The Natural Flow Regime

A paradigm for river conservation and restoration

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Humans have long been fascinated by the dynamism of free-flowing waters. Yet we have expended great effort to tame rivers for transportation, water supply, flood control, agriculture, and power generation. It is now recognized that harnessing of streams and rivers comes at great cost: Many rivers no longer support socially valued native species or sustain healthy ecosystems that provide important goods and services (Naiman et al. 1995, NRC 1992).

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The ecological integrity of river ecosystems depends on their natural dynamic character

The extensive ecological degradation and loss of biological diversity resulting from river exploitation is eliciting widespread concern for conservation and restoration of healthy river ecosystems among scientists and the lay public alike (Allan and Flecker 1993, Hughes and Noss 1992, Karr et al. 1985, TNC 1996, Williams et al. 1996). Extirpation of species, closures of fisheries, groundwater depletion, declines in water quality and availability, and more frequent and intense flooding are increasingly recognized as consequences of current river management and development policies (Abramovitz 1996, Collier et al. 1996, Naiman et al. 1995). The broad social support in the United States for the Endangered Species Act, the recognition of the intrinsic value of noncommercial native species, and the proliferation of watershed councils and riverwatch teams are evidence of society's interest in maintaining the ecological integrity and self-sustaining productivity of free-flowing river systems.

Society's ability to maintain and restore the integrity of river ecosystems requires that conservation and management actions be firmly grounded in scientific understanding. However, current management approaches often fail to recognize the fundamental scientific principle that the integrity of flowing water systems depends largely on their natural dynamic character; as a result, these methods frequently prevent successful river conservation or restoration. Streamflow quantity and timing are critical components of water supply, water quality, and the ecological integrity of river systems. Indeed, streamflow, which is strongly correlated with many critical physicochemical characteristics of rivers, such as water temperature, channel geomorphology, and habitat diversity, can be considered a "master variable" that limits the distribution and abundance of riverine species (Power et al. 1995, Resh et al. 1988) and regulates the ecological integrity of flowing water systems (Figure 1). Until recently, however, the importance of natural streamflow variability in maintaining healthy aquatic ecosystems has been virtually ignored in a management context.

Historically, the "protection" of river ecosystems has been limited in scope, emphasizing water quality and only one aspect of water quantity: minimum flow. Water resources management has also suffered from the often incongruent perspectives and fragmented responsibility of agencies (for example, the US Army Corps of Engineers and Bureau of Reclamation are responsible for water supply and flood control, the US Environmental Protection Agency and state environmental agencies for water quality, and the US Fish &

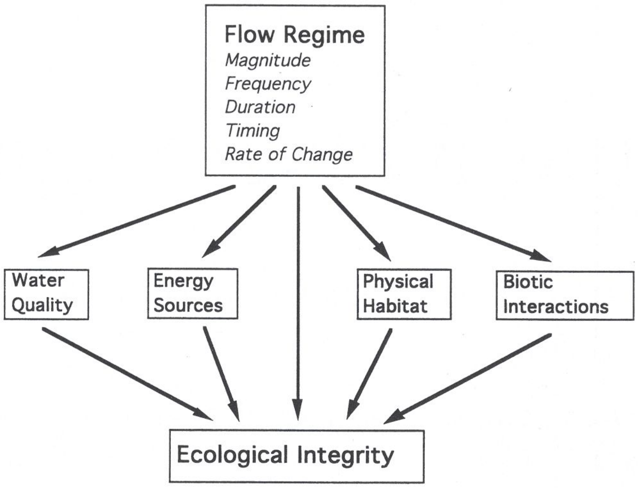

Figure 1. Flow regime is of central importance in sustaining the ecological integrity of flowing water systems. The five components of the flow regime—magnitude, frequency, duration, timing, and rate of change—influence integrity both directly and indirectly, through their effects on other primary regulators of integrity. Modification of flow thus has cascading effects on the ecological integrity of rivers. After Karr 1991.

Wildlife Service for water-dependent species of sporting, commercial, or conservation value), making it difficult, if not impossible, to manage the entire river ecosystem (Karr 1991). However, environmental dynamism is now recognized as central to sustaining and conserving native species diversity and ecological integrity in rivers and other ecosystems (Holling and Meffe 1996, Hughes 1994, Pickett et al. 1992, Stanford et al. 1996), and coordinated actions are therefore necessary to protect and restore a river's natural flow variability.

In this article, we synthesize existing scientific knowledge to argue that the natural flow regime plays a critical role in sustaining native biodiversity and ecosystem integrity in rivers. Decades of observation of the effects of human alteration of natural flow regimes have resulted in a well-grounded scientific perspective on why altering hydrologic variability in rivers is ecologically harmful (e.g., Arthington et al. 1991, Castleberry et al. 1996, Hill et al. 1991, Johnson et al. 1976, Richter et al. 1997, Sparks 1995, Stanford et al. 1996, Toth 1995, Tyus 1990). Current pressing demands on water use and the continuing alteration of watersheds require scientists to help develop management protocols that can accommodate economic uses while protecting ecosystem functions. For humans to continue to rely on river ecosystems for sustainable food production, power production, waste assimilation, and flood control, a new, holistic, ecological perspective on water management is needed to guide society's interactions with rivers.

The natural flow regime

The natural flow of a river varies on time scales of hours, days, seasons, years, and longer. Many years of observation from a streamflow gauge are generally needed to describe the characteristic pattern of a river's flow quantity, timing, and variability—that is, its natural flow regime. Components of a natural flow regime can be characterized using various time series (e.g., Fourier and wavelet) and probability analyses of, for example, extremely high or low flows, or of the entire range of flows expressed as average daily discharge (Dunne and Leopold 1978). In watersheds lacking long-term streamflow data, analyses can be extended statistically from gauged streams in the same geographic area. The frequency of large-magnitude floods can be estimated by paleohydrologic studies of debris left by floods and by studies of historical damage to living trees (Hupp and Osterkamp 1985, Knox 1972). These historical techniques can be used to extend existing hydrologic records or to provide estimates of flood flows for ungauged sites.

River flow regimes show regional patterns that are determined largely by river size and by geographic variation in climate, geology, topography, and vegetative cover. For example, some streams in regions with little seasonality in precipitation exhibit relatively stable hydrographs due to high groundwater inputs (Figure 2a), whereas other streams can fluctuate greatly at virtually any time of year (Figure 2b). In regions with seasonal precipitation, some streams are dominated by snowmelt, resulting in pronounced, predictable runoff patterns (Figure 2c), and others lack snow accumulation and exhibit more variable runoff patterns during the rainy season, with peaks occurring after each substantial storm event (Figure 2d).

Five critical components of the flow regime regulate ecological processes in river ecosystems: the magnitude, frequency, duration, timing, and rate of change of hydrologic conditions (Poff and Ward 1989, Richter et al. 1996, Walker et al. 1995). These components can be used to characterize the entire range of flows and specific hydrologic phenomena, such as floods or low flows, that are critical to the integrity of river ecosystems. Furthermore, by defining flow regimes in these terms, the ecological consequences of particular human activities that modify one or more components of the flow regime can be considered explicitly.

- The *magnitude* of discharge[1] at any given time interval is simply the amount of water moving past a fixed location per unit time. Magnitude can refer either to absolute or to relative discharge (e.g., the amount of water that inundates a floodplain). Maximum and minimum magnitudes of flow vary with climate and watershed size both within and among river systems.
- The *frequency* of occurrence refers to how often a flow above a given magnitude recurs over some specified time interval. Frequency of occurrence is inversely related to flow magnitude. For example, a 100-year flood is equaled or exceeded on average once every 100 years (i.e., a chance of 0.01 of occurring in any given year). The average (median)

[1]Discharge (also known as streamflow, flow, or flow rate) is always expressed in dimensions of volume per time. However, a great variety of units are used to describe flow, depending on custom and purpose of characterization: Flows can be expressed in near-instantaneous terms (e.g., ft^3/s and m^3/s) or over long time intervals (e.g., acre-ft/yr).

flow is determined from a data series of discharges defined over a specific time interval, and it has a frequency of occurrence of 0.5 (a 50% probability).

•The *duration* is the period of time associated with a specific flow condition. Duration can be defined relative to a particular flow event (e.g., a floodplain may be inundated for a specific number of days by a ten-year flood), or it can be a defined as a composite expressed over a specified time period (e.g., the number of days in a year when flow exceeds some value).

•The *timing*, or *predictability*, of flows of defined magnitude refers to the regularity with which they occur. This regularity can be defined formally or informally and with reference to different time scales (Poff 1996). For example, annual peak flows may occur with low seasonal predictability (Figure 2b) or with high seasonal predictability (Figure 2c).

•The *rate of change*, or *flashiness*, refers to how quickly flow changes from one magnitude to another. At the extremes, "flashy" streams have rapid rates of change (Figure 2b), whereas "stable" streams have slow rates of change (Figure 2a).

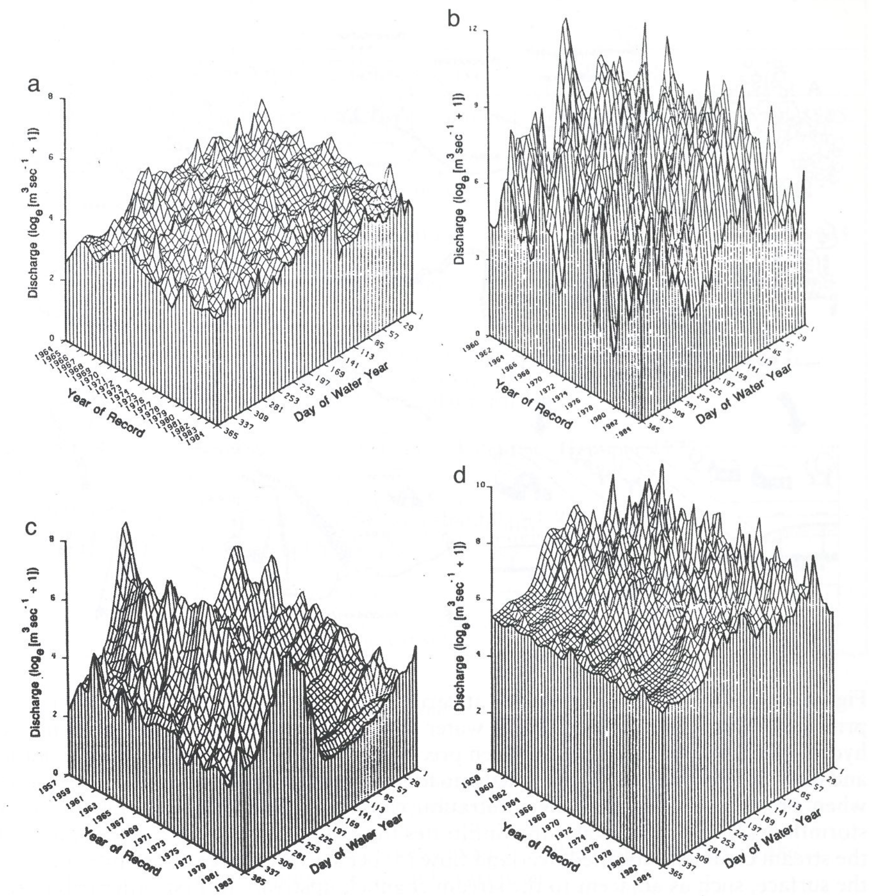

Figure 2. Flow histories based on long-term, daily mean discharge records. These histories show within- and among-year variation for (**a**) Augusta Creek, MI, (**b**) Satilla River, GA, (**c**) upper Colorado River, CO, and (**d**) South Fork of the McKenzie River, OR. Each water year begins on October 1 and ends on September 30. Adapted from Poff and Ward 1990.

Hydrologic processes and the flow regime. All river flow derives ultimately from precipitation, but in any given time and place a river's flow is derived from some combination of surface water, soil water, and groundwater. Climate, geology, topography, soils, and vegetation help to determine both the supply of water and the pathways by which precipitation reaches the channel. The water movement pathways depicted in Figure 3a illustrate why rivers in different settings have different flow regimes and why flow is variable in virtually all rivers. Collectively, overland and shallow subsurface flow pathways create hydrograph peaks, which are the river's response to storm events. By contrast, deeper groundwater pathways are responsible for baseflow, the form of delivery during periods of little rainfall.

Variability in intensity, timing, and duration of precipitation (as rain or as snow) and in the effects of terrain, soil texture, and plant evapotranspiration on the hydrologic cycle combine to create local and regional flow patterns. For example, high flows due to rainstorms may occur over periods of hours (for permeable soils) or even minutes (for impermeable soils), whereas snow will melt over a period of days or weeks, which slowly builds the peak snowmelt flood. As one proceeds downstream within a watershed, river flow reflects the sum of flow generation and routing processes operating in multiple small tributary watersheds. The travel time of flow down the river system, combined with nonsynchronous tributary inputs and larger downstream channel and floodplain storage capacities, act to attenuate and to dampen flow peaks. Consequently, annual hydrographs in large streams typically show peaks created by widespread storms or snowmelt events and broad seasonal influences that affect many tributaries together (Dunne and Leopold 1978).

The natural flow regime organizes and defines river ecosystems. In rivers, the physical structure of the environment and, thus, of the habitat, is defined largely by physical processes, especially the movement of water and sediment within the channel and between the channel and floodplain. To understand the biodiversity, production, and sustainability of river ecosystems, it is necessary to appreciate the central organizing role played by a dynamically varying physical environment.

The physical habitat of a river includes sediment size and heterogeneity, channel and floodplain morphology, and other geomorphic features. These features form as the available sediment, woody debris, and other transportable materials are moved and deposited by flow. Thus, habitat conditions associated with channels and floodplains vary among

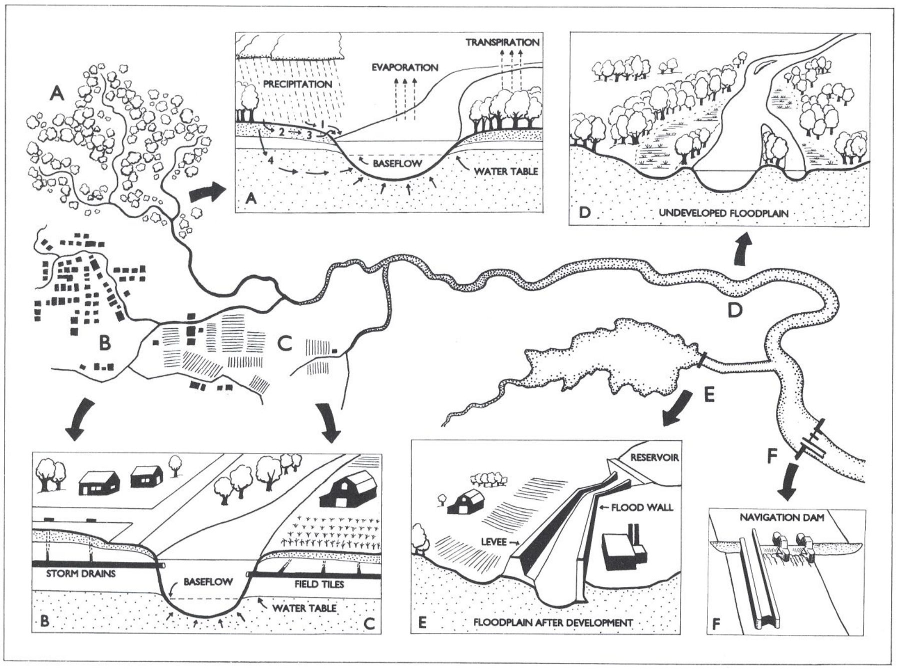

Figure 3. Stream valley cross-sections at various locations in a watershed illustrate basic principles about natural pathways of water moving downhill and human influences on hydrology. Runoff, which occurs when precipitation exceeds losses due to evaporation and plant transpiration, can be divided into four components (**a**): overland flow (1) occurs when precipitation exceeds the infiltration capacity of the soil; shallow subsurface stormflow (2) represents water that infiltrates the soil but is routed relatively quickly to the stream channel; saturated overland flow (3) occurs where the water table is close to the surface, such as adjacent to the stream channel, upstream of first-order tributaries, and in soils saturated by prior precipitation; and groundwater flow (4) represents relatively deep and slow pathways of water movement and provides water to the stream channel even during periods of little or no precipitation. Collectively, overland and shallow subsurface flow pathways create the peaks in the hydrograph that are a river's response to storm events, whereas deeper groundwater pathways are responsible for baseflow. Urbanized (**b**) and agricultural (**c**) land uses increase surface flow by increasing the extent of impermeable surfaces, reducing vegetation cover, and installing drainage systems. Relative to the unaltered state, channels often are scoured to greater depth by unnaturally high flood crests and water tables are lowered, causing baseflow to drop. Side-channels, wetlands, and episodically flooded lowlands comprise the diverse floodplain habitats of unmodified river ecosystems (**d**). Levees or flood walls (**e**) constructed along the banks retain flood waters in the main channel and lead to a loss of floodplain habitat diversity and function. Dams impede the downstream movement of water and can greatly modify a river's flow regime, depending on whether they are operated for storage (**e**) or as "run-of-river," such as for navigation (**f**).

rivers in accordance with both flow characteristics and the type and the availability of transportable materials.

Within a river, different habitat features are created and maintained by a wide range of flows. For example, many channel and floodplain features, such as river bars and riffle–pool sequences, are formed and maintained by dominant, or bankfull, discharges. These discharges are flows that can move significant quantities of bed or bank sediment and that occur frequently enough (e.g., every several years) to continually modify the channel (Wolman and Miller 1960). In many streams and rivers with a small range of flood flows, bankfull flow can build and maintain the active floodplain through stream migration (Leopold et al. 1964). However, the concept of a dominant discharge may not be applicable in all flow regimes (Wolman and Gerson 1978). Furthermore, in some flow regimes, the flows that build the channel may differ from those that build the floodplain. For example, in rivers with a wide range of flood flows, floodplains may exhibit major bar deposits, such as berms of boulders along the channel, or other features that are left by infrequent high-magnitude floods (e.g., Miller 1990).

Over periods of years to decades, a single river can consistently provide ephemeral, seasonal, and persistent types of habitat that range from free-flowing, to standing, to no water. This predictable diversity of in-channel and floodplain habitat types has promoted the evolution of species that exploit the habitat mosaic created and maintained by hydrologic variability. For many riverine species, completion of the life cycle requires an array of different habitat types, whose availability over time is regulated by the flow regime (e.g., Greenberg et al. 1996, Reeves et al. 1996, Sparks 1995). Indeed, adaptation to this environmental dynamism allows aquatic and floodplain species to persist in the face of seemingly harsh conditions, such as floods and droughts, that regularly destroy and re-create habitat elements.

From an evolutionary perspective, the pattern of spatial and temporal habitat dynamics influences the relative success of a species in a particular environmental setting. This habitat template (Southwood 1977), which is dictated largely by flow regime, creates both subtle and profound differences in the natural histories of species in different segments of their ranges. It also influences species distribution and abundance, as well as ecosystem function (Poff and Allan 1995, Schlosser 1990, Sparks 1992, Stanford et al. 1996). Human alteration of flow regime changes the established pattern of natural hydrologic variation and disturbance, thereby altering habitat dynamics and creating new conditions to which the native biota may be poorly adapted.

Human alteration of flow regimes

Human modification of natural hydrologic processes disrupts the dynamic equilibrium between the movement of water and the movement of sediment that exists in free-flowing rivers (Dunne and Leopold 1978). This disruption alters both gross- and fine-scale geomorphic features that constitute habitat for aquatic and riparian species (Table 1). After

Table 1. Physical responses to altered flow regimes.

Source(s) of alteration	Hydrologic change(s)	Geomorphic response(s)	Reference(s)
Dam	Capture sediment moving downstream	Downstream channel erosion and tributary headcutting	Chien 1985, Petts 1984, 1985, Williams and Wolman 1984
		Bed armoring (coarsening)	Chien 1985
Dam, diversion	Reduce magnitude and frequency of high flows	Deposition of fines in gravel	Sear 1995, Stevens et al. 1995
		Channel stabilization and narrowing	Johnson 1994, Williams and Wolman 1984
		Reduced formation of point bars, secondary channels, oxbows, and changes in channel planform	Chien 1985, Copp 1989, Fenner et al. 1985
Urbanization, tiling, drainage	Increase magnitude and frequency of high flows	Bank erosion and channel widening	Hammer 1972
		Downward incision and floodplain disconnection	Prestegaard 1988
	Reduced infiltration into soil	Reduced baseflows	Leopold 1968
Levees and channelization	Reduce overbank flows	Channel restriction causing downcutting	Daniels 1960, Prestegaard et al. 1994
		Floodplain deposition and erosion prevented	Sparks 1992
		Reduced channel migration and formation of secondary channels	Shankman and Drake 1990
Groundwater pumping	Lowered water table levels	Streambank erosion and channel downcutting after loss of vegetation stability	Kondolf and Curry 1986

such a disruption, it may take centuries for a new dynamic equilibrium to be attained by channel and floodplain adjustments to the new flow regime (Petts 1985); in some cases, a new equilibrium is never attained, and the channel remains in a state of continuous recovery from the most recent flood event (Wolman and Gerson 1978). These channel and floodplain adjustments are sometimes overlooked because they can be confounded with long-term responses of the channel to changing climates (e.g., Knox 1972). Recognition of human-caused physical changes and associated biological consequences may require many years, and physical restoration of the river ecosystem may call for dramatic action (see box on the Grand Canyon flood, page 774).

Dams, which are the most obvious direct modifiers of river flow, capture both low and high flows for flood control, electrical power generation, irrigation and municipal water needs, maintenance of recreational reservoir levels, and navigation. More than 85% of the inland waterways within the continental United States are now artificially controlled (NRC 1992), including nearly 1 million km of rivers that are affected by dams (Echeverria et al. 1989). Dams capture all but the finest sediments moving down a river, with many severe downstream consequences. For example, sediment-depleted water released from dams can erode finer sediments from the receiving channel. The coarsening of the streambed can, in turn, reduce habitat availability for the many aquatic species living in or using interstitial spaces. In addition, channels may erode, or downcut, triggering rejuvenation of tributaries, which themselves begin eroding and migrating headward (Chien 1985, Petts 1984). Fine sediments that are contributed by tributaries downstream of a dam may be deposited between the coarse particles of the streambed (e.g., Sear 1995). In the absence of high flushing flows, species with life stages that are sensitive to sedimentation, such as the eggs and larvae of many invertebrates and fish, can suffer high mortality rates.

For many rivers, it is land-use activities, including timber harvest, livestock grazing, agriculture, and urbanization, rather than dams, that are the primary causes of altered flow regimes. For example, logging and the associated building of roads have contributed greatly to degradation of salmon streams in the Pacific Northwest, mainly through effects on runoff and sediment delivery (NRC 1996). Converting forest or prairie lands to agricultural lands generally decreases soil infiltration and results in increased overland flow, channel incision, floodplain isolation, and headward erosion of stream channels (Prestegaard 1988). Many agricultural areas were drained by the construction of ditches or tile-and-drain systems, with the result that many channels have become entrenched (Brookes 1988).

These land-use practices, combined with extensive draining of wetlands or overgrazing, reduce retention of water in watersheds and,

A controlled flood in the Grand Canyon

Since the Glen Canyon dam first began to store water in 1963, creating Lake Powell, some 430 km (270 miles) of the Colorado River, including Grand Canyon National Park, have been virtually bereft of seasonal floods. Before 1963, melting snow in the upper basin produced an average peak discharge exceeding 2400 m^3/s; after the dam was constructed, releases were generally maintained at less than 500 m^3/s. The building of the dam also trapped more than 95% of the sediment moving down the Colorado River in Lake Powell (Collier et al. 1996).

This dramatic change in flow regime produced drastic alterations in the dynamic nature of the historically sediment-laden Colorado River. The annual cycle of scour and fill had maintained large sandbars along the river banks, prevented encroachment of vegetation onto these bars, and limited bouldery debris deposits from constricting the river at the mouths of tributaries (Collier et al. 1997). When flows were reduced, the limited amount of sand accumulated in the channel rather than in bars farther up the river banks, and shallow low-velocity habitat in eddies used by juvenile fishes declined. Flow regulation allowed for increased cover of wetland and riparian vegetation, which expanded into sites that were regularly scoured by floods in the constrained fluvial canyon of the Colorado River; however, much of the woody vegetation that established after the dam's construction is composed of an exotic tree, salt cedar (*Tamarix* sp.; Stevens et al. 1995). Restoration of flood flows clearly would help to steer the aquatic and riparian ecosystem toward its former state and decrease the area of wetland and riparian vegetation, but precisely how the system would respond to an artificial flood could not be predicted.

In an example of adaptive management (i.e., a planned experiment to guide further actions), a controlled, seven-day flood of 1274 m^3/s was released through the Glen Canyon dam in late March 1996. This flow, roughly 35% of the pre-dam average for a spring flood (and far less than some large historical floods), was the maximum flow that could pass through the power plant turbines plus four steel drainpipes, and it cost approximately $2 million in lost hydropower revenues (Collier et al. 1997). The immediate result was significant beach building: Over 53% of the beaches increased in size, and just 10% decreased in size. Full documentation of the effects will continue to be monitored by measuring channel cross-sections and studying riparian vegetation and fish populations.

instead, route it quickly downstream, increasing the size and frequency of floods and reducing baseflow levels during dry periods (Figure 3b; Leopold 1968). Over time, these practices degrade in-channel habitat for aquatic species. They may also isolate the floodplain from overbank flows, thereby degrading habitat for riparian species. Similarly, urbanization and suburbanization associated with human population expansion across the landscape create impermeable surfaces that direct water away from subsurface pathways to overland flow (and often into storm drains). Consequently, floods increase in frequency and intensity (Beven 1986), banks erode, and channels widen (Hammer 1972), and baseflow declines during dry periods (Figure 3c).

Whereas dams and diversions affect rivers of virtually all sizes, and land-use impacts are particularly evident in headwaters, lowland rivers are greatly influenced by efforts to sever channel–floodplain linkages. Flood control projects have shortened, narrowed, straightened, and leveed many river systems and cut the main channels off from their floodplains (NRC 1992). For example, channelization of the Kissimmee River above Lake Okeechobee, Florida, by the US Army Corps of Engineers transformed a historical 166 km meandering river with a 1.5 to 3 km wide floodplain into a 90 km long canal flowing through a series of five impoundments, resulting in great loss of river channel habitat and adjacent floodplain wetlands (Toth 1995). Because levees are designed to prevent increases in the width of flow, rivers respond by cutting deeper channels, reaching higher velocities, or both.

Channelization and wetland drainage can actually increase the magnitude of extreme floods, because reduction in upstream storage capacity results in accelerated water delivery downstream. Much of the damage caused by the extensive flooding along the Mississippi River in 1993 resulted from levee failure as the river reestablished historic connections to the floodplain. Thus, although elaborate storage dam and levee systems can "reclaim" the floodplain for agriculture and human settlement in most years, the occasional but inevitable large floods will impose increasingly high disaster costs to society (Faber 1996). The severing of floodplains from rivers also stops the processes of sediment erosion and deposition that regulate the topographic diversity of floodplains. This diversity is essential for maintaining species diversity on floodplains, where relatively small differences in land elevation result in large differences in annual inundation and soil moisture regimes, which regulate plant distribution and abundance (Sparks 1992).

Ecological functions of the natural flow regime

Naturally variable flows create and maintain the dynamics of in-channel and floodplain conditions and habitats that are essential to aquatic and riparian species, as shown schematically in Figure 4. For purposes of illustration, we treat the components of a flow regime individually, although in reality they interact in complex ways to regulate geomorphic and ecological processes. In describing the ecological functions associated with the components of a flow regime, we pay particular attention to high- and low-flow events, because they often serve as ecological "bottlenecks" that present critical stresses and opportunities for a wide array of riverine species (Poff and Ward 1989).

The magnitude and frequency of high and low flows regulate numerous ecological processes. Frequent, moderately high flows effectively transport sediment through the channel (Leopold et al. 1964). This sediment movement, combined with the force of moving water, exports organic resources, such as detritus and attached algae, rejuvenating the biological community and allowing many species with fast life cycles and good colonizing ability to reestablish (Fisher 1983). Consequently, the composition and relative abundance of species that are present in a stream or river often reflect the frequency and intensity of high flows (Meffe and Minckley 1987, Schlosser 1985).

High flows provide further ecological benefits by maintaining ecosystem productivity and diversity. For example, high flows remove and transport fine sediments that would otherwise fill the interstitial spaces in productive gravel habitats (Beschta and Jackson 1979). Floods import woody debris into the channel (Keller and Swanson 1979), where it creates new, high-quality habitat (Figure 4; Moore and Gregory 1988, Wallace and Benke 1984). By connecting the channel to the floodplain, high overbank flows also maintain broader productivity and diversity. Floodplain wetlands provide important nursery grounds for fish and export organic matter and organisms back into the main channel (Junk et al. 1989, Sparks 1995, Welcomme 1992). The scouring of floodplain soils rejuvenates habitat for plant species that germinate only on barren, wetted surfaces that are free of competition (Scott et al. 1996) or that require access to shallow water tables (Stromberg et al. 1997). Flood-resistant, disturbance-adapted riparian communities are maintained by flooding along river corridors, even in river sections that have steep banks and lack floodplains (Hupp and Osterkamp 1985).

