May 28, 1996

CONF-950937б--1

A GENERAL PROTOCOL
FOR RESTORATION OF ENTIRE RIVER CATCHMENTS

by

Jack A. Stanford
Flathead Lake Biological Station
The University of Montana
Polson, MT 59860 USA
stanford@selway.umt.edu

J. V. Ward
Department of Limnology
EAWAG/ETH
Uberlandstrasse 133
CH-8600 Dubendorf, Switzerland

William J. Liss
Department of Fisheries and Wildlife
Oregon State University
Corvallis, OR 97331

Christopher A. Frissell
Flathead Lake Biological Station
The University of Montana
Polson, MT 59860 USA

Richard N. Williams
510 Clear Creek Drive
Meridian, ID 83642 USA

James A. Lichatowich
159 Don Schmith Road
Sequim, WA 98382 USA

and

Charles C. Coutant
Oak Ridge National Laboratory
Box 2008
Oak Ridge, TN 37831 USA

A contribution to the symposium on Restoration of Regulated Rivers,
Lycksele, Sweden, 25-28 September 1995;
proceedings in press in Regulated Rivers: Research and Management,
a scientific journal published by Wiley, Chichester, UK.

All correspondence should be addressed to the first author

DLC

May 28, 1996

ABSTRACT

Large catchment basins may be viewed as ecosystems with interactive natural and cultural attributes. Human activities in catchments reduce ecosystem capacity for native biodiversity and bioproduction through the combined effects of stream regulation, pollution and food web manipulation. Contemporary river ecology emphasizes is on the four dimensional nature of the river continuum and the propensity for riverine biodiversity and bioproduction to be largely controlled by habitat maintenance processes and attributes such as cut and fill alluviation mediated by catchment water yield and seasonality of temperature patterns. Stream regulation severs ecological connectivity between channels and flood plains by reducing the range of natural flow and temperature variation, reduces the capacity of the ecosystem to sustain native biodiversity and bioproduction and promotes proliferation of non-native biota. However, regulated rivers regain normative attributes, which promote recovery of native biota, as distance from the dam increases and in relation to the mode of regulation.

Therefore, reregulation of flow and temperature to normative pattern, coupled with elimination of pollutants and constrainment of nonnative biota, can naturally restore damaged habitats from headwaters to mouth. The expectation is rapid recovery of depressed populations of native species. The protocol requires: restoration of seasonal temperature patterns (e.g., by construction of depth-selective withdrawal systems on storage dams); restoration of peak flows (flushing flows capable of transporting median-sized substratum) needed to reconnect and periodically reconfigure channel and floodplain habitats; stabilization of base flows to revitalize the shallow water habitats; maximization of dam passage to allow restoration of metapopulation structure; change in the management belief system to rely on natural habitat restoration as opposed to artificial propagation, installation of artificial instream structures (river engineering) and artificial food web control; and, practice of adaptive ecosystem management.

Our restoration protocol for entire catchments should be viewed as an hypothesis drawn from key principles of river ecology. Although restoration to aboriginal state is not expected nor necessarily desired, recovery some large portion of lost capacity to sustain native biodiversity and bioproduction is possible by management for processes that maintain normative habitat conditions. The cost may be less than expected because the river can do most of the work.

DISCLAIMER

INTRODUCTION

Flow regulation perhaps is the most pervasive change wrought by humans on rivers worldwide. Dynesius and Nilsson (1994) recently showed that all of the largest rivers in the northern third of the world are regulated; flow in most is totally controlled by dams and diversions, except for some free-flowing reaches and during extreme floods.

Much research in stream ecology worldwide is now devoted to understanding and mitigating flow regulation and interactive effects of land and water use by humans within catchment basins. A primary goal of The Freshwater Imperative, a recent synthesis of research direction by limnologists in the USA, is understanding and predicting the influences of flow regulation on the integrity (e.g., maintenance of biotic diversity) and resiliency (e.g., natural ability of ecosystems to detoxify and immobilize pollutants) of epicontinental aquatic ecosystems (Naiman *et al.*, 1995a; summarized in Naiman *et al.*, 1995b).

River corridors were the arteries for development of modern societies and they remain central to local and global economies. Quality of life in countries worldwide can be assessed in terms of quality and quantity of environmental goods (e.g., potable and irrigable water, fisheries) and services (e.g., sustained discharge and bioproduction) that humans are able to obtain from river ecosystems (*sensu* Lubchenco *et al.*, 1991). Conservation and restoration of rivers clearly should be a national priority for responsible governments and a wide array of actions have been proposed or discussed (e.g., Gore, 1985; Toth et al., 1993; Gore and F. D. Shields, 1995; Shuman, 1995; Van Dijk *et al.*, 1995)

However, governments struggle with designation of specific elements of river environments that need to be conserved or restored, because of conflict between human use of riverine goods and services and different perceptions of how those finite resources can be sustained as human populations burgeon. Moreover, fixing problems in a particular reach or segment usually is compromised to some extent by the natural upstream-downstream connectivity of rivers; management actions targeted at a particular segment or species too often fail to meet objectives because rivers are not viewed as interconnected ecosystems from headwaters to ocean confluence.

Indeed, a strong tendency has emerged to focus river conservation and restoration on charismatic or economically important fauna, such as trout and salmon, without thorough consideration of the attributes and processes of the catchment that control biodiversity and bioproduction (Sparks, 1995). In the USA, Federal legislation requiring timely recovery of species deemed in danger of extinction has fostered management and research emphasis on the biology of the organisms rather than ecosystem processes that control their survival (Minckley and Deacon, 1991). For example, the decade-old restoration program for anadromous salmon runs in the Columbia River has cost well over $1 billion dollars; yet, native populations are rapidly approaching nonviable levels (Nehlsen *et al.*, 1991; 1996; National Research Council, 1995).

To be successful, river restoration plans must be based on a thorough understanding of the biogeochemical processes that control the distribution and production of biota and human influences on those processes. In this paper we examine general principles of river ecology and stream regulation in an ecosystem context and we use these principles as the basis for proposition of a general protocol for restoration of entire catchments.

NATURAL-CULTURAL ELEMENTS OF CATCHMENT ECOSYSTEMS

Rivers cannot be separated in theory or practice from the lands they drain (Hynes, 1975). Hence, the catchment basin (often referred to as watershed in the USA) defines the spatial dimensions of river ecosystems and understanding the linkages between terrestrial and aquatic components and processes is essential.

The catchment landscape is composed of interactive, biophysical resources (e.g., water, minerals, nutrients, habitats, food webs) that are used by the assembledge of animals and plants (biodiversity) that live within the ecosystem. Biodiversity encompasses such phenomena as genetic variation, morphological variation, life history variation within species and the richness, distributions, biomass and productivity of populations, species, guilds and other taxonomic and trophic categories across the landscape. It also encompasses the myriad of biophysical processes (functional attributes) that control these phenomena (Noss, 1994; Hall *et al.*, 1992, Doppelt *et al.*, 1993, and many others). However, the salient features of biodiversity, species numbers (alpha diversity) and distribution (beta diversity), are determined by availability of resources that are needed by animals and plants in order to successfully reproduce (i.e., complete their life cycle) (Andrewartha and Birch, 1954) and thereby sustain ecosystem integrity (Frissell and Bayles, 1996). Life history stages are determined by the genome of each species as derived from its legacy of genetic responses to changes in the availability of resources. Hence, the dynamic biophysical components of the landscape are controlled in space and time by environmental changes (e.g., forest fires, drought, disease, earthquakes) that vary in intensity and duration.

Similarly, human societies within catchments usually are derived from a mix of cultures (e.g., natives, immigrants) that use or market goods and services to produce wealth or some other measure of the quality of life desired by individuals. Desires and perceptions that individuals have about life style are dynamic and influenced by heritage, education, earning power, shortages and surpluses of goods such as fossil fuels, laws, taxes and natural resource management policies, among many other social and economic concerns. The point is that both natural and cultural components of catchments are complex and highly interactive. Humans change catchment landscapes by using or extracting environmental goods and services, whereas societies change in relation to the quality or ecological integrity of landscapes in which they reside (Blikie and Brookfield, 1987; Schinberg and Gould, 1994; and many others in the rapidly expanding environmental sociology and ecological economics literature).

Within this natural-cultural framework, we recognize that river ecosystems have a certain natural capacity to maintain biota and produce biomass (Warren *et al.*, 1979; Frissell *et. al.* 1996; Ebersole *et al.*, in press) and that biodiversity and bioproduction are dynamic in time and space in relation to availability of resources (Benke *et al.*, 1988). Biotic dynamics derive from natural variation in the environmental setting; equilibrium conditions (e.g., logistic relationship between resources and bioproduction) rarely exist for very long because environmental changes are constantly reconfiguring resource availability. Periodic constraints on species-specific productivity increases opportunities for other species to use resources, inferring that levels of ecosystem biodiversity and bioproduction generally are related to the intensity, frequency and duration of disturbance events (Huston, 1979; Resh *et al.*, 1988; Pimm, 1991; Huston, 1994; Reice, 1994).

Ecological capacity therefore varies from place to place and higher levels of biological richness (speciosity) and bioproduction are most likely to occur in ecosystems with a long legacy of high spatial and temporal environmental heterogeneity (Connell, 1978; Ward and Stanford, 1983; Salo *et al.*, 1986; Poff and Ward, 1990). In contrast, total unit area biomass (standing crop) of a few species, while also constrained by inherent ecosystem capacity, may be high under sustained conditions of environmental constancy owing to slow turnover rates. For example, a few species often are extremely abundant and persistent in springbrooks, lake outlets and reservoir tailwaters, where disturbance events are relatively benign (e.g., scouring floods, very dynamic diel and annual temperature patterns and rapid changes in transport of particulate matter do not occur because of the buffering effect of the lake or reservior) (Richardson, 1984; Gislason, 1985; Perry and Sheldon, 1986; Valett and Stanford, 1987; Wooton, 1987; Shannon *et al.*, 1994).

Humans tend to dominate ecosystems thereby superimposing pervasive, continual disturbance that manifests in many forms over very short time frames. The result is suppression, and in some cases permanent loss, of the spatial and temporal diversity of habitats and biodiversity, fundamentally reducing the productive capacity of biotic resources (Warren and Liss, 1980; Frissell *et al.*, 1993; Frissell *et al.*, in press; Ebersole *et. al.*, in press). The goal of river restoration is to remove or at least minimize human-mediated constraints thereby allowing natural re-expression of productive capacity. In some, if not most, intensely regulated rivers, human-mediated constraints may have progressed to the point that full re-expression of capacity is neither desired nor possible. Nonetheless, the implication is that basic ecological principles applied to rivers in a natural-cultural context can lead to restoration of biodiversity and bioproduction in space and time; but, the constraints must be removed, not mitigated.

GENERAL PRINCIPLES OF RIVER ECOLOGY

Conservation and management strategies for large rivers must have a solid conceptual basis or they likely will fail to sustain biodiversity and bioproduction. Contemporary river ecology is guided by a number of intertwined concepts or principles that have a solid empirical basis. No two rivers are exactly alike and no single theory encompasses the myriad of biophysical interactions and responses to natural and human disturbances that make each river unique. However, fundamental principles do apply to all rivers and too many conservation and restoration efforts become myopic, costly and too often fail because plans and actions overlook ecological fundamentals.

Unregulated rivers exist as geohydraulic continua from continental divides to the oceans. They are networks of surface and groundwater flow paths that drain catchment landscapes (Gibert *et al.*, 1990). The energy of flowing water constantly reconfigures the physical form of these interconnected flow pathways, primarily by the process of cut and fill alluviation (Leopold *et al.*, 1964) although dissolution can dominate in limestone massifs (Mangin, 1994) and a few other situations. Inorganic and organic materials are eroded upstream and deposited downstream primarily in relation to: a) long- and short-term flow dynamics, b) the resistivity of geologic formations to erosion and dissolution and c) the geometry of the catchment.

Channel morphologies are determined by the legacy of flooding. Big floods fill channels with inorganic and organic materials eroded laterally and vertically, thereby producing a continuum of instream structures (pools, runs, riffles, gravel bars, avulsion channels, islands, debris jams) and lateral floodplain terraces in many sizes and shapes. Local morphologies resulting from infrequent very big floods may persist in the same general form (quasi-equilibrium) for long time periods until the next big flood, even though interim flow dynamics gradually and subtly reconfigure instream structures and features (Schumm and Lichty, 1956). For example, the channel of the Snake River upstream from Hells Canyon in Idaho, USA, persists as an incised gravel-bed channel containing a chain of elevated, midchannel islands that have not been overtopped since the cataclysmic glacial flood that formed them receded over 8000 years ago (Connor, 1993). Other river channels with a greater sediment supply and frequent overbank flooding are constantly and visibly moving around, braiding or meandering, on the valley bottom from year to year as the channel fills with material in one place causing the flow pathway to avulse and downcut (Best, 1993).

