change with scale, and the effect of a single process may change in magnitude, or even direction, with scale. Examples of key processes shifting with scale are growing in the literature on salmonid fishes (see Cooper *et al.*, 1998 for examples with other aquatic taxa). Fausch *et al.* (1994) studied the distribution of two charr (*Salvelinus*) species, and found that fish distributions were related to climatic gradients at larger-scales, while biotic interactions controlled distributions at smaller scales. Dunham *et al.* (1999) reported a similar pattern for cutthroat trout (*Oncorhynchus clarki*). Baxter and Hauer (2000) found areas of upwelling groundwater to be related to the distribution of spawning bull trout (*Salvelinus confluentus*) among stream reaches, but the distribution of redds at smaller scales was tied to localized downwelling. Reeves *et al.* (1995) suggested that patterns of disturbance, such as those following stand-replacing wildfires, may be detrimental to Pacific coastal salmonid populations in the short-term (e.g., one to several years following disturbance), but in the longer-term (e.g., decades to centuries), such events are key to generating high-quality habitat. Rieman *et al.* (1997), and Rieman and Clayton (1997) suggested similar patterns for the effects of fire on inland salmonids in the Pacific Northwest, but on shorter time scales (e.g., the frequency of disturbance is higher and recovery is faster).

An important theme in large-scale or “landscape” ecology is the effect of pattern on process (Turner, 1989, 2005). Our recent work on inland salmonids at larger-scales suggests spatial pattern, including habitat size and isolation, may drive processes affecting species persistence (Rieman and McIntyre, 1995; Dunham *et al.*, 1997; Rieman and Dunham, 2000; Dunham *et al.*, 2002). The importance of habitat size and isolation at large scales implies the potential for “metapopulation” dynamics. Metapopulations are defined as interacting groups of two or more local or “sub-” populations (see Hanski, 1999; Rieman and Dunham, 2000). Within a metapopulation, local populations occupy discrete habitats, and patterns of habitat occupancy may vary

according to habitat-specific rates of extinction and recolonization. A major area of uncertainty for salmonid fishes and many other species is the relationship between metapopulation structure (e.g., patterns of habitat occupancy) and metapopulation processes (e.g., dispersal and extinction-recolonization dynamics), and scale. Patterns of habitat occupancy observed within metapopulations may be the result of a balance between rates of extinction and recolonization on a relatively stable network of habitat patches. The alternative is that patterns of occurrence reflect long-term changes in habitat occupancy and (potentially lagged) biological responses to disturbance and habitat changes, including natural disturbance and succession, and human-caused habitat modification and loss (Rieman and Dunham, 2000).

While our work on salmonids points to the importance of habitat size at large scales, the mechanism driving this pattern is not clear. A common explanation for this widespread pattern is that habitat diversity is greater in larger habitats, and diversity in space and time may confer greater stability to species assemblages (Dunham *et al.*, 2003). This explanation for patterns of species persistence on landscapes has important implications for land management. Management practices that tend to homogenize landscapes or alter the frequency and magnitude of disturbance events may strongly influence species persistence (Landres *et al.*, 1999; Hilborn *et al.*, 2003). Physical science can make important contributions to conservation of aquatic species by providing a better understanding of spatial and temporal scaling of different sources of disturbance to physical systems (e.g., Reeves *et al.*, 1995; Benda *et al.*, 1998; Montgomery, 1999; Miller *et al.*, 2003). The short and long-term effects of these disturbance events must be more clearly linked to relevant biological responses. Understanding of these linkages is tied to appropriate scaling of both physical process and biological responses in space and time.

4 Synthesis

In this paper, we have characterized physical systems as the processes that influence and constrain the creation and maintenance of aquatic habitats, which in turn serve as a template for the expression, maintenance, and evolution of ecological diversity. From this view the biological system defines the relevant physical system and together they represent an ecosystem. The term ecological “integrity” has been proposed to represent an ecosystem’s “ability to generate and maintain adaptive biotic elements through natural evolutionary processes” (Angermeier and Karr, 1994; Angermeier, 1997). Integrity should reflect evolutionary adaptations to a diverse and dynamic physical environment through a complementary suite of ecological forms, strategies, and temporal/spatial patterns of occurrence that serve to stabilize systems and maximize their productivity (Chapin *et al.*, 2000). Managers focused on ecological integrity will strive to restore or maintain physical systems that can sustain ecological elements and products, and that can also respond and adapt to change, disturbance, or the effects of management that we cannot foresee. The concepts of natural process and variability, diversity, and scale provide a foundation for implementation of

watershed management intended to conserve ecological integrity when faced with uncertainty. The challenge to implementation rests on our ability to define clearly what these concepts mean in terms of management objectives, and how to manipulate and monitor systems to ensure that these objectives are met. While it is clear that much of the current regulatory guidance for managers is oversimplified, the complexities, potential costs, and uncertainties of implementing new concepts are significant obstacles.