Flows of low magnitude also provide ecological benefits. Periods of low flow may present recruitment opportunities for riparian plant species in regions where floodplains are frequently inundated (Wharton et al. 1981). Streams that dry temporarily, generally in arid regions, have aquatic (Williams and Hynes 1977) and riparian (Nilsen et al. 1984) species with special behavioral or physiological adaptations that suit them to these harsh conditions.

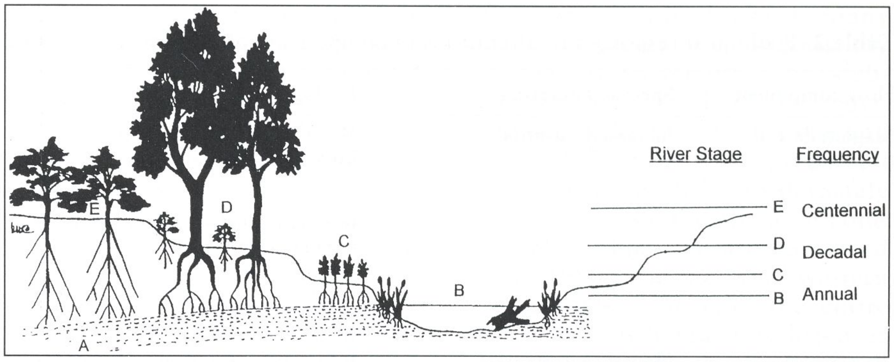

Figure 4. Geomorphic and ecological functions provided by different levels of flow. Water tables that sustain riparian vegetation and that delineate in-channel baseflow habitat are maintained by groundwater inflow and flood recharge (A). Floods of varying size and timing are needed to maintain a diversity of riparian plant species and aquatic habitat. Small floods occur frequently and transport fine sediments, maintaining high benthic productivity and creating spawning habitat for fishes (B). Intermediate-size floods inundate low-lying floodplains and deposit entrained sediment, allowing for the establishment of pioneer species (C). These floods also import accumulated organic material into the channel and help to maintain the characteristic form of the active stream channel. Larger floods that recur on the order of decades inundate the aggraded floodplain terraces, where later successional species establish (D). Rare, large floods can uproot mature riparian trees and deposit them in the channel, creating high-quality habitat for many aquatic species (E).

The duration of a specific flow condition often determines its ecological significance. For example, differences in tolerance to prolonged flooding in riparian plants (Chapman et al. 1982) and to prolonged low flow in aquatic invertebrates (Williams and Hynes 1977) and fishes (Closs and Lake 1996) allow these species to persist in locations from which they might otherwise be displaced by dominant, but less tolerant, species.

The timing, or predictability, of flow events is critical ecologically because the life cycles of many aquatic and riparian species are timed to either avoid or exploit flows of variable magnitudes. For example, the natural timing of high or low streamflows provides environmental cues for initiating life cycle transitions in fish, such as spawning (Montgomery et al. 1983, Nesler et al. 1988), egg hatching (Næsje et al. 1995), rearing (Seegrist and Gard 1978), movement onto the floodplain for feeding or reproduction (Junk et al. 1989, Sparks 1995, Welcomme 1992), or migration upstream or downstream (Trépanier et al. 1996). Natural seasonal variation in flow conditions can prevent the successful establishment of nonnative species with flow-dependent spawning and egg incubation requirements, such as striped bass (*Morone saxatilis*; Turner and Chadwick 1972) and brown trout (*Salmo trutta*; Moyle and Light 1996, Strange et al. 1992).

Seasonal access to floodplain wetlands is essential for the survival of certain river fishes, and such access can directly link high wetland productivity with fish production in the stream channel (Copp 1989, Welcomme 1979). Studies of the effects on stream fishes of both extensive and limited floodplain inundation (Finger and Stewart 1987, Ross and Baker 1983) indicate that some fishes are adapted to exploiting floodplain habitats, and these species decline in abundance when floodplain use is restricted. Models indicate that catch rates and biomass of fish are influenced by both maximum and minimum wetland area (Power et al. 1995, Welcomme and Hagborg 1977), and empirical work shows that the area of floodplain water bodies during nonflood periods influences the species richness of those wetland habitats (Halyk and Balon 1983). The timing of floodplain inundation is important for some fish because migratory and reproductive behaviors must coincide with access to and avail-

Table 2. Ecological responses to alterations in components of natural flow regime.[a]

Flow component	Specific alteration	Ecological response	Reference(s)
Magnitude and frequency	Increased variation	Wash-out and/or stranding	Cushman 1985, Petts 1984
		Loss of sensitive species	Gehrke et al. 1995, Kingsolving and Bain 1993, Travnichek et al. 1995
		Increased algal scour and wash-out of organic matter	Petts 1984
		Life cycle disruption	Scheidegger and Bain 1995
		Altered energy flow	Valentin et al. 1995
	Flow stabilization	Invasion or establishment of exotic species, leading to:	
		Local extinction	Kupferberg 1996, Meffe 1984
		Threat to native commercial species	Stanford et al. 1996
		Altered communities	Busch and Smith 1995, Moyle 1986, Ward and Stanford 1979
		Reduced water and nutrients to floodplain plant species, causing:	
		Seedling desiccation	Duncan 1993
		Ineffective seed dispersal	Nilsson 1982
		Loss of scoured habitat patches and secondary channels needed for plant establishment	Fenner et al. 1985, Rood et al. 1995, Scott et al. 1997, Shankman and Drake 1990
		Encroachment of vegetation into channels	Johnson 1994, Nilsson 1982
Timing	Loss of seasonal flow peaks	Disrupt cues for fish:	
		Spawning	Fausch and Bestgen 1997, Montgomery et al. 1993, Nesler et al. 1988
		Egg hatching	Næsje et al. 1995
		Migration	Williams 1996
		Loss of fish access to wetlands or backwaters	Junk et al. 1989, Sparks 1995
		Modification of aquatic food web structure	Power 1992, Wootton et al. 1996
		Reduction or elimination of riparian plant recruitment	Fenner et al. 1985
		Invasion of exotic riparian species	Horton 1977
		Reduced plant growth rates	Reily and Johnson 1982
Duration	Prolonged low flows	Concentration of aquatic organisms	Cushman 1985, Petts 1984
		Reduction or elimination of plant cover	Taylor 1982
		Diminished plant species diversity	Taylor 1982
		Desertification of riparian species composition	Busch and Smith 1995, Stromberg et al. 1996
		Physiological stress leading to reduced plant growth rate, morphological change, or mortality	Kondolf and Curry 1986, Perkins et al. 1984, Reily and Johnson 1982, Rood et al. 1995, Stromberg et al. 1992
	Prolonged baseflow "spikes"	Downstream loss of floating eggs	Robertson 1997
	Altered inundation duration	Altered plant cover types	Auble et al. 1994
	Prolonged inundation	Change in vegetation functional type	Bren 1992, Connor et al. 1981
		Tree mortality	Harms et al. 1980
		Loss of riffle habitat for aquatic species	Bogan 1993
Rate of change	Rapid changes in river stage	Wash-out and stranding of aquatic species	Cushman 1985, Petts 1984
	Accelerated flood recession	Failure of seedling establishment	Rood et al. 1995

[a]Only representative studies are listed here. Additional references are located on the Web at http://lamar.colostate.edu/~poff/natflow.html.

ability of floodplain habitats (Welcomme 1979). The match of reproductive period and wetland access also explains some of the yearly variation in stream fish community composition (Finger and Stewart 1987).

Many riparian plants also have life cycles that are adapted to the seasonal timing components of natural flow regimes through their "emergence phenologies"—the seasonal sequence of flowering, seed dispersal, germination, and seedling growth. The interaction of emergence phenologies with temporally varying environmental stress from flooding or drought helps to maintain high species diversity in, for example, southern floodplain forests (Streng et al. 1989). Productivity of riparian forests is also influenced by flow timing and can increase when short-duration flooding occurs in the growing season (Mitsch and Rust 1984, Molles et al. 1995).

The rate of change, or flashiness, in flow conditions can influence species persistence and coexistence. In many streams and rivers, particularly in arid areas, flow can change dramatically over a period of hours due to heavy storms. Non-native fishes generally lack the behavioral adaptations to avoid being displaced downstream by sudden floods (Minckley and Deacon 1991). In a dramatic example of how floods can benefit native species, Meffe (1984) documented that a native fish, the Gila topminnow (*Poeciliopsis occidentalis*), was locally extirpated by the introduced predatory mosquitofish (*Gambusia affinis*) in locations where natural flash floods were regulated by upstream dams, but the native species persisted in naturally flashy streams.

Rapid flow increases in streams of the central and southwestern United States often serve as spawning cues for native minnow species, whose rapidly developing eggs are either broadcast into the water column or attached to submerged structures as floodwaters recede (Fausch and Bestgen 1997, Robertson in press). More gradual, seasonal rates of change in flow conditions also regulate the persistence of many aquatic and riparian species. Cottonwoods (*Populus* spp.), for example, are disturbance species that establish after winter–spring flood flows, during a narrow "window of opportunity" when competition-free alluvial substrates and wet soils are available for germination. A certain rate of floodwater recession is critical to seedling germination because seedling roots must remain connected to a receding water table as they grow downward (Rood and Mahoney 1990).

Ecological responses to altered flow regimes

Modification of the natural flow regime dramatically affects both aquatic and riparian species in streams and rivers worldwide. Ecological responses to altered flow regimes in a specific stream or river depend on how the components of flow have changed relative to the natural flow regime for that particular stream or river (Poff and Ward 1990) and how specific geomorphic and ecological processes will respond to this relative change. As a result of variation in flow regime within and among rivers (Figure 2), the same human activity in different locations may cause different degrees of change relative to unaltered conditions and, therefore, have different ecological consequences.

Flow alteration commonly changes the magnitude and frequency of high and low flows, often reducing variability but sometimes enhancing the range. For example, the extreme daily variations below peaking power hydroelectric dams have no natural analogue in freshwater systems and represent, in an evolutionary sense, an extremely harsh environment of frequent, unpredictable flow disturbance. Many aquatic populations living in these environments suffer high mortality from physiological stress, from wash-out during high flows, and from stranding during rapid dewatering (Cushman 1985, Petts 1984). Especially in shallow shoreline habitats, frequent atmospheric exposure for even brief periods can result in massive mortality of bottom-dwelling organisms and subsequent severe reductions in biological productivity (Weisberg et al. 1990). Moreover, the rearing and refuge functions of shallow shoreline or backwater areas, where many small fish species and the young of large species are found (Greenberg et al. 1996, Moore and Gregory 1988), are severely impaired by frequent flow fluctuations (Bain et al. 1988, Stanford 1994). In these artificially fluctuating environments, specialized stream or river species are typically replaced by generalist species that tolerate frequent and large variations in flow. Furthermore, life cycles of many species are often disrupted and energy flow through the ecosystem is greatly modified (Table 2). Short-term flow modifications clearly lead to a reduction in both the natural diversity and abundance of many native fish and invertebrates.

At the opposite hydrologic extreme, flow stabilization below certain types of dams, such as water supply reservoirs, results in artificially constant environments that lack natural extremes. Although production of a few species may increase greatly, it is usually at the expense of other native species and of systemwide species diversity (Ward and Stanford 1979). Many lake fish species have successfully invaded (or been intentionally established in) flow-stabilized river environments (Moyle 1986, Moyle and Light 1996). Often top predators, these introduced fish can devastate native river fish and threaten commercially valuable stocks (Stanford et al. 1996). In the southwestern United States, virtually the entire native river fish fauna is listed as threatened under the Endangered Species Act, largely as a consequence of water withdrawal, flow stabilization, and exotic species proliferation. The last remaining strongholds of native river fishes are all in dynamic, free-flowing rivers, where exotic fishes are periodically reduced by natural flash floods (Minckley and Deacon 1991, Minckley and Meffe 1987).

Flow stabilization also reduces the magnitude and frequency of overbank flows, affecting riparian plant species and communities. In rivers with constrained canyon reaches or multiple shallow channels, loss of high flows results in increased cover of plant species that would otherwise be removed by flood scour (Ligon et al. 1995, Williams and Wolman 1984). Moreover, due to other related effects of flow regulation, including increased water salinity, non-native vegetation often dominates, such as the salt cedar (*Tamarix* sp.) in the semiarid western United States (Busch and Smith 1995). In alluvial valleys, the loss of overbank flows can greatly modify riparian communities by causing plant desiccation, reduced growth, competitive exclusion, ineffective seed dispersal, or failure of seedling establishment (Table 2).

The elimination of flooding may also affect animal species that depend on terrestrial habitats. For example, in the flow-stabilized Platte River of the United States Great Plains, the channel has narrowed dramatically (up to 85%) over a period of decades (Johnson 1994). This narrowing has been facilitated by vegetative colonization of sandbars that formerly provided nesting habitat for the threatened piping plover (*Charadius melodius*) and endangered least tern (*Sterna antillarum*; Sidle et al. 1992). Sandhill cranes (*Grus canadensis*), which made the Platte River famous, have abandoned river segments that have narrowed the most (Krapu et al. 1984).

Changes in the duration of flow conditions also have significant biological consequences. Riparian plant species respond dramatically to channel dewatering, which occurs frequently in arid regions due to surface water diversion and groundwater pumping. These biological and ecological responses range from altered leaf morphology to total loss of riparian vegetation cover (Table 2). Changes in duration of inundation, independent of changes in annual volume of flow, can alter the abundance of plant cover types (Auble et al. 1994). For example, increased duration of inundation has contributed to the conversion of grassland to forest along a regulated Australian river (Bren 1992). For aquatic species, prolonged flows of particular levels can also be damaging. In the regulated Pecos River of New Mexico, artificially prolonged high summer flows for irrigation displace the floating eggs of the threatened Pecos bluntnose shiner (*Notropis sinius pecosensis*) into unfavorable habitat, where none survive (Robertson in press).

Modification of natural flow timing, or predictability, can affect aquatic organisms both directly and indirectly. For example, some native fishes in Norway use seasonal flow peaks as a cue for egg hatching, and river regulation that eliminates these peaks can directly reduce local population sizes of these species (Næsje et al. 1995). Furthermore, entire food webs, not just single species, may be modified by altered flow timing. In regulated rivers of northern California, the seasonal shifting of scouring flows from winter to summer indirectly reduces the growth rate of juvenile steelhead trout (*Oncorhyncus mykiss*) by increasing the relative abundance of predator-resistant invertebrates that divert energy away from the food chain leading to trout (Wootton et al. 1996). In unregulated rivers, high winter flows reduce these predator-resistant insects and favor species that are more palatable to fish.

Riparian plant species are also strongly affected by altered flow timing (Table 2). A shift in timing of peak flows from spring to summer, as often occurs when reservoirs are managed to supply irrigation water, has prevented reestablishment of the Fremont cottonwood (*Populus fremontii*), the dominant plant species in Arizona, because flow peaks now occur after, rather than before, its germination period (Fenner et al. 1985). Non-native plant species with less specific germination requirements may benefit from changes in flood timing. For example, salt cedar's (*Tamarix* sp.) long seed dispersal period allows it to establish after floods occurring any time during the growing season, contributing to its abundance on floodplains of the western United States (Horton 1977).

Altering the rate of change in flow can negatively affect both aquatic and riparian species. As mentioned above, loss of natural flashiness threatens most of the native fish fauna of the American Southwest (Minckley and Deacon 1991), and artificially increased rates of change caused by peaking power hydroelectric dams on historically less flashy rivers creates numerous ecological problems (Table 2; Petts 1984). A modified rate of change can devastate riparian species, such as cottonwoods, whose successful seedling growth depends on the rate of groundwater recession following floodplain inundation. In the St. Mary River in Alberta, Canada, for example, rapid drawdowns of river stage during spring have prevented the recruitment of young trees (Rood and Mahoney 1990). Such effects can be reversed, however. Restoration of the spring flood and its natural, slow recession in the Truckee River in California has allowed the successful establishment of a new generation of cotton-

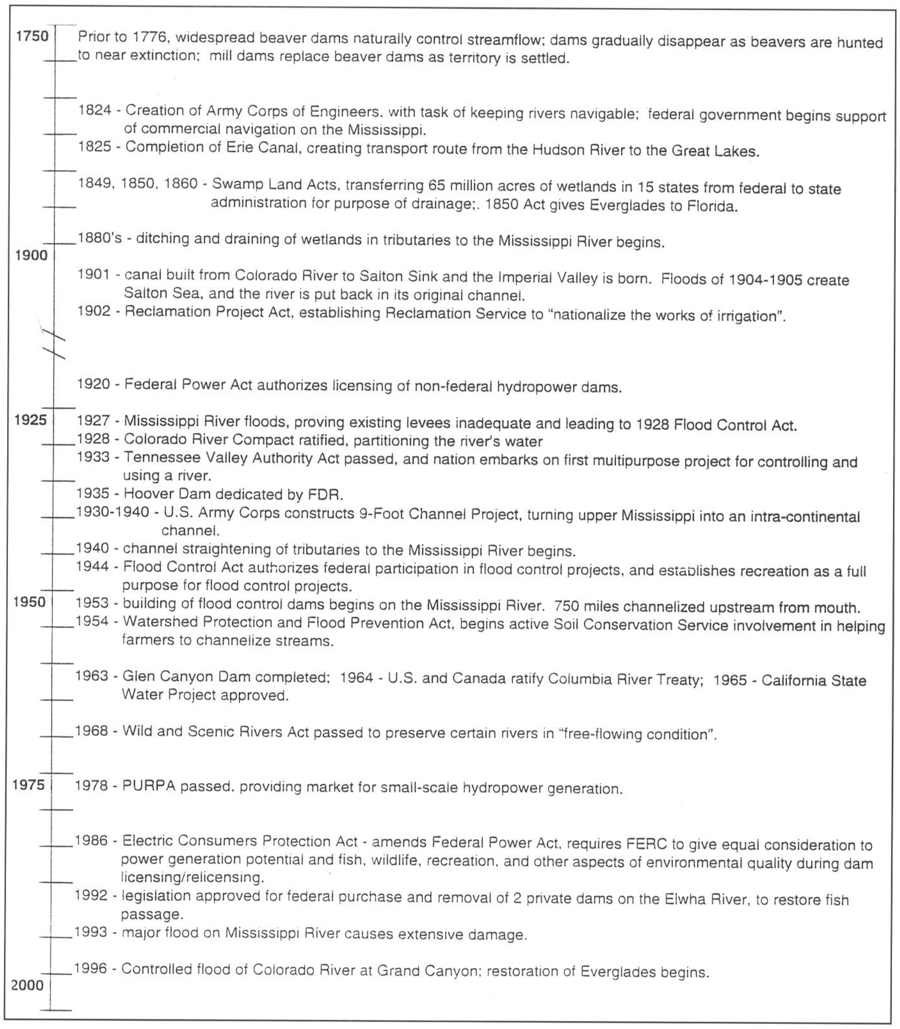

Figure 5. A brief history of flow alteration in the United States.

Table 3. Recent projects in which restoration of some component(s) of natural flow regimes has occurred or been proposed for specific ecological benefits.

Location	Flow component(s)	Ecological purpose(s)	Reference
Trinity River, CA	Mimic timing and magnitude of peak flow	Rejuvenate in-channel gravel habitats; restore early riparian succession; provide migration flows for juvenile salmon	Barinaga 1996[a]
Truckee River, CA	Mimic timing, magnitude, and duration of peak flow, and its rate of change during recession	Restore riparian trees, especially cottonwoods	Klotz and Swanson 1997
Owens River, CA	Increase base flows; partially restore overbank flows	Restore riparian vegetation and habitat for native fishes and non-native brown trout	Hill and Platts in press
Rush Creek, CA (and other tributaries to Mono Lake)	Increase minimum flows	Restore riparian vegetation and habitat for waterfowl and non-native fishes	LADWP 1995
Oldman River and tributaries, southern Alberta, Canada	Increase summer flows; reduce rates of postflood stage decline; mimic natural flows in wet years	Restore riparian vegetation (cottonwoods) and cold-water (trout) fisheries	Rood et al. 1995
Green River, UT	Mimic timing and duration of peak flow and duration and timing of nonpeak flows; reduce rapid baseflow fluctuations from hydropower generation	Recovery of endangered fish species; enhance other native fishes	Stanford 1994
San Juan River, UT/NM	Mimic magnitude, timing, and duration of peak flow; restore low winter baseflows	Recovery of endangered fish species	—[b]
Gunnison River, CO	Mimic magnitude, timing, and duration of peak flow; mimic duration and timing of nonpeak flows	Recovery of endangered fish species	—[b]
Rio Grande River, NM	Mimic timing and duration of floodplain inundation	Ecosystem processes (e.g., nitrogen flux, microbial activity, litter decomposition)	Molles et al. 1995
Pecos River, NM	Regulate duration and magnitude of summer irrigation releases to mimic spawning flow "spikes"; maintain minimum flows	Determine spawning and habitat needs for threatened fish species	Robertson 1997
Colorado River, AZ	Mimic magnitude and timing	Restore habitat for endangered fish species and scour riparian zone	Collier et al. 1997
Bill Williams River, AZ (proposed)	Mimic natural flood peak timing and duration	Promote establishment of native trees	USCOE 1996
Pemigewasset River, NH	Reduce frequency (i.e., to no more than natural frequency) of high flows during summer low-flow season; reduce rate of change between low and high flows during hydropower cycles	Enhance native Atlantic salmon recovery	FERC 1995
Roanoke River, VA	Restore more natural patterning of monthly flows in spring; reduce rate of change between low and high flows during hydropower cycles	Increased reproduction of striped bass	Rulifson and Manooch 1993
Kissimmee River, FL	Mimic magnitude, duration, rate of change, and timing of high- and low-flow periods	Restore floodplain inundation to recover wetland functions; reestablish in-channel habitats for fish and other aquatic species	Toth 1995

[a]J. Polos, 1997, personal communication. US Fish & Wildlife Service, Arcata, CA.
[b]F. Pfeifer, 1997, personal communication. US Fish & Wildlife Service, Grand Junction, CO.

wood trees (Klotz and Swanson 1997).

Recent approaches to streamflow management

Methods to estimate environmental flow requirements for rivers focus primarily on one or a few species that live in the wetted river channel. Most of these methods have the narrow intent of establishing minimum allowable flows. The simplest make use of easily analyzed flow data, of assumptions about the regional similarity of rivers, and of professional opinions of the minimal flow needs for certain fish species (e.g., Larson 1981).

A more sophisticated assessment of how changes in river flow affect aquatic habitat is provided by the Instream Flow Incremental Methodology (IFIM; Bovee and Milhous

1978). IFIM combines two models, a biological one that describes the physical habitat preferences of fishes (and occasionally macroinvertebrates) in terms of depth, velocity, and substrate, and a hydraulic one that estimates how the availability of habitat for fish varies with discharge. IFIM has been widely used as an organizational framework for formulating and evaluating alternative water management options related to production of one or a few fish species (Stalnaker et al. 1995).

As a predictive tool for ecological management, the IFIM modeling approach has been criticized both in terms of the statistical validity of its physical habitat characterizations (Williams 1996) and the limited realism of its biological assumptions (Castleberry et al. 1996). Field tests of its predictions have yielded mixed results (Morehardt 1986). Although this approach continues to evolve, both by adding biological realism (Van Winkle et al. 1993) and by expanding the range of habitats modeled (Stalnaker et al. 1995), in practice it is often used only to establish minimum flows for "important" (i.e., game or imperiled) fish species. But current understanding of river ecology clearly indicates that fish and other aquatic organisms require habitat features that cannot be maintained by minimum flows alone (see Stalnaker 1990). A range of flows is necessary to scour and revitalize gravel beds, to import wood and organic matter from the floodplain, and to provide access to productive riparian wetlands (Figure 4). Interannual variation in these flow peaks is also critical for maintaining channel and riparian dynamics. For example, imposition of only a fixed high-flow level each year would simply result in the equilibration of in-channel and floodplain habitats to these constant peak flows.

Moreover, a focus on one or a few species and on minimum flows fails to recognize that what is "good" for the ecosystem may not consistently benefit individual species, and that what is good for individual species may not be of benefit to the ecosystem. Long-term studies of naturally variable systems show that some species do best in wet years, that other species do best in dry years, and that overall biological diversity and ecosystem function benefit from these variations in species success (Tilman et al. 1994). Indeed, experience in river restoration clearly shows the impossibility of simultaneously engineering optimal conditions for all species (Sparks 1992, 1995, Toth 1995). A holistic view that attempts to restore natural variability in ecological processes and species success (and that acknowledges the tremendous uncertainty that is inherent in attempting to mechanistically model all species in the ecosystem) is necessary for ecosystem management and restoration (Franklin 1993).

Managing toward a natural flow regime

The first step toward better incorporating flow regime into the management of river ecosystems is to recognize that extensive human alteration of river flow has resulted in widespread geomorphic and ecological changes in these ecosystems. The history of river use is also a history of flow alteration (Figure 5). The early establishment of the US Army Corps of Engineers is testimony to the importance that the nation gave to developing navigable water routes and to controlling recurrent large floods. However, growing understanding of the ecological impacts of flow alteration has led to a shift toward an appreciation of the merits of free-flowing rivers. For example, the Wild and Scenic Rivers Act of 1968 recognized that the flow of certain rivers should be protected as a national resource, and the recent blossoming of natural flow restoration projects (Table 3) may herald the beginning of efforts to undo some of the damage of past flow alterations. The next century holds promise as an era for renegotiating human relationships with rivers, in which lessons from past experience are used to direct wise and informed action in the future.

A large body of evidence has shown that the natural flow regime of virtually all rivers is inherently variable, and that this variability is critical to ecosystem function and native biodiversity. As we have already discussed, rivers with highly altered and regulated flows lose their ability to support natural processes and native species. Thus, to protect pristine or nearly pristine systems, it is necessary to preserve the natural hydrologic cycle by safeguarding against upstream river development and damaging land uses that modify runoff and sediment supply in the watershed.

Most rivers are highly modified, of course, and so the greatest challenges lie in managing and restoring rivers that are also used to satisfy human needs. Can reestablishing the natural flow regime serve as a useful management and restoration goal? We believe that it can, although to varying degrees, depending on the present extent of human intervention and flow alteration affecting a particular river. Recognizing the natural variability of river flow and explicitly incorporating the five components of the natural flow regime (i.e., magnitude, frequency, duration, timing, and rate of change) into a broader framework for ecosystem management would constitute a major advance over most present management, which focuses on minimum flows and on just a few species. Such recognition would also contribute to the developing science of stream restoration in heavily altered watersheds, where, all too often, physical channel features (e.g., bars and woody debris) are re-created without regard to restoring the flow regime that will help to maintain these re-created features.

Just as rivers have been incrementally modified, they can be incrementally restored, with resulting improvements to many physical and biological processes. A list of recent efforts to restore various components of a natural flow regime (that is, to "naturalize" river flow) demonstrates the scope for success (Table 3). Many of the projects summarized in Table 3 represent only partial steps toward full flow restoration, but they have had demonstrable ecological benefits. For example, high flood flows followed by mimicked natural rates of flow decline in the Oldman River of Alberta, Canada, resulted in a massive cottonwood recruitment that extended for more than 500 km downstream from the Oldman Dam. Dampening of the unnatural flow fluctuations caused by hydroelectric generation on the Roanoke River in

Virginia has increased juvenile abundances of native striped bass. Mimicking short-duration flow spikes that are historically caused by summer thunderstorms in the regulated Pecos River of New Mexico has benefited the reproductive success of the Pecos bluntnose shiner.

We also recognize that there are scientific limits to how precisely the natural flow regime for a particular river can be defined. It is possible to have only an approximate knowledge of the historic condition of a river, both because some human activities may have preceded the installation of flow gauges, and because climate conditions may have changed over the past century or more. Furthermore, in many rivers, year-to-year differences in the timing and quantity of flow result in substantial variability around any average flow condition. Accordingly, managing for the "average" condition can be misguided. For example, in human-altered rivers that are managed for incremental improvements, restoring a flow pattern that is simply proportional to the natural hydrograph in years with little runoff may provide few if any ecological benefits, because many geomorphic and ecological processes show nonlinear responses to flow. Clearly, half of the peak discharge will not move half of the sediment, half of a migration-motivational flow will not motivate half of the fish, and half of an overbank flow will not inundate half of the floodplain. In such rivers, more ecological benefits would accrue from capitalizing on the natural between-year variability in flow. For example, in years with above-average flow, "surplus" water could be used to exceed flow thresholds that drive critical geomorphic and ecological processes.

If full flow restoration is impossible, mimicking certain geomorphic processes may provide some ecological benefits. Well-timed irrigation could stimulate recruitment of valued riparian trees such as cottonwoods (Friedman et al. 1995). Strategically clearing vegetation from river banks could provide new sources of gravel for sediment-starved regulated rivers with reduced peak flows (e.g., Ligon et al. 1995). In all situations, managers will be required to make judgments about specific restoration goals and to work with appropriate components of the natural flow regime to achieve those goals. Recognition of the natural flow variability and careful identification of key processes that are linked to various components of the flow regime are critical to making these judgments.