In any case all rivers fundamentally are alluvial in nature as a consequence of cut and fill alluviation mediated by flooding. Most rivers have deeply bedded and expansive floodplains interspersed between constrained and often incised reaches (canyons) where the bedrock may be very near or exposed on the stream bottom. Hence, river ecosystems have three important spatial dimensions that are temporally dynamic (Figure 1). The longitudinal (upstream-downstream) dimension is described in detail in the ecological literature, including the occurrence and ecological significance (discussed below) of streamside (riparian) vegetation and associated faunal assemblages in the surficial transition zone from riverine to terrestrial environments. However, critically important lateral and vertical attributes and connections often are overlooked or ignored. Owing to the high porosity of the bed sediments in gravel bed rivers, river water penetrates the bottom and saturates the alluvial bedding of the channel and floodplain down to substantially less porous bedrock thereby creating complex groundwater (hyporheic) habitats. As the valley constricts or due to changes in local bedrock geometry, the water table may intersect the surface creating floodplain (riparian) wetlands; permanent springbrooks and ponds in downcut areas may be observed at the downstream end of flood channels. Indeed, a prominent feature of alluvial rivers is sequential down- and upwelling of river water into and out of the bed sediments, which interacts with overland flooding to create complex habitat mosaics on the floodplain surface. The floodplain with its hyporheic and riparian habitats therefore is the transition zone or ecotone linking aquatic and terrestrial components of river ecosystem above and below ground level. Also, groundwater flowing from uplands may mix with river water flowing within the hyporheic zone creating yet another important lateral ecotone. These lateral and vertical transition zones alternate in juxtaposition with the channel from headwaters to mouth, forming hyporheic and riparian corridors (Naiman *et al.*, 1988; Stanford and Ward, 1993; Ward and Weins, in press).

The mosaic of channel and floodplain structures creates a constantly changing habitat template (*sensu* Southwood, 1977; Southwood, 1978) for a myriad of plants and animals that compose riverine food webs. Resources needed by particular life history stages of organisms have discrete or "patchy" distributions within this heterogeneous landscape. As flows change, not only does the ability of the river to move substratum change, but the way in which water moves around and/or over instream structures, such as boulders and gravel bars, also changes. Hence, biota must adapt to resources arrayed as patches that manifest from local (e.g., a single rock on a single riffle in a particular river reach; Townsend, 1989) to catchment scale. Moreover, as biota attempt to find and utilize these patches efficiently enough to sustain growth and reproduction over the long term, they also must adapt to the physical forces of water movement (Statzner *et al.*, 1988). Therefore, biota often are arrayed in precise locations within the river channel and along the river continuum (Poff and Allan, 1995). For example, a large, behaviorally-dominant trout may occupy the optimal position within an eddy for capturing drifting insects; if that fish is removed, the next fish in the pecking order of the stream will move into the sweet spot for foraging (Bachman, 1983). Trout are found only in the colder, rocky reaches (rhithron) of the stream continuum and are replaced by warm water species (catfish, carp) in the slow-moving, sandy and often turbid reaches downstream (potamon) (Illies, 1956; Illies and Botosaneanu, 1963).

The river continuum essentially then is a complex, dynamic gradient of habitat types from headwaters to oceanic confluence and flora and fauna usually are distributed rather predictably along that gradient (Figure 2) according to the requirements specified by each stage in their life cycle (Vannote *et al.*, 1980). Each species or unique life history type (stock or population) is most abundant where the resources they require are most abundant and/or most efficiently obtained. They will be present wherever they can maintain a positive energy balance, that is, they have enough resources to sustain growth and reproduction and thereby sustain the presence of the species or stock in the river food web at that location (Hall *et al.*, 1992). For some species a positive life history energy balance can be maintained without much movement and suites of organisms appear to occur in zones along the river continuum; others must move long distances in search of resources needed for each life stage, sometimes involving migrations into the lakes (e.g., adfluvial bull charr, *Salvelinus confluentus*) or the ocean (e.g., anadromous salmon and trout: *Onchorynchus* spp.; *Salmo salar and S. trutta; Salvelinus* spp.).

Widely dispersed species often exist in what is referred to as metapopulations because local populations or subpopulations are linked by dispersal and gene flow into larger regional populations that may encompass the entire catchment (Hanski, 1991; Hanski and Gilpin, 1991). For example, metapopulation structure is thought to be particularly evident in many salmonid populations (Reisenbichler *et al.*, 1992; Rieman and McIntyre, 1993; Williams *et al.*, in press) and likely influences the probability of persistence for a species (Stacy and Taper, 1992). Metapopulation linkages allow for local extinction of populations, which can be reestablished via colonization from adjacent populations (Leider, 1989; Milner and Bailey, 1989). The spatial arrangement of large and small scale habitat features within a catchment may serve as a template for metapopulation organization of fishes (Schlosser and Angermeier, 1995). The mosaic of floodplain reaches and constrained segments (Figure 2) within the mainstem and tributaries influences size, spatial distribution, and proximity of local spawning populations. Proximity of populations and favorability of connecting habitats can affect exchange of individuals among local populations (Reiman and McIntyre, 1993; Li *et al.*, 1995; Schlosser and Angermeier, 1995) and thus influence potential for recolonization of habitats where local extinction has occurred.

Since most river fauna are ectotherms, growth and reproduction also is vitally influenced by river temperature. Organisms adapted to cold climes of the headwater reaches simply cannot survive in warmer reaches downstream and vice versa. Indeed, species found in a particular thermal environment in one river generally will be found in very similar environments in other rivers within the geographical range of that species, if all other resource needs also are met. Because growth of ectotherms is strictly temperature dependent, temperature is a critical habitat attribute (Ward, 1985; Hall *et al.*, 1992). Stream insects and fish will be found in areas of the stream where their thermal needs are met and substratum, food (nutrients) and other resources are marginal, but rarely the inverse, at least for individuals that ultimately reproduce successfully. This is because of the basic thermal energetics of growth and the fact that many life history stages, such as insect emergence (ecdysis) and fish spawning are initiated by precise temperature cues (Brett, 1971; Vannote and Sweeney, 1980; Ward and Stanford, 1982). Also, few riverine organisms have highly specialized food requirements so that food limitation may be less prevalent than thermal limitation most of the time.

For plants of the river food web, availability of light and nutrients is crucial. Headwater streams often are shaded by riparian plants and decomposition of allochthonous (terrestrially derived) coarse particulate organic matter (leaves, grasses) usually drives instream bioproduction (Cummins *et al.*, 1984; Cummins *et al.*, 1989). Plant growth nutrients are released into transport by the decomposition of particulate organic matter entrained on the bottom and are utilized by photosynthetic plants in better light environments downstream where the stream channel is wider and the riparian canopy opens. Of course, nutrients and other dissolved solids also are derived from dissolution of the bedrock and other geochemical reactions. Indeed, streams with high alkalinity from limestone dissolution generally are more productive than streams draining more inert bedrocks, such as granite massifs (Kruger *et al.*, 1983; Waters *et al.*, 1990). Dissolved solids that are required for growth by photosynthetic microbes and hydrophytes spiral downstream, alternatively retained and released into transport by the river food webs (Newbold *et al.*, 1981; 1982). Short spiral length (i.e., the distance molecules travel between uptake points by the food web) reflects nutrient stress (shortage) whereas longer spiral lengths suggest nutrients are more sufficient for efficient growth of the autotrophic community. Conditions may shift back to heterotrophy in turbid, slow moving reaches near the river mouth as a consequence of planktonic microbial decomposition of organic matter transported from upstream reaches, reduced light reaching the bottom owing to deep and often turbid water and shifting, unstable nature sand and silt substratum on the bottom (Vannote and Sweeney, 1980; Minshall *et al.*, 1983; Naiman et al., 1987).

All of this underscores the complex linkages between the spatial dimensions of river ecosystems (Figure 1). These interactive components and attributes are replicated throughout the river course from headwaters to mouth. Floods maintain channel and floodplain habitats and pulse nutrient-enriched waters laterally into backwaters and onto floodplains as well as downstream into the estuary. Because it is a continual habitat forming process, river biota are adapted to frequency and duration of flood pulses (Junk *et al.*, 1989; Copp, 1989). Rivers that flood frequently (annually or more often) maintain different species and food webs than systems that are more ecologically benign by rarely or never experiencing scouring floods (e.g., springbrooks and lake outlet streams). Food webs are complex and change predictably along the stream continuum in direct response to variations in the strength of interconnections between channel, ground water, flood plain, upland elements of the catchment (Ward and Stanford, 1995a).

In our view the primary variables driving the distribution and abundance of animals and plants in flood-prone rivers usually are abiotic and primarily determined by the geologic and climatic setting of the catchment basin (Figure 3). Biotic interactions (e.g., competition, predation, parasitism), while they obviously continually occur within food webs in all habitats, may become progressively more important and apparent as the time between abiotic disturbances increases and hence are most pronounced in springbrooks and lake outlet streams where abiotic drivers are comparatively nonvariable (Ward and Stanford, 1983b; McAuliffe, 1983; 1984; Reice, 1994). All big rivers that are not influenced by large on-channel lakes are naturally flood-prone and biophysical structure ultimately is controlled by the inexorable, but highly dynamic, scouring process of cut and fill alluviation.

Environmental heterogeneity (complexity) maximizes in the alluvial (aggraded) reaches of the river continuum. Owing to the energetics of materials transport through large catchment basins from high elevation to sea level, alluvial reaches are arrayed along the stream continuum between canyon segments like beads on a string (Figure 2). The hyporheic and riparian corridor is expansive on alluvial reaches and seasonal temperature patterns vary within the wide array of aquatic habitats that exist laterally from the channel across the floodplain (Ward, 1984). Large floodplains appear to function as centers of biophysical organization within the river continuum (*sensu* Regier *et al.*, 1989). They likely are "hot spots" of biodiversity and bioproduction that are structurally and functionally linked by the river corridor (Copp, 1989; Gregory *et al.*, 1991; Zwick, 1992; Stanford and Ward, 1993; Ward and Stanford, 1995). Indeed, intermountain and piedmont valley floodplains worldwide are characterized by nutrient rich floodplain soils and diverse and productive backwater and mainstem fisheries (Welcomme, 1979; Davies and Walker, 1986; Lowe-McConnell, 1987; Sparks *et al.*, 1990; Junk and Piedade, 1994; Welcomme, 1995). These reaches also were and are foci for human activities within the catchment basin (Amoros *et al.*, 1987; Petts *et al.*, 1989; Wissmar *et al.*, 1994).

Additional data are needed to confirm explicitly the pattern of biodiversity hypothesized in Figure 2 for a spectrum of rivers worldwide, but the importance of alluvial zones as biological "hot spots" within river continua is very clear (e.g., riparian plants: Junk *et al.*, 1989; Gregory *et al.*, 1991; benthic insects: Zwick, 1992; Roth *et al.*, in press; fishes: Welcomme, 1979; Rieman and McIntyre, 1995). Moreover, metapopulation theory suggests that populations are critical for persistence of metapopulations with core-satellite structures (Schoener 1991; Harrison 1991, 1994). Core populations are relatively large populations occupying high quality habitat. In rivers, large alluvial reaches may support core populations of fishes (Lichatowich and Mobrand, 1995). These productive populations can serve as stable sources of dispersers that can recolonize peripheral habitats where less productive satellite populations have undergone local extinctions (Harrison, 1991, 1994; Reiman and McIntyre 1993; Li *et al.*, 1995; Schlosser and Angermeier, 1995) or "rescue" from extinction satellite populations whose abundance has been severely reduced (Brown and Kodrick-Brown, 1977; Gotelli 1991; Stacey and Taper, 1992). Thus, core populations can buffer metapopulations against environmental change and contribute to resiliency of regional fish production. Certain riparian plant species also appear to exist as metapopulations with cores on alluvial flood plains (Decamps and Tabacchi, 1994). We infer that alluvial reaches also should be foci for large river conservation and restoration.

THE RIVER DISCONTINUUM:
HUMAN ALTERATION OF LARGE RIVER ECOSYSTEMS

Humans vastly reduce the capacity of river ecosystems to sustain natural biodiversity and bioproduction by severing or compromising the dynamic interactive pathways of the river continuum. As described above, native biota of rivers display life history traits that allow populations survive within a certain range of environmental variation that characterizes a particular river. If this range of variation changes, organisms must locally adapt to the new range of environmental conditions or be extirpated. However, recolonization of extirpated areas may occur over time as environmental constraints ameliorate and/or as a consequence of immigration of suitably adapted populations. Human mediated environmental change can be so rapid and so severe that innate biotic resiliency cannot eventuate. The interactive pathways of the river continuum too often are permanently severed by human activities and biodiversity and bioproduction decline.

Pervasive human disturbances that uncouple important ecological processes linking ecosystem components in large river basins can be lumped into three broad classes: a) water pollution of all types, b) food web manipulation by harvest, stocking and exotic invasions and c) alteration of water, temperature and materials flux by dams, diversions and revetment. Human land use creates direct and diffuse inputs of waterborne wastes from the catchment and its airshed (Hynes, 1966; Warren, 1971), including accelerated erosion and sediment loading related to deforestation and road building (Waters, 1995), alters flux rates of materials (e.g., eutrophication, acidification) in rivers and uncouples lotic food webs by toxic effects. Harvest of fishes and invertebrates and the purposeful and accidental introduction of nonnative species induces strong interactions that alter food webs by causing biomass and bioproduction shifts, species replacements and other trophic effects (Mooney, 1986) that may cascade through all trophic levels and even involve terrestrial species that feed on aquatic biota (Spencer *et al.*, 1991). Pollution and food web manipulation are interactive with stream regulation effects in most catchments. However, alteration of flow regimes and associated severing of connectivity in the three spatial dimensions of riverine ecosytems perhaps are the most strikingly pervasive influence of humans on river landscapes worldwide (Dynesius and Nilsson, 1994).

Three first principles of the ecology of stream regulation

At least three fundamental commonalties emerge from the large literature on the ecology regulated rivers (reviewed by Baxter, 1977; Ward and Stanford, 1979; Lillehammer and Saltveit, 1984; Ward and Stanford, 1987; Petts and Wood, 1988; Petts, 1989; Calow and Petts, 1992). These principles must be recognized in the derivation of large river restoration strategies.