What is Natural? A fundamental issue in restoring more natural variation in patterns, processes and disturbance structuring aquatic ecosystems will be recognizing what “natural” is or was. We often lack long enough time series or even enough unaltered landscapes to characterize the patterns that might be expected in the absence of human influence. One perplexing problem is the recognition that natural regimes are not stable, and that historical observations of fire, floods, and erosional events, for example, may not capture near-future conditions, particularly in light of human influence on whole earth systems. Recent and rapid climate changes suggest that hydrologic and temperature regimes, and linked disturbance processes are trending along pathways that have no observational precedent. For example, recent climate assessments relevant to freshwater systems (e.g., Mote *et al.*, 1999; Poff *et al.*, 2002), suggest that river systems in the Pacific Northwest will likely experience earlier snow melt and increased winter flooding. Changing fire regimes (McKenzie *et al.*, 2004) might also lead to more frequent or extensive watershed disruption. In spite of these concerns, new methodologies continue to emerge that allow for longer and more accurate glimpses into the past. For example, in-situ cosmogenic nuclide production and apatite fission track measurements have allowed extension of sediment production estimates in montane watersheds in Idaho from tens of years to millions of years, and have provided a rational basis for estimating periodicity of large events (Kirchner *et al.*, 2001). Paleoecological methods have allowed a tentative reconstruction of historic patterns of flow and erosion in more recent periods (Chatters *et al.*, 1995). Systems modeling focused on fluvial-geomorphic processes with linkages to key drivers such as climate and fire (Benda *et al.*, 1998; Benda and Sias, 2003) may provide useful perspectives when direct reconstruction is impossible. In any case gaining a better sense of the environmental variability that can serve as a management goal seems essential.

Where should it be? Using natural process and variability as a guide for watershed management could be a key step toward conservation and restoration of the template for biological diversity and ecological integrity. A key question is where should, or can, we do it? Do we know enough about natural processes to actually restore or mimic them? Certainly removing dams or channel levies or even providing more natural flow regimes are important and feasible actions. But wildland management tied to roads, timber harvest and prescribed fire represent more uncertain links to hydrologic and geomorphic process. In either case socio-political issues in management requiring long-term commitment consistent with ecological time scales increase that uncertainty. Even assuming that we have the fundamental knowledge required

to conserve and restore those basic processes, there remain two important constraints to progress. (1) The problem is large and resources for work are limited. The demands for development of watershed-based natural resources are likely to grow rather than decline in the foreseeable future (Dale *et al.*, 2000). We cannot hope to conserve or restore all of the watersheds we might wish. Prioritization will be important. (2) We generally lack any detailed inventory to characterize the nature and distribution of the aquatic biological diversity we hope to conserve.

Hunter (1991) and others have argued that our most efficient and effective option might focus on the conservation and restoration of a diverse physical system. This is the strategy embraced by a number of major conservation initiatives such as GAP (Scott *et al.*, 1993) and the Nature Conservancy (Noss *et al.*, 1995; Groves, 2003). The goal is to map distinct conservation units based on the classification of physical attributes ultimately thought to support, or constrain the distribution of distinct biological elements. In essence by focusing conservation or restoration on a representative set of distinct physical environments we could ensure the conservation of distinct biological elements and the components of biological diversity. Understanding the link between diversity in the physical template and diversity in biological elements will be an important step toward a more efficient and effective prioritization of management resources.

At What Scale? The scope of many issues facing managers of aquatic ecosystems necessitates a larger or broader view, but “scaling up” entails more than changing the linear and temporal dimensions of the problem. Management to maintain or restore ecological integrity must consider how different processes operate at different scales, particularly with reference to how physical and biological processes are functionally organized (Urban *et al.*, 1987). Context is important. In the temporal dimension, present conditions must be understood in the context of historical legacies and potential future conditions. In the spatial dimension, conditions within any reach of stream could be driven largely by the connections to and conditions in, the surrounding landscape. For example, most reserves to protect aquatic ecosystems (Frissell and Bayles, 1996) cannot function in isolation of effects from the “matrix” of managed landscapes in which they are embedded (Harris, 1984; Pringle, 1999).

Multi-scale approaches must acknowledge a degree of uncertainty that is not reflected in many current management regulations or applications. Even with perfect information, we cannot precisely predict how aquatic ecosystems will respond to alternative management actions. Complex and stochastic interactions between factors acting at multiple scales ultimately lead to a distribution of potential physical and biological responses. One response may be to view whole river basins as “populations” of watersheds with a characteristic frequency distribution of environmental conditions driven by the periodicity of disturbance and its interaction with hydrologic and geomorphic process (Benda *et al.*, 1998). Another may be to classify watersheds or stream segments by the fundamental processes or regimes that structure them (Montgomery, 1999). In a pragmatic sense “scaling” for managers may require recognizing the system size and time frame

that encompasses a relatively stable, complete, representative or diverse distribution of conditions, populations or classes.

Questions for Integrated Research We believe that by struggling with these questions we begin an outline of a collaborative integration for biologists and physical scientists interested in the conservation management of river ecosystems. New work would necessarily consider more specific questions. Some examples:

- What are the natural patterns of variability and how have they changed? How different are the environments influenced by humans in pattern or variation from those that might have existed in the absence of human effects? How far can natural processes be altered without impairing biological elements of ecosystem integrity?
- How will they change in the future?
- What are the dominant processes structuring aquatic ecosystems? In the Pacific coastal ecoregion, for example, influences of fire and subsequent delivery of wood and sediment (e.g., Reeves *et al.*, 1995; Benda *et al.*, 1998; Cissel *et al.*, 1998; Naiman *et al.*, 2000) are thought to be the dominant drivers in the formation of stream habitats for fish. In other regions, different processes may be important.
- How do we “scale” aquatic ecosystems? Different physical processes may operate on different scales (Benda *et al.*, 1998) or “domains” (Montgomery, 1999) within a single watershed (Frissell *et al.*, 1986; Seyfried and Wilcox, 1995). Patterns of biological organization, such as the distribution of local populations, may or may not conform to different physical gradients or boundaries (Dunham *et al.*, 2002). We need to understand how to scale both, if we are to effectively manage aquatic ecosystems.
- If full restoration of natural processes is not possible, how can we effectively mimic them? Poff *et al.* (1997) summarize the example of attempts to mimic natural flow regimes in the Colorado River. Were flows of sufficient magnitude and duration to restore important physical habitat elements? Is restoration of a natural flow regime sufficient, given that upstream reservoirs have severely altered sediment supply and thermal regimes?
- What are the temporal and spatial patterns of disturbance and variation within any region or scale of interest? Is there some natural ebb and flow in the productivity of some streams that might provide a template for management intent on mimicking that pattern? How does the probability that some portions of a system are productive at any point in time change with the size of the system?
- What are the primary gradients in the physical environment influencing the occurrence and diversity of aquatic organisms? Are some kinds of environments invariably productive and diverse while others are not? Temperature is a physical characteristic of central importance that limits the distribution of species, and constrains species interactions through basic physiological processes. The fundamental differences in geomorphic processes may also constrain distributions through disturbance and direct selection on reproductive strategies. Models that allowed broad spatially and temporally explicit predictions of temperature without detailed site level information could be immensely useful in defining potential habitats.

Physical classification of streams and watersheds reflecting biologically relevant disturbance regimes could have similar power in understanding the distribution of distinct species, life histories, or diversity in general.

5 Conclusions

Retaining the critical types and ranges of natural variability in ecosystems remains, for the present, a management goal or a conceptual underpinning for management rather than an operational dictum. In practice, this requires adopting a conservative approach to changing the complex nature of systems that we understand poorly, but that we wish to manage. Technological fixes that are used should be compatible with natural conditions and the processes that structure aquatic ecosystems not run counter to them. A primary challenge will be to apply these emerging ideas in the real world. Examples of successful applications for aquatic ecosystems are extremely rare, but there is growing optimism and support for management based on concepts of natural variability. The opportunity for conservation or restoration of more natural conditions will depend on our ability to collaborate across disciplines to recognize what those conditions were, where we can hope to do it, and which areas are likely to provide the greatest ecological value.