Setting specific goals to restore a more natural regime in rivers with altered flows (or, equally important, to preserve unaltered flows in pristine rivers) should ideally be a cooperative process involving river scientists, resource managers, and appropriate stakeholders. The details of this process will vary depending on the specific objectives for the river in question, the degree to which its flow regime and other environmental variables (e.g., thermal regime, sediment supply) have been altered, and the social and economic constraints that are in play. Establishing specific criteria for flow restoration will be challenging because our understanding of the interactions of individual flow components with geomorphic and ecological processes is incomplete. However, quantitative, river-specific standards can, in principle, be developed based on the reconstruction of the natural flow regime (e.g., Richter et al. 1997). Restoration actions based on such guidelines should be viewed as experiments to be monitored and evaluated—that is, adaptive management—to provide critical new knowledge for creative management of natural ecosystem variability (Table 3).

To manage rivers from this new perspective, some policy changes are needed. The narrow regulatory focus on minimum flows and single species impedes enlightened river management and restoration, as do the often conflicting mandates of the many agencies and organizations that are involved in the process. Revisions of laws and regulations, and redefinition of societal goals and policies, are essential to enable managers to use the best science to develop appropriate management programs.

Using science to guide ecosystem management requires that basic and applied research address difficult questions in complex, real-world settings, in which experimental controls and statistical replication are often impossible. Too little attention and too few resources have been devoted to clarifying how restoring specific components of the flow regime will benefit the entire ecosystem. Nevertheless, it is clear that, whenever possible, the natural river system should be allowed to repair and maintain itself. This approach is likely to be the most successful and the least expensive way to restore and maintain the ecological integrity of flow-altered rivers (Stanford et al. 1996). Although the most effective mix of human-aided and natural recovery methods will vary with the river, we believe that existing knowledge makes a strong case that restoring natural flows should be a cornerstone of our management approach to river ecosystems.

Acknowledgments

We thank the following people for reading and commenting on earlier versions of this paper: Jack Schmidt, Lou Toth, Mike Scott, David Wegner, Gary Meffe, Mary Power, Kurt Fausch, Jack Stanford, Bob Naiman, Don Duff, John Epifanio, Lori Robertson, Jeff Baumgartner, Tim Randle, David Harpman, Mike Armbruster, and Thomas Payne. Members of the Hydropower Reform Coalition also offered constructive comments. Excellent final reviews were provided by Greg Auble, Carter Johnson, an anonymous reviewer, and the editor of *BioScience*. Robin Abell contributed to the development of the timeline in Figure 5, and graphics assistance was provided by Teresa Peterson (Figure 3), Matthew Chew (Figure 4) and Robin Abell and Jackie Howard (Figure 5). We also thank the national offices of Trout Unlimited and American Rivers for encouraging the expression of the ideas presented here. We especially thank the George Gund Foundation for providing a grant to hold a one-day workshop, and The Nature Conservancy for providing logistical support for several of the authors prior to the workshop.

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North American Journal of Fisheries Management 20:1005–1015, 2000
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Predicting Salmonid Habitat–Flow Relationships for Streams from Western North America

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Abstract.—One of the most widely applied methodologies for developing instream flow recommendations is the instream flow incremental methodology (IFIM) and its component microhabitat model, physical habitat simulation (PHABSIM). In this paper we reviewed over 1,500 habitat–flow curves obtained from 127 PHABSIM studies from western North America to develop predictions for flow needs for salmonids in this region and to test whether habitat–flow relationships for salmonids were related to watershed characteristics and geographic location. We present regressions that predict PHABSIM optima for four life history stages of four salmonid species and for all salmonid species in the database as a group, and we quantify the uncertainty in these estimates. Mean annual discharge (MAD) was the best predictor of optimum flow. The general form of the regressions was $\log_e$(optimum flow) = $A \times \log_e$(MAD), where $A < 1$. Minor improvement in predictive power was sometimes possible with addition of latitude and longitude coordinates to the regression. This relationship is asymptotic and differs considerably from the fixed flow percentages recommended by Tennant. Our results are presented as a planning tool to (1) allow managers and project proponents to conduct a preliminary assessment of proposed water-use development projects, (2) optimize research efforts for instream flow studies and experiments, and (3) set experimental boundaries for adaptive management of stream flow.

Fluvial systems are physically and biologically complex, and consequently understanding instream flow needs for fish can be a daunting task. Fish abundance and biomass are the parameters that managers ultimately consider, but population estimation is difficult and abundance is variable, which makes it difficult to measure relationships between flow and abundance. In their attempts to understand relationships between abundance and flow, scientists have often turned to simpler surrogate measures rather than direct population estimates. For example, fish habitat is often quantified under different flow scenarios because it is relatively easy to measure and is more stable than population abundance.

Numerous methods can be used to determine instream flow needs (see EA Engineering Science and Technology 1986; Jowett 1997), but one of the most widely used is the instream flow incremental methodology (IFIM), developed in the 1970s by physical and biological scientists in the U.S. Fish and Wildlife Service. The method has undergone continual refinements and has remained state of the art. Accepted by many resource managers as an excellent tool for establishing habitat-flow relationships, it is the most widely used method in the United States (Reiser et al. 1989) and is commonly used throughout the rest of the world.

A major component of IFIM is a collection of computer models called the physical habitat simulation model (PHABSIM). It incorporates hydrology, stream morphology, and microhabitat preferences to generate relationships between river flow and habitat availability (Bovee 1982). Habitat availability is measured by an index called the weighted useable area (WUA), which is the wetted area of a stream weighted by its suitability for use by an organism. Because habitat suitability differs among species and changes over the life span of an organism, PHABSIM allows habitat–flow relationships to be developed for any life stage of any species and allows quantitative habitat comparisons at different (hypothetical) flows.

Typically, PHABSIM produces bell-shaped habitat–flow curves (Figure 1). Such a curve indicates a single flow that maximizes the PHABSIM index of microhabitat. For convenience we refer to this flow as the *optimum flow* but acknowledge that it represents only the maximum value of an index

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Received June 8, 1999; accepted June 18, 2000

North American Journal of Fisheries Management 20:1016–1028, 2000
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Measuring and Modeling the Hydraulic Environment for Assessing Instream Flows

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Abstract.—Detailed measurements of water depth and velocity in natural channels, though rare, show that the velocity fields are complex and irregular even in streams with moderate gradients and gravel substrates. This complexity poses a challenge for instream flow studies, most of which use the physical habitat simulation (PHABSIM) model, a set of computer models that combine the results of hydraulic modeling with estimates of channel substrate or cover and habitat suitability criteria to compute weighted usable area (WUA), an index of habitat. Some recent studies have replaced the transect-based one-dimensional hydraulic modeling in PHABSIM with two-dimensional models that allow better definition of the depth and velocity fields in the modeled stream reach. The accuracy of the estimates as a function of channel geometry and data collection effort remains unclear, however, as does the utility of the estimates for evaluating instream flow needs. Here we review the assumptions, accuracy, and precision of hydraulic modeling and the measurements that provide input data for the models; we also consider some implications of the limitations of hydraulic modeling for describing fish habitat and assessing instream flows. Highly accurate hydraulic modeling seems infeasible for streams with complex channel geometry, and in any event practical hydraulic modeling cannot resolve flow patterns at the short length scales at which fish often respond to the hydraulic environment. Information on depth, velocity, and substrate is important for assessing instream flows, but information from hydraulic models should be treated with great caution and is not a substitute for biological understanding.

Detailed measurements of depth and velocity in natural channels are rare, but those that exist show that the velocity fields are complex and irregular, often with substantial cross-stream components (Dietrich and Smith 1983; Petit 1987; Whiting and Dietrich 1991; Larsen 1995; Whiting 1997). This complexity in the flow patterns in natural channels poses a challenge for methods of assessing instream flows that depend on hydraulic modeling, such as the physical habitat simulation (PHABSIM).

PHABSIM consists of a set of computer models that combine hydraulic and biological models to evaluate the habitat value of a reach of stream for a given fish species and life stage. The weighted sum of calculated habitat values for the reach is expressed as the weighted usable area (WUA), which is taken to represent the "living space" available for the organism; water quality and temperature are evaluated separately. PHABSIM is widely used in North America to quantify the biological effects of alterations in flow regimes or the relative benefits of different release regimes from reservoirs (Reiser et al. 1989), and it is increasingly being applied elsewhere as well, either directly or in modified form (Jowett 1989; Pouilly et al. 1995). PHABSIM has even been used to evaluate the instream flow needs of blue ducks *Hymenolaimus malacorhynchos,* which forage for invertebrates in steep, boulder-bedded upland streams in New Zealand (Collier and Wakelin 1996). However, the hydraulic and biological aspects of PHABSIM have also been the subject of continuing criticism (Marthur et al. 1985; Shirvell 1986, 1994; Osborne et al. 1988; Gan and McMahon 1990; Elliott 1994; Castleberry et al. 1996; Ghanem et al. 1996; Heggenes 1996; Williams 1996; Lamouroux et al. 1998).

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Received September 14, 1998; accepted March 30, 2000

Transactions of the American Fisheries Society 126:536–537, 1997
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COMMENTS

Comment: Testing the Independence of Microhabitat Preferences and Flow (Part 1)

Beecher et al. (1995) should be commended for trying to test one of the various assumptions of the physical habitat simulation model (PHABSIM). They noted Shirvell's (1990) report that juvenile steelhead *Oncorhynchus mykiss* used areas of stream with different water velocities at different flows, which suggested that the microhabitat preferences of juvenile steelhead can be a function of flow. Pert and Erman (1994) have found this true for adult rainbow trout, the nonanadromous form of *O. mykiss*. Because PHABSIM depends upon the assumption that microhabitat preferences are independent of flow, Beecher et al. recognized this as a serious problem and tried to test the assumption; however, their test is not persuasive.

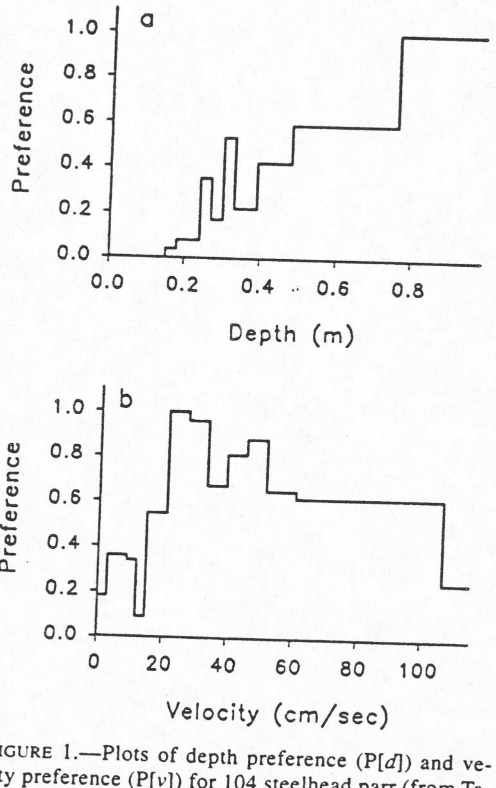

FIGURE 1.—Plots of depth preference (P[*d*]) and velocity preference (P[*v*]) for 104 steelhead parr (from Table 1 of Beecher et al. 1995).

In an earlier study, Beecher et al. (1993) developed preference criteria for depth and velocity from observations of 104 juvenile steelhead at a relatively low flow (Figure 1). In a later study, Beecher et al. (1995) measured depth and velocity at regular intervals along evenly spaced transects in an adjacent reach of the same stream at a relatively high flow. This gave them data at 242 points on a grid, which they took to represent an equal number of PHABSIM cells. (Each cell is centered on one of the grid points.) They also determined the positions of 21 juvenile steelhead, each of which was assigned to the depth–velocity cell nearest to the position.

To analyze the data from the later study, Beecher et al. (1995) used the product (denoted P[*dv*]) of depth preference (P[*d*]) and velocity preference (P[*v*]) for each cell. They divided the P[*dv*] range, which extends from 0.0 to 1.0, into four intervals such that approximately one-fourth of the cells fell into each range. Then they used the distribution of 21 fish among the four P[*dv*] intervals (Figure 2) to test "the hypothesis that depth and velocity preferences determined at one flow predict steelhead parr distribution at a different flow." Their null hypothesis was that fish would be distributed evenly over the four groups of cells. When this hypothesis was rejected by a chi-square test, they took this result as "validating the assumption of flow-independent preferences."

The logic of this claim is not apparent. The question is not whether juvenile steelhead distribute themselves evenly in streams regardless of depth and velocity, but whether their preferences for

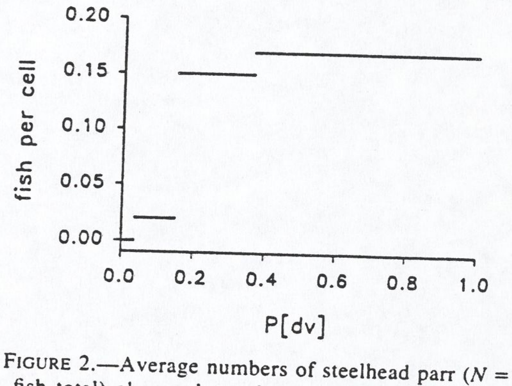

FIGURE 2.—Average numbers of steelhead parr (*N* = 21 fish total) observed per depth–velocity cell in four P[*dv*] intervals (horizontal lines; from Table 2 of Beecher et al. 1995).

depth or velocity change with flow. Should we believe that the depths and velocities at which the 104 and 21 steelhead parr were observed are samples from the same distributions? To answer this requires a different null hypothesis than the one used and probably a larger sample size. In any event, any number of sets of preferences for depth and velocity could give rise to given values of P[*dv*]—or to the observed frequencies (Figure 2), which are flat over a considerable range of P[*dv*]—so analyzing the data in terms of P[*dv*] does not seem helpful. Finally, it seems hard to assign biological meaning to the city-skyline shapes of the preference curves.

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Transactions of the American Fisheries Society 126:537–540, 1997
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Comment: Testing the Independence of Microhabitat Preferences and Flow (Part 2)

Beecher et al. (1995) claimed to have validated an assumption of the instream flow incremental methodology (IFIM) and of its physical habitat simulation model (PHABSIM) that water depths and velocities preferred by fish are independent of streamflow. We disagree. First, the study compared habitat preference (of young steelhead *Oncorhynchus mykiss*) at low flow with habitat use (not preference) at high flow. Second, the statistical approach used can lead to the conclusion that depth and velocity preferences are the same at two flows even when most scientists would consider them different. Here, we address statistical issues that arise when comparisons of habitat distribution are based on fish preferences rather than on depth and velocity, and we recommend new techniques for comparing distributions.

Beecher et al. (1995) addressed the null hypothesis "fish distribution is independent of depth and velocity preferences determined at a different flow." They rejected the hypothesis on the basis of a goodness-of-fit test that compared the observed distribution of fish among preference quartiles at a high flow with the expected uniform distribution that would result if fish selected habitat without regard to preferences derived at a lower flow. (The test statistic was P[*dv*], the product of preferred depth P[*d*] and preferred velocity P[*v*].) We do not believe that rejecting this hypothesis implies similarity in fish preferences over a range of flows.

The comparison was of low-flow preference with high-flow *use*; the question of whether preference changed with flow should have been addressed by calculating preference at both flows. It can be shown mathematically that both habitat use and habitat preference cannot be flow-invariant. Habitat use must change in response to flow (i.e., to habitat availability). The original question remains, because preference might be flow-invariant though habitat use may shift.

Unlike traditional comparisons of habitat preferences in which univariate depth and velocity preference distributions are compared between two fish populations, Beecher et al. used preference ranges instead of depth–velocity ranges. Their frequencies were numbers of fish, but expected fish numbers were calculated with the number of P[*dv*] cells in each of four preference ranges: (expected number of fish) = (fraction of cells in preference range) × (total number of fish). This approach is unlikely to detect shifts in habitat preference because it compares the numbers of fish in each of four preference ranges (quartiles) between two flows. Collapsing data into ranges masks differences in depth and velocity preferences because many depth–velocity combinations can share the same P[*dv*] value. Consider a unimodal depth preference curve for trout at low flow. Intermediate depths are optimal, and both shallow and deep habitats are marginal. As flow increases, fish that had been forced to occupy shallow water may shift to deep water, as they did in Pert and Erman's (1994) study. If the fish distribution data are aggregated within preference ranges, shallow and deep fish would be lumped together in the low-preference category, and their joint proportion of the population might not change between low and high flows. In such a case, the test used by Beecher et al. would not detect the marked habitat shift that fish underwent. The same problem can arise with velocity, and the marginal preference range becomes an even greater catchall when both habitat factors are combined. Whether habitat is unsuitable because depth or another factor is too great or too slight is immaterial for IFIM calculations of weighted usable area (WUA) and instream flows. It does matter for testing and comparing preferences. Having the same proportions of fish in habitat deemed unsuitable, marginal, and optimal at different flows does not imply that the same depths and velocities were preferred.

The test used by Beecher et al. also had low power because their hypothesis was that high-flow use (assume it was preference) is independent of low-flow preference, rather than that preferences at the two flows are equal. The type I error rate is low for the hypothesis tested, and only large differences in preference would be diagnosed as real.

Thomas and Bovee (1993) used a test like that of Beecher et al. to evaluate transferability of IFIM habitat suitability curves. They quantified the relationship between type I and type II error rates and the number of occupied and unoccupied P[*dv*] cells. This test is strongly influenced by habitat availability because it depends on cell frequencies instead of fish frequencies. Its dependence on the quantity and characteristics of unoccupied cells is undesirable, because it seems unreasonable that a difference in preference between two flows should depend on the index values assigned to empty cells. Fish density may influence the degree to which "suitable" cells are occupied.

We suggest alternative tests that can detect smaller differences between preferences than the one used by Beecher et al. (1995), and we propose a way to define ecologically significant differences. As an illustrative example, we use the frequency distributions of preference for depth and velocity shown by adult rainbow trout (nonanadromous *O. mykiss*) at low and high flows (Pert and Erman 1994). Preferences shifted to deeper and faster water when flow increased (Figure 3). We chose this example because most people can agree without statistical confirmation that a clear shift in habitat preference occurred.

In two tests, we evaluated the habitat shift by resampling the joint depth–velocity preference distribution. Resampling provides confidence bounds of statistics with unknown distributional characteristics, such as the preference index. In our proposed tests and in an application of the Beecher et al. test, we used the true bivariate or joint preferences (P[*d,v*]) rather than the usual index (P[*dv*] = P[*d*] × P[*v*]).

In our first test, we resampled the habitat use data for each flow, drawing fish observed in different depth–velocity combinations. For each of 50 replicate samples, we calculated the differences between preferences at high and low flows. The 1% and 99% confidence bounds for several depth and velocity classes did not include zero (zero implies no difference between flows; Table 1). According to this test, preferences were significantly different at the two flows, particularly in deeper habitat.

In the second test, we focused on defining an ecologically meaningful statistic to describe the preference distributions. The peak of the WUA curve would be a good ultimate endpoint, but we chose the peak of the joint preference distribution P[*d,v*] as a simpler surrogate. We tested the hypothesis that the P[*d,v*] peak did not shift in response to flow. For all the low-flow samples we drew, the peak occurred within the depth range of 96–120 cm and the velocity range of 15–30 cm/s. At the high flow, 36% of the samples peaked within these ranges, but 64% peaked in deeper (120–144 cm) and faster (30–60 cm/s) habitat. A binomial test rejected the hypothesis that the peaks were the same at both flows ($|z| = 3.75$; $P < 0.0001$).

Finally, we applied the goodness-of-fit test used by Beecher et al. to the joint preference data organized in the following form:

Low-flow preference range	High-flow percentages of: Expected cells	High-flow percentages of: Observed fish
0.0–0.1	54	40
0.1–0.3	22	26
0.3–1.0	24	34

The null hypothesis of independence from low-flow preferences was rejected ($\chi^2 = 8.46$; df = 2; $P = 0.014$).

These results appear to contradict one another. Although trout did not select habitat without re-

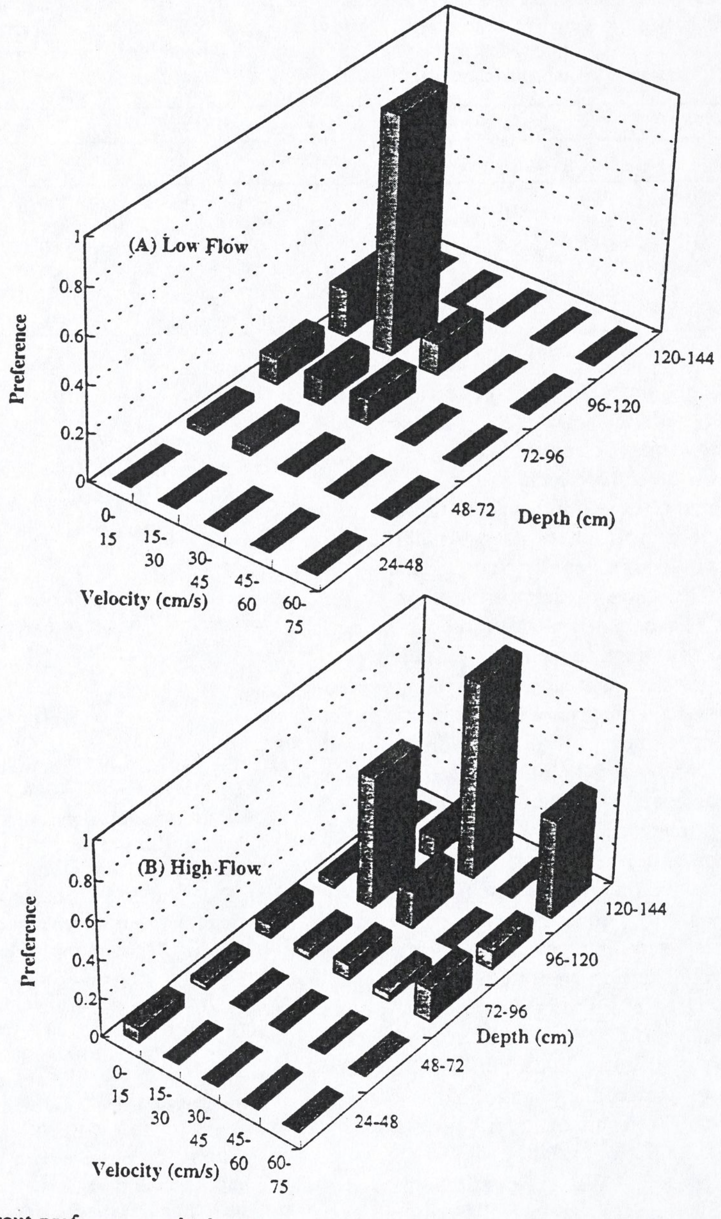

FIGURE 3.—Adult trout preferences calculated as a function of river depth and velocity for (A) a low flow and (B) a high flow.

gard to low-flow P[d,v], their habitat preferences shifted to greater depths and velocities with increased flow. This contradiction is possible because the tests are mirror images of one another and because the probability of a type I error (reject when true) is set to a low value ($\alpha \leq 0.10$) for each. Fish in these samples fell into the wide intermediate area between extremes of complete and no constancy in habitat preference with changes in flow. Which test is better, and which level of type I error is acceptable? Ecologists are coming to realize that the balance between type I and type II errors should be reasonable in terms of ecological significance (Quinn and Dunham 1983; Roughgarden 1983; Toft and Shea 1983). In our case, it is misleading to use a test that rejects the null hypothesis at the slightest similarity and then claim that no shift in preference has occurred.

TABLE 1.—Resampling test of the hypothesis of zero difference between high-flow and low-flow joint preferences of rainbow trout for depth and velocity. Values are the sample differences in preference (high flow minus low flow) and (in parentheses) the nonparametric 1% and 99% confidence bounds determined by resampling. Asterisks indicate significant differences from zero ($P \leq 0.01$; i.e., 98% of the range of simulated differences failed to bracket zero). Parenthetic words in place of confidence bounds mean that a habitat combination was present only at low flow (low), at high flow (high), or at neither flow (neither).

Depth class (cm)	Velocity class (cm/s)				
	0–15	15–30	30–45	45–60	60–75
0–24	0.00 (0.00, 0.00)	(neither)	(neither)	0.00 (low)	0.00 (low)
24–48	0.07 (0.00, 0.18)	0.00 (high)	0.00 (0.00, 0.00)	0.00 (low)	(neither)
48–72	0.01 (−0.08, 0.08)	−0.04 (−0.14, 0.00)	0.00 (0.00, 0.00)	0.00 (0.00, 0.00)	0.00 (high)
72–96	−0.04 (−0.27, 0.18)	−0.07 (−0.22, 0.01)	−0.03 (−0.28, 0.10)	0.09 (0.10, 0.54)*	0.04 (0.00, 0.19)
96–120	−0.16 (−0.56, −0.03)*	−0.34 (−0.77, 0.00)	0.09 (0.04, 0.80)*	0.08 (0.00, 0.26)	0.00 (0.00, 0.00)
120–144	(neither)	0.11 (high)	0.95 (0.55, 1.00)*	0.50 (high)	(neither)

However, small shifts in preference that do not influence the predicted relationship between WUA and streamflow may be tolerable.

How do we detect differences that are ecologically significant? One good way is to determine the magnitude of shift in depth or velocity preference that would significantly change peak WUA. Williams (1996) showed that variation in preference curves can cause large differences in peak WUA. Once the magnitude of a significant preference shift has been defined, one can design habitat studies with adequate power for detecting such a shift. If a compilation of IFIM studies allowed flow-related changes in habitat availability to be characterized, general guidelines might be developed that would circumvent the need for a new IFIM study on every regulated stream.

In summary, we recommend the following protocol for comparing habitat preferences. (1) Conduct comparisons with regard to bivariate depth and velocity distributions, not with regard to preferences. (2) Use resampling methods to obtain confidence bounds on indexes (such as preference) with unknown distributional properties. (3) Define a magnitude of preference change that is ecologically significant in terms of its effect on the predicted WUA-streamflow relationship.

Acknowledgments.—We received helpful reviews from Steven Railsback, Hal Cardwell, and John Beauchamp. Ken Rose suggested the resampling test. Oak Ridge National Laboratory is managed by the Lockheed Martin Energy Research Corp. for the U.S. Department of Energy under contract DE-AC05-96OR22464. This is publication 4678 of the Environmental Sciences Division.

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Transactions of the American Fisheries Society 126:541–542, 1997
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Testing the Independence of Microhabitat Preferences and Flow: Response to Comments

Williams (1997, this issue) and Jager and Pert (1997, this issue) suggest we incorrectly concluded (in Beecher et al. 1995) that depth and velocity preferences (P[*d*] and P[*v*]) of juvenile (parr) steelhead *Oncorhynchus mykiss* do not change with flow. We originally estimated steelhead preferences at low streamflow (Beecher et al. 1993). When we tested the estimates at substantially higher flow, steelhead parr occurred most frequently in areas giving high combined depth–velocity preference values (P[*dv*] = P[*d*] × P[*v*]). Williams and Jager and Pert believe our test was inconclusive because similar values of P[*dv*] can result from several combinations of P[*d*] and P[*v*] and thus can mask flow-related changes in depth and velocity preferences that might have occurred. Nevertheless, we think our results are consistent with our conclusion that depth and velocity preferences determined at one flow predict fish distribution at a different flow.

We did not directly compare depth and velocity preferences at low and high streamflows, as Williams and Jager and Pert urge, but we did recognize from Shirvell's (1990) study that both utilization and preference cannot remain unchanged at different flows. The question that concerned us was: Do depth and velocity preferences determined at one flow predict fish distribution at another flow? If not, then the instream flow incremental methodology (IFIM) will not be useful for evaluating the effect of different flows on fish.

We attempted to validate flow-independent preference by evaluating preferred combinations of depth and velocity (P[*dv*]) in the context of IFIM. In IFIM, P[*d*] and P[*v*] are multiplied together with preference for substrate or cover to determine the value of different microhabitats. We did not evaluate substrate or cover but used P[*dv*] as an indicator of microhabitat quality, as we had done successfully at a flow similar to the preference determination flow (Beecher et al. 1993). We set out to evaluate whether the interaction of habitat preferences and habitat availability would yield a distribution of fish that was consistent with conventional applications of IFIM. If habitat is important to fish and fish select habitat based on its quality, then fish should use higher-quality habitat (higher P[*dv*], equivalent to greater weighted usable area, WUA) more than they use lower-quality habitat if they are not crowded. Behavioral dominance and other intra- and interspecific pressures affect fish distribution within a stream, but we think such confounding effects on preference determination are stronger at high fish densities. The fish in our study were not crowded and left many P[*dv*] cells unoccupied (to which Jager and Pert object). Thus, fish should have occupied high-P[*dv*] cells more frequently than low-P[*dv*] cells, which they did.

Williams proposes that the best test of a change (or lack of change) in depth and velocity preference with a change in flow is to compare the fish distributions, presumably with a goodness-of-fit test. We agree both that this would be a good test of change in preference and that it would require a much larger sample size; at a minimum, the smaller sample should be similar to the larger sample, which was 104 fish for the low-flow determinations. Jager and Pert suggest sampling with replacement and use of different tests to compare preferences at different flows (or sites or seasons). We do not disagree, but although their statistical tests are more powerful than ours, we are not convinced they are suitable for answering the question we asked.