1. Diversity of habitats for native biota is substantially reduced.

Large storage dams worldwide inundate piedmont or mountain valley floodplains thereby severing the river continuum. Mass transport dynamics that create instream and floodplain habitats for riverine biota are drastically altered. Flood peaks are eliminated, daily discharges are more variable (e.g., Figure 4) and temperature seasonality may be reduced or lost (Stanford and Hauer, 1992; Blinn *et al.*, 1995).

As a consequence of reservoir storage of peak flows for flood control, navigation, irrigation and hydropower production, base flows increase substantially and often fluctuate so erratically that aquatic biota cannot survive in shallow, near-shore habitats. The varial zone, shown in Figure 1, constricts owing to loss of peak flows and is sterilized by cyclic dewatering and rewatering that occurs on weekly, daily or even hourly schedules (Cushman, 1985; Jourdonnais and Hauer, 1993). In stark contrast, a natural river pulses water onto often expansive floodplains within a range of variation that allows a diversity of aquatic and riparian biota to exist in multiple successional stages in a complex array of habitats. Persistent shallow or slack water habitats are especially important for survival of early life history stages of fishes that cannot survive in the strong currents of the channel thalweg. Storage of bedload in the reservoir and constant clear-water flushing downstream artificially depletes gravel and finer sediments in the tailwaters causing armoring of the bed with large cobble and boulder substratum (Simons, 1979). Large rocks eroded from the canyon walls and coarse bedload from tributaries jam the channel and increase the size of rapids over time because peak flows are insufficient to scour and transport the largest materials downstream (Dolan *et al.*, 1978). Channel constrictions and habitat simplification occur as the channel downcuts and riparian vegetation invades to the top of the varial zone in aggraded reaches, owing to loss of upstream sediment supply and loss of scouring flood flows (Johnson, 1994; Church, 1995).

The general conclusion is that regulation creates a discontinuum of environmental conditions and severs the connectivity of channel, ground water, flood plain and upland components of the catchment ecosystem; habitats for riverine biota become spatially homogenous, limited to the permanently wetted portion of the channel thalweg that is dominated by conditions dictated by operations of upstream storage reservoirs (Figure 5). Indeed, serial construction of low-head dams has converted virtually the entire mainstems of the largest rivers in USA, Europe, Sweden and Finland into shallow reservoir habitat that is neither truly laucustran nor riverine.

2. *Native biodiversity decreases and non-native species proliferate*

Native biodiversity almost always decreases after regulation (Ward and Stanford, 1991; Minckley and Deacon, 1991; Moyle and Leidy, 1992; Stevens *et al.*., in press) as conceptualized in Figure 5 compared to Figure 2. Vital core populations may be extirpated and satellite populations may become increasingly isolated by regulation schemes. Moreover, mortality resulting from passage through dams and reservoirs may synchronize the dynamics of geographically diverse local populations that use mainstem areas as a common migratory pathway, increasing the probability of metapopulation extinction (Harrison and Quinn, 1989; Reiman and McIntyre, 1993).

Altered temperature patterns and continual export of very fine organic matter and dissolved nutrients, coupled with simplification of the channel, stabilization of bottom substratum and loss of floodplain flooding, promotes environmental conditions to which native species are maladapted, opening opportunities for nonnative plants and animals to establish robust populations (Stanford and Ward, 1986; Li, *et al.*, 1987; Pflieger and Grace, 1987; Bain *et al.*, 1988; Shannon *et al.*, 1994). In some cases one or a few native species are more abundant than they were before regulation (e.g., Poe *et al.*, 1992). But, the most pervasive result of habitat change produced by regulation is the proliferation of non-native species. Non-native invertebrates and fishes are consistently more abundant in regulated compared to unregulated river reaches (Li *et al.*, 1987; Bain *et al.*, 1988). Native riparian plants cannot exist on dewatered flood plains, which opens niches for dryland exotic plants. Moreover, due to loss of scouring flows, exotic and some native riparian plants choke the periodically saturated area of the shoreline above the narrowed varial zone and exotic hydrophytes usually dominate shallow water habitats (Decamps and Tabacchi, 1994; Johnson, 1994) Explicit reasons for non-native proliferation in regulated rivers vary, but in general non-natives simply are better competitors in the homogenous habitats of regulated rivers, plus the fact that managers and publics have purposefully introduced a wide array of non-natives into regulated rivers.

3. Biophysical conditions reset predictably in relation to influences of tributaries.and as distance downstream from the dam increases

The Serial Discontinuity Concept (SDC) (Ward and Stanford, 1983; Ward and Stanford, 1995b) explicitly acknowledges the inherent connectivity of the river continuum and predicts that the conditions described above will ameliorate downstream as a natural consequence of the biophysical energetics of rivers. The spatial rate at which reset occurs and its manifestation relative to position within the river continuum (Figure 5) is related to the limnological attributes (depth, volume, water retention time, trophic state) of the reservoir, the mechanics of water release (surface, bottom or depth-selective), the mode of dam operations and the influence of tributaries entering downstream from the dam. If the tributaries are large and unregulated, they may substantially mediate the reset (Stanford and Hauer, 1992). In any case conditions at some point downstream from the dam will very closely approximate conditions elsewhere in the continuum. Thus, upstream or downstream shifts in biophysical conditions mediated by dams manifest as predictable discontinuities in the river continuum. For example, biophysical conditions at some predictable point downstream from a large bottom (hypolimnial) release (winter warm, summer cold conditions, relative to the pre-regulation environment) dam in the montane transition of a temperate latitude river will be very similar to pristine conditions far upstream. In rivers that are free flowing for long distances downstream from large dams in the montane reaches, the position of the rhithron-potomon transition can be predicted from the operational mode of the dams relative to influence of tributaries.

The predictions of the SDC largely have been substantiated (Stanford *et al.*, 1988; Ward and Voelz, 1988; Hauer *et al.*, 1989; Stanford and Ward, 1989; Ward and Stanford, 1990; Munn and Brusven, 1991; Ward and Stanford, 1991; Sabater *et al.*, in press), although recent incorporation of responses of large floodplains (Ward and Stanford, 1995b) require additional resolution. The main point is that the ecological consequences of specific regulation schemes are largely predictable and environmental degradation associated with regulation can be ameliorated. We recognize that uncertainties derive from interactions with pollution and introduction of exotic biota. However, pollution can be curtailed or eliminated and nonnative biota likely will be substantially less successful as invaders when dams are operated in ways that maximize resets of environmental heterogeneity.

RESTORATION PROTOCOL

The era of dam building may be over in much of the world because high efficiency and affordable dam sites are already developed. Loss of biodiversity and bioproduction, especially riverine and anadromous fisheries (Frissell, 1993; Welcomme 1995), underscores the need for restoration of regulated rivers and enormously expensive reconstructions are underway or are being planned (Gore and Shields, 1995; Dahm *et al.*, 1995). Even removal of large dams on large rivers is included in some restoration plans because the costs of damage to fisheries and other attributes of riverine integrity in some instances far exceeds the commercial value of the dams. Removal of large dams obviously is problematic in a variety of ways, such as the mobilization of large volumes of fine sediments stored in the reservoir basin, and methods for evaluating removal strategies have been proposed (Shuman, 1995). A variety of approaches exist for restoring small streams with substantial emphasis on engineered structures such as weirs, off-channel ponds, rock gardens (Gore and Shields, 1995) and many other artificial habitat structures (Hunter, 1991). Commercial operations advertise engineering expertise for bulldozing damaged streams back to preregulation channel configurations and stories of restored fisheries and improved water quality abound in the popular literature, although scientific, long-term evaluations of such schemes are much less available (Sear, 1994). Structures placed instream often are washed out, fail to restore biodiversity or produce unanticipated negative responses, such as increased bank erosion or accelerated deposition of fine sediments (Frissell and Nawa, 1992) and increased water temperatures (C. Frissell, unpubl. data) associated with weirs and rock gardens. Such problems largely derive from lack of attention to the conceptual foundations of river ecology and first principles of the ecology of regulated streams.

Formalize the problem at catchment scale

Restoration of large regulated rivers begins with recognition of the river continuum and evaluation of the loss of ecosystem capacity to sustain biodiversity and bioproduction. Biological (e.g., past and present distribution of native biota) *and* physical (e.g., channel configuration) indices of ecosystem resilience are needed (Frissell *et al.*, 1993); measures of biological integrity as defined by Angermeier and Karr (1994) may be more useful than biodiversity *per se* because of the difficulty of accurately determining the distribution and abundance of benthos, fish and other river organisms. Habitat requirements for all life history stages and generation times (turnover rates) of native, keystone species (i.e., top carnivores and other strong interactors capable of structuring food webs: Power *et al.*, 1995) may clarify spatial and temporal scales in large river restorations. In general, the entire catchment from headwaters to the ocean is relevant. In the case of rivers that support anadromous fisheries, estuarine and ocean habitats connect functionally to the riverine components. Mathematical models can be very effectively used to formalize understanding of the effects of regulation and interactions with pollution and food web manipulation within the river continuum, but models should not be used *exclusively* to define a restoration strategy (Hall, 1988b). The process must be inferential from the entire body of quantitative and qualitative information about how river regulation and interactive effects have altered ecosystem capacity.

Restore environmental (habitat) heterogeneity but let the river do the work

The main goal is to reduce the range of human disturbances so that interconnected riverine habitats (Figures 1 and 2) can support diverse and productive food webs, including species of special social and economic interest. Management should strive to restore environmental heterogeneity and reduce or eliminate sources of mortality from pollution and overharvest. Keep in mind that riverine biodiversity and bioproduction largely are controlled by abiotic drivers (Figure 3) and that density-dependent relationships, such as stock-recruitment relations often used to determine fisheries harvest prescriptions, rarely manifest predictably due to natural abiotic variation (Hall, 1986; Hall, 1988a; Pimm, 1991; Huston, 1994).

Owing to the importance of flow to habitat maintenance and temperature to food web energetics, significant restoration is possible simply by reregulation to allow more natural seasonality of flow and temperature. We call this restoration of normative habitat conditions, where the baseline is established from what is possible in a natural-cultural context as opposed to striving for pristine conditions which are difficult, if not impossible, to define or achieve, at least for entire catchments. Removal of dams certainly should be considered and, where possible, done; but, in general removal is not desired or possible. However, restoration of normative habitat conditions is possible in many if not most regulated rivers without taking dams out.

Peak flows are needed to scour and rearrange substratum and reconnect floodplain habitats with the channel; spatial and temporal temperature variability promotes re-establishment of native biodiversity (Figures 2 and 5). Peak flows needed to re-establish cut and fill alluviation (called effective flows by geomorphologists) may or may not be equal to bankfull and gravel supply may be limiting due to storage of bedload in the reservoirs (Ligon *et al.*, 1995). Effective flows can rapidly degrade (downcut) entire segments when sediment mass balance relations change as a consequence of regulation (Andrews and Nelson, 1989). Adding sediments to regulated rivers using slurry pipelines from reservoir deltas should not be out of the realm of consideration in situations where instream sediment supply is limited by years of regulation. However, overbank flows in many cases will initiate cut and fill alluviation in an ecologically effective manner supplying sufficient sediment from lateral erosion.

We emphasize that reregulation of flows requires careful evaluation of channel morphometry, bedsediment size distribution and shear stress in relation to the range of possible flows. A great deal of geomorphic study and modeling has been devoted to this problem in recent years (Andrews, 1980; Andrews and Nelson, 1989; Kellerhals and Church, 1989; Deitrich *et al.*, 1993; Church, 1995). In general, flows that mobilize substratum of median particle diameter will build bars, cut overflow channels and dig pools. Determination of peak flows is complicated by dense, often senescent, thickets of riparian vegetation on the flood plains of regulated rivers. Repeated scouring flows likely will restore riparian succssional vitality. Annual temperature patterns similar to preregulation conditions, which will directly mediate restoration of biota, often can be attained by depth-selective withdrawal structures on the dams (Gore, 1985).

Of course restoration of overbank flows may be problematic in many rivers where humans have colonized the flood plains. In these cases revetments often have been extensively built to restrain flood flows. Reregulation to produce overbank flows may not be practical. However, floods of record likely will result in overbank flow even in intensely regulated rivers because storage throughout the continuum usually is insufficient to control very large floods. Revetments tend to act as dams during very large floods on aggraded rivers and extensive scouring of floodplain surfaces occurs if revetments are breached. Recent floods (1993-5) of such magnitude in large rivers of western Europe, southern Scandinavia, Bangladesh and the United States provided evidence of the value of vacating flood plains to reduce the human costs and exploit natural flood pulsing (Sparks, 1995).

The strong inference for management is to protect uncolonized floodplains by re-establishing periodic overbank flooding, allowing the river to rebuild habitats. Elsewhere, incentives will be needed to get people to vacate flood plains. If that is not practical or desired by stakeholders, development of strategies for reconnecting severed lowland floodplain wetlands and backwaters by use of lateral flow control structures may be useful (Gore, 1985; Gore and Shields, 1995). In situations where alluvial areas have been inundated, it may be possible to permanently lower the full pool level of the reservoir allowing riverine cut and fill alluviation to reconfigure and restore drowned flood plains. As in dam removal, this scenario requires careful evaluation because sediment transport dynamics may be different than occurred prior to regulation.