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References

- ADKISON, M. (1995). "Population Differentiation in Pacific Salmon: Local Adaptation, Genetic Drift, or the Environment," *Can. J. Fish. Aquat. Sci.*, 52, 2762–2777.
- ALLENDORF, F. and LEARY, R. (1988). "Conservation and Distribution of Genetic Variation in a Polytypic Species the Cutthroat Trout," *Cons. Biol.*, 2, 170–184.
- ANGERMEIER, P. (1997). Conceptual roles of biological integrity and diversity, in J. Williams, C. Wood and M. Dombeck (eds.), *Watershed Restoration: Principles and Practices*, American Fisheries Society: Bethesda MD, pp. 49–65.
- ANGERMEIER, P. and KARR, J. (1994). "Biological Integrity versus Biological Diversity as Policy Directives," *BioScience*, 44, 690–697.
- BAXTER, C. and HAUER, F. (2000). "Geomorphology, Hyporheic Exchange, and Selection of Spawning Habitat by Bull Trout (*Salvelinus confluentus*)," *Can. J. Fish. Aquat. Sci.*, 57, 1470–1481.
- BEECHIE, T. and BOLTON, S. (1999). "An Approach to Restoring Salmonid Habitat-Forming Processes in Pacific Northwest Watersheds," *Fisheries*, 24(4), 6–15.
- BEISSINGER, S. and WESTPHAL, M. (1998). "On the Use of Demographic Models of Population Viability in Endangered Species Management," *J. Wild. Manage.*, 62, 821–841.
- BENDA, L., MILLER, D., DUNNE, T., REEVES, G. and AGE, J. (1998). Dynamic landscape systems, in R. Naiman and R. Bilby (eds.), *River Ecology and Management: Lessons from the Pacific Coastal Ecoregion*, Springer Verlag, New York, pp. 261–288.
- BENDA, L.E. and SIAS, J.C. (2003). "A Quantitative Framework for Evaluating the Mass Balance of In-Stream Organic Debris," *Forest Ecol. Manage.*, 172, 1–16.
- BENDA, L.E., MILLER, D., BIGELOW, P. and ANDRAS, K. (2003). "Effects of Post-Wildfire Erosion on Channel Environments, Boise River, Idaho," *Forest Ecol. Manage.*, 178(1–2), 105–119.
- BENDA, L., POFF, N.L., MILLER, D., DUNNE, T., REEVES, G., PESS, G. and POLLOCK, M. (2004). "The Network Dynamics Hypothesis: How Channel Networks Structure Riverine Habitats," *BioScience*, 54, 413–427.
- BESCHTA, R., BILBY, R., BROWN, G., HOLTBY, L. and HOFSTRA, T. (1987). Stream temperature and aquatic habitat: Fisheries and forestry interactions, in E. Salo and T. Cundy (eds.), *Streamside Management: Forestry and Fishery Interactions Contribution No. 57*, Institute of Forest Resources/University of Washington, Seattle, pp. 132–191.
- BILBY, R.E. *et al.* (2003). A review of strategies for recovering tributary habitat. Northwest Power Planning Council, National Marine Fisheries Service, 2003-2, OR.
- BISSON, P., REEVES, G., BILBY, R. and SEDELL, J. (1997). Desired future conditions? in *Pacific Salmon and Their Ecosystems: Status and Future Options*, Chapman and Hall, New York, pp. 447–474.
- BRANNON, E.L., POWELL, M.S., QUINN, T.P. and TALBOT, A. (2004). "Population Structure of Columbia River Basin Chinook Salmon and Steelhead Trout," *Reviews in Fisheries Science*, 12, 99–232.
- CALLICOTT, J. and MUMFORD, K. (1997). "Ecological Sustainability as a Conservation Concept," *Cons. Biol.*, 11, 32–40.
- CHANDLER, G. and BJORN, T. (1988). "Abundance, Growth, and Interactions of Juvenile Steelhead Relative to Time of Emergence," *Trans. Am. Fish. Soc.*, 117, 432–443.
- CHAPIN, F. *et al.* (2000). "Consequences of Changing Biodiversity," *Nature*, 405, 234–242.
- CHATTERS, J., BUTLER, V., SCOTT, M., ANDERSON, D. and NEITZEL, D. (1995). A paleoscience approach to estimating the effects of climatic warming on salmonid fisheries of the Columbia River basin, in R. Beamish (ed.), *Climate Change and Northern Fish Populations*, Canadian Special Publications in Fisheries Aquatic Sciences 121, pp. 489–496.
- CHRISTENSEN, N. *et al.* (1995). The scientific basis for ecosystem management: An assessment by the Ecological Society of America. Ecological Society of America: Washington DC.