Multiple combinations of depth and velocity can produce the same P[*dv*] value, as noted by Williams, Jager, and Pert. This does affect the distribution of P[*dv*], and it implies an assumption of IFIM that fish respond to a composite of habitat variables rather than to one at a time. We do not see that it affects the logic of our study, however. Our study was prompted by Shirvell's (1990) finding that steelhead parr used different combinations of depth and velocity at different flows. Was the apparent change in velocity use the result of a change in preference or of a change in the combination of depths and velocities that optimized P[*dv*] among available conditions? If the change in depths and velocities occupied resulted from a change in available combinations of depth and velocity alone, then distributions of the fish should be predictable from the original depth and velocity preferences. If the preferences for depth and velocity changed significantly, then we would expect a poor match between fish and their preferred combinations of depth and velocity. For any given value of P[*dv*], once the value of either P[*d*] or P[*v*] is known, the other is known. We found few locations where both P[*d*] and P[*v*] were near 1.00. In many locations P[*d*] was 0.00, resulting in many cells with P[dv] = 0.00. Some of the P[d] and P[v] bands were wider than others, so several individual values of depth and velocity could lead to the same P[dv]. Jager and Pert make a distinction between P[dv] and P[d,v], but we have not seen studies that made a clear biological distinction between them.

We share Williams' concern for the "city-skyline shapes of the preference curves," and we would (and do) smooth these curves for water management use. We have since developed a composite set of depth and velocity preference curves for steelhead parr from the Morse Creek data set, two sets from the Dungeness River, and other sets from other Washington streams (unpublished). The patterns from our Morse Creek curves holds true in the larger data sets (about 1,000 fish observations in each), but transitions between adjacent intervals are smoother. However, for the purpose of testing the preferences for predicting fish distribution, we felt it was more appropriate to use the data as they were rather than to superimpose our own judgments about the nature of the underlying biological response to depth and velocity. Small samples (and 104 fish distributed among 10 depth and 13 velocity intervals constitutes a small sample) are unlikely to represent the population with complete fidelity. In an adjacent stream (Dungeness River; unpublished data), we found differences in the depth and velocity preferences of steelhead parr between two flows, as did Pert and Erman (1994) for rainbow trout *O. mykiss*. Did these reflect true differences in preference or consistent preferences interacting with a different set of available depths and velocities? We cannot rule out the latter, which we believe requires a less complicated behavioral mechanism than preferences that change with flow.

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Uncertainty and Instream Flow Standards

By Daniel T. Castleberry, Joseph J. Cech Jr., Don C. Erman, David Hankin, Michael Healey, G. Mathias Kondolf, Marc Mangel, Michael Mohr, Peter B. Moyle, Jennifer Nielsen, Terence P. Speed, and John G. Williams

Several years ago, *Science* published an important essay (Ludwig et al. 1993) on the need to confront the scientific uncertainty associated with managing natural resources. The essay did not discuss instream flow standards explicitly, but its arguments apply. At an April 1995 workshop in Davis, California, all 12 participants agreed that currently no scientifically defensible method exists for defining the instream flows needed to protect particular species of fish or aquatic ecosystems (Williams, in press). We also agreed that acknowledging this fact is an essential step in dealing rationally and effectively with the problem.

Practical necessity and the protection of fishery resources require that new instream flow standards be established and that existing standards be revised. However, if standards cannot be defined scientifically, how can this be done? We join others in recommending the approach of *adaptive management*. Applied to instream flow standards, this approach involves at least three elements.

First, conservative (i.e., protective) interim standards should be set based on whatever information is available but with explicit recognition of its deficiencies. The standards should prescribe a reasonable annual hydrograph as well as minimum flows. Such standards should try to satisfy the objective of conserving the fishery resource, the first principle of adaptive management (Lee and Lawrence 1986).

Second, a monitoring program should be established and should be of adequate quality to permit the interim standards to serve as experiments. Active manipulation of flows, including temporary imposition of flows expected to be harmful, may be necessary for the same purpose. This element embodies the adaptive management principles that management programs should be experiments and that information should both motivate and result from management action. Often, it also will be necessary to fund ancillary scientific work to allow more robust interpretation of the monitoring results.

Third, an effective procedure must be established whereby the interim standards can be revised in light of new information. Interim commitments of water that are in practice irrevocable must be avoided.

The details of the monitoring program should vary from case to case. Where protection of particular populations is emphasized, the monitoring program should produce estimates of population size. However, population estimates by themselves often will not provide useful guides to action. This is particularly likely with anadromous fishes such as salmon, where populations of adults depend on harvest, ocean conditions, and other factors not related to instream flows, and populations of juveniles are hard to estimate accurately. Managers will learn more if the monitoring program also includes a suite of indices of the growth, condition, and development of the target species. These indices need to be interpreted with awareness of the complications arising from variations in life history patterns within and among populations. However, the indices and population estimates together will offer the best evidence of the mechanisms by which flows affect the survival and reproduction of individuals and thus the persistence of populations.

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The 1990 "Hodge Decision" in the case of *Environmental Defense Fund v East Bay Municipal Utility District* [Superior Court of Alameda County (California) No. 425955], with which several of us have been involved, exemplifies this approach. Judge Richard Hodge set flow standards for the American River, a major tributary to the Sacramento, that are intended to protect chinook salmon and other public trust resources from diversions by the East Bay Municipal Utility District. However, Hodge recognized the "fundamental inadequacy" of existing information regarding flow needs, so he retained jurisdiction and ordered parties to the litigation to cooperate in studies intended to clarify what the flow standards should be. Experience with these studies motivated the April 1995 workshop.

Our claim that there is now no scientifically defensible method for defining flow standards implies that the Physical Habitat Simulation Model (PHABSIM), the heart of the Instream Flow Incremental Methodology (IFIM), is not such a method. We have divergent views on PHABSIM. Some of us think that, with modification and careful use, it might produce useful information. Others think it should simply be abandoned. However, we agree that those who would use PHABSIM, or some modification of it, must take into account the following problems: (1) sampling and measurement problems associated with representing a river reach with selected transects and with the hydraulic and substrate data collected at the transects; (2) sampling and measurement problems associated with developing the suitability curves; and (3) problems with assigning biological meaning to weighted usable area (WUA), the statistic estimated by PHABSIM. Estimates of WUA should not be presented without confidence intervals, which can be developed by bootstrap methods (Efron and Tibshirani 1991; Williams 1996). Nor should any analytic method become a substitute for common sense, critical thinking about stream ecology, or careful evaluation of the consequences of flow modification, as has sometimes happened with the implementation of the IFIM.

Establishing instream flows involves both policy and science, and scientists and resource managers have challenging roles in the process. Managers need to accept the existing uncertainty regarding instream flow needs and make decisions that will both protect instream resources and allow development of knowledge that will reduce the uncertainty. Scientists need to develop and implement monitoring methods that will realize the potential of adaptive management, and develop the basic biological knowledge that will provide a more secure foundation for decisions that must balance instream and consumptive uses of water.

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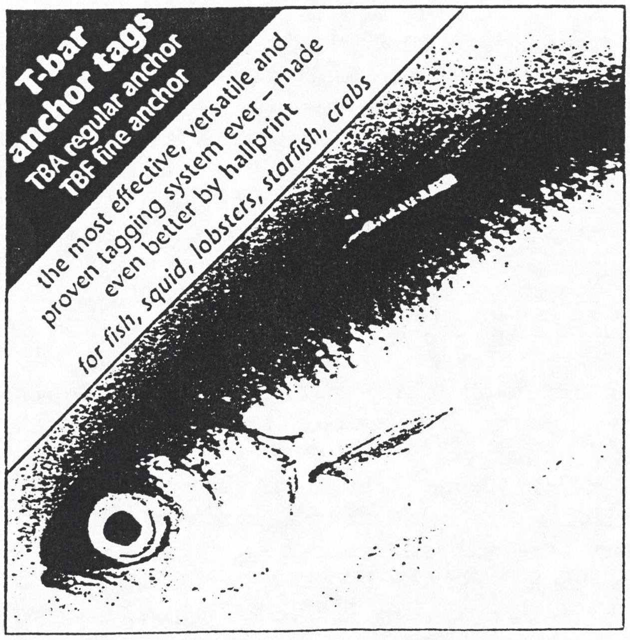

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COMMENTS

Comment: Testing the Independence of Microhabitat Preferences and Flow (Part 1)

Beecher et al. (1995) should be commended for trying to test one of the various assumptions of the physical habitat simulation model (PHABSIM). They noted Shirvell's (1990) report that juvenile steelhead *Oncorhynchus mykiss* used areas of stream with different water velocities at different flows, which suggested that the microhabitat preferences of juvenile steelhead can be a function of flow. Pert and Erman (1994) have found this true for adult rainbow trout, the nonanadromous form of *O. mykiss*. Because PHABSIM depends upon the assumption that microhabitat preferences are independent of flow, Beecher et al. recognized this as a serious problem and tried to test the assumption; however, their test is not persuasive.

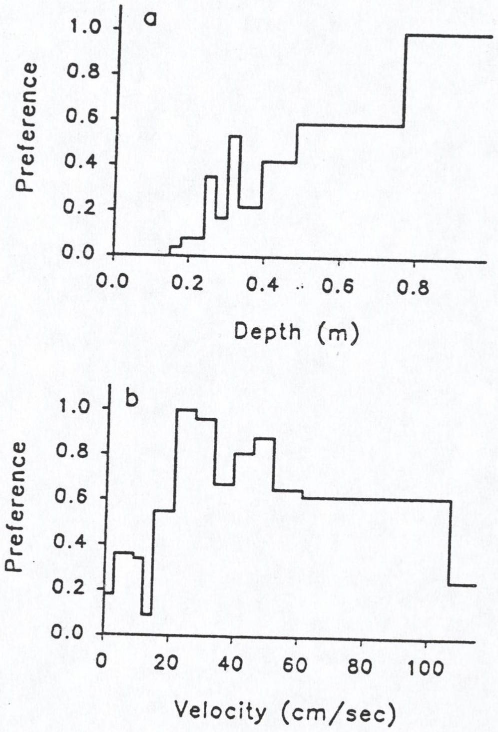

FIGURE 1.—Plots of depth preference (P[*d*]) and velocity preference (P[*v*]) for 104 steelhead parr (from Table 1 of Beecher et al. 1995).

In an earlier study, Beecher et al. (1993) developed preference criteria for depth and velocity from observations of 104 juvenile steelhead at a relatively low flow (Figure 1). In a later study, Beecher et al. (1995) measured depth and velocity at regular intervals along evenly spaced transects in an adjacent reach of the same stream at a relatively high flow. This gave them data at 242 points on a grid, which they took to represent an equal number of PHABSIM cells. (Each cell is centered on one of the grid points.) They also determined the positions of 21 juvenile steelhead, each of which was assigned to the depth–velocity cell nearest to the position.

To analyze the data from the later study, Beecher et al. (1995) used the product (denoted P[*dv*]) of depth preference (P[*d*]) and velocity preference (P[*v*]) for each cell. They divided the P[*dv*] range, which extends from 0.0 to 1.0, into four intervals such that approximately one-fourth of the cells fell into each range. Then they used the distribution of 21 fish among the four P[*dv*] intervals (Figure 2) to test "the hypothesis that depth and velocity preferences determined at one flow predict steelhead parr distribution at a different flow." Their null hypothesis was that fish would be distributed evenly over the four groups of cells. When this hypothesis was rejected by a chi-square test, they took this result as "validating the assumption of flow-independent preferences."

The logic of this claim is not apparent. The question is not whether juvenile steelhead distribute themselves evenly in streams regardless of depth and velocity, but whether their preferences for

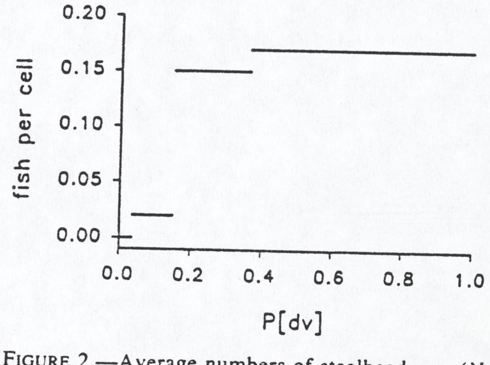

FIGURE 2.—Average numbers of steelhead parr (N = 21 fish total) observed per depth–velocity cell in four P[*dv*] intervals (horizontal lines; from Table 2 of Beecher et al. 1995).

depth or velocity change with flow. Should we believe that the depths and velocities at which the 104 and 21 steelhead parr were observed are samples from the same distributions? To answer this requires a different null hypothesis than the one used and probably a larger sample size. In any event, any number of sets of preferences for depth and velocity could give rise to given values of P[*dv*]—or to the observed frequencies (Figure 2), which are flat over a considerable range of P[*dv*]—so analyzing the data in terms of P[*dv*] does not seem helpful. Finally, it seems hard to assign biological meaning to the city-skyline shapes of the preference curves.

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Comment: Testing the Independence of Microhabitat Preferences and Flow (Part 2)

Beecher et al. (1995) claimed to have validated an assumption of the instream flow incremental methodology (IFIM) and of its physical habitat simulation model (PHABSIM) that water depths and velocities preferred by fish are independent of streamflow. We disagree. First, the study compared habitat preference (of young steelhead *Oncorhynchus mykiss*) at low flow with habitat use (not preference) at high flow. Second, the statistical approach used can lead to the conclusion that depth and velocity preferences are the same at two flows even when most scientists would consider them different. Here, we address statistical issues that arise when comparisons of habitat distribution are based on fish preferences rather than on depth and velocity, and we recommend new techniques for comparing distributions.

Beecher et al. (1995) addressed the null hypothesis "fish distribution is independent of depth and velocity preferences determined at a different flow." They rejected the hypothesis on the basis of a goodness-of-fit test that compared the observed distribution of fish among preference quartiles at a high flow with the expected uniform distribution that would result if fish selected habitat without regard to preferences derived at a lower flow. (The test statistic was P[*dv*], the product of preferred depth P[*d*] and preferred velocity P[*v*].) We do not believe that rejecting this hypothesis implies similarity in fish preferences over a range of flows.

The comparison was of low-flow preference with high-flow *use*; the question of whether preference changed with flow should have been addressed by calculating preference at both flows. It can be shown mathematically that both habitat use and habitat preference cannot be flow-invariant. Habitat use must change in response to flow (i.e., to habitat availability). The original question remains, because preference might be flow-invariant though habitat use may shift.

Unlike traditional comparisons of habitat preferences in which univariate depth and velocity preference distributions are compared between two fish populations, Beecher et al. used preference ranges instead of depth–velocity ranges. Their frequencies were numbers of fish, but expected fish numbers were calculated with the number of P[*dv*] cells in each of four preference ranges: (expected number of fish) = (fraction of cells in preference range) × (total number of fish). This approach is unlikely to detect shifts in habitat preference because it compares the numbers of fish in each of four preference ranges (quartiles) between two flows. Collapsing data into ranges masks differences in depth and velocity preferences because many depth–velocity combinations can share the same P[*dv*] value. Consider a unimodal depth preference curve for trout at low flow. Intermediate depths are optimal, and both shallow and deep habitats are marginal. As flow increases, fish that had been forced to occupy shallow water may shift to deep water, as they did in Pert and Erman's (1994) study. If the fish distribution data are aggregated within preference ranges, shallow and deep fish would be lumped together in the low-preference category, and their joint proportion of the population might not change between low and high flows. In such a case, the test used by Beecher et al. would not detect the marked habitat shift that fish underwent. The same problem can arise with velocity, and the marginal preference range becomes an even greater catchall when both habitat factors are combined. Whether habitat is unsuitable because depth or another factor is too great or too slight is immaterial for IFIM calculations of weighted usable area (WUA) and instream flows. It does matter for testing and comparing preferences. Having the same proportions of fish in habitat deemed unsuitable, marginal, and optimal at different flows does not imply that the same depths and velocities were preferred.

The test used by Beecher et al. also had low power because their hypothesis was that high-flow use (assume it was preference) is independent of low-flow preference, rather than that preferences at the two flows are equal. The type I error rate is low for the hypothesis tested, and only large differences in preference would be diagnosed as real.

Thomas and Bovee (1993) used a test like that of Beecher et al. to evaluate transferability of IFIM habitat suitability curves. They quantified the relationship between type I and type II error rates and the number of occupied and unoccupied P[*dv*] cells. This test is strongly influenced by habitat availability because it depends on cell frequencies instead of fish frequencies. Its dependence on the quantity and characteristics of unoccupied cells is undesirable, because it seems unreasonable that a difference in preference between two flows should depend on the index values assigned to empty cells. Fish density may influence the degree to which "suitable" cells are occupied.

We suggest alternative tests that can detect smaller differences between preferences than the one used by Beecher et al. (1995), and we propose a way to define ecologically significant differences. As an illustrative example, we use the frequency distributions of preference for depth and velocity shown by adult rainbow trout (nonanadromous *O. mykiss*) at low and high flows (Pert and Erman 1994). Preferences shifted to deeper and faster water when flow increased (Figure 3). We chose this example because most people can agree without statistical confirmation that a clear shift in habitat preference occurred.

In two tests, we evaluated the habitat shift by resampling the joint depth–velocity preference distribution. Resampling provides confidence bounds of statistics with unknown distributional characteristics, such as the preference index. In our proposed tests and in an application of the Beecher et al. test, we used the true bivariate or joint preferences (P[*d,v*]) rather than the usual index (P[*dv*] = P[*d*] × P[*v*]).

In our first test, we resampled the habitat use data for each flow, drawing fish observed in different depth–velocity combinations. For each of 50 replicate samples, we calculated the differences between preferences at high and low flows. The 1% and 99% confidence bounds for several depth and velocity classes did not include zero (zero implies no difference between flows; Table 1). According to this test, preferences were significantly different at the two flows, particularly in deeper habitat.

In the second test, we focused on defining an ecologically meaningful statistic to describe the preference distributions. The peak of the WUA curve would be a good ultimate endpoint, but we chose the peak of the joint preference distribution P[*d,v*] as a simpler surrogate. We tested the hypothesis that the P[*d,v*] peak did not shift in response to flow. For all the low-flow samples we drew, the peak occurred within the depth range of 96–120 cm and the velocity range of 15–30 cm/s. At the high flow, 36% of the samples peaked within these ranges, but 64% peaked in deeper (120–144 cm) and faster (30–60 cm/s) habitat. A binomial test rejected the hypothesis that the peaks were the same at both flows ($|z| = 3.75$; $P < 0.0001$).

Finally, we applied the goodness-of-fit test used by Beecher et al. to the joint preference data organized in the following form:

Low-flow preference range	High-flow percentages of: Expected cells	High-flow percentages of: Observed fish
0.0–0.1	54	40
0.1–0.3	22	26
0.3–1.0	24	34

The null hypothesis of independence from low-flow preferences was rejected ($\chi^2 = 8.46$; df = 2; $P = 0.014$).

These results appear to contradict one another. Although trout did not select habitat without re-

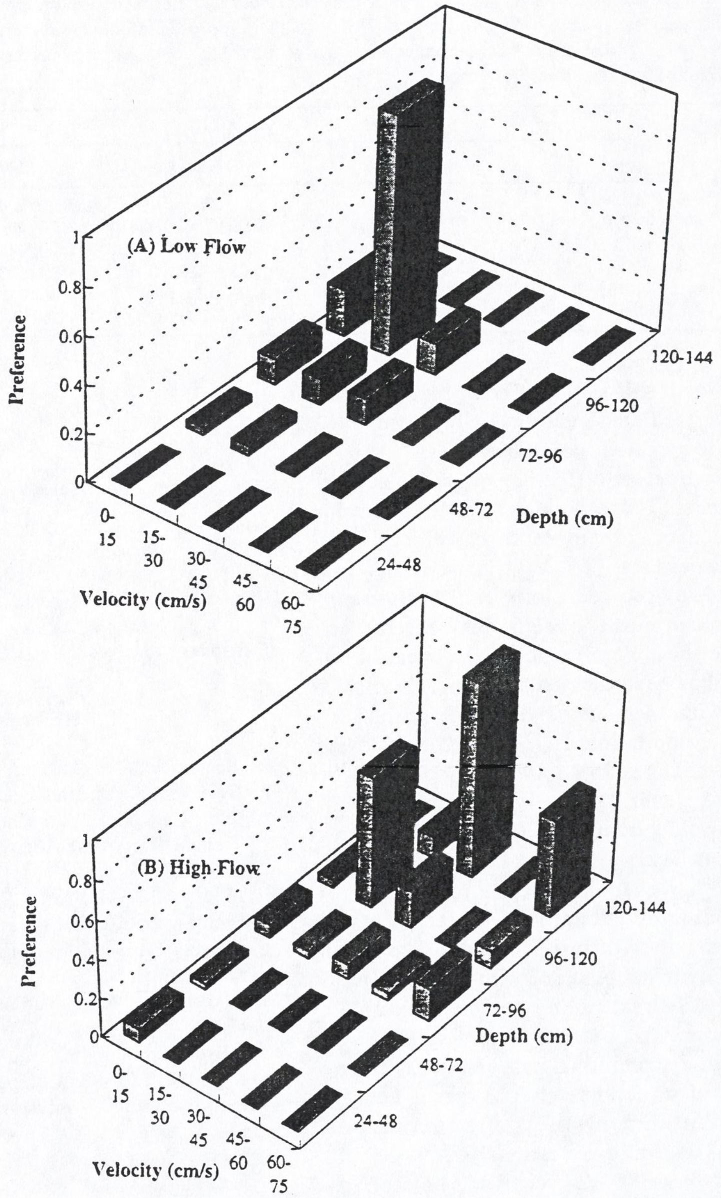

FIGURE 3.—Adult trout preferences calculated as a function of river depth and velocity for (A) a low flow and (B) a high flow.

gard to low-flow P[*d*,*v*], their habitat preferences shifted to greater depths and velocities with increased flow. This contradiction is possible because the tests are mirror images of one another and because the probability of a type I error (reject when true) is set to a low value ($\alpha \leq 0.10$) for each. Fish in these samples fell into the wide intermediate area between extremes of complete and no constancy in habitat preference with changes in flow. Which test is better, and which level of type I error is acceptable? Ecologists are coming to realize that the balance between type I and type II errors should be reasonable in terms of ecological significance (Quinn and Dunham 1983; Roughgarden 1983; Toft and Shea 1983). In our case, it is misleading to use a test that rejects the null hypothesis at the slightest similarity and then claim that no shift in preference has occurred.

TABLE 1.—Resampling test of the hypothesis of zero difference between high-flow and low-flow joint preferences of rainbow trout for depth and velocity. Values are the sample differences in preference (high flow minus low flow) and (in parentheses) the nonparametric 1% and 99% confidence bounds determined by resampling. Asterisks indicate significant differences from zero ($P \leq 0.01$; i.e., 98% of the range of simulated differences failed to bracket zero). Parenthetic words in place of confidence bounds mean that a habitat combination was present only at low flow (low), at high flow (high), or at neither flow (neither).

Depth class (cm)	Velocity class (cm/s)				
	0–15	15–30	30–45	45–60	60–75
0–24	0.00 (0.00, 0.00)	(neither)	(neither)	0.00 (low)	0.00 (low)
24–48	0.07 (0.00, 0.18)	0.00 (high)	0.00 (0.00, 0.00)	0.00 (low)	(neither)
48–72	0.01 (−0.08, 0.08)	−0.04 (−0.14, 0.00)	0.00 (0.00, 0.00)	0.00 (0.00, 0.00)	0.00 (high)
72–96	−0.04 (−0.27, 0.18)	−0.07 (−0.22, 0.01)	−0.03 (−0.28, 0.10)	0.09 (0.10, 0.54)*	0.04 (0.00, 0.19)
96–120	−0.16 (−0.56, −0.03)*	−0.34 (−0.77, 0.00)	0.09 (0.04, 0.80)*	0.08 (0.00, 0.26)	0.00 (0.00, 0.00)
120–144	(neither)	0.11 (high)	0.95 (0.55, 1.00)*	0.50 (high)	(neither)

However, small shifts in preference that do not influence the predicted relationship between WUA and streamflow may be tolerable.

How do we detect differences that are ecologically significant? One good way is to determine the magnitude of shift in depth or velocity preference that would significantly change peak WUA. Williams (1996) showed that variation in preference curves can cause large differences in peak WUA. Once the magnitude of a significant preference shift has been defined, one can design habitat studies with adequate power for detecting such a shift. If a compilation of IFIM studies allowed flow-related changes in habitat availability to be characterized, general guidelines might be developed that would circumvent the need for a new IFIM study on every regulated stream.

In summary, we recommend the following protocol for comparing habitat preferences. (1) Conduct comparisons with regard to bivariate depth and velocity distributions, not with regard to preferences. (2) Use resampling methods to obtain confidence bounds on indexes (such as preference) with unknown distributional properties. (3) Define a magnitude of preference change that is ecologically significant in terms of its effect on the predicted WUA-streamflow relationship.

Acknowledgments.—We received helpful reviews from Steven Railsback, Hal Cardwell, and John Beauchamp. Ken Rose suggested the resampling test. Oak Ridge National Laboratory is managed by the Lockheed Martin Energy Research Corp. for the U.S. Department of Energy under contract DE-AC05-96OR22464. This is publication 4678 of the Environmental Sciences Division.

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Transactions of the American Fisheries Society 126:541–542, 1997
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Testing the Independence of Microhabitat Preferences and Flow: Response to Comments

Williams (1997, this issue) and Jager and Pert (1997, this issue) suggest we incorrectly concluded (in Beecher et al. 1995) that depth and velocity preferences (P[*d*] and P[*v*]) of juvenile (parr) steelhead *Oncorhynchus mykiss* do not change with flow. We originally estimated steelhead preferences at low streamflow (Beecher et al. 1993). When we tested the estimates at substantially higher flow, steelhead parr occurred most frequently in areas giving high combined depth–velocity preference values (P[*dv*] = P[*d*] × P[*v*]). Williams and Jager and Pert believe our test was inconclusive because similar values of P[*dv*] can result from several combinations of P[*d*] and P[*v*] and thus can mask flow-related changes in depth and velocity preferences that might have occurred. Nevertheless, we think our results are consistent with our conclusion that depth and velocity preferences determined at one flow predict fish distribution at a different flow.

We did not directly compare depth and velocity preferences at low and high streamflows, as Williams and Jager and Pert urge, but we did recognize from Shirvell's (1990) study that both utilization and preference cannot remain unchanged at different flows. The question that concerned us was: Do depth and velocity preferences determined at one flow predict fish distribution at another flow? If not, then the instream flow incremental methodology (IFIM) will not be useful for evaluating the effect of different flows on fish.

We attempted to validate flow-independent preference by evaluating preferred combinations of depth and velocity (P[*dv*]) in the context of IFIM. In IFIM, P[*d*] and P[*v*] are multiplied together with preference for substrate or cover to determine the value of different microhabitats. We did not evaluate substrate or cover but used P[*dv*] as an indicator of microhabitat quality, as we had done successfully at a flow similar to the preference determination flow (Beecher et al. 1993). We set out to evaluate whether the interaction of habitat preferences and habitat availability would yield a distribution of fish that was consistent with conventional applications of IFIM. If habitat is important to fish and fish select habitat based on its quality, then fish should use higher-quality habitat (higher P[*dv*], equivalent to greater weighted usable area, WUA) more than they use lower-quality habitat if they are not crowded. Behavioral dominance and other intra- and interspecific pressures affect fish distribution within a stream, but we think such confounding effects on preference determination are stronger at high fish densities. The fish in our study were not crowded and left many P[*dv*] cells unoccupied (to which Jager and Pert object). Thus, fish should have occupied high-P[*dv*] cells more frequently than low-P[*dv*] cells, which they did.

Williams proposes that the best test of a change (or lack of change) in depth and velocity preference with a change in flow is to compare the fish distributions, presumably with a goodness-of-fit test. We agree both that this would be a good test of change in preference and that it would require a much larger sample size; at a minimum, the smaller sample should be similar to the larger sample, which was 104 fish for the low-flow determinations. Jager and Pert suggest sampling with replacement and use of different tests to compare preferences at different flows (or sites or seasons). We do not disagree, but although their statistical tests are more powerful than ours, we are not convinced they are suitable for answering the question we asked.

Multiple combinations of depth and velocity can produce the same P[*dv*] value, as noted by Williams, Jager, and Pert. This does affect the distribution of P[*dv*], and it implies an assumption of IFIM that fish respond to a composite of habitat variables rather than to one at a time. We do not see that it affects the logic of our study, however. Our study was prompted by Shirvell's (1990) finding that steelhead parr used different combinations of depth and velocity at different flows. Was the apparent change in velocity use the result of a change in preference or of a change in the combination of depths and velocities that optimized P[*dv*] among available conditions? If the change in depths and velocities occupied resulted from a change in available combinations of depth and velocity alone, then distributions of the fish should be predictable from the original depth and velocity preferences. If the preferences for depth and velocity changed significantly, then we would expect a poor match between fish and their preferred combinations of depth and velocity. For any given value of P[*dv*], once the value of either P[*d*] or P[*v*] is known, the other is known. We found few locations where both P[*d*] and P[*v*] were near 1.00. In many locations P[*d*] was 0.00, resulting in many cells with P[dv] = 0.00. Some of the P[d] and P[v] bands were wider than others, so several individual values of depth and velocity could lead to the same P[dv]. Jager and Pert make a distinction between P[dv] and P[d,v], but we have not seen studies that made a clear biological distinction between them.