Whereas peak flows are needed to restore natural habitat heterogeneity, usually stabilization of base flow fluctuations also will be needed to revitalize the varial zone of the channel (Figure 1). Establishment of sustained base flows restores biodiversity and bioproduction in shallow water habitats that are critically important to benthic insects that must emerge from the shorelines of rivers and small fishes that must reside on or near substratum in low velocity habitats (Perry and Perry, 1986; Weisberg *et al.*, 1990; Travnichek *et al.*, 1995).

Reregulation in most rivers likely can be accomplished without substantially compromising storage or hydropower (Figure 6). Peak flows are built from storage and runoff and released in concert with natural runoff timing in the catchment (Figure 4). On wet years, peaks can be re-regulated to approach floods of record, depending on the release capability of the dam. Very high flows are not needed every year to maintain instream and floodplain habitats nor is the historical duration of floods likely required because most of the sediment is moved on the rising limb of the hydrograph. On years of average catchment water yield, a modest peak flow can be generated, while also elevating baseflow to accomplish the purposes for which the dams were built. On dry years, peak flows can be minimal or nonexistent (Figure 4). The strategy simply is to lower the baseflow some to build peaks in relation to catchment runoff. On all years it is essential to prevent massive dewatering of the varial zone during base flow periods; explicitly, this means that daily changes in flow (ramping rates) should not exceed the range of variation that occurred before regulation (Figure 4).

Operators of hydroelectric dams may object to reregulation recommendations as depicted in Figure 6, because of potential constraints on generation of peak power and often concern exists that legal requirements for electrical load control cannot be met. On the contrary, load control can be done without ramping flow beyond the range of variation observed in preregulation periods (Jourdonnais and Hauer, 1993). Loss of peaking is problematic. However, most large dams are part of large electrical marketing grids and alternatives to hydropower peaking exist today that were not available a decade ago. For example, modern fuel turbines are very effective peaking units, natural gas reserves are large worldwide and local utilities are finding gas powered turbines to be preferred alternatives to purchase of regional hydropower. Need for hydropower peaking may wane in the next decade, particularly as the cost of downstream environmental mitigation increases.

Maximize passage efficiency to allow recovery of metapopulations

Maintenance of instream and floodplain habitats by restoration of peak flows and revitalization of shallow and slack water habitats by stabilization of baseflows likely will remediate the "beads on the string." In the absence of dam and reservoir removal, optimization of dam and reservoir passage efficiency for biota is required to reconnect the beads in the continuum context (Figure 2). A body of largely gray literature describes efficiency of mechanisms for significantly reducing mortality of juvenile and adult fishes as they pass hydroelectric dams (Harmon and Park, 1980; Mundy *et al.*, 1994). Flowing ladders, traveling screens, surface-release attractors and other bypass devices have been devised (Gore, 1985). The main point is that dams with no or very inefficient bypass systems maintain the discontinuum and isolate populations thereby limiting gene flow that may be needed to restore and maintain metapopulations. On the other hand, presence of impassable dams in some cases has prevented immigration of nonnative species into native food webs and effectively isolated viable native populations (Stanford and Hauer, 1992).

In many large regulated rivers, viable populations of native species remain in segments isolated by dams. Restoration of flow and temperature seasonality and reconnection of these refugia may restore critically important core areas, revitalize metapopulation structure and rapidly lead to recovery of genetically and numerically depressed populations (Sedell *et al.*, 1990; DeVore *et al.*, 1995). Indeed, a primary strategy of large river restoration should be to identify, stabilize, restore and reconnect river segments to core areas containing native food webs. The expectation is that native species will recolonize restored habitat from the core area (Lichatowich *et al.*, 1995; Frissell and Bayles, 1996). The process can be mediated by artificial supplementation (replanting) of the vestigial stock if the native gene pool is properly cultured. However, this strategy is fraught with risk owing to the complexity of locally adapted stocks (Lichatowich *et al.*, 1995). Perhaps a better strategy is to reconnect the beads and allow the biota to adapt as they will (i.e., build the ball field and they will come to play!). How long it will take is a key question; biology itself can be limiting. Time frames for recovery likely will vary from years to decades depending on the degree of habitat degradation, the strength of normative conditions and the species involved. We note, though, that salmon and other biota already have re-established in the rivers devastated by the eruption of Mount St. Helens, Washington, USA, in 1982and chinook salmon in New Zealand rivers developed locally adapted life histories within 50 years after initial introduction (Quinn and Irwin, 1993).

Minimize planting of cultured stocks

Contemporary fisheries management is based on a belief system that embraces the concept that loss of bioproduction and biodiversity from stream regulation can be mitigated by construction and operation of artificial culture systems. In other words, the belief is habitat loss caused by stream regulation can be replaced, if not enhanced, by artificial propagation. Perhaps no greater myth exists in ecology. While economically important nonnative salmonid and other fisheries have been established from cultured stocks in river segments worldwide, in almost every case this practice has failed miserably to meet its objective of replacing lost fisheries (Lichatowich, in press). Stocking of native and nonnative fishes has irresponsibly compromised native food webs worldwide and is rightfully called the Frankenstein Effect (Moyle *et al.*, 1986). A large body of literature debates this problem and the bottom line is that culture operations should be avoided unless native biota clearly are headed for extinction as a consequence of habitat loss (Minckley and Deacon, 1991; Hilborn, 1992). Even then cultured stocks cannot be expected to re-establish if they are simply released back into the same degraded habitats. Ecological bottlenecks that compromised endangered species in the first place have to be fixed and the only way to do that in large river systems is to restore habitat in a continuum context.

Be wary of management actions that attempt to control riverine food webs.

Perhaps the greatest uncertainty in re-regulating river systems to restore hot spot connectivity (Figure 2) is unexpected consequences of the inexorable proliferation of nonnative biota. Wendell Minckley and James Deacon, the sages of fish ecology in the species-rich American Southwest often rightly noted that locally adapted fishes of the desert clearly are able to deal with environmental variation, but they are quickly driven to extinction by food web change associated with invasions of nonnative species (e.g., Minckley and Douglas, 1991). However, restoration of natural flow and temperature dynamics compromises the ability of nonnative species to sustain viable populations and promotes native species (Li et al, 1987; Meffe and Minckley, 1987; Bain et al, 1988). But, even with restoration of the full range of natural flow variation interactions with nonnative plants and animals likely will continue to be a problem for native biodiversity management and conservation.

The alternative is to control nonnative populations by aggressive harvest. However, it is very difficult to do this without also impacting natives and prediction of the influence of food web structure is tenuous at best. Moreover, in some cases one or a few native species have become very abundant in regulated rivers along with nonnatives. For example, native squawfish (*Ptychocheilus oregonensis*) in the Columbia River, USA, are thought to be a major source of mortality for juvenile salmon, which exist in very depressed populations (Poe *et al.*, 1991; Rieman *et al.*, 1991) and a very aggressive control program has been initiated by paying fishermen a bounty for each squawfish caught. However, food web structure in the lower Columbia River is poorly known and a wide variety of nonnative predators are present and predicting food web responses as well as influences on salmon mortality is tenuous. A congener (*P. lucius*) in the Colorado River is listed as endangered and a very expensive recovery program has been initiated. For many publics these strategies seem at cross purposes even though the ecology of the two species is very different.

In general effectiveness of predator control programs is minimal or poorly demonstrated even though it is a very popular management strategy. We agree with Goodrich and Buskirk (1995) that population control of abundant native vertebrates should be a strategy of last resort for conservation of rare natives. Columbia River salmon evolved with squawfish predation and proper habitats for salmon smolts clearly should reduce smolt mortality. However, constraining proliferation of nonnative plants and animals is an obvious need for conservation of native biodiversity.

Again, the preferred approach may be to implement reregulation to restore lost habitat and allow the food web to adjust as it will. The available body of information suggests that natives will fare better than nonnatives. Clearly it is advisable to carefully document and monitor food web dynamics from a community ecology perspective.

Use adaptive ecosystem management

Any strategy to remediate the effects of large river regulation will require an adaptive approach. Scientists can be relied upon to document ecological problems by research and synthesis of empirical information on cause and effect but problem solution must involve knowledge of human perceptions and desires, which often are different than inferred by strict interpretation of the science (Ludwig *et al.*, 1993). In most cases inefficient information transfer between science, management, policy makers (government) and the general public hinders attainment of common ground.

Adaptive ecosystem management (Lee and Lawrence, 1986) is a useful process for solving catchment scale problems discussed herein. We agree with Stanford and Poole (1996) who advocate an iterative, stepwise approach that involves synthesis of available information in an ecosystem context to define the problem, public participation in goal setting (e.g., protection and restoration of native biodiversity), research and peer review to define science-based management actions (e.g., reregulation), effective monitoring and evaluation of management actions and adaptive revision of actions based on new information from scientific research.

CONCLUSION

Reregulation of large river systems from headwaters to mouth for the purpose of restoring and reconnecting hot spots of native biodiversity and bioproduction has not been accomplished anywhere to date. Our protocol should be viewed as an hypothesis in need of an experimental catchment. Many candidate rivers exist. We recognize that this analysis has not adequately considered economic and social ramifications of our protocol. A fundamental problem is that metrics for linking natural and cultural elements of ecosystems remain elusive. Perhaps that shortcoming can be solved through multidisciplinary examination of large river ecosystems using adaptive management. However, the reality is that sustainability of natural attributes of large river ecosystems is vastly compromised by regulation. Tweaking the system with site-specific mitigation activities that ignore the biophysical continuum hold little promise, even though collectively tweaking can be very costly. Perhaps it is time to try restoring biophysical connectivity of an entire regulated river ecosystem using the protocol proposed herein. Restoration of some large portion of lost capacity to sustain native biodiversity and bioproduction seems possible, especially in large rivers with a substantial portion of the continuum remaining in a free-flowing state. The cost may be less than expected because the river can do the most of the work.

ACKNOWLEDGMENT

Financial support for this paper was provided in part by the Northwest Power Planning Council, Portland, Oregon, USA, and National Science Foundation grant number BSR ------- but no endorsement of the paper was made or implied. We thank Geoffrey C. Poole for help with graphics and three anonymous reviewers for their constructive comments.

Oak Ridge National Laboratory is managed by Lockheed Martin Energy Research Corp., under contract DE-AC05-96OR22464 with the U. S. Department of Energy.

LITERATURE CITED

Amoros, C., A. L. Roux, J. L. Reygrobellet, J. P. Bravard and G. Pautou. 1987. 'A method for applied ecological studies of fluvial hydrosystems', *Regulated Rivers: Research and Management*, 1, 17-36.

Andrewartha, H. G. and L. C. Birch. 1954. *The Distribution and Abundance of Animals.* University of Chicago Press, Chicago, Illinois. 281 pp.

Andrews, E. D. 1980. 'Effective and bankfull discharges in the Yampa River Basin, Colorado and Wyoming', *Journal of Hydrology,* 43, 311-330.

Andrews, E. D. and J. M. Nelson. 1989. 'Topographic response of a bar in the Green River, Utah to variation in discharge', in Ikeda, S. and G. Parker (Eds), *River Meandering.* American Geophysical Union. pp. 463-485.

Angermeier, P. L. and J. R. Karr. 1994. 'Biological integrity versus biological diversity as policy directives', *BioScience*, 44/10, 690-697.

Bachman, R. A. 1983. 'Foraging behavior of free-ranging wild brown trout (*Salmo trutta*) in a stream', *Transactions of the American Fisheries Society,* 113, 1-32.

Bain, M. B., J. T. Finn and H. E. Booke. 1988. Stream-flow regulation and fish community structure. Ecology 69:382-392.

Baxter, R. M. 1977. Environmental effects of dams and impoundments. Ann. Rev. Ecol. Syst. 8:255-283.

Benke, A. C., C. A. S. Hall, C. P. Hawkins, R. H. Lowe-McConnell, J. A. Stanford, K. Suberkropp and J. V. Ward. 1988. 'Bioenergetic considerations in the analyses of stream ecosystems', *Journal of the North American Benthological Society,* 7/4, 480-502.

Best, J. L. and C. S. Bristow, (ed.). 1993. Braided Rivers. Geological Society Special Publications. The Geological Society,London.

Blikie, P. and H. Brookfield. 1987. Land Degradation and Society. Methuen Press, New York, NY. USA. 453 pp.

Blinn, D. W., J. P. Shannon, L. E. Stevens and J. P. Carder. 1995. Consequences of fluctuating discharge for lotic communities. J. North Am. Benthol. Soc. 14(2):233-248.

Brett, J. R. 1971. 'Energetic responses of salmon to temperature. A study of some thermal relations in the physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*)', *Am. Zool.*, 11, 99-113.

Brown, J.H. and A. Kodric-Brown. 1977. Turnover rates in insular biogeography: effects of immigration on extinction. Ecology 58: 445-449.

Calow, P. and G. E. Petts, (Eds). 1992. *The Rivers Handbook, Volume 1: Hydrological and Ecological Principles.* Blackwell Scientific, Oxford, England.

Church, M. 1995. 'Geomorphic response to river flow regulation: case studies and time-scales', *Regulated Rivers: Research and Management,* 11/1, 3-22.

Connell, J. H. 1978. 'Diversity in tropical rain forests and coral reefs', *Science,* 199, 1302-1310.

Connor, J. E. 1993. *Hydrology, Hydraulics and Geomorphology of the Bonneville Flood.* US Geological Survey Special Paper 274. US Govt. Printing Office, Washington, DC.

Copp, G. H. 1989. 'The habitat diversity and fish reproductive function of floodplain ecosystems', *Envir. Biol. Fish.,* 26, 1-27.

Cummins, K. W., G. W. Minshall, J. R. Sedell, C. E. Cushing and R. C. Petersen. 1984. 'Stream ecosystem theory', *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie,* 22, 1818-1827.