21. CISSEL, J. *et al.* (1998). A landscape plan based on historical fire regimes for a managed forest ecosystem: The Augusta Creek study, *Gen. Tech. Rept. PNW-GTR-422*, USDA Forest Service, Portland, OR.
22. CISSEL, J., SWANSON, F. and WEISBERG, P. (1999). "Landscape Management Using Historical Fire Regimes: Blue River, Oregon," *Ecol. Appl.*, 9, 1217–1234.
23. CLAYTON, J. and KENNEDY, D. (1985). "Nutrient Losses from Timber Harvest in the Idaho Batholith," *Soil Sci. Soc. Am. J.*, 49(4), 1041–1049.
24. CONROY, M., COHEN, Y., JAMES, F., MATSINOS, Y. and MAURER, B. (1995). "Parameter Estimation, Reliability, and Model Improvement for Spatially Explicit Models of Animal Populations," *Ecol. Appl.*, 5, 17–19.
25. COOPER, S., DIEHL, S., KRATZ, K. and SARNELLE, O. (1998). "Implications of Scale for Patterns and Processes in Stream Ecology," *Aust. J. Ecol.*, 23, 27–40.
26. DALE, V. *et al.* (2000). "Ecological Principles and Guidelines for Managing the Use of Land," *Ecol. Appl.*, 10, 639–670.
27. DUNHAM, J. and RIEMAN, B. (1999). "Metapopulation Structure of Bull Trout: Influences of Physical, Biotic and Geometrical Landscape Characteristics," *Ecol. Appl.*, 9, 642–655.
28. DUNHAM, J. and VINYARD, G. (1997). "Incorporating Stream Level Variability into Analyses of Fish-Habitat Relationships: Some Cautionary Examples," *Trans. Am. Fish. Soc.*, 126, 323–329.
29. DUNHAM, J., PEACOCK, M., RIEMAN, B., SCHROETER, R. and VINYARD, G. (1999). "Local and Geographic Variability in the Distribution of Stream-Living Lahontan Cutthroat Trout," *Trans. Am. Fish. Soc.*, 128, 875–889.
30. DUNHAM, J., RIEMAN, B. and PETERSON, J. (2002). Patch-based models to predict species occurrence: Lessons from salmonid fishes in streams, in J. Scott, P. Heglund, M. Morrison, M. Raphael, J. Haufler and B. Wall (eds.), *Predicting Species Occurrences: Issues of Accuracy and Scale*, Island Press: Covelo, CA, pp. 327–334.
31. DUNHAM, J.B., VINYARD, G.L. and RIEMAN, B.E. (1997). "Habitat Fragmentation and Extinction Risk of Lahontan Cutthroat Trout," *N. Am. J. Fish. Manage.*, 17, 1126–1133.
32. DUNHAM, J.B., YOUNG, M.K., GRESSWELL, R.E. and RIEMAN, B.E. (2003). "Effects of Fires on Fish Populations: Landscape Perspectives on Persistence of Native Fishes and Nonnative Fish Invasions," *Forest Ecol. Manage.*, 178(1,2), 183–196.
33. DUTTILLEUL, P. (1998a). Incorporating scale in ecological experiments: Study design, in D. Peterson and V. Parker (eds.), *Ecological Scale: Theory and Applications*, Columbia University Press, New York, pp. 369–386.
34. DUTTILLEUL, P. (1998b). Incorporating scale in ecological experiments: Data analysis, in D. Peterson and V. Parker (eds.), *Ecological Scale: Theory and Applications*, Columbia University Press, New York, pp. 387–428.
35. ENGSTROM, D., FRITZ, S., ALMENDINGER, J. and JUGGINS, S. (2000). "Chemical and Biological Trends During Lake Evolution in Recently Deglaciated Terrain," *Nature*, 408, 161–166.
36. FAUSCH, K., HAWKES, C. and PARSONS, M. (1988). Models that predict standing crop of stream fish from habitat variables: 1950–85, *Gen. Tech. Rept. PNW-GTR-213*, USDA Forest Service, Portland, OR.
37. FAUSCH, K., NAKANO, S. and ISHIGAKI, K. (1994). "Distribution of Two Congeneric Charrs in Streams of Hokkaido Island, Japan: Considering Multiple Factors Across Scales," *Oecologia*, 100, 1–12.
38. FAUSCH, K.D., TORGENSEN, C.E., BAXTER, C.V. and LI, H.W. (2002). "Landscapes to Riverscapes: Bridging the Gap between Research and Conservation of Stream Fishes," *BioScience*, 52.
39. FORBES, S. (1887). The Lake as a Microcosm, *Bulletin of the Science Association of Peoria, Illinois*, pp. 77–87.
40. FRANKLIN, J. (1993). "Preserving Biodiversity: Species, Ecosystems, or Landscapes?" *Ecol. Appl.*, 3, 202–205.
41. FRISSELL, C. (1993). "Topology of Extinction and Endangerment of Native Fishes in the Pacific Northwest and California (USA)," *Cons. Biol.* 7(2), 342–354.
42. FRISSELL, C. and BAYLES, D. (1996). "Ecosystem Management and the Conservation of Aquatic Biodiversity and Ecological Integrity," *Water Resour. Bull.*, 229–240.
43. FRISSELL, C., LISS, W., GRESSWELL, R., NAWA, R. and EBERSOLE, J. (1997). A resource in crisis: Changing the measure of salmon management, in D. Stouder, R. Bisson and R. Naiman (eds.), *Pacific Salmon and Their Ecosystems: Status and Future Options*, Chapman and Hall, New York, pp. 411–446.
44. FRISSELL, C., LISS, W., WARREN, C. and HURLEY, M. (1986). "A Hierarchical Framework for Stream Habitat Classification: Viewing Streams in a Watershed Context," *Environ. Manage.*, 10, 199–214.
45. GREGORY, S. and BISSON, P. (1997). Degradation and loss of anadromous salmonid habitat in the Pacific Northwest, in D. Stouder, P. Bisson and R. Naiman (eds.), *Pacific Salmon and Their Ecosystems: Status and Future Options*, Chapman and Hall, New York, pp. 277–314.
46. GRESSWELL, R. (1999). "Fire and Aquatic Ecosystems in Forested Biomes of North America," *Trans. Am. Fish. Soc.*, 128, 193–221.
47. GROSS, M. (1991). "Salmon Breeding Behavior and Life History Evolution in Changing Environments," *Ecology*, 72(4), 1180–1186.
48. GROVES, C.R. (2003). *Drafting a Conservation Blueprint: A Practitioner's Guide to Planning for Biodiversity*. Island Press, Washington, DC.
49. HALUPKA, K.C., WILLSON, M.F., BRYANT, M.D., EVEREST, F.H. and GHARRETT, A.J. (2003). "Conservation of Population Diversity of Pacific Salmon in Southeast Alaska," *N. Am. J. Fish. Manage.*, 23, 1057–1086.
50. HANKSI, I. (1999). *Metapopulation Ecology*, Oxford University Press, Oxford.