We share Williams' concern for the "city-skyline shapes of the preference curves," and we would (and do) smooth these curves for water management use. We have since developed a composite set of depth and velocity preference curves for steelhead parr from the Morse Creek data set, two sets from the Dungeness River, and other sets from other Washington streams (unpublished). The patterns from our Morse Creek curves holds true in the larger data sets (about 1,000 fish observations in each), but transitions between adjacent intervals are smoother. However, for the purpose of testing the preferences for predicting fish distribution, we felt it was more appropriate to use the data as they were rather than to superimpose our own judgments about the nature of the underlying biological response to depth and velocity. Small samples (and 104 fish distributed among 10 depth and 13 velocity intervals constitutes a small sample) are unlikely to represent the population with complete fidelity. In an adjacent stream (Dungeness River; unpublished data), we found differences in the depth and velocity preferences of steelhead parr between two flows, as did Pert and Erman (1994) for rainbow trout *O. mykiss.* Did these reflect true differences in preference or consistent preferences interacting with a different set of available depths and velocities? We cannot rule out the latter, which we believe requires a less complicated behavioral mechanism than preferences that change with flow.

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mussel should serve as a wake-up call to align the aquaculture interests in the United States. There is no question about it—the zebra mussel is here to stay. It can serve to either unify or shatter the industry—to make it viable and sustainable, or not. The choice is clear and is up to each American aquaculturist to ultimately make.

—*Rick Kastner*

Another look at instream flow standards

I read with interest the essay, "Uncertainty and Instream Flow Standards," in the August *Fisheries*. I must say that I was astounded that 12 people had to come together in that forum, similar to the 12 Apostles, to come to so obvious a conclusion. I have taken five or six 40-hour courses from the Fort Collins Instream Flow Incremental Methodology (IFIM) group since 1983, and I have used the methods. The IFIM training group stresses that the results of the IFIM should be used with caution and to supplement other information prepared for the decision-making process. I am a careful user of the method that provides various types of valuable information to help in the decision-making process. Let's not discard the method just because it does not give us "the answer." I did not see Bob Milhous, Ken Bovee, Terry Waddles, or others who are or were part of the IFIM training group in the forum (which could add considerable credibility) and perhaps could be a leader of the 12 to help clarify the appropriate uses of the IFIM.

The fact that they did come together in a forum suggests a question: Why did they have to come together? Probably because there was so much misunderstanding about the expections of the method. I hope this misunderstanding was an honest difference of opinion, but emotionalism and sophistry should not be ruled out in negotiations regarding use of water resources.

This leads to another question: How do we educate us all so that we can understand the limitations of the method? The educational process is embodied in critical thinking, intuitive reasoning, and the ability to understand how the IFIM works. So many entities take for granted that the results of the method are the end point of the analysis that will take a large effort of reeducation.

This begs the question: Who shall do the educating? Here the answer is perhaps obvious in a trilogy of sorts. The primary leaders will be the professors who teach the complex nature of ecological relationships and lead students to question and develop their reasoning ability. The secondary leaders will be the IFIM trainers. It is their duty to put into perspective how the results fit into the complex ecological environment and how difficult performing a limiting factor analysis consisting of more than three or four parameters in a complex ecosystem is. The tertiary leaders are the practitioners of the IFIM. They and they alone must make their clients and decision makers understand that the results of the IFIM are not the final answer. It is only one tool in combition with many others that will help to define the habitat or environmental conditions necessary for fish.

The results of the IFIM have been used as the final answer in a complex analysis of water resource issues. These issues have social, political, and even technical ramifications. As educated ecologists, we should know better than to take the results of any analysis that upon examination is simplistic and that obviously does not include room for the complexities. However, this is what has occurred when some practitioners of the IFIM have applied the method over the years. The IFIM uses basically three or four parameters in the development of weighted usable area. These are depth, substrate, and water velocity. Sometimes cover and other parameters are used. Based on common sense and the rigorous course in ecology that I took at Oklahoma State in the early 1960s (taught by Adolph Stebler) and the enlightening research methods at Oregon State in the late 1960s (taught by Charles Warren), I believe that there are more than three or four factors affecting distribution and abundance of fish, and it seems obvious that a species response is a result of a complex of environmental conditions, species interactions, human interference/harvest, and other factors.

—*Richard E. Craven*

Walleye-trout conflict airing appreciated

I want to thank the American Fisheries Society (AFS) for publishing the "Walleye and Northern Pike: Boost or Bane to Northwest Fisheries?" article by Thomas McMahon and David Bennett in your August 1996 issue of *Fisheries*. It is controversial, as noted, with some anglers supporting these species' introduction and a few taking it upon themselves to


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Uncertainty and Instream Flow Standards: Perspectives Based on Hydropower Research and Assessment

By Webster Van Winkle, Charles C. Coutant, Henriette I. Jager, Jack S. Mattice, Donald J. Orth, Robert G. Otto, Steven F. Railsback, and Michael J. Sale

In a thought-provoking essay, "Uncertainty and Instream Flow Standards," Castleberry et al. (1996) argue that currently no scientifically defensible method exists [including the Physical Habitat Simulation System component (PHABSIM) of the Instream Flow Incremental Methodology (IFIM)] for defining instream flows needed to protect fish or aquatic ecosystems. They suggest (1) that an adaptive management approach is preferable, involving protective interim standards, a monitoring program, and an effective [institutional] procedure for revising interim standards in light of new information; and (2) that scientists and managers need to understand and consider the uncertainties in instream flow methods, develop and implement monitoring methods that will realize the potential of adaptive management, and develop the basic (mechanistic) biological knowledge about how flows affect the survival and reproduction of individuals.

We want to add to these constructive ideas to promote further discussion on the important issue of instream flow management. The scientific defensibility of any predictive assessment methodology needs to be judged based on its scientific foundations and its proven track record of use in specific environmental assessments. The adaptive management approach, while having a sound scientific foundation, is still developing a proven track record. Many perceive this approach as trial-and-error manipulations that provide an excuse for maintaining the status quo. Stated more strongly, adaptive management can be primarily a political process of adapting to changing political pressures, rather than a scientific process of adapting to increased scientific understanding. In reality, adaptive management requires dramatic experiments, including predictive models. We identify three additional needs to obtain the benefits of more flexible approaches such as adaptive management.

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Decision-making Framework

Adaptive management requires a high level of institutional, legal, and political flexibility—more than now typically occurs (Castleberry et al. 1996). Many fisheries agencies have insufficient resources for the current backlog of hydropower instream flow studies (Railsback et al. 1990), much less for long-term monitoring and adaptive management at each site. In addition, deregulation of electricity generation in the United States is creating a competitive climate such that hydropower operators will be less able to afford adaptive management experiments.

However, the benefits of flexible requirements are being recognized and gradually implemented. In addition to the "Hodge Decision" (Castleberry et al. 1996), examples include the settlement agreements for the Skagit River Project in Washington and the New Don Pedro Project in California, both of which allow flows to be varied according to agreed rules as more information and better models are obtained from monitoring studies. Additional opportunities for adaptive management lie with federal water projects [e.g., the Glen Canyon Project (U.S. Bureau of Reclamation 1995)]. Federal projects are not bound by the

> adaptive management can be primarily a political process of adapting to changing political pressures, rather than a scientific process of adapting to increased scientific understanding

procedures of the Federal Energy Regulatory Commission, and study and mitigation costs (including funding of resource agency participation) are heavily subsidized.

Management Objectives

A challenge to any approach based on population- or community-level effects is achieving agreement on management objectives that are acceptable to the public, simple to understand, ecologically meaningful, and measurable before designing a monitoring program or a model. The objective could range from target values for adult population density or production of a key fish species to maintainance of a balanced and indigenous fish community. Many of these objectives are difficult to measure. For example, providing a specified long-term average number of outmigrating salmon smolts per spawner may seem like a simple, well-defined management objective. However, determining whether this objective is being met based on variable and uncertain data gathered throughout the years is not simple. Nonetheless, the need to define such management objectives can be viewed as a strength of population- and community-level approaches (Orth 1995); while difficult, it does force decision makers to focus on real project effects, management options, and uncertainty.

Flow Manipulations, Monitoring Programs, and Models

The adaptive management approach requires several key components. The flow manipulation must involve a major change in the base flow regime for regulators and scientists to expect a measurable change. Minor flow changes may not provide the contrast needed to test the knowledge base and models used to develop management regulations and, thus, would fail to serve the decision-making purpose. While necessary for the adaptive management approach, flow manipulations and monitoring programs alone are not sufficient. For the adaptive management approach to be successful, it must include a methodology that provides two critical functions. First, it must provide the qualitative framework for identification and consensus-building concerning management objectives, flow manipulations, and monitoring. Second, it must provide a quantitative predictive tool [always combined with common sense, critical thinking about stream ecology, and careful evaluation of the actual consequences of flow modification (Castleberry et al. 1996)] that synthesizes the results from the monitoring program and makes quantitative predictions (absolute or relative) of fish population responses to alternative instream flow regimes and mitigation measures. Adaptive management can treat these predictions as hypotheses and design experiments to test their validity and improve predictions.

Although it has its weaknesses because of its limited focus on physical habitat, PHABSIM is such a tool. The individual-based modeling approach is another such tool that does not have this limitation. It replaces PHABSIM's reliance on habitat suitability curves with a mechanistic representation of the processes underlying fish growth, survival, and reproduction (e.g., Van Winkle et al. 1993). This representation varies with the life history of the species of interest, and density dependence (i.e., compensation) is an emergent population property of what happens to the individual model fish.

One such individual-based instream flow model (Van Winkle et al. 1996) is being developed in conjunction with a field evaluation of PHABSIM (Studley et al. 1996). By monitoring fish populations and habitat at 9 hydropower sites throughout 11 years and experimentally changing minimum flows (Studley et al. 1996), this study indicates that population responses to flow can be complex yet predictable. For example, at sites within one 5-km reach of the Tule River, California, factors that limited trout populations included base flows, scouring of redds by floods, winter temperatures too high for incubation, high summer temperatures, scarce spawning habitat, and interspecies competition. Physical habitat assessments alone cannot be expected to do well in such situations, yet many of these population-limiting factors have been successfully captured in the individual-based model and could be represented in a more comprehensive suite of models in IFIM. Preliminary results also indicate that relatively simple improvements to typical PHABSIM methods can produce instream flow assessments that are reasonably accurate and far less expensive than an adaptive management approach. At the very least, they can provide the initial predictions on which adaptive management can build.

Castleberry et al. (1996) correctly point out the uncertainties in simplistic instream flow assessments. We agree that the adaptive management approach has potential benefits and, in fact, we see a gradual trend toward more flexible assessment and management of water projects. However, before the adaptive management approach can be fully successful, it is clear that (1) decision-making frameworks; (2) management objectives; and (3) flow manipulations, monitoring programs, and models all need improvement. We emphasize that mechanistic models that depict the factors affecting the target aquatic resources (and not just physical habitat) must be key components of the adaptive management process. Without such models, the uncertainties may be greater than those currently encountered with habitat models, and as a consequence, eventual costs may be much higher than necessary.

Acknowledgments

The authors appreciate the constructive comments and perspectives of C. B. Stalnaker and two other reviewers. Preparation of this essay was supported by the Electric Power Research Institute under contract RP2932-2 (DOE ERD-87-672) with the U. S. Department of Energy, under contract DE-AC05-96OR22464 with Lockheed Martin Energy Research Corporation. This is Publication No. 4649 of the Environmental Sciences Division, Oak Ridge National Laboratory.

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ESSAY

Uncertainty and Instream Flow Standards

By Daniel T. Castleberry, Joseph J. Cech Jr., Don C. Erman, David Hankin, Michael Healey, G. Mathias Kondolf, Marc Mangel, Michael Mohr, Peter B. Moyle, Jennifer Nielsen, Terence P. Speed, and John G. Williams

Several years ago, *Science* published an important essay (Ludwig et al. 1993) on the need to confront the scientific uncertainty associated with managing natural resources. The essay did not discuss instream flow standards explicitly, but its arguments apply. At an April 1995 workshop in Davis, California, all 12 participants agreed that currently no scientifically defensible method exists for defining the instream flows needed to protect particular species of fish or aquatic ecosystems (Williams, in press). We also agreed that acknowledging this fact is an essential step in dealing rationally and effectively with the problem.

Practical necessity and the protection of fishery resources require that new instream flow standards be established and that existing standards be revised. However, if standards cannot be defined scientifically, how can this be done? We join others in recommending the approach of *adaptive management*. Applied to instream flow standards, this approach involves at least three elements.

First, conservative (i.e., protective) interim standards should be set based on whatever information is available but with explicit recognition of its deficiencies. The standards should prescribe a reasonable annual hydrograph as well as minimum flows. Such standards should try to satisfy the objective of conserving the fishery resource, the first principle of adaptive management (Lee and Lawrence 1986).

Second, a monitoring program should be established and should be of adequate quality to permit the interim standards to serve as experiments. Active manipulation of flows, including temporary imposition of flows expected to be harmful, may be necessary for the same purpose. This element embodies the adaptive management principles that management programs should be experiments and that information should both motivate and result from management action. Often, it also will be necessary to fund ancillary scientific work to allow more robust interpretation of the monitoring results.

Third, an effective procedure must be established whereby the interim standards can be revised in light of new information. Interim commitments of water that are in practice irrevocable must be avoided.

The details of the monitoring program should vary from case to case. Where protection of particular populations is emphasized, the monitoring program should produce estimates of population size. However, population estimates by themselves often will not provide useful guides to action. This is particularly likely with anadromous fishes such as salmon, where populations of adults depend on harvest, ocean conditions, and other factors not related to instream flows, and populations of juveniles are hard to estimate accurately. Managers will learn more if the monitoring program also includes a suite of indices of the growth, condition, and development of the target species. These indices need to be interpreted with awareness of the complications arising from variations in life history patterns within and among populations. However, the indices and population estimates together will offer the best evidence of the mechanisms by which flows affect the survival and reproduction of individuals and thus the persistence of populations.

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The 1990 "Hodge Decision" in the case of *Environmental Defense Fund v East Bay Municipal Utility District* [Superior Court of Alameda County (California) No. 425955], with which several of us have been involved, exemplifies this approach. Judge Richard Hodge set flow standards for the American River, a major tributary to the Sacramento, that are intended to protect chinook salmon and other public trust resources from diversions by the East Bay Municipal Utility District. However, Hodge recognized the "fundamental inadequacy" of existing information regarding flow needs, so he retained jurisdiction and ordered parties to the litigation to cooperate in studies intended to clarify what the flow standards should be. Experience with these studies motivated the April 1995 workshop.

Our claim that there is now no scientifically defensible method for defining flow standards implies that the Physical Habitat Simulation Model (PHABSIM), the heart of the Instream Flow Incremental Methodology (IFIM), is not such a method. We have divergent views on PHABSIM. Some of us think that, with modification and careful use, it might produce useful information. Others think it should simply be abandoned. However, we agree that those who would use PHABSIM, or some modification of it, must take into account the following problems: (1) sampling and measurement problems associated with representing a river reach with selected transects and with the hydraulic and substrate data collected at the transects; (2) sampling and measurement problems associated with developing the suitability curves; and (3) problems with assigning biological meaning to weighted usable area (WUA), the statistic estimated by PHABSIM. Estimates of WUA should not be presented without confidence intervals, which can be developed by bootstrap methods (Efron and Tibshirani 1991; Williams 1996). Nor should any analytic method become a substitute for common sense, critical thinking about stream ecology, or careful evaluation of the consequences of flow modification, as has sometimes happened with the implementation of the IFIM.

Establishing instream flows involves both policy and science, and scientists and resource managers have challenging roles in the process. Managers need to accept the existing uncertainty regarding instream flow needs and make decisions that will both protect instream resources and allow development of knowledge that will reduce the uncertainty. Scientists need to develop and implement monitoring methods that will realize the potential of adaptive management, and develop the basic biological knowledge that will provide a more secure foundation for decisions that must balance instream and consumptive uses of water.

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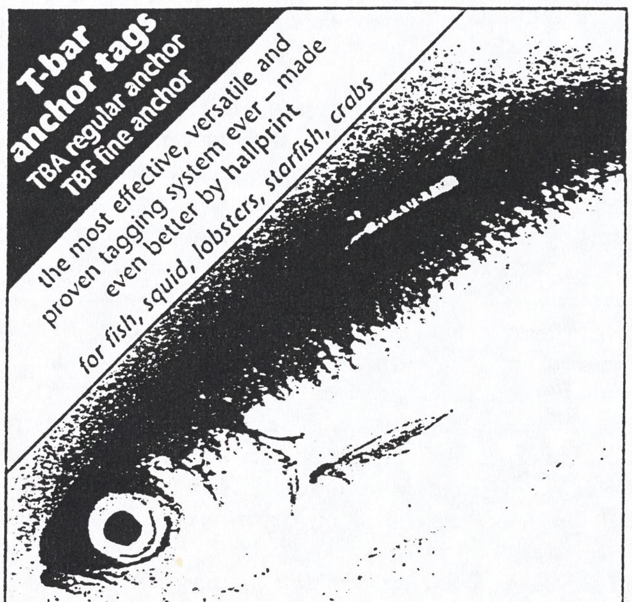

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COPY 1

The Watershed Protection Approach: Is the Promise About To Be Realized?

William E. Taylor and Mark Gerath

The concept of managing water resources and protecting water quality on a geographical or watershed basis has been evolving since the late 1800s. Only in the last few years, however, have water resource and protection organizations, both public and private, begun to focus seriously on a watershed approach to address remaining water quality problems. Until recently, water quality regulation and management focused on control of point source dischargers of pollutants. Technology and water quality-based effluent limitations on point sources, in conjunction with implementation of antibacksliding and antidegradation requirements, have resulted in a substantial reduction in point source pollutant loadings to waters and consequent upgrading of many receiving waters.

To achieve further cost-effective improvements in water quality, water resource managers recognize that they must now focus on a more comprehensive approach to water quality management, including continued control of point source discharges as well as control of nonpoint source discharges, preservation of habitat, and ground water protection and flow.

This article gives a brief history of watershed protection efforts and an analysis of why the watershed approach makes technical sense. Recent case studies from throughout the country illustrate various types of watershed protection approaches now being used.

Historical Development of the Watershed Protection Approach

For several decades, agencies such as the Army Corps of Engineers, the Soil Conservation Service (now known as the Natural Resources Conservation Service) and the Federal Energy Regulatory Commission (FERC) have funded and approved water resource projects designed to achieve multiple objectives which in turn required watershed-based planning and management. Early federal initiatives typically involved basinwide projects for flood control, municipal water supply, irrigation, hydroelectric power generation, recreation, and water quality improvement as part of a single project.

Section 3 of the 1917 Newland Act, 33 U.S.C. § 701 (1988) (repealed 1994), gave the Corps authority to undertake a comprehensive study of watersheds for flood control improvements. The Corps reports served as the basis for most river planning documents for the next several decades. Early basinwide plans tended to address water resource development rather than quality and focus on structural solutions rather than nonstructural pollution control-based planning. In the early 1960s, the focus of water resources management turned from a large basinwide economic development approach to a more regional development and water quality protection approach.

The Water Resources Planning Act of 1965 (WRPA), 42 U.S.C. § 1962 (1988 & Supp. V. 1993), evolved from several years of congressional review of river basin management plans. The WRPA recognized water pollution as a major national concern and attempted to coordinate federal programs to address both water quantity and quality. It did not result in significant change in national water policy, however, because Congress was unwilling to put regulatory teeth into the law or to cede any authority to local or regional basin entities.

The Federal Water Pollution Control Act of 1972, Pub. L. No. 92-500, 86 Stat. 816 (1972) (Clean Water Act or CWA), provided the United States Environmental Protection Agency (EPA) with authority and funding mechanisms specifically directed to watershed protection. The Clean Water Act's principal purpose was the restoration and maintenance of the "chemical, physical and biological integrity of the nation's waters." Section 102(a) of the Act directed EPA, in cooperation with other federal agencies, states and dischargers, to "prepare or develop comprehensive plans for preventing, reducing or eliminating pollution in navigable waters and ground waters." Section 102(c) and (d) provided federal grants for states to develop comprehensive water control plans consistent with the basin planning process under the Water Resources Planning Act. Section 208 of the CWA required states to develop "area wide waste treatment management plans" including land use-based pollution sources.

Of particular importance, section 303(d) of the CWA requires that Total Maximum Daily Loads (TMDLs) be established for water bodies where water quality standards have not been met. A TMDL includes consideration of the waste load allocation from point sources and an estimate of the pollutant load from nonpoint sources. States were required to identify water quality limited waters (those waters not meeting applicable water quality standards), rank them by priority, and submit the list of waters to EPA by June 26, 1979. Following approval by

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EPA, states were to develop TMDLs for listed waters, implement control actions, and assess the effectiveness of the control actions. When states have not acted, courts have required EPA to implement the TMDL program. *See William J. Scott v. City of Hammond, Indiana*, 741 F.2d 992 (7th Cir. 1984). Unfortunately, even today very few states have fulfilled their obligations under section 303(d). The result is a series of citizen suits against EPA requiring the agency to begin preparing TMDLs for impaired water bodies.

In the past three years, various environmental and citizens groups have filed nearly twenty lawsuits (or notices of suits) against EPA for failure to approve state section 303(d) lists or to implement TMDLs in the absence of state action. These suits have been filed in every EPA Region except Region V (Chicago). EPA's Office of Regional Counsel expects several new notices to be filed, particularly in Region V, where many of the states have failed to meet the biennial April 1 deadline for submission of section 303(d) lists. In one recently decided case, the United States District Court for the Northern District of Georgia ruled that Georgia's section 303(d) submissions were inadequate and that EPA's approval of the state's submissions was arbitrary and capricious. The court ordered EPA to take over Georgia's total maximum daily load program. *Sierra Club v. Hankinson*, 1:94-CV-2501 (N.D. Ga. 1996).

In a similar case brought against EPA's Regional Administrator in Region II, *Natural Resources Defense Council, Inc. v. Fox*, 909 F. Supp. 153 (S.D.N.Y. 1995), the district court determined that there were triable issues of fact as to whether the State of New York has created and submitted the appropriate TMDLs to EPA Region II. The state must now spend time reconstructing its TMDL filings of the last fifteen years to establish that it has met the specific requirements of section 303(d). These two recent lawsuits have spurred EPA to begin a dialogue with environmental groups, states and other interested stakeholders with the principal purpose of overhauling EPA's TMDL program.

Despite all the available CWA statutory authority to begin watershed protection, implementation of these provisions has been limited because EPA and states initially focused on point source dischargers under section 402 of the CWA, the National Pollutant Discharge Elimination System (NPDES) permit program. The Water Quality Act of 1987, P.L. 100-4 (Feb. 4, 1987), added more specific planning-based approaches to the Clean Water Act, including section 319, which specifically required states to develop watershed-based approaches to polluted nonpoint source runoff. In addition, Section 320 established the national estuary program which adopts the planning and implementation of water quality management activities for an estuary's entire drainage area. Currently, there are twenty-eight approved national estuary projects.

Since the 1987 amendments to the Clean Water Act, states and federal agencies have begun to embrace watershed protection approaches seriously. A 1993 watershed management conference drew well over 1,000 participants from state and federal water resource agencies as well as other public and private organizations. The proceedings from that conference have served as a guide for many states implementing watershed protection approaches and for EPA's development of its watershed protection guidance. In a series of guidance documents published within the last year, EPA has finally begun to define and establish a framework for implementing a watershed protection approach.

Watershed Protection: Does It Make Technical Sense?

Although each watershed will have different aquatic resources, pollutant loadings, land uses and regulatory programs, it is possible to define a watershed protection approach. In its latest guidance, *Watershed Approach Framework* (Final Draft May 15, 1996), EPA defined a watershed approach as a "coordinating framework for environmental management that focuses public and private sector efforts to address the highest priority problems within hydrologically-defined geographic areas, taking into consideration both ground and surface water flow." The goals are to protect and restore aquatic ecosystems and to protect human health. To be successful, the approach must include consideration of all environmental concerns, including protection of critical habitats, such as wetlands within the watershed, in addition to protection of surface and ground waters.

Much of the momentum behind the watershed approach derives from its very clear advantages for enhancing water quality. Water quality and quantity within a receiving water are affected by the sum of human activities and environmental processes in the hydrologic basin. It makes sense to coordinate water quality management in recognition of the sum of activities. Table 1, on page 18, presents a list of management activities that might be coordinated under the watershed approach. For example, the simple act of synchronizing wastewater discharge permits within a basin helps the permitting agency coordinate its data collection and modeling while more readily considering the combined impacts of the various dischargers and background loadings. The logical extension of this technique is the explicit consideration and management of nonpoint sources of pollutants and water consumption within the basin. The alternative approach of considering each pollutant source in isolation is not only less efficient, but also not suitable for assessing the full range of potential pollutant loads and necessary control measures.

While the watershed approach provides significant technical advantages, it can be very difficult to administer. The watershed approach is by its nature more complex than either traditional technology or water quality-based permitting. Full implementation of the watershed approach requires an understanding of: (1) the sources of each important pollutant throughout the basin; (2) the source and frequency of different rates of water flow through the system; and (3) how pollution control strategies are likely to affect the loadings and/or flows. For many pollutants (e.g., nutrients or short-lived toxics), it is desirable to understand the rate of pollutant loss from the system to avoid overestimation of loadings. The site-specific chemistry (e.g., bioavailability and toxicity) of the pollutant may bear consideration to develop effluent limitations appropriate for the specific watershed. Finally, it may be necessary to consider two critical flow periods: the low flow events traditionally examined in wasteload allocations at which point source effluents tend to dominate, and wet weather events during which nonpoint source pollutant loadings increase. Thus, permitting agencies face a data collection effort with significant spatial and temporal demands. Table 2, on page 19, lists some of the data utilized to implement watershed-based permitting.

A key element of most watershed protection strategies is the use of mathematical modeling to estimate water quality. A narrowly focused point source permitting approach often allowed the discharge to be considered in isolation, and background receiving water concentration was usually assumed rather than measured. The watershed approach puts all contaminant sources on an equal footing and requires a relatively sophisticated model to track all the loadings, dilutions, and attenuation mechanisms. In fact, lack of modeling resources is commonly cited as a reason that agencies have failed to develop TMDLs.

Another complexity associated with the watershed approach is the issue of regulatory jurisdiction. The watershed approach, by its very nature, recognizes watershed boundaries but it must also acknowledge political ones. Many significant loadings (e.g., mercury from atmospheric deposition and nutrients from septic tanks) come from diffuse and remote (from a regulatory and geographical sense) sources. Controlling these types of sources will likely require new regulatory initiatives such as evaluation and regulation of air emissions for long-distance and long-term impacts. Conversely, many of the critical issues in watershed management are under local or regional control. For example, control of development, with simultaneous control of water consumption, runoff, and septic loadings, is generally local. To be successful, watershed management must motivate local officials and taxpayers to consider impacts across jurisdictional and geographical lines.

As discussed above, a key premise of the watershed approach is that nonpoint sources can and will be controlled on a basis similar to point source dischargers. This assumption is questionable. The agencies charged with regulating water quality through the NPDES program have little or no authority over many important nonpoint sources. This regulatory gap was the subject of a recent debate within EPA regarding trading of point source and nonpoint source pollutants. The EPA Office of Enforcement, recognizing EPA's tenuous ability to regulate many nonpoint sources, wants to hold the point source discharger responsible for the performance of the nonpoint source controls. On the other hand, the Office of Water, wishing to facilitate trading, wants to minimize the point source discharger's responsibility following the trade.

While pollutant trading is relatively well established under the Clean Air Act, it is more complicated under the watershed approach because the location and timing of the relevant loadings within the watershed greatly affect the results. It may be necessary, for example, to assure that the partners in a trade affect the water quality within the same river reaches. EPA is currently developing an effluent trading guidance document to clarify how such trades may be accomplished and credited.

Complexities such as jurisdictional questions and pollutant trading associated with watershed protection have led and will continue to lead to a proliferation of different approaches. Most states are rapidly moving to a watershed based approach and many hundreds of citizen groups are becoming directly involved in those efforts. EPA has published a number of watershed protection guidance documents in the last year and maintains a site on the World Wide Web to discuss the approaches different states are adopting. EPA has even established a Watershed Academy to educate state managers on watershed protection strategies.

The need and benefits of the watershed approach are

Table 1

Management Activities that Might be Incorporated into Watershed Permitting

NPDES Permitting	Habitat Improvement Programs
Wellhead Protection Programs	Water Use Regulation
Management of Hazardous Waste Sites	Control of Household Wastewater Systems
Control of Agricultural Runoff	Regulation of Residential Development
Control of Urban Runoff	Flood Control Programs
Management of Forest Lands	Wetlands Conservation and Protection Programs

becoming increasingly clear. Local, state and federal agencies are beginning to use any regulatory mandates available to them to further the watershed approach. Efforts are underway to reorganize regulatory agencies, to revamp the data collection and permitting processes, and to involve stakeholders to an unprecedented degree. In many cases, the state agencies and even the citizen watershed groups are out in front of EPA as the case studies below illustrate. Water pollution control agencies agree that the low-hanging fruit has been picked on the water pollution control tree. The watershed approach, despite its complexity, is a cost-effective means to provide the next highest level of water quality.