Cummins, K. W., M. A. Wilzbach, D. M. Gates, J. B. Perry and W. B. Taliaferro. 1989. 'Shredders and riparian vegetation. Leaf litter that falls into streams influences communities of stream invertebrates', *BioScience,* 39/1, 24-30.

Cushman, R. M. 1985. 'Review of ecological effects of rapidly varying flows downstream of hydroelectric facilities', *N. Am. J. Fish. Mgmt.,* 5, 330-339.

Dahm, C. N., K. W. Cummins, H. M. Valett and R. L. Coleman. 1995. An ecosystem view of the restoration of the Kissimmee River. Restoration Ecology 3(3):225-238.

Davies, B. R. and K. F. Walker, (Ed.). 1986. *The Ecology of River Systems.* Dr. W. Junk, Dordrecht, The Netherlands. 793 pp.

Decamps, H. and E. Tabacchi. 1994. Species richness in vegetation along river margins, IN: P. S. Giller, A. G. Hildrew and D. G. Raffaelli (ed.), Aquatic Ecology: Scale, Pattern and Process. Blackwell Scientific Publications, London.

DeVore, J. D., B. W. James, C. A. Tracy and D. A. Hale. 1995. 'Dynamics and potential production of white sturgeon in the unimpounded Lower Columbia River', *Transactions of the American Fisheries Society,* 124/6, 845-856.

Dolan, R., A. Howard and D. Trimble. 1978. 'Structural control of the rapids and pools of the Colorado River in the Grand Canyon', *Science,* 202, 629-631.

Doppelt, B., M. Scurlock, C. Frissell and J. Karr. 1993. *Entering the Watershed.* Island Press, Washington, D.C. 462 pp.

Dynesius, M. and C. Nilsson. 1994. 'Fragmentation and flow regulation of river systems in the northern third of the world', *Science,* 266, 753-762.

Ebersole, J.L., W.J. Liss, and C.A. Frissell. In Press. Restoration of stream habitats in managed landscapes in the western USA: restoration as re-expression of habitat capacity. Environmental Management.

Frissell, C. A. 1993. 'Topology of extinction and endangerment of native fishes in the Pacific northwest and California (U.S.A.)', *Conservation Biology,* 7/2, 342-354.

Frissell, C. A. and D. Bayles. 1996. Ecosystem management and the conservation of aquatic biodiversity and ecological integrity. *Water Resources Bulletin* 32(2): 229-240.

Frissell, C. A., W. J. Liss and D. Bayles. 1993. 'An integrated, biophysical strategy for ecological restoration of large watersheds', in Spangenborg, N. E. and D. E. Potts (Ed.), *Proceedings of the Symposium on Changing Roles in Water Resources Management and Policy.* American Water Resources Association, Bethesda, Maryland. pp. 449-456.

Frissell, C. A., W. J. Liss, R. E. Gresswell, R. K. Nawa, and J. L. Ebersole. In press. 'A resource in crisis: changing the measure of salmon management', in Stouder, D. J., P. A. Bisson, and R. J. Naiman (Eds). *Pacific Salmon and their Ecosystems: Status and Future Options.* Chapman and Hall, New York, New York.

Frissell, C. A. and R. K. Nawa. 1992. 'Incidence and causes of physical failure of artificial habitat structures in streams of western Oregon and Washington', *North American Journal of Fisheries Management,* 12, 182-197.

Gibert, J., M. J. Dole-Olivier, P. Marmonier and P. Vervier. 1990. 'Surface water-groundwater ecotones' in Naiman, R. J. and H. Decamps (Eds), *Ecology and Management of Aquatic-Terrestrial Ecotones.* Partenon Publ., London, England. pp. 199-255.

Gislason, G. M. 1985. The life cycle and production of Simulium vittatum Zett. in the River Laxa, North-East Iceland. 22:3281-3287

Goodrich, J. M. and S. W. Buskirk. 1995. 'Control of abundant native vertebrates for conservation of endangered species', *Conservation Biology,* 9/6, 1357-1364.

Gore, J. A., (Ed.). 1985. *The Restoration of Rivers and Streams: Theories and Experience.* Butterworth Publishers, Stoneham, Massachusetts. 280 pp.

Gore, J. A. and J. F. D. Shields. 1995. 'Can large rivers be restored?', *BioScience,* 45/3, 142-152.

Gotelli, N.J. 1991. Metapopulation modesl: the rescue effect, the propagule rain, and the core-satellite hypothesis. The American Naturalist 138: 768-776.

Gregory, S. V., F. J. Swanson, W. A. McKee and K. W. Cummins. 1991. 'An ecosystem perspective of riparian zones', *BioScience,* 41/8, 540-551.

Hall, C. A. S. 1986. 'The changing intellectual climate of fisheries management', *Environmental Management,* 10/3, 331-334.

Hall, C. A. S. 1988a. 'An assessment of several of the historically most influential theoretical models used in ecology and of the data provided in their support', *Ecological Modelling,* 43, 5-31.

Hall, C. A. S. 1988b. 'What constitutes a good model and by whose criteria?', *Ecological Modelling,* 43, 125-127.

Hall, C. A. S., J. A. Stanford and F. R. Hauer. 1992. 'The distribution and abundance of organisms as a consequence of energy balances along multiple environmental gradients', *Oikos,* 65, 377-390.

Hanski, I. 1991. 'Single species metapopulation dynamics: concepts, models and observations', *Biol. Jour. Linnean Soc.,* 42:17-38.

Hanski, I. and M. Gilpin. 1991. 'Metapopulation dynamics: brief history and conceptual domain', *Biol. Jour. Linnean Soc.,* 42, 3-16.

Harmon, J. R. and D. L. Park. 1980. 'Evaluation of a bypass sytem for juvenile salmonids at Little Goose Dam', *Marine Fisheries Review,* June, 25-28.

Harrison, S. 1991. Local extinction in a metapopulation context: an empirical evaluation. Biological Journal of the Linnean Society 42: 73-88.

Harrison, S. 1994. Metapopulations and Conservation. In Large-scale Ecology and Conservation Biology. P.J. Edwards, R.M. May, and N.R. Webb (eds.). Blackwell Scientific Publications, Oxford. 375 pages.

Harrison, S. and J.F. Quinn. 1989. Correlated environments and the persistence of metapopulations. Oikos 56: 293-298.

Hauer, F. R., J. A. Stanford and J. V. Ward. 1989. 'Serial discontinuities in a Rocky Mountain river. II. Distribution and abundance of Trichoptera', *Regulated Rivers: Research and Management,* 3, 177-182.

Hilborn, R. 1992. 'Hatcheries and the future of salmon in the Northwest', *Fisheries,* 17/1, 5.

Hunter, C. J. 1991. *Better Trout Habitat: A Guide to Stream Restoration and Management.* Island Press, Washington, District of Columbia. 320 pp.

Huston, M. 1979. 'A general hypothesis of diversity', *American Naturalist,* 113, 81-101.

Huston, M. A. 1994. *Biological Diversity: The Coexistence of Species on Changing Landscapes.* Cambridge University Press, Cambridge, Great Britain. 681 pp.

Hynes, H. B. N. 1966. *The Biology of Polluted Waters.* Liverpool University Press, Liverpool, England. 202 pp.

Hynes, H. B. N. 1975. 'The stream and its valley', *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie,* 19, 1-15.

Illies, J. 1956. 'Seeausfluss-Biozönosen lappländischer Waldbäche', *Ent. Tidskr.*, 77, 138-153.

Illies, J. and L. Botosaneanu. 1963. 'Problemes et methodes de la classification et de la zonation ecologique des eaux courantes, considerees surtout du point de vue faunistique', *Mitteilungen der Internationalen Vereinigung für Theoreticshe und Angewandte Limnologie,* 12, 1-57.

Johnson, W. C. 1994. 'Woodland expansion in the Platte River, Nebraska: Patterns and causes', *Ecological Monographs,* 64/1, 45-84.

Jourdonnais, J. H. and F. R. Hauer. 1993. 'Electrical frequency control and its effects on flow and river ecology in the lower Flathead River, Montana', *Rivers,* 4/2, 132-145.

Junk, W. J., P. B. Bayley and R. E. Sparks. 1989. 'The flood pulse concept in river-floodplain systems' in Dodge, D. P. (Ed.), *Proceedings of the International Large River Symposuim.* Canadian Special Publication of Fisheries and Aquatic Sciences 106. pp. 110-127.

Junk, W. J. and M. T. F. Piedade. 1994. 'Species diversity and distribution of herbaceous plants in the floodplain of the middle Amazon', *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie,* 25, 1862-1865.

Heiler, G., T. Hein, F. Schiemer and G. Bornette. 1995. Hydrological connectivity and flood pulses as the central aspects for the integrity of a river-floodplain system. Reg. Rivers 11(3 & 4):351-361.

Kellerhals, R. and M. Church. 1989. 'The morphology of large rivers: characterization and management', *Canadian Special Publication of Fisheries and Aquatic Sciences,* 106, 31-48.

Kondolf, G. M. and M. Larson. 1995. Historical channel analysis and its application to riparian and aquatic habitat restoration. Aquat. Conservation: Marine and Freshwater Ecosystems 5(2):109-126.

Krueger, C. C. and T. F. Waters. 1983. 'Annual production of macroinvertebrates in three streams of different water quality', *Ecology,* 64, 840-850.

Lee, K. N. and J. Lawrence. 1986. 'Adaptive management: learning from the Columbia River Basin fish and wildlife program', *Environmental Law,* 16, 431-460.

Leider, S. A. 1989. 'Increased straying by adult steelhead trout, *Salmo gairdneri,* following the 1980 eruption of Mount St. Helens', *Envir. Biol. Fishes,* 24, 219-229.

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 Matthews, W. J. and D. C. Heins (Eds), *Community and Evolutionary Ecology of North American Stream Fishes.* University of Oklahoma Press, Norman, Oklahoma. pp. 193-202.

Li, H. W., K. Currens, D. Bottom, S. Clarke, J. Dambacher, C. Frissell, P. Harris, R. M. Hughes, D. McCullough, A. McGie, K. Moore and S. Thiele. 1995. Safe havens: refuges and evolutionarily significant units. American Fisheries Society Symposium 17

Lichatowich, J. In Press. 'Components of management baselines' in Stouder, D. J., P. A. Bisson and R. J. N. (Eds), *Pacific Salmon and Their Ecosystems.* Chapman and Hall, New York, New York.

Lichatowich, J., L. Mobrand, L. Lestelle and T. Vogel. 1995. 'An approach to the diagnosis and treatment of depleted Pacific salmon populations in Pacific Northwest watersheds', *Fisheries,* 20/1, 10-18.

Ligon, F. K., W. E. Dietrich and W. J. Trush. 1995. 'Downstream ecological effects of dam', *BioScience,* 45(3), 183-192.

Lillehammer, A. and S. J. Saltveit, (Eds). 1984. *Regulated Rivers.* Oslo University Press, Oslo, Norway. 540 pp.

Lowe-McConnell, R. H. 1987. *Ecological Studies in Tropical Fish Communities.* Cambridge Univ. Press, Cambridge.

Lubchenco, J., A. M. Olson, L. B. Brubaker, S. R. Carpenter, M. M. Holland, S. P. Hubbell, S. A. Levin, J. A. MacMahon, P. A. Matson, J. M. Melillo, H. A. Mooney, C. H. Peterson, H. R. Pulliam, L. A. Real, P. J. Regal and P. G. Risser. 1991. 'The sustainable biosphere initiative: An ecological research agenda', *Ecology,* 72/2, 371-412.

Ludwig, D., R. Hillborn and C. Walters. 1993. 'Uncertainty, resource exploitation and conservation: Lessons from history', *Science,* 260, 17-36.

Mangin, A. 1994. 'Karst hydrogeology' in Gibert, J., D. L. Danielopol and J. A. Stanford (Eds), *Groundwater Ecology.* Academic Press, Inc., San Diego, California. pp. 43-68.

McAuliffe, J. R. 1983. Competition, colonization patterns and disturbance in stream benthic communities. IN: Barnes, J. R. and G. W. Minshall (eds.), Stream ecology: application and testing of general ecological theory. Plenum Press, New York.

McAuliffe, J. R. 1984. Competition for space, disturbance, and the structure of a benthic stream community. Ecology 65:894-908.

Meffe, G. K. and W. L. Minckley. 1987. 'Persistence and stability of fish and invertebrate assemblages in a repeatedly disturbed Sonoran Desert stream', *American Midland Naturalist,* 117, 177-191.

Milner, A. M. and R. G. Bailey. 1989. 'Salmonid colonization of new streams in Glacier Bay National Park, Alaska', *Aquaculture and Fisheries Mgmt.,*. 20, 179-192.

Minckley, W. L. and J. E. Deacon, (Eds). 1991. *Battle Against Extinction: Native Fish Management in the American West.* University of Arizona Press, Tucson, Arizona. 535 pp.

Minckley, W. L. and M. E. Douglas. 1991. 'Discovery and extinction of western fishes: A blink of the eye in geologic time' in Minckley, W. L. and J. E. Deacon (Eds), *Battle Against Extinction: Native Fish Management in the American West.* University of Arizona Press, Tucson, Arizona. pp. 7-17.

Minshall, G. W. 1978. 'Autotrophy in stream ecosystems', *BioScience,* 28/12, 767-771.

Minshall, G. W., R. C. Petersen, K. W. Cummins, T. L. Bott, J. R. Sedell, C. E. Cushing and R. L. Vannote. 1983. Interbiome comparison of stream ecosystem dynamics. Ecol. Monogr. 53(1):1-25.