51. HARRIS, L. (1984). *The Fragmented Forest*, University of Chicago Press, Chicago.
52. HAWKINS, C. *et al.* (1993). "A Hierarchical Approach to Classifying Stream Habitat Features," *Fisheries*, 18(6), 3–12.
53. HEALEY, M. (1991). Life history of chinook salmon, in C. Groot and L. Margolis (eds.), *Pacific Salmon Life Histories*, UBC Press, British Columbia Canada, pp. 311–393.
54. HEALEY, M. (1994). "Variation in the Life History Characteristics of Chinook Salmon and its Relevance to Conservation of the Sacramento Winter Run of Chinook Salmon," *Cons. Biol.*, 8(3), 876–877.
55. HEALEY, M. and PRINCE, A. (1995). Scales of variation in life history tactics of Pacific salmon and the conservation of phenotype and genotype, in J. Nehlsen (ed.), *Evolution and the Aquatic Ecosystem*, American Fisheries Society, Bethesda MD, pp. 176–184.
56. HILBORN, R., QUINN, T.P., SCHINDLER, D.E. and ROGERS, D.E. (2003). "Biocomplexity and Fisheries Sustainability," *Proc. Nat. Acad. Sci.*, 100, 6564–6568.
57. HOLLING, C.S. and MEFFE, G.K. (1995). "Command and Control and the Pathology of Natural Resource Management," *Cons. Biol.*, 10(2), 328–337.
58. HUNTER, JR. M. (1991). Coping with ignorance: the coarse-filter strategy for maintaining biodiversity, in K. Kohm (ed.), *Balancing on the Brink of Extinction*, Island Press: CA, pp. 266–281.
59. HYNES, H. (1970). *The Ecology of Running Waters*, University of Toronto Press.
60. IMHOF, J., FITZGIBBON, J. and ANNABLE, W. (1996). "A Hierarchical Evaluation System for Characterizing Watershed Ecosystems for Fish Habitat," *Can. J. Fish. Aquat. Sci.*, 52(1), 312–326.
61. JOHNSON, L. and GAGE, S. (1997). "Landscape Approaches to the Analysis of Aquatic Ecosystems," *Freshwater Biol.*, 37, 113–132.
62. KETCHESON, G., MEGAHAN, W. and KING, J. (1999). "R1–R4" and "BOISED" Sediment Prediction Model Tests using Forest Roads in Granitics," *J. Am. Water Resour. As.*, 35(1), 83–98.
63. KING, A. (1997). Hierarchy theory: a guide to system structure for wildlife biologists, in J. Bissonette (ed.), *Wildlife and Landscape Ecology: Effects of Pattern and Scale*, Springer-Verlag, New York, pp. 185–214.
64. KING, J. (1994). Streamflow and sediment yield responses to forest practices in north Idaho, in D. Baumgartner, J. Lotan and J. Tonn (eds.), *Proceedings of the Interior Cedar-Hemlock-White Pine Forests: Ecology and Management*, March 2–4, 1993, Spokane, WA, Washington State University, Pullman, pp. 213–220.
65. KIRCHNER, J.W., FINKEL, R.C., RIEBE, C.S., GRANGER, D.E., CLAYTON, J.L., KING, J.G., and MEGAHAN, W.F. (2001). "Mountain Erosion Over 10 yr, 10 k.y. and 10 m.y. Time Scales," *Geology*, 29(7), 591–594.
66. LABBE, T. and FAUSCH, K. (2000). "Dynamics of Intermittent Stream Habitat Regulate Persistence of a Threatened Fish at Multiple Scales," *Ecol. Appl.*, 10, 1774–1791.
67. LANDRES, P., MORGAN, P. and SWANSON, F. (1999). "Overview of the Use of Natural Variability Concepts in Managing Ecological Systems," *Ecol. Appl.*, 9, 1179–1188.
68. LEE, D., SEDELL, J., RIEMAN, B., THUROW, R. and WILLIAMS, J. (1997). Broadscale assessment of aquatic species and habitats, *Gen. Tech. Rept. PNW-GTR-328*, USDA Forest Service, Portland, OR.
69. LICHTOWICH, J. (1999). *Salmon Without Rivers: A History of the Pacific Salmon Crisis*. Island Press, Covelo, CA.
70. LUDWIG, D., HILBORN, R. and WALTERS, C. (1993). "Uncertainty, Resource Exploitation and Conservation: Lessons from History," *Science*, 260, 17–36.
71. LYTLE, D.A. and POFF, N.L. (2004). "Adaptation to Natural Flow Regimes," *Trends Ecol. Evol.*, 19(2), 94–100.
72. MAGURRAN, A. (1998). *Ecological Diversity and its Measurement*. Princeton University Press, Princeton, NJ.
73. MANTUA, N., HARE, S., ZHANG, Y., WALLACE, J. and FRANCIS, R. (1997). "A Pacific Interdecadal Climate Oscillation with Impacts on Salmon Production," *B. Am. Meteorol. Soc.*, 78, 1069–1079.
74. MCKENZIE, D., GEDALOF, Z., PETERSON, D.L. and MOTE, P. (2004). "Climate Change, Wildfire and Conservation," *Cons. Biol.*, 18, 890–902.
75. MEGAHAN, W., KING, J. and SEYEDBAGHERI, K. (1995). "Hydrologic and Erosional Responses of a Granitic Watershed to Helicopter Logging and Broadcast Burning," *Forest Sci.*, 41(4), 777–795.
76. MILLER, D., LUCE, C. and BENDA, L. (2003). "Time, Space and Episodicity of Physical Disturbance in Streams," *Forest Ecol. Manage.*, 178(1–2), 121–140.
77. MONTGOMERY, D. (1999). "Process Domains and the River Continuum," *J. Am. Water Resour. As.*, 35, 397–410.
78. MONTGOMERY, D., BEAMER, E., PESS, G. and QUINN, T. (1999). "Channel Type and Salmonid Spawning Distribution and Abundance," *Can. J. Fish. Aquat. Sci.*, 56, 377–387.
79. MOTE, P. *et al.* (1999). *Impacts of Climate Variability and Change in the Pacific Northwest*, JISAO/SMA Climate Impacts Group, University of Washington, Seattle.
80. NAIMAN, R. and TURNER, M. (2000). "A Future Perspective on North America's Freshwater Ecosystems," *Ecol. Appl.*, 10, 958–970.
81. NAIMAN, R.J. (1998). Biotic stream classification, in R.J. Naiman and R.E. Bilby (eds.), *River Ecology and Management: Lessons from the Pacific Coastal Ecoregion*, Springer-Verlag, NY, pp. 97–119.
82. NAIMAN, R., BILBY, R. and BISSON, P. (2000). "Riparian Ecology and Management in the Pacific Coastal Rain Forest," *BioScience*, 50, 996–1011.
83. NEHLSSEN, W., WILLIAMS, J. and LICHTOWICH, J. (1991). "Pacific Salmon at the Crossroads: Stocks at Risk from