Watershed Protection Case Studies

Four current watershed programs from around the country provide examples of innovative state approaches to watershed protection.

Case 1: State Agency Reorganizes and Citizen Group Is Empowered. The Charles River watershed in Massachusetts is highly developed. The river drains into Boston Harbor and has urban and residential development along its entire length. The river is also considered to be a important cultural, scenic, and recreational resource. Among the problems facing the river are the presence of fecal coliform bacteria at concentrations above the water quality criteria. In addition, there was widespread concern about the quantity of river flow as affected by groundwater and surface water withdrawals from the basin. Both of these problems clearly stem from development on which the traditional wastewater permitting process has little effect.

Statewide, these issues have contributed to the reorganization of the state water regulation divisions (e.g., water supply, wastewater permitting) around watershed boundaries as well as formation of basin teams with other state and federal agencies (e.g., U.S. Fish and Wildlife, EPA). Wastewater permitting has been coordinated in time to facilitate data collection and wasteload allocations. In addition, the Massachusetts Department of Environmental Protection has integrated its program of water withdrawal permitting into a program of watershed management. This program modification greatly facilitates data collection on critical stream flows as well as subjecting water withdrawals to evaluation relative to ecological issues and wasteload allocations. Multidisciplinary and multiagency teams within each basin now facilitate planning.

In the Charles River basin, the Charles River Watershed Association (CRWA), a nonprofit citizen group, has begun a study of the basin because of the problems of nonpoint source pollution and management of water quantity. In an ambitious five-year program, the organization will collect water quality samples, develop mathematical models of water quantity and quality, perform stakeholder outreach, and help to develop water quality management plans. The CRWA study uses local academic resources and citizen volunteers and is funded by government grants and the stakeholders.

In many ways, the CRWA is performing a function that might be expected to be fulfilled by a government agency. They are attempting to act as a fair arbiter of the issues while allowing stakeholders to make their own conclusions with unbiased data. One of the early conclusions of this effort is that a large percentage of the fecal coliform contamination derives from many sources in the upper- and mid-basin area. This finding runs counter to some expectations that combined sewer overflows in the lower, urbanized basin area would dominate the loading of fecal coliform. The CRWA and the regulatory agencies may conclude, therefore, that the large expenditures necessary to control combined sewer overflows in the lower basin would not be effective in achieving compliance with water quality standards. Rather, the control of nonpoint sources is likely to be more important. For this reason, the CRWA is focusing its outreach on local authorities that regulate development, household wastewater disposal, and urban runoff.

Table 2

Factors Affecting Permitting under the Watershed Approach

- Pollutant Concentration in Wastewater
- Rate of Wastewater Discharge
- Rate of Receiving Water Flow under Critical Conditions
- Pollutants in Receiving Water Sediments
- Rate of Pollutant Loading from Soil Erosion/Sedimentation
- Rate of Pollutant Decay/Settling/Volatilization

While this effort is still relatively new, it illustrates the power of the watershed approach. Careful evaluation of the situation indicates that the most obvious source of the problem, urban CSOs, are not, in fact, dominating the loading. Instead, more diffuse sources under local control are the apparent culprit. Importantly, an active citizen group is empowered to provide information and make recommendations to local authorities to effect change. By reaching out to the public, the citizens and agencies can more easily shape a solution to the problem. It is not clear that an agency acting alone and demanding change would be as likely to succeed.

Case 2: Pollutant Trading in North Carolina Watersheds. Nutrient loading to the Nuese and Tar-Pemlico watersheds in North Carolina has led to significant water quality impacts. The North Carolina environmental agency determined that the loadings to the watershed derive from both point sources (such as municipal treatment works) and nonpoint sources (e.g., animal wastes). Following the development of a TMDL for each system, the state established a program that effectively allows pollutant trading between the regulated entity, the dischargers, and an unregulated one, the nonpoint sources. The state sets targets for effluent nutrient concentrations for certain major NPDES-registered dischargers. If the discharger cannot meet those targets, the discharger pays into a state-administered fund to be used for the control of nutrients from nonpoint sources. The amount of the payment is proportional to the degree of noncompliance. This is a promising program that illustrates the importance of creativity in developing a management system in which the discharger gains flexibility, yet the agency retains requisite authority to further water quality goals. Of course, it is likely that the point sources will bear a heavier burden than the nonpoint sources but they may achieve "compliance" at a lower cost than in the absence of trading.

Case 3: Pollutant Trading of Toxic Metal in California. Copper loading from point sources and nonpoint sources to south San Francisco Bay has led to noncompliance with the water quality criteria. The Regional Water Quality Control Board oversaw the permitting of point sources. Following an inventory of copper sources and development of a TMDL, the Board found that copper loading to the basin should be reduced by 950 pounds per year. The major point sources were already well controlled with respect to copper. The various basin stakeholders (e.g., the POTWs, the municipalities, and environmental groups) and the Board concluded that control of nonpoint sources (notably sediment transport in stormwater) was likely to be the most cost-effective solution to the problem. Other, less obvious controls (e.g., curtailment of copper sulfate application for aquatic weed control and removal of copper from automobile brake pads) were also investigated. The resulting agreements on copper control measures were to be incorporated into a basin plan and the NPDES permits of the major point source dischargers.

Despite the planned trading of copper loading from the nonpoint to point sources, the major wastewater dischargers were still dissatisfied with their effluent limits. They appealed the basin plan to the State Water Quality Control Board, which overturned the plan. They based their challenge on the applicability of the water quality criterion as well as on the technical basis of the TMDL. This case study highlights the technical and regulatory complexity of the TMDL process and the high stakes involved in water quality management. Despite the failure of the basin management plan for copper, the major municipal wastewater dischargers have reduced their copper loading by 50 percent through better management of indirect dischargers and optimization of their treatment processes. Thus, increased awareness of the problem led to substantial water quality gains.

Case 4: Washington State Department of Ecology (DOE) Implements TMDLs. The State of Washington reorganized its wastewater permitting functions around watersheds, by synchronizing permits and by establishing schedules for basin investigations and modeling and evaluation. DOE has developed TMDLs for a variety of pollutants including nutrients and toxics. The TMDL process led to the use of innovative methods for addressing some of the more difficult problems facing the watershed. For example, in some cases, development of a conservative water quality model has eliminated the requirement that an explicit reserve for uncertainty be included in the development of a TMDL. Thus, the reserve is implicit in the TMDL and the full, modeled TMDL can be distributed among the sources.

Washington DOE has an interesting approach to pollutant trading. Rather than organizing explicit trades, DOE modeled its watershed management on the Clean Lakes Program which presents the costs and benefits of a number of management schemes to the stakeholders and reaches a consensus on the best one. This approach is more likely to result in buy-in on the part of the regulated parties and has the potential to lead to cost-sharing.

In summary, while the watershed approach to water quality management has significant technical and economic advantages, it also involves substantially increasing the scope and complexity of water quality management. The approach is driven in large part by CWA requirements that waters in noncompliance with water quality standards be brought into compliance through a budget and allocation of all contaminant loadings. Unfortunately, the control of nonpoint sources of pollution is not easy because such loadings are hard to quantify, agencies often have little or no authority over them, and control measures may be extremely expensive. Implementation of the watershed approach will result in a substantial improvement in water quality only if the nonpoint sources are appropriately involved. Undue emphasis on point sources is likely to result, in many cases, in significant expenditures without substantial improvements in water quality. In any case, improvements in water quality will only occur with the implementation of a more complex and comprehensive water policy approach as well as more focused expenditures.

Despite these problems, rapid progress is occurring in the implementation of the watershed protection approach. Most notably, regulatory agencies are reorganizing the permitting process and themselves around watersheds, thus leading to greater agency efficiency and better stakeholder awareness of remaining water quality problems. Although it will take time to implement fully and require innovative regulatory decisionmaking, the promise of the watershed approach is cost-effective control of remaining pollutant sources.

COPY 1

Procedural Justice in Fishery Resource Allocations

By Cheryl Perusse Daigle, David K. Loomis, and Robert B. Ditton

ABSTRACT

Demands on scarce fishery resources have resulted in the need for allocation decisions. These decisions often entail choosing among various groups; some receive the resources they desire, others do not. Dissatisfaction with such allocation decisions and procedures is problematic for allocators, recipients, and nonrecipients. Thus, allocators should develop decision-making processes that minimize or prevent conflict yet continue to allocate resources wisely. Research on *distributive justice*, defined as "the fairness of the actual distribution of resources," provides insight into how those affected by proposed allocations are likely to react. A second approach is *procedural justice*, or "the fairness of the decision-making process that leads to a distribution of resources." An understanding of procedural justice can help resource managers determine whether perceptions of fairness or satisfaction arise from the final allocation decision, the manner in which a decision was made, or a combination of the two. This paper introduces the concept of procedural justice as it relates to fishery resource decision-making and management, describes its potential for understanding what causes or increases dissatisfaction with allocation decisions, and suggests procedures to minimize or prevent conflict. A case study involving sport-fishery management in East Matagorda Bay, Texas, is analyzed from a procedural justice perspective.

Because of demands on increasingly scarce fishery resources, allocation decisions are required. Often these decisions entail choosing among various groups; some will obtain the resources they desire, some will not. Conflicts caused by dissatisfaction regarding allocation decisions and procedures cause problems for allocators, recipients, and nonrecipients, and time and money spent on conflict resolution efforts can be costly. Thus, allocators should develop decision-making processes that minimize or prevent conflict yet continue to allocate resources wisely.

Recent resource allocation research has taken a human dimensions perspective to better understand why conflicts occur. In particular, research has focused on the fairness of allocation decision making. Research on *distributive justice*, defined as 'the fairness of the actual distribution of resources' (Loomis and Ditton 1993), shows potential in predicting the likely reaction of those affected by proposed allocations. Also, research on distributive justice is useful for understanding the behavior of recipients and nonrecipients after an allocation decision has been made (Ritter 1991; Loomis and Ditton 1993).

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Another approach for understanding fairness issues is *procedural justice*, or "the fairness of the decision-making process that leads to a distribution of resources" (Folger et al. 1983). Concepts of procedural justice can help determine whether perceptions of fairness or satisfaction arise from the final decision, the manner in which a decision was made, or a combination of the two.

Little attention has been given to procedures used to allocate natural resources and the reaction of affected groups to the actual distribution of resources as well as to the procedures that led to the distribution. Previous research in organizational and court settings has application value toward solving problems in the area of natural resource allocations.

The purpose of this paper is to introduce the concept of procedural justice as it relates to fishery resource decision making and management, suggest its potential for understanding what causes or increases dissatisfaction with allocation decisions, and suggest procedures that can minimize or prevent conflict. Finally, we analyze from a procedural justice perspective a case study involving sport-fishery management in East Matagorda Bay, Texas, reported earlier (Matlock et al. 1988; Ritter 1991; Loomis and Ditton 1993).

Procedural Justice

In contrast with distributive justice, which deals with the fairness of a distribution of resources, procedural justice deals with the fairness of the mechanisms, structures, and processes that lead to the distribution (Folger et al. 1983). Although distributive and procedural justice are related and influence each other, individuals perceive them to be distinct when reacting to allocation decisions (Thibaut and Walker 1975; Leventhal et al. 1980). Distributive and procedural justice are independent to the extent that an unfair procedure may produce a fair outcome, or a fair procedure may result in an unfair outcome (Folger 1977). However, certain aspects of the procedures used may influence perception of the distribution and vice versa. Whereas early work in this field suggested a positive relationship between distributive and procedural justice, subsequent efforts have demonstrated that procedural justice is important in its own right (Tyler 1988). Today, the broad concept of procedural justice is composed of several developing models. Two independent approaches to procedural justice provide a foundation for current knowledge: Leventhal's (1980) expansion of his justice judgment model and Thibaut's and Walker's (1975) control theory of procedural justice.

Some Basics of Procedural Justice

To judge the fairness of an allocation process, Leventhal (1980) suggested that individuals form a cognitive map of the procedural components of the process that shapes their evaluation of procedural fairness. Leventhal proposed seven categories of procedural components; these may be evaluated individually or in combination by those affected by an allocation. They include (1) the selection of decision makers; (2) the setting of ground rules concerning the availability of information about an allocation and how to obtain it; (3) the way information is gathered to evaluate the potential recipients; (4) the decision-making structure; (5) the appeals process; (6) the safeguards that exist to monitor the integrity of decision makers; and (7) the change mechanisms available if existing procedures fail (Leventhal 1980).

An individual may then use one or more of six procedural justice rules to evaluate each component. A *justice rule* is "an individual's belief that a distribution of outcomes, or procedure for distributing outcomes, is fair and appropriate when it satisfies certain criteria" (Leventhal 1980:30).

(1) *Consistency rule*—The process is perceived to be consistent across persons and through time ("equality of opportunity").
(2) *Bias-suppression rule*—The allocator's personal self-interest or blind allegiance to narrow preconceptions is suppressed at all times.
(3) *Accuracy rule*—The information used in the decision-making process is believed to be accurate.
(4) *Correctability rule*—The potential exists for modification or reversal of decisions throughout the process.
(5) *Representativeness rule*—The opportunity to voice opinions or concerns is open to all individuals or groups affected by the decision.
(6) *Ethicality rule*—The procedures used are consistent with the individual's or group's moral and ethical values.

Thibaut and Walker (1975) approached the concept of procedural justice from a narrower perspective. They developed a model to explain procedural preferences and understand how people determine procedural fairness within the context of dispute resolution. Two types of control over resolution of a dispute were distinguished: decision control and process control. *Decision control* is the individual's control over actual decisions made (v third-party control), while *process control* refers to an individual's control over the presentation of "facts" (or the opportunity to state one's case) to a third party. Thibaut and Walker (1975) suggest that the key characteristic in forming an individual's perception of procedural justice is the distribution of control between the individual and the decision maker (Lind and Tyler 1988).

Providing individuals with an opportunity to voice their opinions and concerns regarding allocations leads them to believe they have been treated fairly...and increases satisfaction with decision makers.

Individuals are thought to prefer to maximize their control over decisions by directly participating in the decision-making process (decision control) (Thibaut and Walker 1975). If unable to do so, they seek to *indirectly* influence the decision by maximizing control over the process that leads to a decision. This concept of procedural justice was termed the *instrumental perspective* when subsequent research led to speculation that control was not always an important factor when individuals were considering the fairness of procedures used in an allocation (Tyler et al. 1985; Tyler 1988). Alternately, the noninstrumental or *value-expressive effect* claims that "people value having the chance to state their case, irrespective of whether their statement influences the decisions of the authorities" (Tyler 1987). This is in contrast to Thibaut's and Walker's perspective in which the emphasis is on having some type of control over the decision (Lind and Tyler 1988; Tyler 1988).

The value-expressive effect is more thoroughly explored as the concept of *voice*, or "having some form of participation in decision making by expressing one's own opinion" (Folger 1977:109). Providing individuals with an opportunity to voice their opinions and concerns regarding allocations leads them to believe they have been treated more fairly whether or not their input influences the decision (Tyler 1987; Lind et al. 1990). This perception also increases satisfaction with decision makers, suggesting that public support for decisions may be increased by paying more attention to efforts that allow public input. Fairness is perceived to be greater when the opportunity to voice one's concerns is combined with the possibility of influencing the decision (Lind et al. 1990).

However, increased perceptions of fairness are not due solely to the opportunity to voice an opinion. Individuals affected by a decision must believe that their views are being considered by decision makers and that decision makers have made an effort to be fair. Prior expectations concerning fair treatment influence how an individual behaves when given the opportunity to speak. If individuals believe previous experience with decision makers has led to fair decisions, they are more likely to respond favorably to a situation that allows participation in the process but little control over the decision (Tyler 1987).

> **...an interest in maintaining harmony and a concern for all involved increases the importance of procedural justice**

These early approaches to procedural justice have limitations. Leventhal's justice rules have been criticized as being too broad (Tyler 1988). In particular, some of Leventhal's rules involve multiple criteria that have different effects on an individual's perception of procedural fairness (Tyler 1988). For example, Leventhal's representativeness rule is ambiguous; it could be better explained using the concepts of process control and voice.

Thibaut's and Walker's approach focuses on representation within the narrow context of dispute resolution. Disputes are only one context within which individuals or groups must deal with decision makers. In this article emphasis is given to allocation as a proactive distribution decision rather than as a dispute resolution, which would be a reactive attempt to resolve an existing distribution perceived to be unfair. Integrating these perspectives enhances the potential to generalize procedural justice to nondispute or allocation settings.

The Importance of Procedural Justice Criteria

An individual's perception and behavior are affected by many motivational concerns—fairness is only one. Whether or not an individual views procedural justice as important depends on the circumstances (Barrett-Howard and Tyler 1986). In a given situation, the perceived importance of fairness may be influenced by the social role of the individual, the importance of other goals, whether or not a violation may have occurred, the stability of the social system, and the existence of quasi-fair behavior (Leventhal 1980; Leventhal et al. 1980). *Quasi-fair behavior* is defined as "behavior that appears to arise out of concern for fairness but is actually used to manipulate or deceive others" (Leventhal 1980; Leventhal et al. 1980). Also, an interest in maintaining harmony and a concern for all involved increases the importance of procedural justice (Barrett-Howard and Tyler 1986).

should be "pseudo"

Tyler (1988) developed seven aspects of procedural justice that contribute independently to assessments of fair process: (1) the perceived effort of the decision makers to be fair, (2) their perceived honesty, (3) the consistency of their behavior in terms of ethical standards of the individual, (4) opportunities of representation, (5) the quality of the decisions made, (6) opportunities to appeal decisions, and (7) possible bias by decision makers at any time during the decision-making process. Further, Tyler (1988) reported a strong correlation between criteria used to assess the fairness of a decision-making experience and those used to assess the fairness of the authorities involved.

Finally, the extent to which different criteria are used by different people or by people in different circumstances to assess whether procedures are fair plays a significant role. Tyler (1988) found that the circumstances of allocation strongly influence how individuals define procedural justice. For example, when the outcome was favorable, individuals emphasized the perceived honesty of decision makers; when the outcome was negative, individuals were more concerned with decision makers' perceived efforts to be fair and their consistency with past similar situations. In cases involving a dispute, the most important determinant of procedural justice appears to be the level of control over the outcome or decision-making process (Thibaut and Walker 1975). Since the meaning of procedural justice changes with each circumstance, any universally fair procedures are unlikely to exist; procedures are more or less appropriate as the circumstances of an allocation change (Barrett-Howard and Tyler 1986; Tyler 1988).

The Group-Value Model of Procedural Justice

The group-value model of procedural justice developed by Lind and Tyler (1988) can be readily applied to fishery resource allocations. It incorporates previously defined procedural justice criteria, an understanding of individuals' perceptions of their relationships with decision makers, and an understanding of how this affects their interpretation of decision-making procedures. Furthermore, this model assumes that people are concerned about a long-term social relationship with decision makers and do not view this relationship as a "one-shot deal" (Tyler 1989). *Group membership*, defined here as "an individual or group of individuals that belong to a larger group," is important because it provides a source of self-validation via feedback about the appropriateness of attitudes and values. It also provides emotional support and a sense of belonging and is an important source of material resources (Tyler 1989). This model highlights three issues that influence procedural fairness judgments: the neutrality of the decision-making procedure; trust in the third party; and evidence of social standing (Lind and Tyler 1988; Tyler 1989).

The issue of *neutrality* incorporates four of Leventhal's (1980) six criteria—consistency across people and through time, bias-suppression, accuracy, and correctability. *Trust* involves the belief that the decision makers want to treat people in a fair and reasonable way. *Social standing* refers to the perception that if individuals are treated unfairly, they are likely to interpret that as evidence that the decision makers regard them as having low standing within the group. Conversely, if they are shown fair and respectful treatment, they will interpret it as meaning they have high status within the group (Tyler 1989).

Trust and standing within the group have been shown to be important in shaping people's judgments about whether they have received procedural justice and how they should react to their experience (Tyler 1989). Both appear to be more important than either judgments of control or favorability of outcomes. However, when the issue of concern is outcome fairness, people place more weight on the neutrality of the decision-making procedures.

Group-value issues are usually more important among individuals (or groups) with a greater commitment to legal authorities (Tyler 1989). People high in group loyalty define procedural justice in terms of the neutrality of the decision-making process; in contrast, people who show little group support are more concerned about the favorability of the outcome (Tyler 1989). Possibly, people or groups who view group membership as important because it is an important source of material resources, may out of necessity show a greater commitment to legal authorities. Research suggests these people in particular would show more concern about the group-value issues of neutrality, trust, and social standing than they would for outcome favorability (Tyler 1989).

In summary, the above review shows that early research examined procedural justice in terms of the criteria individuals use to evaluate decision-making procedures; the individuals preference to have control over either the decision, the process, or both; and the importance of participating in decision making through expressing one's own opinion. The group-value model integrates key aspects of the early research on procedural justice and is most applicable to analyses of people's response to natural resource allocations.

Case Study: What Was Unfair about Fishery Regulations in East Matagorda Bay?

An analysis of a case study involving a fishery resource allocation conflict provides an example of how procedural justice concepts can be used. In January 1984, the Texas Parks and Wildlife Commission (TPWC) adopted emergency regulations in response to a major fish kill along the Texas coastline in December 1983 (Ritter 1991). Several days of severely low temperatures killed approximately 567,000 spotted seatrout (*Cynoscion nebulosus*) and 90,000 red drum (*Sciaenops ocellatus*), both favored species of Texas anglers (Matlock et al. 1988; Ritter 1991). These regulations reduced red drum and spotted seatrout daily bag and possession limits, increased minimum size limits, and prohibited use of various nets and trotlines coastwide. The intent of these regulations was to protect the smaller fish for future spawning to replenish fish stocks.

Retention of the two species was prohibited in East Matagorda Bay alone so it could be used as a control area to assess managers' response to the freeze. East Matagorda Bay was selected from all other bays as a sanctuary because TPWC believed it was a small bay with limited access, low fishing pressure, and smaller economic impact than other local bays (Matlock et al. 1988). The TPWC would have considered a complete ban on recreational fishing coastwide for a period, if necessary, but agency staff saw no need for such drastic action (TPWC 1984).

The TPWC is delegated emergency powers to promulgate regulations without prior notice to the public or public hearings if there is imminent danger of depletion of a species or natural resource (V.T.C.A. Parks and Wildlife Code 61.104). Emergency regulations are effective for a period not to exceed 120 days and may be renewed once for up to 60 days by the agency's executive director. At that point they may be proposed and adopted on a permanent basis, following normal agency decision-making procedures.

Initially, the emergency regulations were regarded as a temporary means of dealing with the fish kill. However,

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immediately following their implementation on 12 January 1994, TPWC proposed that they be adopted as a part of the statewide hunting and fishing regulations. Since no one knew the full extent of the fish kill, and since the agency was continuing its assessment efforts, the move to make the emergency rules permanent was done to acquire the option if conditions warranted (Ritter 1991). If the regulations had not been proposed as permanent rules, the TPWC would have had no further recourse to protect fish stocks if conditions necessitated it when the emergency rules expired. Certain procedures and deadlines had to be met to make the emergency rules permanent (TPWC 1980), which is why these efforts began almost immediately after adoption of emergency rules. Accordingly, the agency urged anglers who fished in the bay, local residents, and all other interested parties to submit comments to the agency about the closure and to participate in a statewide series of public hearings regarding new fishing regulations that were concluding February 1994. Statewide regulations are considered at the same time each year.

The emergency regulations were generally well accepted coastwide. However, opposition to the prohibition of retention of red drum and spotted seatrout in East Matagorda Bay on a permanent basis was considerable, as demonstrated at a public hearing in Matagorda County 6 February 1984. Although many local residents claimed they did not oppose the 120-day emergency closure, they opposed its extension (even if for only 60 days) because of the impact it would have on recreational fishing and the local economy.

The TPWC met 30 March 1994 (78 days into the 120-day emergency period) to discuss proposed changes in statewide hunting and fishing regulations. According to staff, there was no longer a need to prohibit retention of red drum and spotted seatrout in the bay so prohibition should be discontinued. Accordingly, and with considerable pressure to do so, the TPWC voted to repeal this emergency rule. Because of procedural problems associated with public notification, discontinuing the emergency rule was not possible immediately. The measure was to be enacted as quickly as possible but before May 1984. Interestingly, the TPWC adopted all of the other emergency regulations for coastwide application on a permanent basis effective 2 May 1984 (Ritter 1991).

Analysis

Previously, the behavior of area residents was evaluated in terms of the concept of distributive justice (Ritter 1991; Loomis and Ditton 1993) and, in particular, their feelings of relative deprivation:

> "...East Matagorda Bay anglers (1) wanted the opportunity to retain the fish they caught, (2) felt they deserved to be able to retain the fish they caught, (3) believed it possible to retain the fish they caught, and (4) lacked the sense they were responsible for not being allowed to retain the fish they caught. Therefore, we would predict they would have felt deprived relative to anglers who fished other bays (who were allowed retention of fish)" (Loomis and Ditton 1993:17)."

Extending this analysis to recognize the importance of procedural justice allows for a broader understanding of the rationale behind public opposition. The group-value model of procedural justice is relevant because of its emphasis on neutrality and trust, and its recognition of the importance of group membership and the related tendency for people to compare their treatment in an allocative process with that of other individuals or groups affected by the decision. In this case, *group membership* refers to the group of individuals or groups interested in the fishery resource, i.e., concerned residents, anglers, and business owners. Whereas the East Matagorda Bay area is one part of the coastal bay system, the group of individuals representing this bay would be considered part of a larger group of individuals representing respective bay systems. The TPWC is the decision maker allocating the resource between bay systems.

With this model people are assumed to be concerned about the long-term social relationship with the decision-making body and to not view this relationship as a one-shot deal (Lind and Tyler 1988). The residents of the East Matagorda Bay area who are affected by fishery resource decisions have little choice but to maintain a relationship with the resource allocator (TPWC) if they are to maintain continued access to the resource. In other words, they cannot make up their own rules and regulations regarding the resource; they must deal with the allocating agency if they want to change the way the resource is managed or allocated. The relationship can be one of support or opposition—either way, a relationship must exist.

Trust in the decision maker strongly influences individuals' judgments about whether they received procedural justice and their reactions to their experience.

The three issues of concern in the group-value model relate directly to concerns raised by East Matagorda Bay residents opposing TPWC's proposal to permanently close the bay to retention of spotted seatrout and red drum. These concerns included the following:

(1) Residents were convinced the choice of the bay as a sanctuary was a politically based decision and did not understand the rationale behind the decision.
(2) The decision lacked scientific justification and was based on an inadequate assessment of fishing pressure on the bay and an inadequate economic assessment.
(3) The restrictions were unnecessary because the kill was not as severe as reported.
(4) The closure of only East Matagorda Bay was unfair and discriminatory without basis (Ritter 1991).

Trust in the decision maker and the perceived neutrality of decision making are reflected prominently in these local concerns. Trust in the decision maker strongly influences individuals' judgments about whether they received procedural justice and their reactions to their experience. Those opposed to the proposal did not trust either the data provided by the TPWD or the commission's subsequent interpretation of the data (Ritter 1991). This lack of trust in the agency allocating the resource contributed greatly to the subsequent failure of individuals to accept the proposed regulations as permanent.

Accuracy of information is a key component of the issue of neutrality (residents did not perceive either the economic data or the fish kill data to be accurate in terms of consistency across people), and in the past, TPWC was not consistent in its proposal across groups (the agency elected to prohibit retention only in East Matagorda Bay). Locals believed TPWC had no basis for discriminating against the bay.

Residents of East Matagorda Bay believed they were treated unfairly by TPWC, and this perceived injustice provided them with evidence as to their standing among other coastal areas statewide. This feeling of low status compared to other areas probably added to the strength of their opposition. The process by which the emergency regulations were to become permanent was an issue of concern because the normal TPWD decision-making procedures were bypassed due to time constraints, and initially the procedures did not involve public participation (Ritter 1991). This led some residents to believe TPWD was intentionally trying to make the regulation permanent without allowing ample time for them to respond to the proposal (Ritter 1991). The influence of this perception on their subsequent reaction to the proposal cannot be underestimated. Providing people with an opportunity to voice their opinions and concerns regarding an allocation lets people think they have been treated fairly and increases satisfaction with decision makers. Public support for the proposal may have been more widespread had residents perceived themselves as more active participants in the decision to propose permanent regulations. Sensitivity to issues of public perceptions of fair process may have increased the probabilities of implementing regulations that TPWD believed were appropriate and biologically sound.

Implications for Fisheries Management

Procedural justice involves an awareness and understanding of complex social and psychological processes that occur within individuals and groups. This has certain implications for fisheries management.

(1) Fisheries managers often may be confused about what causes conflict; only recently have they begun to take advantage of the growing body of research emphasizing the social dimensions of natural resource management.

(2) Increased attention to procedural justice in natural resources decision making would require that managers better understand the behavior of groups, both recipients and nonrecipients, before and after decisions are made.

(3) Fisheries managers also need to be able to predict the response of public groups affected by resource decisions before those decisions are made. This could save agencies considerable time, money, and effort.

(4) Finally, fisheries managers must begin to view their decision-making process and procedures from a fairness perspective, one that includes the perceptions of recipients and nonrecipients of resource allocations.