Mooney, H. A. and J. A. Drake, (Ed.). 1986. *Ecology of Biological Invasions of North America and Hawaii.* Springer-Verlag, New York, New York.

Moyle, P. B. and R. A. Leidy. 1992. 'Loss of biodiversity in aquatic ecosystems: Evidence from fish faunas' in Fielder, P. L. and S. K. Jain (Ed.), *Conservation Biology: The Theory and Practice of Nature, Conservation, Preservation and Management.* Chapman and Hall, New York, New York. pp. 128-169.

Moyle, P. B., H. W. Li and B. A. Barton. 1986. 'The Frankenstein effect: Impact of introduced fishes on native fishes in North America', in Stroud, R. H. (Ed.), *Fish Culture in Fisheries Management.* Am. Fish. Soc., Maryland. pp. 415-426.

Mundy, P. R., D. Neeley, C. R. Stewart, T. P. Quinn, B. A. Barton, R. N. Williams, D. Goodman, R. R. Whiney, M. W. Erho and L. W. Botsford. 1994. *Transportation of Juvenile Salmonids from Hydroelectric Projects in the Columbia River Basin; An Independent Peer Review.* U. S. Fish & Wildlife Service, Portland, Oregon. 149 pp.

Munn, M. and M. A. Brusven. 1991. 'Benthic macroinvertebrate communities in nonregulated and regulated waters of the Clearwater River, Idaho', *Regulated Rivers: Research and Management,* 6, 1-11.

Naiman, R. J., H. Decamps, J. Pastor and C. A. Johnston. 1988. 'The potential importance of boundaries to fluvial ecosystems', *Journal of the North American Benthological Society,* 7/4, 289-306.

Naiman, R. J., J. J. Magnuson, D. M. McKnight and J. A. Stanford (Eds). 1995a. *Freshwater Imperative: A Research Agenda.* (1st ed.). Island Press, Washington, District of Columbia. 165 pp.

Naiman, R. J., J. J. Magnuson, D. M. McKnight, J. A. Stanford and J. R. Karr. 1995b. 'Freshwater ecosystems and their management: a national initiative', *Science,* 270/5236, 584-585.

Naiman, R. J., J. M. Melillo, M. A. Lock, T. E. Ford and S. R. Reice. 1987. Longitudinal patterns of ecosystem processes and community structure in a subarctic river continuum. Ecology 68:1139-1156.

National Research Council. 1995. *Upstream: Salmon and Society in the Pacific Northwest.* National Academy of Sciences, Washington, District of Columbia. 388 pp.

Nehlsen, W., J. E. Williams and J. A. Lichatowich. 1991. 'Pacific salmon at the crossroads: Stocks at risk from California, Oregon, Idaho, and Washington', *Fisheries,* 16/2, 4-21.

Newbold, J. D., J. W. Elwood, R. V. O'Neill and W. Van Winkle. 1981. 'Measuring nutrient spiralling in streams', *Canadian Journal of Fisheries and Aquatic Sciencem* 38/7, 860-863.

Newbold, J. D., R. V. O'Neill, J. W. Elwood, and W. Van Winkle. 1982. 'Nutrient spiralling in streams: implications for nutrient limitation and invertebrate activity', *Am. Nat.*m120/5, 628-652.

Noss, R.F. and A. Y. Cooperrider. 1994. Saving Nature's Legacy: Protecting and Restoring Biodiversity. Island Press, Washington, D.C.

Perry, S. A. and A. L. Sheldon. 1986. Effects of exported seston on aquatic insect faunal similarity and species richness in lake outlet streams in Montana, USA. Hydrobiologia 137:65-77.

Perry, S. A. and W. B. Perry. 1986. 'Effects of experimental flow regulation on invertebrate drift and stranding in the Flathead and Kootenai Rivers, Montana, USA', *Hydrobiologia* ,134, 171-182.

Petts, G. E., H. Moller and A. L. Roux, (Ed.). 1989. *Historical Change of Large Alluvial Rivers: Western Europe.* John Wiley & Sons, Chichester, England. 355 pp.

Petts, G. E. and R. Wood (Eds). 1988. 'River regulation in the United Kingdom', *Regulated Rivers: Research and Management,* 2/3.

Pflieger, W. L. and T. B. Grace. 1987. 'Changes in the fish fauna of the Lower Missouri River, 1940-1983' in Matthews, W. J. and D. C. Heins (Eds), *Community and Evolutionary Ecology of North American Stream Fishes.* University of Oklahoma Press, Norman, Oklahoma. pp. 166-177.

Pimm, S. L. 1991. *The Balance of Nature? Ecological Issues in the Conservation of Species and Communities.* University of Chicago Press, Chicago, Illinois. 447 pp.

Poe, T. P., H. C. Hansel, S. Vigg, D. E. Palmer and L. A. Prendergast. 1991. 'Feeding of predaceous fishes on out-migrating salmonids in John Day Reservoir, Columbia River', *Transactions of the American Fisheries Society,* 120/4, 405-420.

Poff, N. L. and J. D. Allan. 1995. 'Functional organization of stream fish assemblages in relation to hydrological variability', *Ecology,* 76/2, 606-627.

Poff, N. L. and J. V. Ward. 1990. 'Physical habitat template of lotic systems: recovery in the context of historical pattern of spatiotemporal heterogeneity', *Environmental Management,* 14, 629-645.

Power, M. E., A. Sun, G. Parker, W. E. Dietrich and J. T. Wootton. 1995. 'Hydraulic food-chain models', *BioScience,* 45/3, 159-167.

Quinn, T. P. and M. J. Unwin. 1993. Variation in life history patterns among New Zealand chinook salmon (*Oncorhynchus tshawytscha*) populations. Can. J. Fish. Aq. Sci. 50:1414-1421.

Regier, H. A., R. L. Welcomme, R. J. Stedman and H. F. Henderson. 1989. 'Rehabilitation of degraded river ecosystems' in *Proceedings of the International Large River Symposium,* Can. Spec. Publ. Fish. Aquat. Sci. pp. 86-89.

Reice, S. R. 1994. 'Nonequilibrium determinants of biological community structure', *American Scientist,* 82/5, 424-435.

Reisenbichler, R. R., J. D. McIntyre, M. F. Solazzi and S. W. Landino. 1992. 'Genetic variation in steelhead of Oregon and Northern California', *Transactions of the American Fisheries Society,* 121, 158-169.

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', *Journal of the North American Benthological Society,* 7, 433-455.

Rieman, B. E., R. C. Beamesderfer, S. Vigg and T. P. Poe. 1991. 'Estimated loss of juvenile salmonids to predation by northern squawfish, walleyes, and smallmouth bass in John Day reservoir, Columbia River', *Transactions of the American Fisheries Society,* 120, 448-458.

Rieman, B. E. and J. D. McIntyre. 1993. Demographic and habitat requirements for conservation of bull trout. US Forest Service, Intermountain Research Station. INT-308, 38 pp.

Rieman, B. E. and J. D. McIntyre. 1995. 'Occurrence of bull trout in naturally fragmented habitat patches of varies size', *Transactions of the American Fisheries Society,* 124/3, 285-296.

Roth, N. E., J. D. Allan and D. L. Erickson. In press. 'Landscape influences on stream biotic integrity assessed at multiple spatial scales', *Landscape Ecology.*

Sabater, F., J. Armengol and S. Sabater. In press. Measuring discontinuities in the Ter River.

Salo, J., R. Kalliola, I. Häkkinen, Y. Mäkinen, P. Niemelä, M. Puhakka and P. D. Coley. 1986. 'River dynamics and the diversity of Amazon lowland forest', *Nature,* 322, 254-258.

Schlosser, I.J. and P.L. Angermeier. 1995. Spatial variation in demographic processes of lotic fishes: conceptual models, empirical evidence, and implications for conservation.American Fisheries Society Symposium 17: 392-401.

Schoener, T. 1991. Extinction and the nature of the metapopulation. Acta Oecologia 12: 53-75.

Schinberg, A. and K. A. Gould. 1994. Environment and Society: the Enduring Conflict. St. Martins Press, New York, NY. USA. 324pp.

Schumm, S. A. and R. W. Lichty. 1956. 'Time, space and causality in geomorphology', *American Journal of Science,* 263, 110-119.

Sear, D. A. 1994. 'River restoration and geomorphology', *Aquatic Conservation: Marine & Freshwater Ecosystems,* 4, 169-177.

Sedell, J. R., G. H. Reeves, F. R. Hauer, J. A. Stanford and C. P. Hawkins. 1990. 'Role of refugia in recovery from disturbances: Modern fragmented and disconnected river systems', *Environmental Management,* 14/5, 711-724.

Shannon, J. P., D. W. Blinn and L. E. Stevens. 1994. 'Trophic interactions and benthic animal community structure in the Colorado River, Arizona, U.S.A.', *Freshwater Biology,* 31, 213-220.

Shuman, J. R. 1995. 'Environmental considerations for assessing dam removal alternatives for river restoration', *Regulated Rivers: Research and Management,* 11/3&4, 249-261.

Simons, D. B. 1979. 'Effects of stream regulation on channel morphology' in Ward, J. V. and J. A. Stanford (Eds), *The Ecology of Regulated Streams.* Plenum Press, New York. pp. 95-111.

Southwood, T. R. E. 1977. 'Habitat, the templet for ecological strategies?', *Journal of Animal Ecology,* 46, 337-365.

Southwood, T. R. E. 1978. *Ecological Methods.* (2nd ed.). Chapman and Hall, London, Great Britain. 524 pp.

Sparks, R. E. 1995. 'Need for ecosystem management of large rivers and their floodplains', *BioScience,* 45/3, 168-182.

Sparks, R. E., P. B. Bayley, S. L. Kohler and L. L. Osborne. 1990. 'Disturbance and recovery of large floodplain rivers', *Environmental Management,* 14, 699-709.

Spencer, C. N., B. R. McClelland and J. A. Stanford. 1991. 'Shrimp stocking, salmon collapse, and eagle displacement: cascading interactions in the food web of a large aquatic ecosystem', *BioScience,* 41/1, 14-21.

Stacy, P. B. and M. Taper. 1992. 'Environmental variation and the persistence of small populations', *Ecol. Applic.,* 2, 18-29.

Stanford, J. A. 1996. in Hauer, F. R. and G. -. Lamberti (Eds), *Methods in Stream Ecology.* Academic Press, San Diego, California, USA. pp ----

Stanford, J. A. and F. R. Hauer (Eds) 1993. 'Fifth International Symposium on Regulated Streams', *Regulated Rivers: Research and Management,* 8/1&2.

Stanford, J. A. and F. R. Hauer. 1992. 'Mitigating the impacts of stream and lake regulation in the Flathead River Catchment, Montana, USA: An ecosystem perspective', *Aquatic Conservation,* 2, 35-63.

Stanford, J. A., F. R. Hauer and J. V. Ward. 1988. 'Serial discontinuity in a large river system', *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie,* 23, 1114-1118.

Stanford, J. A. and G. C. Poole. in press. 'A protocol for ecosystem management', *Ecological Applications.*

Stanford, J. A. and J. V. Ward. 1986. 'Fish of the Colorado system' in Davies, B. R. and K. F. Walker (Eds), *The Ecology of River Systems.* Dr. W. Junk Publishers, Dordrecht, The Netherlands. pp. 385-402.

Stanford, J. A. and J. V. Ward. 1989. 'Serial discontinuities in a Rocky Mountain river. I. Distribution and abundance of Plecoptera', *Regulated Rivers: Research and Management,* 3, 169-175.

Stanford, J. A. and J. V. Ward. 1992. 'Management of aquatic resources in large catchments: Recognizing interactions between ecosystem connectivity and environmental disturbance' in Naiman, R. J. (Ed.), *Watershed Management.* Springer-Verlag, New York, New York. pp. 91-124.

Stanford, J. A. and J. V. Ward. 1993. 'An ecosystem perspective of alluvial rivers: Connectivity and the hyporheic corridor', *Journal of the North American Benthological Society,* 12/1, 48-60.

Statzner, B., J. A. Gore and V. H. Resh. 1988. 'Hydraulic stream ecology: Observed patterns and potential applications', *Journal of the North American Benthological Society,* 7/4, 307-360.

Stevens, L. E., J. P. Shannon and D. W. Blinn. In press. Colorado River benthic ecology in Grand Canyon, Arizona: dam, tributary and geomorphic influences. Regulated Rivers

Taylor, E.B. 1991. A review of local adaptation in Salmonidae, with particular reference to Pacific and Atlantic salmon. Aquaculture 98: 185-207.

Toth, L. A., J. T. B. Obeysekera, W. A. Perkin and M. K. Loftin. 1993. 'Flow regulation and restoration of Florida's Kissimmee River', *Regulated Rivers: Research and Management,* 8/1&2, 155-166.

Townsend, C. R. 1989. 'The patch dynamics concept of stream community ecology', *Journal of the North American Benthological Society,* 8, 36-50.

Travnichek, V. H., M. B. Bain and M. J. Maceina. 1995. 'Recovery of a warmwater fish assemblage after the initiation of a minimum-flow release downstream from a hydroelectric dam', *Transactions of the American Fisheries Society,* 124/6, 836-844.

Valett, H. M. and J. A. Stanford. 1987. 'Food quality and hydropsychid caddisfly density in a lake outlet stream in Glacier National Park, Montana, USA.', *Canadian Journal of Fisheries and Aquatic Sciences,* 44, 77-82.