- California, Oregon, Idaho and Washington," *Fisheries*, 16(2), 4–21.
84. NIKOL'SKIY, G. (1969). "Parallel Intraspecific Variation in Fishes," *Probl. Ichthyol.*, 9, 4–8.
 85. NITSCHKE, C.R. (2005). "Does Forest Harvesting Emulate Fire Disturbance? A Comparison of Effects on Selected Attributes in Coniferous-Dominated Headwater Systems," *Forest Ecol. Manage.*, 214, 305–319.
 86. NORTON, B. and ULANOWICZ, R. (1992). "Scale and Biodiversity Policy: A Hierarchical Approach," *AMBIO*, 21(3), 244–249.
 87. NOSS, R. (1990). "Indicators for Monitoring Biodiversity: A Hierarchical Approach," *Cons. Biol.*, 4(4), 355–364.
 88. NOSS, R. and COOPERIDER, A. (1994). *Saving Nature's Legacy: Protecting and Restoring Biodiversity*. Island Press, Covelo CA.
 89. NOSS, R., LAROE, E. and SCOTT, J. (1995). Endangered ecosystems of the United States: A preliminary assessment of loss and degradation, *Biological Report 28*, USDI National Biological Service, Washington DC.
 90. PALMER, M.A. et al. (2005). "Standards for Ecologically Successful River Restoration," *J. Appl. Ecol.*, 42, 208–217.
 91. PETCHEY, O.L. and GASTON, K.J. (2002). "Functional Diversity (FD), Species Richness and Community Composition," *Ecology Letters*, 5, 402–411.
 92. PICKETT, S. and WHITE, P. (1985). *The Ecology of Natural Disturbance and Patch Dynamics*. Academic Press, New York.
 93. POFF, N. (1997). "Landscape Filters and Species Traits: Towards Mechanistic Understanding and Prediction in Stream Ecology," *J. N. Am. Benthol. Soc.*, 16, 391–409.
 94. POFF, N. and ALLAN, J. (1995). "Functional Organization of Stream Fish Assemblages in Relation to Hydrological Variability," *Ecology*, 76(2), 606–627.
 95. POFF, N. et al. (1997). "The Natural Flow Regime: A Paradigm for River Conservation and Restoration," *BioScience*, 47, 769–784.
 96. POFF, N. and WARD, J. (1990). "Physical Habitat Template of Lotic Systems: Recovery in the Context of Historical Pattern of Spatiotemporal Heterogeneity," *Environ. Manage.*, 14(5), 629–645.
 97. POFF, N.L., BRINSON, M.M. and DAY, JR. J.W. (2002). Aquatic ecosystems and global climate change: Potential impacts on inland freshwater and coastal wetland ecosystems in the United States. Report from the Pew Center on Global Climate Change on line at: http://www.pewclimate.org/global-warming-in-depth/all_reports/aquatic_ecosystems/index.cfm.
 98. POOLE, G.C. et al. (2004). "The Case for Regime-Based Water Quality Standards," *BioScience*, 54(2), 155–161.
 99. POOLE, G.C. and BERMAN, C.H. (2001). "An Ecological Perspective on Instream Temperature: Natural Heat Dynamics and Mechanisms of Human-Caused Thermal Degradation," *Environ. Manage.*, 27, 787–802.
 100. PRINGLE, C. (1999). "Threats to U.S. Public Lands from Cumulative Hydrologic Alterations Outside Their Boundaries," *Ecol. Appl.*, 10, 971–989.
 101. PURVIS, A. and HECTOR, A. (2000). "Getting the Measure of Biodiversity," *Nature*, 405, 212–219.
 102. QUINN, T., UNWIN, M. and KINNISON, M. (2000). "Evolution of Temporal Isolation in the Wild: Genetic Divergence in Timing of Migration and Breeding by Introduced Chinook Salmon Populations," *Evolution*, 54, 1372–1385.
 103. QUINN, T.P. (2005). *The Behavior and Ecology of Pacific Salmon and Trout*. University of Washington Press, WA.
 104. REEVES, G., BENDA, L., BURNETT, K., BISSON, P. and SEDELL, J. (1995). "A Disturbance-Based Approach to Maintaining and Restoring Freshwater Habitats of Evolutionary Significant Units of Anadromous Salmonids in the Pacific Northwest," *Am. Fish. Soc. Symp.*, 17, 334–349.
 105. REEVES, H., BISSON, P. and DAMBACHER, J. (1998). Fish communities, in R. Naiman and R. Bilby (eds.), *River Ecology and Management: Lessons from the Pacific Coastal Ecoregion*, Springer-Verlag, New York, pp. 200–234.
 106. REICE, S., WISSMAR, R. and NAIMAN, R. (1990). "Disturbance Regimes, Resilience and Recovery of Animal Communities and Habitats in Lotic Ecosystems," *Environ. Manage.*, 14, 647–659.
 107. RIEMAN, B. and CLAYTON, J. (1997). "Fire and Fish: Issues of Forest Health and Conservation of Native Fishes," *Fisheries*, 22(11), 6–15.
 108. RIEMAN, B. and DUNHAM, J. (2000). "Metapopulations and Salmonid Fishes: A Synthesis of Life History Patterns and Empirical Observations," *Ecol. Freshw. Fish*, 9, 51–64.
 109. RIEMAN, B. and MCINTYRE, J. (1995). "Occurrence of Bull Trout in Naturally Fragmented Habitat Patches of Varied Size," *Trans. Am. Fish. Soc.*, 124, 285–296.
 110. RIEMAN, B., HESSBURG, P., LEE, D., THUROW, R. and SEDELL, J. (2000). "Toward an Integrated Classification of Ecosystems: Defining Opportunities for Managing Fish and Forest Health," *Environ. Manage.*, 25, 425–444.
 111. RIEMAN, B., LEE, D. and THUROW, R. (1997). "Distribution, Status and Likely Future Trends of Bull Trout within the Columbia River and Klamath Basins," *N. Am. J. Fish. Manage.*, 17, 1111–1125.
 112. RIEMAN, B.E., LEE, D., BURNS, D., GRESSWELL, R., YOUNG, M., STOWELL, R. and HOWELL, P. (2003). "Status of Native Fishes in the Western United States and Issues for Fire and Fuels Management," *Forest Ecol. Manage.*, 178(1–2), 197–211.
 113. ROOT, T. and SCHNEIDER, S. (1995). "Ecology and Climate: Research Strategies and Implications," *Science*, 269, 334–341.
 114. RUCKELSHAUS, M.H., LEVIN, P., JOHNSON, J.B. and KAREIVA, P.M. (2002). "The Pacific Salmon Wars: What Science Brings to the Challenge of Recovering Species," *Annu. Rev. Ecol. Syst.*, 33, 665–706.