The potential for continued misuse of fishery resources is high when agencies responsible for their protection lack the awareness and knowledge to handle the social conflicts that arise as a result of agency decisions. Political pressure often overrides ecologically sound management decisions; to better handle the politics, an understanding of the social psychology of the affected parties is extremely important.

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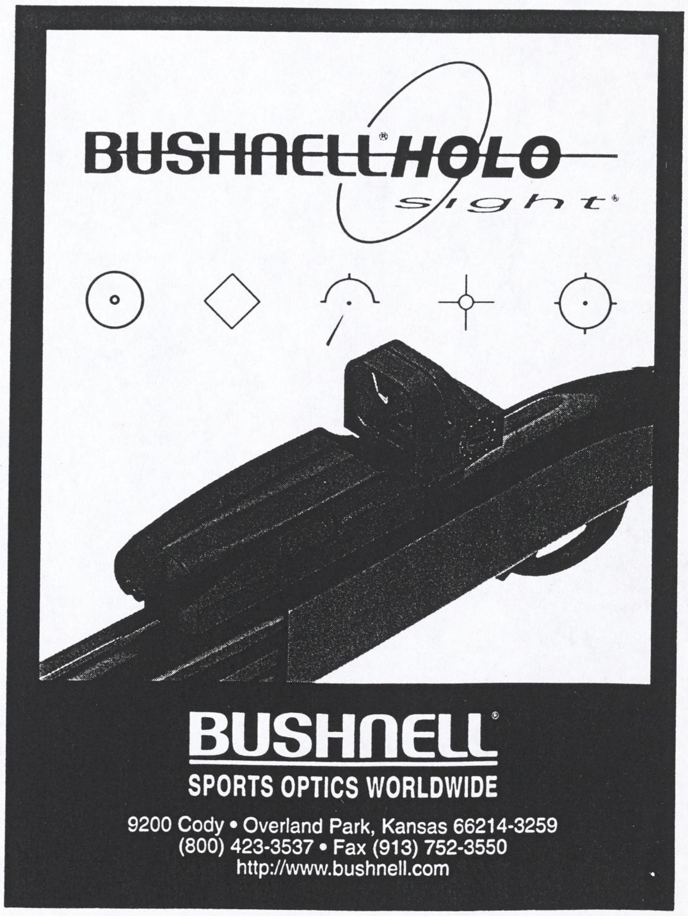

Minimum Flow is a Myth

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During the warmwater stream symposium in 1980, when discussing low flow as a limiting factor in warmwater streams, I warned fisheries management personnel that the concept of a single minimum or base flow for fishery habitat maintenance that has evolved in the western region of the United States could very well become a real threat to low gradient, eastern, warmwater stream fisheries (Stalnaker 1981). The minimum flow concept rose from western water law as a mechanism to either reserve an amount of water from future appropriations or as a means of granting an instream water right for fishery purposes. This led to the myth that a consistent methodology could be used to establish a single minimum discharge value for any given stream. Experience has shown that as water becomes fully appropriated to upstream use or storage, the minimum flow, if not frequently violated in time, tends to become the average flow condition. Too often the minimum becomes the objective rather than the means to achieve some riverine fishery or recreation management goal. Such persistent low flows are not necessarily desirable from the water management perspective, being inflexible in the face of competitive uses or during unusual water supply conditions (e.g., drought), and certainly do not meet all the desired environmental needs. This difficulty with minimum flows arises in part because all the instream uses for which flows may be needed are not identified. Most often overlooked are necessary periodic high flows that move bedload, flush sediments, rejuvenate the floodplain, and generally maintain the structural characteristics of a stream channel, which should be maintained in dynamic equilibrium with its watershed (Stalnaker 1979).

A common misconception among water management personnel and consumers is that inclusion of all the identifiable instream uses of water in an instream flow requirement will dictate an additive treatment of their respective needs. This, it is further assumed, will result in total allocation of the stream flow to instream uses. Contrary to this view, a considerable degree of compatibility exists among many instream uses and downstream delivery requirements for offstream or consumptive uses. However, in order to deal with these compatible uses, the instream flow advocate and the water resource manager must be aware of both the timing and the magnitude of all the demands being placed on the stream system. Such a common understanding, which should lead to the identification of instream flow requirements, will protect all complimentary uses as well as meet downstream delivery requirements.

It is evident from reviewing the literature and from the discussions during this workshop that many methods for evaluating instream flow needs have evolved since the 1960's. I prefer to categorize such methods as "standard setting" or "incremental." Standard setting methodologies, on one hand, refer to those measurements and interpretive techniques designed to generate a flow value (or values) intended to maintain the fishery or recreational use at some acceptable level (usually dictated by policy). Incremental methodologies, on the other hand, are organized and repeatable processes by which (1) a fishery habitat–stream flow relation and the hydrology of the stream are transformed into a baseline habitat time series, (2) proposed water management alternatives are simulated and compared with the baseline, and (3) project operating rules are negotiated.

Trihey and Stalnaker (1985) suggested that a hierarchical approach to hydro licensing and relicensing be followed that in essence takes advantage of both the standard setting and incremental approaches. A three-tiered hierarchy was suggested including reconnaissance, feasibility, and operational or design studies for evaluating hydro projects. It is important to recognize that such licensing is

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generally a multiyear process. Adopting the suggested hierarchical approach can lead to greater understanding among the resource agencies, the applicant, and the general public, leading to negotiated conditions for the license. Specifically, the reconnaissance study identifies the stream segments of potential impact, the project location configuration, and possible operating scheme. With- and without-project hydrologic conditions are compared to determine whether the project seems to be "benign" and compatible with resource agency policies. In other words, there is little change in the flow pattern below the project. In the feasibility study, the use of a previously set standard can be quite advantageous. At this level of analysis, comparison is made between the projected stream flow conditions and the stream flow maintenance standard to identify major issues and periods of incompatibility. Standard setting methods (such as the New England Flow Method and the Arkansas and North Carolina methods) were discussed during this workshop; they and the optimum flow proposed for western Virginia are excellent examples by which one can screen for hydro projects that seem to be incompatible with agency policy and environmental protection goals. When it becomes obvious that project operations and the maintenance of stream flow standards are incompatible, impacts need to be quantified and mitigation measures agreed on. Then much more detailed operational level studies are appropriate. Only during this third study phase do the incremental methods become useful and, in fact, necessary.

The majority of States now recognize instream flows and have identified procedures for incorporating such uses in water planning (Reiser et al. 1989). Adoption of a standard setting approach by the State Water Resources and Fisheries Management agencies greatly facilitates identification of incompatible water development projects during feasibility studies. Stream flow assessment methods, such as the Instream Flow Incremental Methodology used by the U.S. Fish and Wildlife Service, have consequently evolved to become environmental assessment techniques and are used for evaluating the effects of proposed reservoir construction, water diversions, or hydroelectric operations on downstream fish habitats. Quite often such impact assessments become a matter of comparison among several possible, but not always measurable, water management schemes, leading to the necessity of simulation modeling for making these comparisons. Only the physical-chemical aspects of the habitat are evaluated, and comparisons are judged on the potential habitat limitations that may result from a proposed change in the way stream flows are controlled and routed through stream segments. It is important to realize that minimum flows, optimal flows, and even stream flow standards are not impact assessment tools. When it comes to relicensing of hydroelectric projects, the questions really are focused on the effects that may result from a change in project operations. Minimum flow has no logical argument in such an institutional process and, in fact, as hydro projects go to increased peaking operations (involving daily and hourly rapid fluctuations in the tailwater releases), it is often the high flows that are of more concern from a biological standpoint than the low or minimum flows.

The challenge now before us is to progress beyond the minimum flow and even habitat impact assessment and to focus on scientific principles in understanding riverine systems. Management biologists must get involved with water management in riverine environments. By definition, management is a designed and directed change in a system. The improvement of basic understanding of ecology of our stream systems, coupled with the use of engineering tools and simulation modeling, provides an opportunity for fisheries to be enhanced downstream of the many hydroelectric projects coming up for relicensing in the 1990's. This will occur only if fishery managers and natural resource agencies do the designing and directing of the change in the operating systems, working hand-in-hand with the hydro project applicants and the Federal Energy Regulatory Commission.

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COPY 1

a public employee is fired for uttering speech on a matter of public concern that is not unduly disruptive of the operations of the relevant agency. The violation does not vanish merely because the firing was based upon a reasonable mistake about what the employee said.[5] A First Amendment claimant need not allege bad faith; the controlling question is not the regularity of the agency's investigative procedures, or the purity of its motives, but whether the employee's freedom of speech has been "abridged."

The risk that a jury may ultimately view the facts differently from even a conscientious employer, is not, as the plurality would have it, a needless fetter on public employers' ability to discharge their duties. It is the normal means by which our legal system protects legal rights and encourages those in authority to act with care. Here, for example, attention to "conclusions a jury would later draw," *ante*, at 13, about the content of Churchill's speech might have caused petitioners to talk to Churchill about what she said before deciding to fire her. There is nothing unfair or onerous about putting the risk of error on an employer in these circumstances.[6]

Government agencies are often the site of sharp differences over a wide range of important public issues. In offices where the First Amendment commands respect for candid deliberation and individual opinion, such disagreements are both inevitable and desirable. When those who work together disagree, reports of speech are often skewed, and supervisors are apt to misconstrue even accurate reports. The plurality, observing that managers "can spend only so much of their time on any one employment decision," *ante*, at 17, adopts a rule that invites discipline, rather than further discussion, when such disputes arise. That rule is unwise, for deliberation within the government, like deliberation about it, is an essential part of our "profound national commitment" to the freedom of speech. Cf. *New York Times*, 376 U. S., at 270. A proper regard for that principle requires that, before firing a public employee for her speech, management get its facts straight.

I would affirm the judgment of the Court of Appeals.

his exercise of First and Fourteenth Amendment rights"); *ibid.* ("[A] teacher's public criticism of his superiors on matters of public concern may be constitutionally protected and may, therefore, be an impermissible basis for termination of his employment."); *Pickering*, 391 U. S., at 574 ("In sum, . . . a teacher's exercise of his right to speak on issues of public importance may not furnish the basis for his dismissal from public employment."). Precedent certainly does not command JUSTICE SCALIA's approach, and nothing in the First Amendment recommends a rule that makes ignorance or mistake a complete defense for a discharge based on fully protected speech. JUSTICE O'CONNOR appropriately rejects that position, at least for those instances in which the employer unreasonably believes an incorrect report concerning speech that was in fact protected and disciplines an employee based upon that misunderstanding. I, of course, agree with JUSTICE O'CONNOR that discipline in such circumstances violates the First Amendment.

[5] The reasonableness of the public employer's mistake would, of course, bear on whether that employer should be liable for damages. See *Butz* v. *Economou*, 438 U. S. 478, 507 (1978) ("Federal officials will not be liable for mere mistakes in judgment, whether the mistake is one of fact or one of law"). It is wrong, however, to constrict the substantive reach of a public employee's right of free speech in response to such remedial considerations. See *ante*, at 14 (government employers who use reasonable procedures should be free to act "without fear [of] *liability*") (emphasis added).

[6] Because there is no dispute that Churchill was fired for the content of her speech, this case does not involve the problem of determining whether the public employee would have been terminated anyway for reasons unrelated to speech. See *Mount Healthy City Bd. of Ed.* v. *Doyle*, 429 U. S. 274 (1977).

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No. 92-1911

PUD NO. 1 OF JEFFERSON COUNTY AND CITY OF TACOMA, PETITIONERS *v.* WASHINGTON DEPARTMENT OF ECOLOGY ET AL.

ON WRIT OF CERTIORARI TO THE SUPREME COURT OF WASHINGTON

Syllabus

No. 92-1911. Argued February 23, 1994—Decided May 31, 1994

Section 303 of the Clean Water Act requires each State, subject to federal approval, to institute comprehensive standards establishing water quality goals for all intrastate waters, and requires that such standards "consist of the designated uses of the navigable waters involved and the water quality criteria for such waters based upon such uses." Under Environmental Protection Agency (EPA) regulations, the standards must also include an antidegradation policy to ensure that "[e]xisting instream water uses and the level of water quality necessary to protect [those] uses [are] maintained and protected." States are required by §401 of the Act to provide a water quality certification before a federal license or permit can be issued for any activity that may result in a discharge into intrastate navigable waters. As relevant here, the certification must "set forth any effluent limitations and other limitations . . . necessary to assure that any applicant" will comply with various provisions of the Act and "any other appropriate" state law requirement. §401(d). Under Washington's comprehensive water quality standards, characteristic uses of waters classified as Class AA include fish migration, rearing, and spawning. Petitioners, a city and a local utility district, want to build a hydroelectric project on the Dosewallips River, a Class AA water, which would reduce the water flow in the relevant part of the River to a minimal residual flow of between 65 and 155 cubic feet per second (cfs). In order to protect the River's fishery, respondent state environmental agency issued a §401 certification imposing, among other things, a minimum stream flow requirement of between 100 and 200 cfs. A state administrative appeals board ruled that the certification condition exceeded respondent's authority under state law, but the State Superior Court reversed. The State Supreme Court affirmed, holding that the antidegradation provisions of the State's water quality standards require the imposition of minimum stream flows, and that §401 authorized the stream flow condition and conferred on States power to consider all state action related to water quality in imposing conditions on §401 certificates.

Held: Washington's minimum stream flow requirement is a permissible condition of a §401 certification.

(a) A State may impose conditions on certifications insofar as necessary to enforce a designated use contained in the State's water quality standard. Petitioners' claim that the State may only impose water quality limitations specifically tied to a "discharge" is contradicted by §401(d)'s reference to an applicant's compliance, which allows a State to impose "other limitations" on a project. This view is consistent with EPA regulations providing that activities—not merely discharges—must comply with state water quality standards, a reasonable interpretation of §401 which is entitled to deference. State standards adopted pursuant to §303 are among the "other limitations" with which a State may ensure compliance through the §401 certification process. Although §303 is not specifically listed in §401(d), the statute allows States to impose limitations to ensure compliance with §301 of the Act, and §301 in turn incorporates §303 by reference. EPA's view supports this interpretation. Such limitations are also permitted by §401(d)'s reference to "any other appropriate" state law requirement.

(b) Washington's requirement is a limitation necessary to enforce the designated use of the River as a fish habitat. Petitioners err in asserting that §303 requires States to protect such uses solely through implementation of specific numerical "criteria." The section's language makes it plain that water quality standards contain two components and is most naturally read to require that a project be consistent with both: the designated use and the water quality criteria. EPA has not interpreted §303 to require the States to protect designated uses exclusively through enforcement of numerical criteria. Moreover, the Act permits enforcement of broad, narrative criteria based on, for example, "aesthetics." There is no anomaly in the State's reliance on both use designations and criteria to protect water quality. Rather, it is petitioners' reading that leads to an unreasonable interpretation of the Act, since specified criteria cannot reasonably be expected to anticipate all the water quality issues arising from every activity which can affect a State's hundreds of individual water bodies. Washington's requirement also is a proper application of the state and federal antidegradation regulations, as it ensures that an existing instream water use will be "maintained and protected."

(c) Petitioners' assertion that the Act is only concerned with water quality, not quantity, makes an artificial distinction, since a sufficient lowering of quantity could destroy all of a river's designated uses, and since the Act recognizes that reduced stream flow can constitute water pollution. Moreover, §§101(g) and 510(2) of the Act do not limit the scope of water pollution controls that may be imposed on users who have obtained, pursuant to state law, a water allocation. Those provisions preserve each State's authority to allocate water quantity as between users, but the §401 certification does not purport to determine petitioners' proprietary right to the River's water. In addition, the Court is unwilling to read implied limitations into §401 based on petitioners' claim that a conflict exists between the condition's imposition and the Federal Energy Regulatory Commission's authority to license hydroelectric projects under the Federal Power Act, since FERC has not yet acted on petitioners' license application and since §401's certification requirement also applies to other statutes and regulatory schemes.

121 Wash. 2d 179, 849 P. 2d 646, affirmed.

O'CONNOR, J., delivered the opinion of the Court, in which REHNQUIST, C. J., and BLACKMUN, STEVENS, KENNEDY, SOUTER, and GINSBURG, JJ., joined. STEVENS, J., filed a concurring opinion. THOMAS, J., filed a dissenting opinion, in which SCALIA, J., joined.

JUSTICE O'CONNOR delivered the opinion of the Court.

Petitioners, a city and a local utility district, want to build a hydroelectric project on the Dosewallips River in Washington State. We must decide whether respondent, the state environmental agency, properly conditioned a permit for the project on the maintenance of specific minimum stream flows to protect salmon and steelhead runs.

I

This case involves the complex statutory and regulatory scheme that governs our Nation's waters, a scheme which implicates both federal and state administrative responsibilities. The Federal Water Pollution Control Act, commonly known as the Clean Water Act, 86 Stat. 816, as amended, 33 U. S. C. §1251 *et seq.*, is a comprehensive water quality statute designed to "restore and maintain the chemical, physical, and biological integrity of the Nation's waters." §1251(a). The Act also seeks to attain "water quality which provides for the protection and propagation of fish, shellfish, and wildlife." §1251(a)(2).

To achieve these ambitious goals, the Clean Water Act establishes distinct roles for the Federal and State Governments. Under the Act, the Administrator of the Environmental Protection Agency is required, among other things, to establish and enforce technology-based limitations on individual discharges into the country's navigable waters from point sources. See §§1311, 1314. Section 303 of the Act also requires each State, subject to federal approval, to institute comprehensive water quality standards establishing water quality goals for all intrastate waters. §§1311(b)(1)(C), 1313. These state water quality standards provide "a supplementary basis . . . so that numerous point sources, despite individual compliance with effluent limitations, may be further regulated to prevent water quality from falling below acceptable levels." *EPA* v. *California ex rel. State Water Resources Control Bd.*, 426 U. S. 200, 205, n. 12 (1976).

A state water quality standard "shall consist of the designated uses of the navigable waters involved and the water quality criteria for such waters based upon such uses." 33 U. S. C. §1313(c)(2)(A). In setting standards, the State must comply with the following broad requirements:

> "Such standards shall be such as to protect the public health or welfare, enhance the quality of water and serve the purposes of this chapter. Such standards shall be established taking into consideration their use and value for public water supplies, propagation of fish and wildlife, recreational [and other purposes.]" *Ibid.*

See also §1251(a)(2).

A 1987 amendment to the Clean Water Act makes clear that §303 also contains an "antidegradation policy"—that is, a policy requiring that state standards be sufficient to maintain existing beneficial uses of navigable waters, preventing their further degradation. Specifically, the Act permits the revision of certain effluent limitations or water quality standards "only if such revision is subject to and consistent with the antidegradation policy established under this section." §1313(d)(4)(B). Accordingly, EPA's regulations implementing the Act require that state water quality standards include "a statewide antidegradation policy" to ensure that "[e]xisting instream water uses and the level of water quality necessary to protect the existing uses shall be maintained and protected." 40 CFR §131.12 (1992). At a minimum, state water quality standards must satisfy these conditions. The Act also allows States to impose more stringent water quality controls. See 33 U. S. C. §§1311(b)(1)(C), 1370. See also 40 CFR 131.4(a) ("As recognized by section 510 of the Clean Water Act [33 U. S. C. §1370], States may develop water quality standards more stringent than required by this regulation").

The State of Washington has adopted comprehensive water quality standards intended to regulate all of the State's navigable waters. See Washington Administrative Code (WAC) 173-201-010 to 173-201-120 (1990). The State created an inventory of all the State's waters, and divided the waters into five classes. 173-201-045. Each individual fresh surface water of the State is placed into one of these classes. 173-201-080. The Dosewallips River is classified AA, extraordinary. 173-201-080(32). The water quality standard for Class AA waters is set forth at 173-201-045(1). The standard identifies the designated uses of Class AA waters as well as the criteria applicable to such waters.[1]

In addition to these specific standards applicable to Class AA waters, the State has adopted a statewide antidegradation policy. That policy provides:

> "(a) Existing beneficial uses shall be maintained and protected and no further degradation which would interfere with or become injurious to existing beneficial uses will be allowed.
>
> "(b) No degradation will be allowed of waters lying in national parks, national recreation areas, national wildlife refuges, national scenic rivers, and other areas of national ecological importance.
>
> . . . . .
>
> "(f) In no case, will any degradation of water quality be allowed if this degradation interferes with or becomes injurious to existing water uses and causes long-term and irreparable harm to the environment. 173–201–035(8).

As required by the Act, EPA reviewed and approved the State's water quality standards. See 33 U. S. C. §1313(c)(3); 42 Fed. Reg. 56792 (1977). Upon approval by EPA, the state standard became "the water quality standard for the applicable waters of that State." 33 U. S. C. §1313(c)(3).

States are responsible for enforcing water quality standards on intrastate waters. 33 U. S. C. §1319(a). In addition to these primary enforcement responsibilities, §401 of the Act requires States to provide a water quality certification before a federal license or permit can be issued for activities that may result in any discharge into intrastate navigable waters. 33 U. S. C. §1341. Specifically, §401 requires an applicant for a federal license or permit to conduct any activity "which may result in any discharge into the navigable waters" to obtain from the state a certification "that any such discharge will comply with the applicable provisions of sections 1311, 1312, 1313, 1316, and 1317 of this title." 33 U. S. C. §1341(a). Section 401(d) further provides that "[a]ny certification . . . shall set forth any effluent limitations and other limitations, and monitoring requirements necessary to assure that any applicant . . . will comply with any applicable effluent limitations and other limitations, under section 1311 or 1312 of this title . . . and with any other appropriate requirement of State law set forth in such certification." 33 U. S. C. §1341(d). The limitations included in the certification become a condition on any Federal license. *Ibid.*[2]

II

Petitioners propose to build the Elkhorn Hydroelectric Project on the Dosewallips River. If constructed as presently planned, the facility would be located just outside the Olympic National Park on federally owned land within the Olympic National Forest. The project would divert water from a 1.2–mile reach of the River (the bypass reach), run the water through turbines to generate electricity and then return the water to the River below the bypass reach. Under the Federal Power Act (FPA), 41 Stat. 1063, as amended, 16 U. S. C. §791 *et seq.*, the Federal Energy Regulatory Commission has authority to license new hydroelectric facilities. As a result, the petitioners must get a FERC license to build or operate the Elkhorn Project. Because a federal license is required, and because the project may result in discharges into the Dosewallips River, petitioners are also required to obtain State certification of the project pursuant to §401 of the Clean Water Act, 33 U. S. C. §1341.

The water flow in the bypass reach, which is currently undiminished by appropriation, ranges seasonally between 149 and 738 cubic feet per second (cfs). The Dosewallips supports two species of salmon, Coho and Chinook, as well as Steelhead trout. As originally proposed, the project was to include a diversion dam which would completely block the river and channel approximately 75% of the River's water into a tunnel

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[1] WAC 173–201–045(1) provides in pertinent part:

(1) **Class AA (extraordinary).**

(a) General characteristic. Water quality of this class shall markedly and uniformly exceed the requirements for all or substantially all uses.

(b) Characteristic uses. Characteristic uses shall include, but not be limited to, the following:

(i) Water supply (domestic, industrial, agricultural).

(ii) Stock watering.

(iii) Fish and shellfish:

Salmonid migration, rearing, spawning, and harvesting.

Other fish migration, rearing, spawning, and harvesting. . . .

(iv) Wildlife habitat.

(v) Recreation (primary contact recreation, sport fishing, boating, and aesthetic enjoyment).

(vi) Commerce and navigation.

(c) Water quality criteria

(i) Fecal coliform organisms.

(A) Freshwater - fecal coliform organisms shall not exceed a geometric mean value of 50 organisms/100 mL, with not more than 10 percent of samples exceeding 100 organisms/100mL.

(B) Marine water - fecal coliform organisms shall not exceed a geometric mean value of 14 organisms/100 mL, with not more than 10 percent of samples exceeding 43 organisms/100 mL.

(ii) Dissolved oxygen [shall exceed specific amounts].

(iii) Total dissolved gas shall not exceed 110 percent of saturation at any point of sample collection.

(vi) Temperature shall not exceed [certain levels].

(v) pH shall be within [a specified range].

(vi) Turbidity shall not exceed [specific levels].

(vii) Toxic, radioactive, or deleterious material concentrations shall be less than those which may affect public health, the natural aquatic environment, or the desirability of the water for any use.

(viii) Aesthetic values shall not be impaired by the presence of materials or their effects, excluding those of natural origin, which offend the senses of sight, smell, touch, or taste.

[2] Section 401 provides in relevant part:

> "(a) Compliance with applicable requirements; application; procedures; license suspension
>
> "(1) Any applicant for a Federal license or permit to conduct any activity including, but not limited to, the construction or operation of facilities, which may result in any discharge into the navigable waters, shall provide the licensing or permitting agency a certification from the State . . . that any such discharge will comply with the applicable provisions of sections 1311, 1312, 1313, 1316, and 1317 of this title.
>
> . . . . .
>
> "(d) Limitations and monitoring requirements of certification "Any certification provided under this section shall set forth any effluent limitations and other limitations, and monitoring requirements necessary to assure that any applicant for a Federal license or permit will comply with any applicable effluent limitations and other limitations, under section 1311 or 1312 of this title, standard of performance under section 1316 of this title, or prohibition, effluent standard, or pretreatment standard under section 1317 of this title, and with any other appropriate requirement of State law set forth in such certification, and shall become a condition on any Federal license or permit subject to the provisions of this section." 33 U. S. C. §1341.

alongside the streambed. About 25% of the water would remain in the bypass reach, but would be returned to the original riverbed through sluice gates or a fish ladder. Depending on the season, this would leave a residual minimum flow of between 65 and 155 cfs in the River. Respondent undertook a study to determine the minimum stream flows necessary to protect the salmon and steelhead fisheries in the bypass reach. On June 11, 1986, respondent issued a §401 water quality certification imposing a variety of conditions on the project, including a minimum stream-flow requirement of between 100 and 200 cfs depending on the season.

A state administrative appeals board determined that the minimum flow requirement was intended to enhance, not merely maintain, the fishery, and that the certification condition therefore exceeded respondent's authority under state law. App. to Pet. for Cert. 55a—57a. On appeal, the state Superior Court concluded that respondent could require compliance with the minimum flow conditions. *Id.*, at 29a-45a. The Superior Court also found that respondent had imposed the minimum flow requirement to protect and preserve the fishery, not to improve it, and that this requirement was authorized by state law. *Id.*, at 34a.

The Washington Supreme Court held that the antidegradation provisions of the State's water quality standards require the imposition of minimum stream flows. 121 Wash. 2d 179, 186–187, 849 P.2d 646, 650 (1993). The court also found that § 401(d), which allows States to impose conditions based upon several enumerated sections of the Clean Water Act and "any other appropriate requirement of State law," 33 U. S. C. §1341(d), authorized the stream flow condition. Relying on this language and the broad purposes of the Clean Water Act, the court concluded that §401(d) confers on States power to "consider all state action related to water quality in imposing conditions on section 401 certificates." 121 Wash. 2d, at 192, 849 P.2d, at 652. We granted certiorari, 510 U. S. — (1993), to resolve a conflict among the state courts of last resort. See 121 Wash. 2d 179, 849 P. 2d 646 (1993); *Georgia Pacific Corp.* v. *Dept. of Environmental Conservation*, 628 A. 2d 944 (1992) (table); *Power Authority of New York* v. *Williams*, 60 N.Y. 2d 315, 457 N. E. 2d 726 (1983). We now affirm.

III

The principal dispute in this case concerns whether the minimum stream flow requirement that the State imposed on the Elkhorn project is a permissible condition of a §401 certification under the Clean Water Act. To resolve this dispute we must first determine the scope of the State's authority under §401. We must then determine whether the limitation at issue here, the requirement that petitioners maintain minimum stream flows, falls within the scope of that authority.

A

There is no dispute that petitioners were required to obtain a certification from the State pursuant to §401. Petitioners concede that, at a minimum, the project will result in two possible discharges—the release of dredged and fill material during the construction of the project, and the discharge of water at the end of the tailrace after the water has been used to generate electricity. Brief for Petitioners 27–28. Petitioners contend, however, that the minimum stream flow requirement imposed by the State was unrelated to these specific discharges, and that as a consequence, the State lacked the authority under §401 to condition its certification on maintenance of stream flows sufficient to protect the Dosewallips fishery.

If §401 consisted solely of subsection (a), which refers to a state certification that a "discharge" will comply with certain provisions of the Act, petitioners' assessment of the scope of the State's certification authority would have considerable force. Section 401, however, also contains subsection (d), which expands the State's authority to impose conditions on the certification of a project. Section 401(d) provides that any certification shall set forth "any effluent limitations and other limitations . . . necessary to assure that *any applicant*" will comply with various provisions of the Act and appropriate state law requirements. 33 U. S. C. §1341(d) (emphasis added). The language of this subsection contradicts petitioners' claim that the State may only impose water quality limitations specifically tied to a "discharge." The text refers to the compliance of the applicant, not the discharge. Section 401(d) thus allows the State to impose "other limitations" on the project in general to assure compliance with various provisions of the Clean Water Act and with "any other appropriate requirement of State law." Although the dissent asserts that this interpretation of §401(d) renders §401(a)(1) superfluous, *infra*, at 4, we see no such anomaly. Section 401(a)(1) identifies the category of activities subject to certification - namely those with discharges. And §401(d) is most reasonably read as authorizing additional conditions and limitations on the activity as a whole once the threshold condition, the existence of a discharge, is satisfied.