Van Dijk, G. M., E. C. L. Marteijn and A. Schulte-Wülwer-Leidig. 1995. 'Ecological rehabilitation of the River Rhine: plans, progress and perspectives', *Regulated Rivers: Research and Management,* 11/3&4, 377-388.

Vannote, R. L., G. W. Minshall, K. W.Cummins, J. R. Sedell and C. E. Cushing. 1980. 'The river continuum concept', *Canadian Journal of Fisheries and Aquatic Sciences,* 37/1, 130-137.

Vannote, R. L. and B. W. Sweeney. 1980. 'Geographic analysis of thermal equilibria; a conceptual model for evaluating the effect of natural and modified thermal regimes on aquatic insect communities', *American Naturalist,* 115/5, 667-695.

Waters, T. F. 1995. *Sediment in Streams: Sources, Biological Effects and Control.* American Fisheries Society, Bethesda, Maryland. 251 pp.

Waters, T. F., M. T. Doherty and C. C. Krueger. 1990. 'Annual production and production: biomass ratios for three species of stream trout in Lake Superior tributaries', *Trans. Am. Fish. Society,* 119, 470-474.

Ward, J. V. 1984. 'Stream regulation of the upper Colorado River: Channel configuration and thermal heterogeneity', *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie,* 22, 1862-1866.

Ward, J. V. 1985. 'Thermal characteristics of running waters', *Hydrobiologia,* 125, 31-46.

Ward, J. V. and J. A. Stanford, (Ed.). 1979. *The Ecology of Regulated Streams.* Plenum Press, New York, New York. 398 pp.

Ward, J. V. and J. A. Stanford. 1982. 'Thermal responses in the evolutionary ecology of aquatic insects', *Ann. Rev. Entomol.,.* 27, 97-117.

Ward, J. V. and J. A. Stanford. 1983a. 'The serial discontinuity concept of lotic ecosystems', in Fontaine, T. D. I. and S. M. Bartell (Eds), *Dynamics of Lotic Ecosystems.* Ann Arbor Science Publishers, Ann Arbor, Michigan. pp. 29-42.

Ward, J. V. and J. A. Stanford. 1983b. 'The intermediate-disturbance hypothesis: An explanation for biotic diversity patterns in lotic ecosystems' in Fontaine III, T. D. and S. M. Bartell (Eds), *Dynamics of Lotic Ecosystems*. Ann Arbor Science, The Butterworth Group, Kent, England. pp. 347-356.

Ward, J. V. and J. A. Stanford. 1987. The ecology of regulated streams: Past accomplishments and directions for future research, pp. 391-409. IN: Craig, J. F. and J. B. Kemper (eds.), Regulated Streams - Advances in Ecology. Plenum, New York.

Ward, J. V. and J. A. Stanford. 1991. 'Benthic faunal patterns along the longitudinal gradient of a Rocky Mountain river system', *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie,* 24/5, 3087-3094.

Ward, J. V. and J. A. Stanford. 1995a. Ecological connectivity in alluvial river ecosystems and its disruption by flow regulation, *Regulated Rivers: Research and Management,* 11(1):105-120.

Ward, J. V. and J. A. Stanford. 1995b. 'The serial discontinuity concept: extending the model to floodplain rivers', *Regulated Rivers: Research and Management,* 10/2-4, 159-168.

Ward, J. V. and N. J. Voelz. 1988. 'Downstream effects of a large, deep-release, high mountain reservoir on lotic zoobenthos', *Verhandlungen der Internationalen Vereinigung für Theoretische und Angewandte Limnologie,* 23/August 1988, 1174-1178.

Ward, J. V. and J. A. Wiens. In press. Ecotones of riverine ecosystems: role and typology, spatio-temporal dynamnics, and river regulation. Regulated Rivers

Warren, C. E. 1971. *Biology and Water Pollution Control.* W. B. Saunders, Philadelphia, Pennsylvania. 434 pp.

Warren, C.E., M.J. Allen, and J.W. Haefner. 1979. Conceptual frameworks and the philisophical foundations of general living systems theory. Behavioral Science 24: 296-310.

Weisberg, S. B., A. J. Janicki, J. Gerritsen and H. T. Wilson. 1990. 'Enhancement of benthic macroinvertebrates by minimum flow from a hydroelectric dam', *Regulated Rivers: Research and Management,* 5, 265-277.

Welcomme, R. L. 1979. *Fisheries Ecology of Floodplain Rivers.* Longman, London, England. 317 pp.

Welcomme, R. L. 1995. 'Relationships between fisheries and the integrity of river systems', *Regulated Rivers: Research and Management,* 11/1, 121-136.

Wissmar, R. C., J. E. Smith, B. A. McIntosh, H. W. Li, G. H. Reeves and J. R. Sedell. 1994. 'A history of resource use and disturbance in riverine basins of eastern Oregon and Washington (early 1800s-1990s)', *Northwest Science,* 68, 1-35.

Wooton, R. S. 1987. 'The ecology of lake-outlet black flies' in Kim, K. C. and R. W. Merritt (Eds), *Black Flies.* The Pennsylvania State University, University Park, Pennsylvania. pp. 146-154.

Zwick, P. 1992. 'Stream habitat fragmentation - a threat to biodiversity', *Biodiversity and Conservation,*.1, 80-97.

FIGURE LEGENDS

Figure 1. Major landscape features of a montane floodplain river, showing the three primary spatial dimensions (lateral, longitudinal or altitudinal, and vertical) that are dynamically molded through time (the fourth dimension) by fluvial processes. Biota may reside in all three spatial dimensions: riparos (streamside or riparian), benthos (channel), hyporheos (river influenced groundwater), and phreatos (deep groundwater). The hatched area is the varial zone or the area of the channel that is periodically dewatered as a consequence of the average amplitude of the discharge regime. Major channel features include a run (A), riffle (B), and pool (C); Sd refers to sites of sediment deposition and Se refers to a major site of bank erosion. The heavy solid line is the thalweg and broken lines conceptualize circulation of water between benthic, hyporheic, and phreatic habitats (after Stanford, 1996; see also Stanford and Ward, 1992).

Figure 2. Conceptualized continuum of a large unregulated river showing biophysical gradients and nodes of environmental heterogeneity (centers of organization) of the major alluvial reaches. Vertical bars on the plot of maximum temperature represent the annual range of annual maximum temperature across all habitats at any point in the river continuum. Numbers indicate stream order. Figure is not drawn to scale; transition reaches are often much longer than inferred.

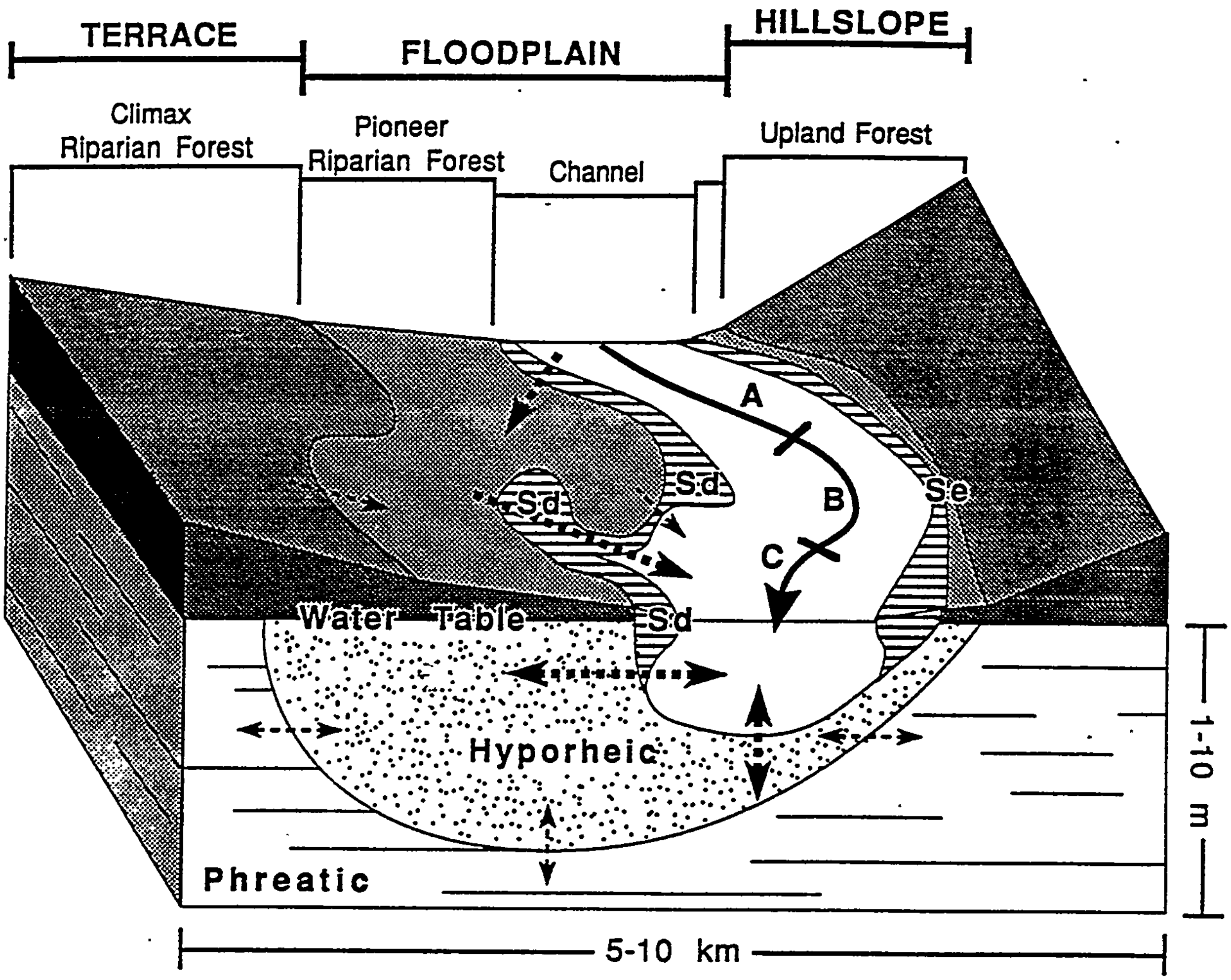
Figure 3. Primary controlling variables and biophysical interactions of river ecosystems.

Figure 4. Left. Discharge of the Columbia River, USA, in the Hanford Reach, an 8th-order segment in the piedmont transition (see Figure 2) between Priest Rapids and the confluence of the Snake River, for the period 1920 - 1929 when no large storage dams were present upstream. In the top panel the solid line is mean daily discharge plotted for each day of the water year beginning October 1 and ending September 30 and the broken line plots standard error. These data were used to calculate average daily change in discharge (middle panel) and average percent daily change (bottom panel).

Right. Same as on the left, except data are for the period 1983 - 1992, when the flow of the Columbia River in this reach was regulated by Priest Rapids and other dams upstream (left and right derived from U. S. Geological Survey data, Reston, Virginia, USA).

Figure 5. Conceptualized continuum of a large river after regulation by high-volume, high-head storage dam in the montane transition (compare to Figure 2). Tributaries downstream from the dam are assumed to be unregulated. Vertical bars on the plot of maximum temperature represent the annual range of annual maximum temperature across all habitats at any point in the river continuum. Numbers indicate stream order. Figure is not drawn to scale; transition reaches are often much longer than inferred.

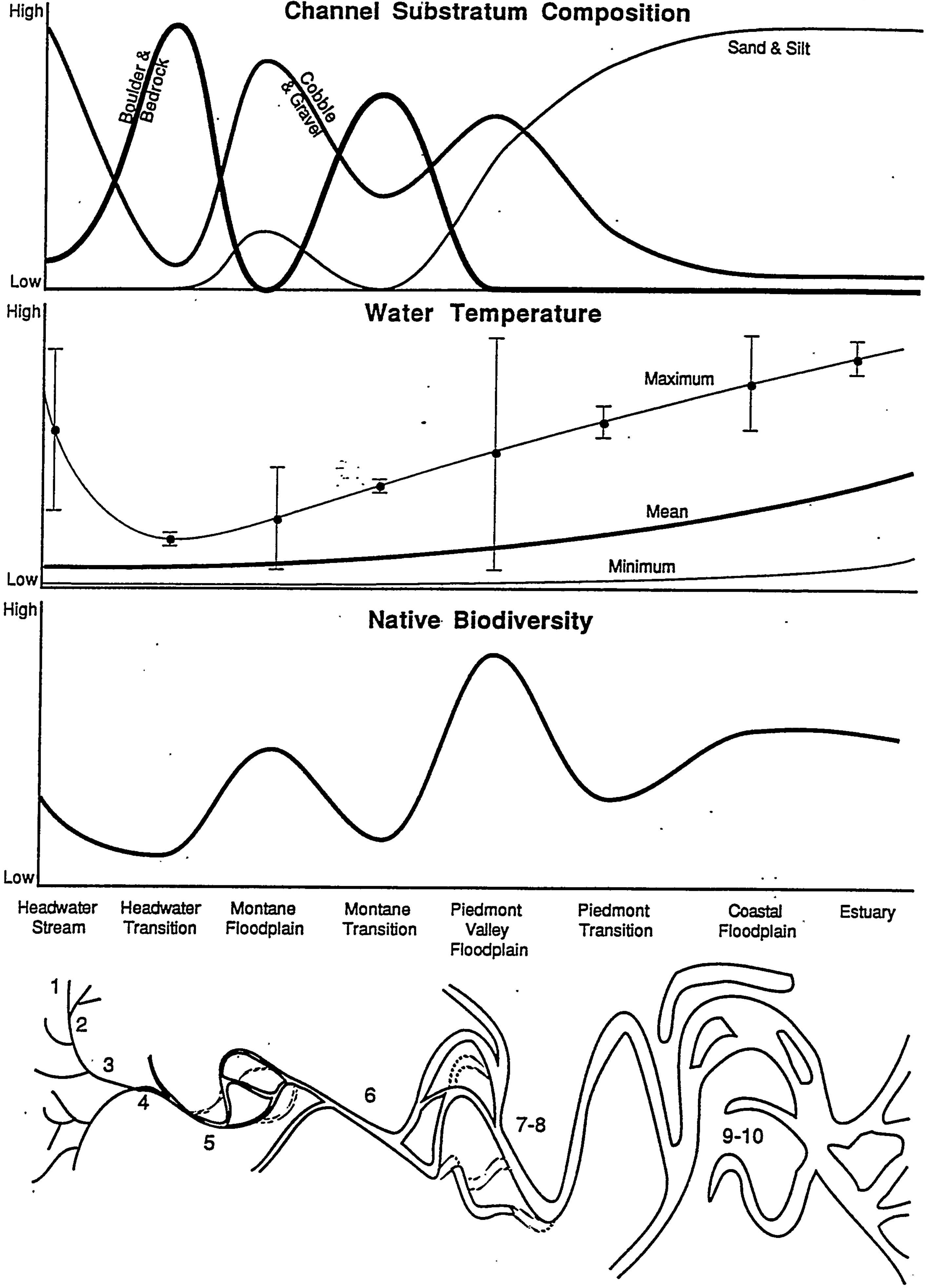
Figure 6. Simulated annual discharge (m^3/s x 10, mean monthly flow) patterns in the Hanford Reach of the Columbia River, USA. The same volume of water passed through the reach in each of the three scenarios (derived from U. S. Geological Survey data, Reston, Virginia, USA).