115. SCHAFER, W.M. (2004). Life histories, evolution and salmonids, in A.P. Hendry and S.C. Stearns, *Evolution Illuminated: Salmon and their Relatives*, Oxford University Press, New York, pp. 20–51.
116. SCHEFFER, M. and BEETS, J. (1994). “Ecological Models and the Pitfalls of Causality,” *Hydrobiologia*, 275/276, 115–124.
117. SCHLOSSER, I. (1995). “Critical Landscape Attributes that Influence Fish Population Dynamics in Headwater Streams,” *Hydrobiologia*, 303, 71–81.
118. SCOTT, J. *et al.* (1993). “Gap Analysis: A Geographic Approach to Protection of Biological Diversity,” *Wildlife Monogr.*, 123, 1–41.
119. SEYFRIED, M. and WILCOX, B. (1995). “Scale and the Nature of Spatial Variability: Field Examples having Implications for Hydrologic Modeling,” *Water Resour. Res.*, 31, 173–184.
120. SKÚLASON, S. and SMITH, T. (1995). “Resource Polymorphisms in Vertebrates,” *Trends Ecol. Evol.*, 10, 366–370.
121. SOUTHWOOD, T. (1977). “Habitat, the Template for Ecological Strategies?” *J. Anim. Ecol.*, 46, 337–365.
122. STOUDE, D., BISSON, P. and NAIMAN R. (eds.) (1997). *Pacific Salmon and Their Ecosystems: Status and Future Options*, Chapman and Hall, New York.
123. SWANSON, F., FRANKLIN, J. and SEDELL, J. (1990). Landscape patterns, disturbance, and management in the Pacific Northwest, USA, in Zonneveld and Forman (eds.), *An Ecological Perspective*, Springer Verlag, New York, pp. 191–213.
124. SWANSON, F., JONES, J., WALLIN, D. and CISSEL, J. (1993). Natural variability: Implications for ecosystem management. *Eastside Forest Ecosystem Health Assessment, Vol. II, Ecosystem Management: Principles and Applications*. USDA Forest Service Research, Washington Office, Washington DC.
125. TAYLOR, E. (1990). “Environmental Correlates of Life-History Variation in Juvenile Chinook Salmon,” *Oncorhynchus tshawytscha* (Walbaum). *J. Fish Biol.*, 37, 1–17.
126. TAYLOR, E. (1991). “A Review of Local Adaptation in Salmonidae, with Particular Reference to Pacific and Atlantic Salmon,” *Aquaculture*, 98, 185–207.
127. TAYLOR, E. (1999). “Species Pairs of North Temperate Freshwater Fishes: Evolution, Taxonomy, and Conservation,” *Rev. Fish Biol. Fisher.*, 9, 299–324.
128. TORGERSEN, C., PRICE, D., LI, H. and MCINTOSH, B. (1999). “Multiscale Thermal Refugia and Stream Habitat Associations of Chinook Salmon in Northeastern Oregon,” *Ecol. Appl.*, 9, 301–319.
129. TURNER, M. (1989). “Landscape Ecology: The Effect of Pattern on Process,” *Annu. Rev. Ecol. Syst.*, 20, 171–197.
130. TURNER, M.G. (2005). “Landscape Ecology: What is the State of the Science?” *Annu. Rev. Ecol. Syst.*, 36, 319–344.
131. URBAN, D., O’NEILL, R. and SHUGART, Jr. H. (1987). “Landscape Ecology,” *BioScience*, 37, 119–127.
132. UTTER, F., SEEB, J. and SEEB, L. (1993). “Complementary Uses of Ecological and Biochemical Genetic Data in Identifying and Conserving Salmon Populations,” *Fish. Res.*, 18, 59–76.
133. WARD, J.V. and TOCKNER, K. (2001). “Biodiversity: Towards a Unifying Theme for River Ecology,” *Freshwater Biol.*, 46, 807–819.
134. WEST-EBERHARD, M. (1989). “Phenotypic Plasticity and the Origins of Diversity,” *Annu. Rev. Ecol. Syst.*, 20, 249–278.
135. WIENS, J.A. (2002). “Riverine Landscapes: Taking Landscape Ecology into the Water,” *Freshwater Biology*, 47, 501–515.
136. WILEY, M., KOHLER, S. and SEELBACH, P. (1997). “Reconciling Landscape and Local Views of Aquatic Communities: Lessons from Michigan Trout Streams,” *Freshwater Biol.*, 37, 133–148.
137. WILLIAMS, R. *et al.* (1999). “Return to the River: Scientific Issues in the Restoration of Salmonid Fishes in the Columbia River,” *Fisheries*, 24, 10–19.
138. WILLSON, M. (1997). Variation in salmonid life histories: patterns and perspectives. *PNW-RP-498*, USDA Forest Service, Pacific Northwest Research Station, Portland, OR.
139. WOOD, C. (1995). Life history variation and population structure in sockeye salmon, in J. Nehlsen (ed.), *Evolution and the Aquatic Ecosystem*, American Fisheries Society, Bethesda MD, pp. 195–216.