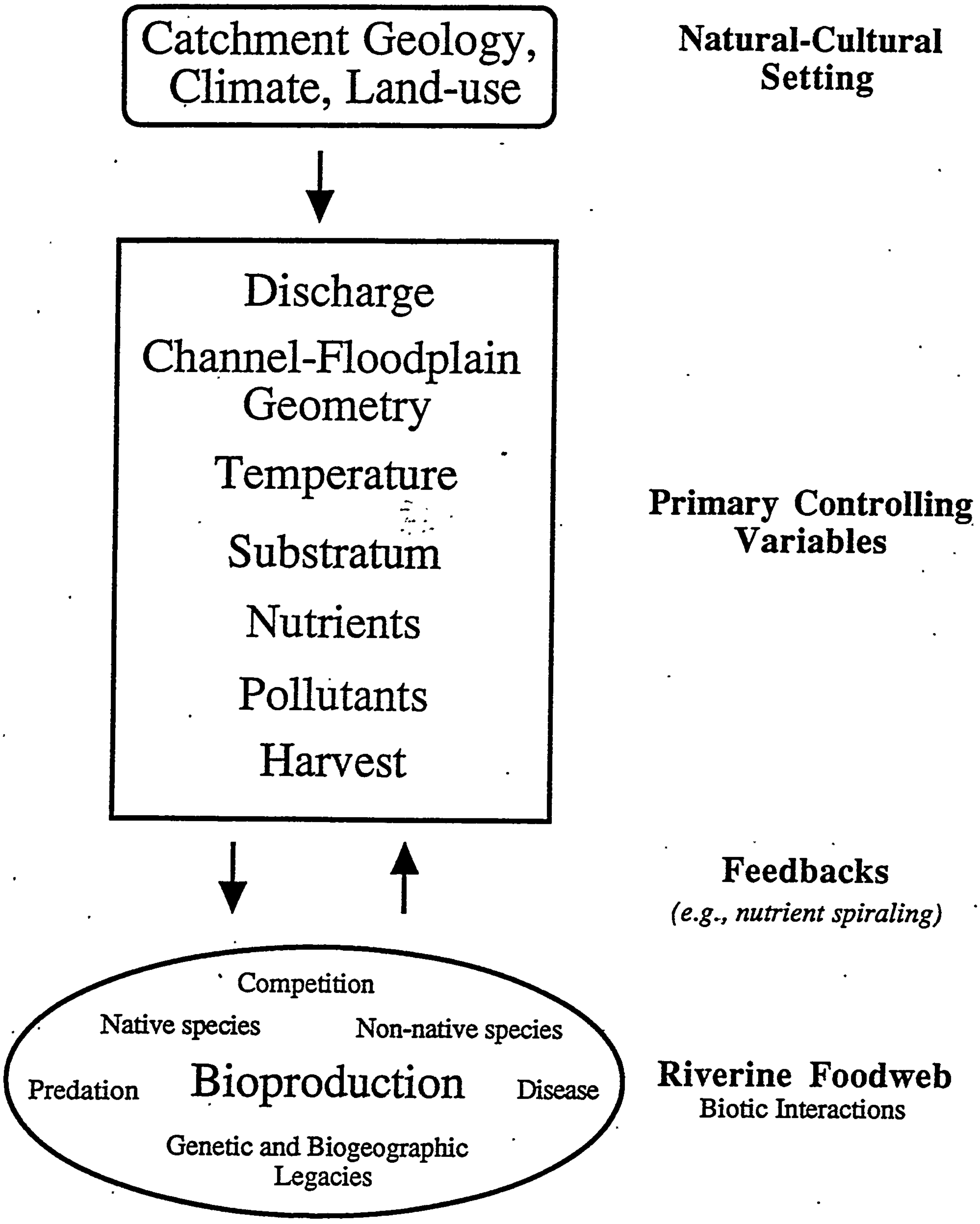


Stanford et al.
Fig 1

Fig 1

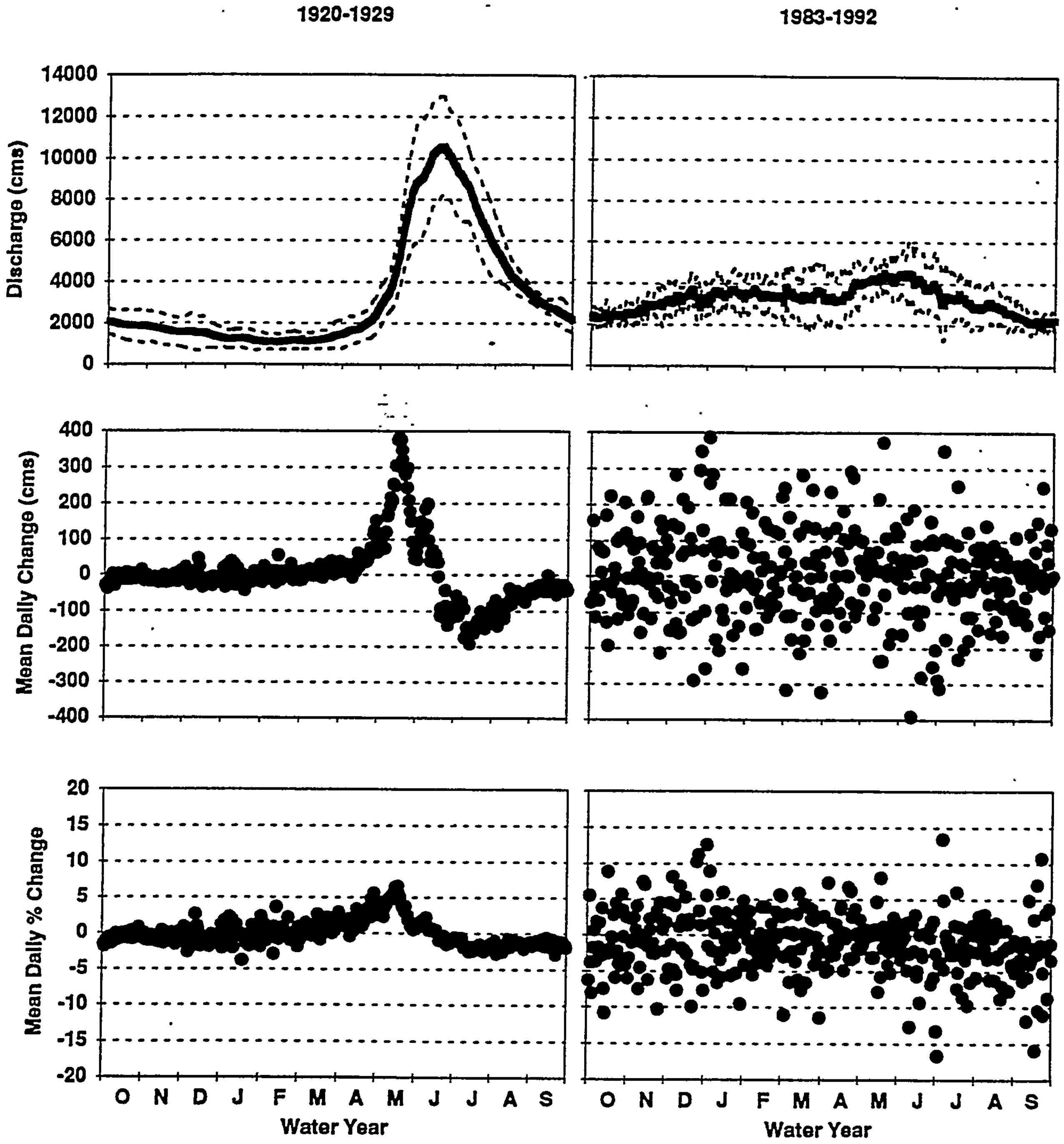
Stanford and Ward, Fig 2



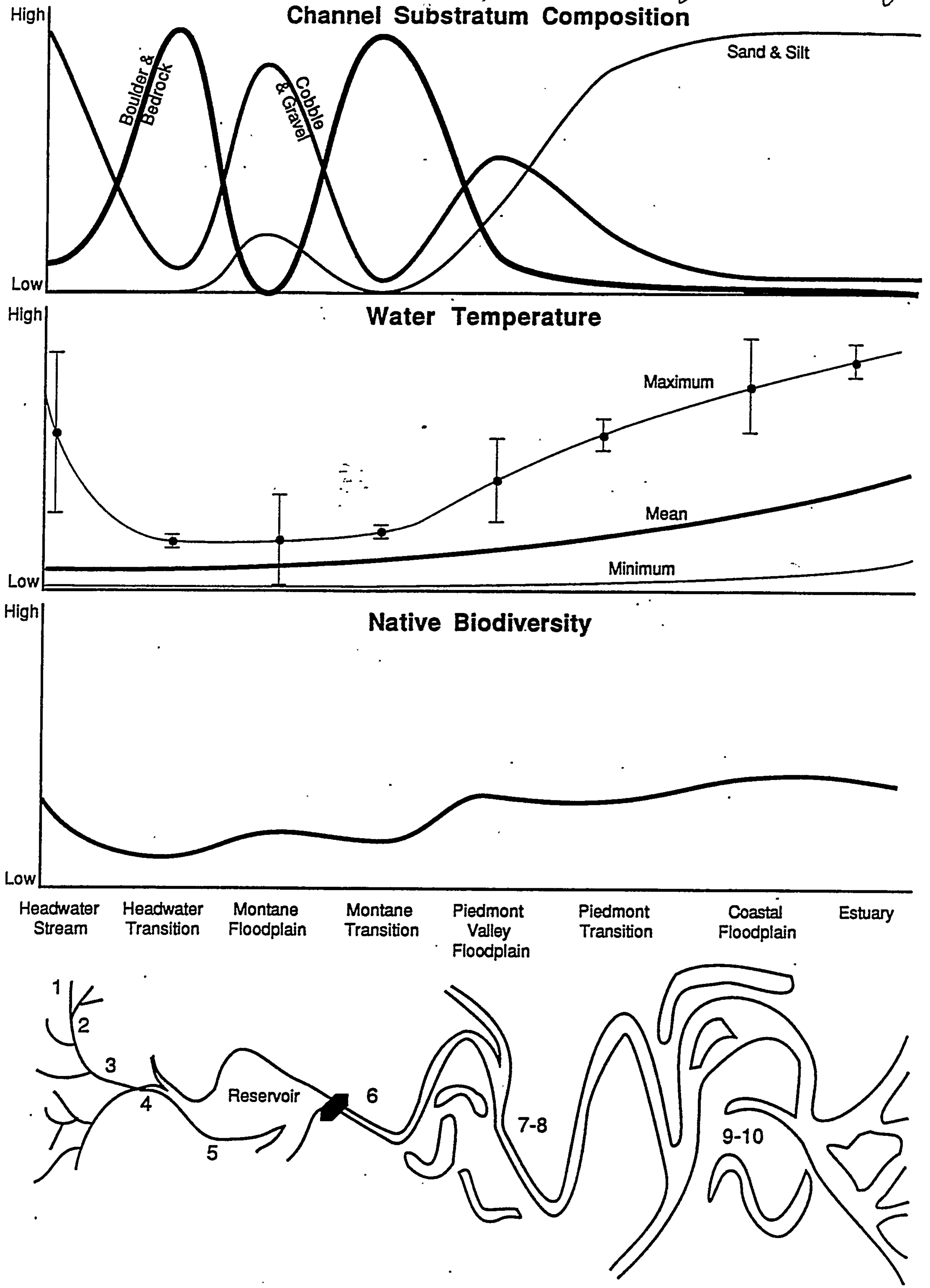


Stanford ~~and Ward Fig 4~~ et al. Fig 3

Stanfield et al. Fig 4



Stanford ~~and Ward~~ et al Fig 3



Stanford et al. Fig. 6B