Our view of the statute is consistent with EPA's regulations implementing §401. The regulations expressly interpret §401 as requiring the State to find that "there is a reasonable assurance that the *activity* will be conducted in a manner which will not violate applicable water quality standards." 40 CFR §121.2(a)(3) (1992) (emphasis added). See also EPA, Wetlands and 401 Certification 23 (Apr. 1989) ("In 401(d), the Congress has given the States the authority to place any conditions on a water quality certification that are necessary to assure that the applicant will comply with effluent limitations, water quality standards, . . . and with 'any other appropriate requirement of State law.'"). EPA's conclusion that *activities*-not merely discharges-must comply with state water quality standards is a reasonable interpretation of §401, and is entitled to deference. See, *e.g.*, *Arkansas* v. *Oklahoma*, 503 U. S. —, — (1992) (slip op., at 18–19); *Chevron U. S.A., Inc.* v. *Natural Resources Defense Council, Inc.*, 467 U. S. 837 (1984).

Although §401(d) authorizes the State to place restrictions on the activity as a whole, that authority is not unbounded. The State can only ensure that the project complies with "any applicable effluent limitations and other limitations, under [33 U. S. C. §§1311, 1312]" or certain other provisions of the Act, "and with any other appropriate requirement of State law." 33 U. S. C. §1341(d). The State asserts that the minimum stream flow requirement was imposed to ensure compliance with the state water quality standards adopted pursuant to §303 of the Clean Water Act, 33 U. S. C. §1313.

We agree with the State that ensuring compliance with §303 is a proper function of the §401 certification. Although §303 is not one of the statutory provisions listed in §401(d), the statute allows states to impose limitations to ensure compliance with §301 of the Act, 33 U. S. C. §1311. Section 301 in turn incorporates §303 by reference. See 33 U. S. C. §1311(b)(1)(C); see also H. R. Conf. Rep. No. 95–830, p. 96 (1977) ("Section 303 is always included by reference where section 301 is listed"). As a consequence, state water quality standards adopted pursuant to §303 are among the "other limitations" with which a State may ensure compliance through the §401 certification process. This interpretation is consistent with EPA's view of the statute. See 40 CFR §121.2(a)(3) (1992); EPA, Wetlands and 401 Certification, *supra*. Moreover, limitations to assure compliance with state water quality standards are also permitted by §401(d)'s reference to "any other appropriate requirement of State law." We do not speculate on what additional state laws, if any, might be incorporated by this language.[3] But at a minimum, limitations imposed pursuant to state water quality standards adopted pursuant to §303 are "appropriate" requirements of state law. Indeed, petitioners appear to agree that the State's authority under §401 includes limitations designed to ensure compliance with state water quality standards. Brief for Petitioners 9, 21.

B

Having concluded that, pursuant to §401, States may condition certification upon any limitations necessary to ensure compliance with state water quality standards or any other "appropriate requirement of State law," we consider whether the minimum flow condition is such a limitation. Under §303, state water quality standards must "consist of the designated uses of the navigable waters involved and the water quality criteria for such waters based upon such uses." 33 U. S. C. §1313(c)(2)(A). In imposing the minimum stream flow requirement, the State determined that construction and operation of the project as planned would be inconsistent with one of the designated uses of Class AA water, namely "[s]almonid [and other fish] migration, rearing, spawning, and harvesting." App. to Pet. for Cert. 83a–84a. The designated use of the River as a fish habitat directly reflects the Clean Water Act's goal of maintaining the "chemical, physical, and biological integrity of the Nation's waters." 33 U. S. C. §1251(a). Indeed, the Act defines pollution as "the man-made or man induced alteration of the chemical, physical, biological, and radiological integrity of water." §1362(19). Moreover, the Act expressly requires that, in adopting water quality standards, the State must take into consideration the use of waters for "propagation of fish and wildlife." 33 U. S. C. §1313(c)(2)(A).

Petitioners assert, however, that §303 requires the State to protect designated uses solely through implementation of specific "criteria." According to petitioners, the State may not require them to operate their dam in a manner consistent with a designated "use"; instead, say petitioners, under §303 the State may only require that the project comply with specific numerical "criteria."

We disagree with petitioners' interpretation of the language of §303(c)(2)(A). Under the statute, a water quality standard must "consist of the designated uses of the navigable waters involved *and* the water quality criteria for such waters based upon such uses." 33 U. S. C. §1313(c)(2)(A) (emphasis added). The text makes it plain that water quality standards contain two components. We think the language of §303 is most naturally read to require that a project be consistent with *both* components, namely the designated use *and* the water quality criteria. Accordingly, under the literal terms of the statute, a project that does not comply with a designated use of the water does not comply with the applicable water quality standards.

Consequently, pursuant to §401(d) the State may require that a permit applicant comply with both the designated uses and the water quality criteria of the state standards. In granting certification pursuant to §401(d), the State "shall set forth any . . . limitations . . . necessary to assure that [the applicant] will comply with any . . . limitations under [§303] . . . and with any other appropriate requirement of State law." A certification requirement that an applicant operate the project consistently with state water quality standards—*i.e.*, consistently with the designated uses of the water body and the water quality criteria—is both a "limitation" to assure "compliance with . . . limitations" imposed under §303, and an "appropriate" requirement of State law.

EPA has not interpreted §303 to require the States to protect designated uses exclusively through enforcement of numerical criteria. In its regulations governing state water quality standards, EPA defines criteria as "*elements* of State water quality standards expressed as constituent concentrations, levels, or narrative statements, representing a quality of water that supports a particular use." §40 CFR 131.3(b) (1992)(emphasis added). The regulations further provide that "[w]hen criteria are met, water quality will *generally* protect the designated use." *Ibid.* (emphasis added). Thus, the EPA regulations implicitly recognize that in some circumstances, criteria alone are insufficient to protect a designated use.

Petitioners also appear to argue that use requirements are too open-ended, and that the Act only contemplates enforcement of the more specific and objective "criteria." But this argument is belied by the open-ended nature of the criteria themselves. As the Solicitor General points out, even "criteria" are often expressed in broad, narrative terms, such as "'there shall be no discharge of toxic pollutants in toxic amounts.'" Brief for United States 18. See *American Paper Institute, Inc.* v. *EPA*, 996 F. 2d 346, 349 (CADC 1993). In fact, under the Clean Water Act, only one class of criteria, those governing "toxic pollutants listed pursuant to section 1317(a)(1)" need be rendered in numerical form. See 33 U. S. C. §1313(c)(2)(B); 40 CFR §131.11(b)(2) (1992).

Washington's Class AA water quality standards are typical in that they contain several open-ended criteria which, like the use designation of the River as a fishery, must be translated into specific limitations for individual projects. For example, the standards state that "[t]oxic, radioactive, or deleterious material concentrations shall be less than those which may affect public health, the

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[3] The dissent asserts that §301 is concerned solely with discharges, not broader water quality standards. *Infra*, 8 n. 2. Although §301 does make certain discharges unlawful, see 33 U. S. C. §1311(a), it also contains a broad enabling provision which requires states to take certain actions, to wit: "In order to carry out the objective of this chapter [*viz.* the chemical, physical, and biological integrity of the Nation's water] there shall be achieved . . . not later than July 1, 1977, any more stringent limitation, including those necessary to meet water quality standards . . . established pursuant to any State law or regulations." 33 U. S. C. §1311(b)(1)(C). This provision of §301 expressly refers to state water quality standards, and is not limited to discharges.

natural aquatic environment, or the desirability of the water for any use." WAC 173-201-045(c)(vii). Similarly, the state standards specify that "[a]esthetic values shall not be impaired by the presence of materials or their effects, excluding those of natural origin, which offend the senses of sight, smell, touch, or taste." 173-201-045(c)(viii). We think petitioners' attempt to distinguish between uses and criteria loses much of its force in light of the fact that the Act permits enforcement of broad, narrative criteria based on, for example, "aesthetics."

Petitioners further argue that enforcement of water quality standards through use designations renders the water quality criteria component of the standards irrelevant. We see no anomaly, however, in the State's reliance on both use designations and criteria to protect water quality. The specific numerical limitations embodied in the criteria are a convenient enforcement mechanism for identifying minimum water conditions which will generally achieve the requisite water quality. And, in most circumstances, satisfying the criteria will, as EPA recognizes, be sufficient to maintain the designated use. See 40 CFR §131.3(b) (1992). Water quality standards, however, apply to an entire class of water, a class which contains numerous individual water bodies. For example, in the State of Washington, the Class AA water quality standard applies to 81 specified fresh surface waters, as well as to all "surface waters lying within the mountainous regions of the state assigned to national parks, national forests, and/or wilderness areas," all "lakes and their feeder streams within the state," and all "unclassified surface waters that are tributaries to Class AA waters." WAC 173-201-070. While enforcement of criteria will in general protect the uses of these diverse waters, a complementary requirement that activities also comport with designated uses enables the States to ensure that each activity—even if not foreseen by the criteria—will be consistent with the specific uses and attributes of a particular body of water.

Under petitioners' interpretation of the statute, however, if a particular criterion, such as turbidity, were missing from the list contained in an individual state water quality standard, or even if an existing turbidity criterion were insufficient to protect a particular species of fish in a particular river, the State would nonetheless be forced to allow activities inconsistent with the existing or designated uses. We think petitioners' reading leads to an unreasonable interpretation of the Act. The criteria components of state water quality standards attempt to identify, for all the water bodies in a given class, water quality requirements generally sufficient to protect designated uses. These criteria, however, cannot reasonably be expected to anticipate all the water quality issues arising from every activity which can affect the State's hundreds of individual water bodies. Requiring the States to enforce only the criteria component of their water quality standards would in essence require the States to study to a level of great specificity each individual surface water to ensure that the criteria applicable to that water are sufficiently detailed and individualized to fully protect the water's designated uses. Given that there is no textual support for imposing this requirement, we are loath to attribute to Congress an intent to impose this heavy regulatory burden on the States.

The State also justified its minimum stream flow as necessary to implement the "antidegradation policy" of §303, 33 U. S. C. §1313(d)(4)(B). When the Clean Water Act was enacted in 1972, the water quality standards of all 50 States had antidegradation provisions. These provisions were required by federal law. See U. S. Dept. of Interior, Federal Water Pollution Control Administration, Compendium of Department of Interior Statements on Non-degradation of Interstate Waters 1-2 (Aug. 1968); see also Hines, A Decade of Nondegradation Policy in Congress and the Courts: The Erratic Pursuit of Clean Air and Clean Water, 62 Iowa L. Rev. 643, 658-660 (1977). By providing in 1972 that existing state water quality standards would remain in force until revised, the Clean Water Act ensured that the States would continue their antidegradation programs. See 33 U. S. C. §1313(a). EPA has consistently required that revised state standards incorporate an antidegradation policy. And, in 1987, Congress explicitly recognized the existence of an "antidegradation policy established under [§303]." §1313(d)(4)(B).

EPA has promulgated regulations implementing §303's antidegradation policy, a phrase that is not defined elsewhere in the Act. These regulations require States to "develop and adopt a statewide antidegradation policy and identify the methods for implementing such policy." 40 CFR §131.12 (1992). These "implementation methods shall, at a minimum, be consistent with the . . . [e]xisting instream water uses and the level of water quality necessary to protect the existing uses shall be maintained and protected." *Ibid.* EPA has explained that under its anti-degradation regulation, "no activity is allowable . . . which could partially or completely eliminate any existing use." EPA, *Questions and Answers re: Antidegradation* 3 (1985). Thus, States must implement their antidegradation policy in a manner "consistent" with existing uses of the stream. The State of Washington's antidegradation policy in turn provides that "[e]xisting beneficial uses shall be maintained and protected and no further degradation which would interfere with or become injurious to existing beneficial uses will be allowed." WAC 173-201-035(8)(a). The State concluded that the reduced streamflows would have just the effect prohibited by this policy. The Solicitor General, representing EPA, asserts, Brief for United States 18-21, and we agree, that the State's minimum stream flow condition is a proper application of the state and federal antidegradation regulations, as it ensures that an "existing instream water us[e]" will be "maintained and protected." 40 CFR §131.12(a)(1) (1992).

Petitioners also assert more generally that the Clean Water Act is only concerned with water "quality," and does not allow the regulation of water "quantity." This is an artificial distinction. In many cases, water quantity is closely related to water quality; a sufficient lowering of the water quantity in a body of water could destroy all of its designated uses, be it for drinking water, recreation, navigation or, as here, as a fishery. In any event, there is recognition in the Clean Water Act itself that reduced stream flow, *i.e.*, diminishment of water quantity, can constitute water pollution. First, the Act's definition of pollution as "the man-made or man induced alteration of the chemical, physical, biological, and radiological integrity of water" encompasses the effects of reduced water quantity. 33 U. S. C. §1362(19). This broad conception of pollution—one which expressly evinces Congress' concern with the physical and biological integrity of water—refutes petitioners' assertion that the Act draws a sharp distinction between the regulation of water "quantity" and water "quality." Moreover, §304 of the Act expressly recognizes that water "pollution" may result from "changes in the movement, flow, or circulation of any navigable waters . . . including changes caused by the construction of dams." 33 U. S. C. §1314(f). This concern with the flowage effects of dams and other diversions is also embodied in the EPA regulations, which expressly require existing dams to be operated to attain designated uses. 40 CFR §131.10(g)(4).

Petitioners assert that two other provisions of the Clean Water Act, §§101(g) and 510(2), 33 U. S. C. §§1251(g) and 1370(2), exclude the regulation of water quantity from the coverage of the Act. Section 101(g) provides "that the authority of each State to allocate quantities of water within its jurisdiction shall not be superseded, abrogated or otherwise impaired by this chapter." 33 U. S. C. §1251(g). Similarly, §510(2) provides that nothing in the Act shall "be construed as impairing or in any manner affecting any right or jurisdiction of the States with respect to the waters . . . of such States." 33 U. S. C. §1370. In petitioners' view, these provisions exclude "water quantity issues from direct regulation under the federally controlled water quality standards authorized in §303." Brief for Petitioners 39 (emphasis omitted).

This language gives the States authority to allocate water rights; we therefore find it peculiar that petitioners argue that it prevents the State from regulating stream flow. In any event, we read these provisions more narrowly than petitioners. Sections 101(g) and 510(2) preserve the authority of each State to allocate water quantity as between users; they do not limit the scope of water pollution controls that may be imposed on users who have obtained, pursuant to state law, a water allocation. In *California* v. *FERC*, 495 U. S. 490, 498 (1990), construing an analogous provision of the Federal Power Act,[4] we explained that "minimum stream flow requirements neither reflect nor establish 'proprietary rights'" to water. Cf. *First Iowa Hydro-Electric Cooperative* v. *FPC*, 328 U. S. 152, 176, and n. 20 (1946). Moreover, the certification itself does not purport to determine petitioners' proprietary right to the water of the Dosewallips. In fact, the certification expressly states that a "State Water Right Permit (Chapters 90.03.250 RCW and 508-12 WAC) must be obtained prior to commencing construction of the project." App. to Pet. for Cert. 83a. The certification merely determines the nature of the use to which that proprietary right may be put under the Clean Water Act, if and when it is obtained from the State. Our view is reinforced by the legislative history of the 1977 amendment to the Clean Water Act adding §101(g). See 3 Legislative History of the Clean Water Act of 1977 (Committee Print compiled for the Committee on Environment and Public Works by the Library of Congress), Ser. No. 95-14, p. 532 (1978) ("The requirements [of the Act] may incidentally affect individual water rights. . . . It is not the purpose of this amendment to prohibit those incidental effects. It is the purpose of this amendment to insure that State allocation systems are not subverted, and that effects on individual rights, if any, are prompted by legitimate and necessary water quality considerations").

IV

Petitioners contend that we should limit the State's authority to impose minimum flow requirements because FERC has comprehensive authority to license hydroelectric projects pursuant to the FPA, 16 U. S. C. §791a *et seq*. In petitioners' view, the minimum flow requirement imposed here interferes with FERC's authority under the FPA.

The FPA empowers FERC to issue licenses for projects "necessary or convenient . . . for the development, transmission, and utilization of power across, along, from, or in any of the streams . . . over which Congress has jurisdiction." §797(e). The FPA also requires FERC to consider a project's effect on fish and wildlife. §§797(e), 803(a)(1). In *California* v. *FERC*, *supra*, we held that the California Water Resources Control Board, acting pursuant to state law, could not impose a minimum stream flow which conflicted with minimum stream flows contained in a FERC license. We concluded that the FPA did not "save" to the States this authority. *Id*., at 498.

No such conflict with any FERC licensing activity is presented here. FERC has not yet acted on petitioners' license application, and it is possible that FERC will eventually deny petitioners' application altogether. Alternatively, it is quite possible, given that FERC is required to give equal consideration to the protection of fish habitat when deciding whether to issue a license, that any FERC license would contain the same conditions as the State §401 certification. Indeed, at oral argument the Solicitor General stated that both EPA and FERC were represented in this proceeding, and that the Government has no objection to the stream flow condition contained in the §401 certification. Tr. of Oral Arg. 43-44.

Finally, the requirement for a state certification applies not only to applications for licenses from FERC, but to all federal licenses and permits for activities which may result in a discharge into the Nation's navigable waters. For example, a permit from the Army Corps of Engineers is required for the installation of any structure in the navigable waters which may interfere with navigation, including piers, docks, and ramps. Rivers and Harbors Appropriation Act of 1899, 30 Stat. 1151, §10, 33 U. S. C. §403. Similarly, a permit must be obtained from the Army Corps of Engineers for the discharge of dredged or fill material, and from the Secretary of the Interior or Agriculture for the construction of reservoirs, canals and other water storage systems on federal land. See 33 U. S. C. §§1344(a), (e); 43 U. S. C. §1761 (1988 ed. and Supp. IV). We assume that a §401 certification would also be required for some licenses obtained pursuant to these statutes. Because §401's certification requirement applies to other statutes and regulatory schemes, and because any conflict with FERC's authority under the FPA is hypothetical, we are unwilling to read implied limitations into §401. If FERC issues a license containing a stream flow condition with which petitioners disagree, they may pursue judicial remedies at that time. Cf. *Escondido Mut. Water Co.* v. *La Jolla Band of Mission Indians*, 466 U. S. 765, 778, n. 20 (1984).

[4] The relevant text of the Federal Power Act provides: "That nothing herein contained shall be construed as affecting or intending to affect or in any way to interfere with the laws of the respective States relating to the control, appropriation, use, or distribution of water used in irrigation or for municipal or other uses, or any vested right acquired therein." 41 Stat. 1077, 16 U. S. C. §821.

In summary, we hold that the State may include minimum stream flow requirements in a certification issued pursuant to §401 of the Clean Water Act insofar as necessary to enforce a designated use contained in a state water quality standard. The judgment of the Supreme Court of Washington, accordingly, is affirmed.

So ordered.

JUSTICE STEVENS, concurring.

While I agree fully with the thorough analysis in the Court's opinion, I add this comment for emphasis. For judges who find it unnecessary to go behind the statutory text to discern the intent of Congress, this is (or should be) an easy case. Not a single sentence, phrase, or word in the Clean Water Act purports to place any constraint on a State's power to regulate the quality of its own waters more stringently than federal law might require. In fact, the Act explicitly recognizes States' ability to impose stricter standards. See, *e.g.*, §301(b)(1)(C), 33 U. S. C. §1311(b)(1)(C).

JUSTICE THOMAS, with whom JUSTICE SCALIA joins, dissenting.

The Court today holds that a State, pursuant to §401 of the Clean Water Act, may condition the certification necessary to obtain a federal license for a proposed hydroelectric project upon the maintenance of a minimum flow rate in the river to be utilized by the project. In my view, the Court makes three fundamental errors. First, it adopts an interpretation that fails adequately to harmonize the subsections of §401. Second, it places no meaningful limitation on a State's authority under §401 to impose conditions on certification. Third, it gives little or no consideration to the fact that its interpretation of §401 will significantly disrupt the carefully crafted federal-state balance embodied in the Federal Power Act. Accordingly, I dissent.

I

A

Section 401(a)(1) of the Federal Water Pollution Control Act, otherwise known as the Clean Water Act (CWA or Act), 33 U. S. C. §1251 *et seq.*, provides that "[a]ny applicant for a Federal license or permit to conduct any activity . . . , which may result in any discharge into the navigable waters, shall provide the licensing or permitting agency a certification from the State in which the discharge originates . . . that any such discharge will comply with . . . applicable provisions of [the CWA]." 33 U. S. C. §1341(a)(1). The terms of §401(a)(1) make clear that the purpose of the certification process is to ensure that discharges from a project will meet the requirements of the CWA. Indeed, a State's authority under §401(a)(1) is limited to certifying that "any discharge" that "may result" from "any activity," such as petitioners' proposed hydroelectric project, will "comply" with the enumerated provisions of the CWA; if the discharge will fail to comply, the State may "den[y]" the certification. *Ibid.* In addition, under §401(d), a State may place conditions on a §401 certification, including "effluent limitations and other limitations, and monitoring requirements," that may be necessary to ensure compliance with various provisions of the CWA and with "any other appropriate requirement of State law." §1341(d).

The minimum stream flow condition imposed by respondents in this case has no relation to any possible "discharge" that might "result" from petitioners' proposed project. The term "discharge" is not defined in the CWA, but its plain and ordinary meaning suggests "a flowing or issuing out," or "something that is emitted." Webster's Ninth New Collegiate Dictionary 360 (1991). Cf. 33 U. S. C. §1362(16) ("The term 'discharge' when used without qualification includes a discharge of a pollutant, and a discharge of pollutants"). A minimum stream flow requirement, by contrast, is a limitation on the amount of water the project can take in or divert from the river. See *ante,* at 7. That is, a minimum stream flow requirement is a limitation on intake—the opposite of discharge. Imposition of such a requirement would thus appear to be beyond a State's authority as it is defined by §401(a)(1).

The Court remarks that this reading of §401(a)(1) would have "considerable force," *ante*, at 9, were it not for what the Court understands to be the expansive terms of §401(d). That subsection provides that

> "[a]ny certification provided under this section shall set forth any effluent limitations and other limitations, and monitoring requirements necessary to assure that *any applicant* for a Federal license or permit will comply with any applicable effluent limitations and other limitations, under section 1311 or 1312 of this title, standard of performance under section 1316 of this title, or prohibition, effluent standard, or pretreatment standard under section 1317 of this title, and with any other appropriate requirement of State law set forth in such certification, and shall become a condition on any Federal license or permit subject to the provisions of this section." 33 U. S. C. §1341(d) (emphasis added).

According to the Court, the fact that §401(d) refers to an "applicant," rather than a "discharge," complying with various provisions of the Act "contradicts petitioners' claim that the State may only impose water quality limitations specifically tied to a 'discharge.'" *Ante*, at 9. In the Court's view, §401(d)'s reference to an applicant's compliance "expands" a State's authority beyond the limits set out in §401(a)(1), *ante*, at 9, thereby permitting the State in its certification process to scrutinize the applicant's proposed "activity as a whole," not just the discharges that may result from the activity. *Ante*, at 10. The Court concludes that this broader authority allows a State to impose conditions on a §401 certification that are unrelated to discharges. *Ante*, at 9–10.

While the Court's interpretation seems plausible at first glance, it ultimately must fail. If, as the Court asserts, §401(d) permits States to impose conditions unrelated to discharges in §401 certifications, Congress' careful focus on discharges in §401(a)(1)—the provision that describes the scope and function of the certification process—was wasted effort. The power to set conditions that are unrelated to discharges is, of course, nothing but a conditional power to deny certification for reasons unrelated to discharges. Permitting States to impose conditions unrelated to discharges, then, effectively eliminates the constraints of §401(a)(1).

Subsections 401(a)(1) and (d) can easily be reconciled to avoid this problem. To ascertain the nature of the conditions permissible under §401(d), §401 must be read as a whole. See *United Savings Assn. of Texas* v. *Timbers of Inwood Forest Associates, Ltd.*, 484 U. S. 365, 371 (1988) (statutory interpretation is a "holistic endeavor"). As noted above, §401(a)(1) limits a State's authority in the certification process to addressing concerns related to discharges and to ensuring that any discharge resulting from a project will comply with specified provisions of the Act. It is reasonable to infer that the conditions a State is permitted to impose on certification must relate to the very purpose the certification process is designed to serve. Thus, while §401(d) permits a State to place conditions on a certification to ensure compliance of the "applicant," those conditions must still be related to discharges. In my view, this interpretation best harmonizes the subsections of §401. Indeed, any broader interpretation of §401(d) would permit that subsection to swallow §401(a)(1).

The text of §401(d) similarly suggests that the conditions it authorizes must be related to discharges. The Court attaches critical weight to the fact that §401(d) speaks of the compliance of an "applicant," but that reference, in and of itself, says little about the nature of the conditions that may be imposed under §401(d). Rather, because §401(d) conditions can be imposed only to ensure compliance with specified provisions of law—that is, with "applicable effluent limitations and other limitations, under section 1311 or 1312 of this title, standard[s] of performance under section 1316 of this title, . . . prohibition[s], effluent standard[s], or pretreatment standard[s] under section 1317 of this title, [or] . . . any other appropriate requirement[s] of State law"—one should logically turn to those provisions for guidance in determining the nature, scope, and purpose of §401(d) conditions. Each of the four identified CWA provisions describes discharge-related limitations. See §1311 (making it unlawful to discharge any pollutant except in compliance with enumerated provisions of the Act); §1312 (establishing effluent limitations on point source discharges); §1316 (setting national standards of performance for the control of discharges); and §1317 (setting pretreatment effluent standards and prohibiting the discharge of certain effluents except in compliance with standards).

The final term on the list—"appropriate requirement[s] of State law"—appears to be more general in scope. Because this reference follows a list of more limited provisions that specifically address discharges, however, the principle *ejusdem generis* would suggest that the general reference to "appropriate" requirements of state law is most reasonably construed to extend only to provisions that, like the other provisions in the list, impose discharge-related restrictions. Cf. *Cleveland* v. *United States*, 329 U. S. 14, 18 (1946) ("Under the *ejusdem generis* rule of construction the general words are confined to the class and may not be used to enlarge it"); *Arcadia* v. *Ohio Power Co.*, 498 U. S. 73, 84 (1990). In sum, the text and structure of §401 indicate that a State may impose under §401(d) only those conditions that are related to discharges.

B

The Court adopts its expansive reading of §401(d) based at least in part upon deference to the "conclusion" of the Environmental Protection Agency (EPA) that §401(d) is not limited to requirements relating to discharges. *Ante*, at 10. The agency regulation to which the Court defers is 40 CFR §121.2(a)(3) (1993), which provides that the certification shall contain "[a] statement that there is a reasonable assurance that the activity will be conducted in a manner which will not violate applicable water quality standards." *Ante*, at 10. According to the Court, "EPA's conclusion that *activities*—not merely discharges—must comply with state water quality standards . . . is entitled to deference" under *Chevron U. S. A. Inc.* v. *Natural Resources Defense Council, Inc.*, 467 U. S. 837 (1984). *Ante*, at 10.

As a preliminary matter, the Court appears to resort to deference under *Chevron* without establishing through an initial examination of the statute that the text of the section is ambiguous. See *Chevron*, *supra*, at 842–843. More importantly, the Court invokes *Chevron* deference to support its interpretation even though the Government does not seek deference for the EPA's regulation in this case.[1] That the Government itself has not contended that an agency interpretation exists reconciling the scope of the conditioning authority under §401(d) with the terms of §401(a)(1) should suggest to the Court that there is no "agenc[y] construction" directly addressing the question. *Chevron*, *supra*, at 842.

In fact, the regulation to which the Court defers is hardly a definitive construction of the scope of §401(d). On the contrary, the EPA's position on the question whether conditions under §401(d) must be related to discharges is far from clear. Indeed, the only EPA regulation that specifically addresses the "conditions" that may appear in §401 certifications speaks exclusively in terms of limiting discharges. According to the EPA, a §401 certification shall contain "[a] statement *of any conditions* which the certifying agency deems necessary or desirable *with respect to the discharge of the activity*." 40 CFR §121.2(a)(4) (1993) (emphases added). In my view, §121.2(a)(4) should, at the very least, give the Court pause before it resorts to *Chevron* deference in this case.

II

The Washington Supreme Court held that the State's water quality standards, promulgated pursuant to §303 of the Act, 33 U. S. C. §1313, were "appropriate" requirements of state law under §401(d), and sustained the stream flow condition imposed by respondents as necessary to ensure compliance with a "use" of the river as specified in those standards. As an alternative to their argument that §401(d) conditions must be discharge-related, petitioners assert that the state court erred when it sustained the stream flow condition under the "use" component of the State's water quality standards without reference to the corresponding "water quality criteria" contained in those standards. As explained above, petitioners' argument with regard to the scope of a State's authority to impose conditions under §401(d) is correct. I also find petitioners' alternative argument persuasive. Not only does the Court err in rejecting that §303 argument, in the process of doing so it essentially removes all limitations on a State's conditioning authority under §401.

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[1]The Government, appearing as *amicus curiae* "supporting affirmance," instead approaches the question presented by assuming, *arguendo*, that petitioners' construction of §401 is correct: "Even if a condition imposed under Section 401(d) were valid only if it assured that a 'discharge' will comply with the State's water quality standards, the [minimum flow condition set by respondents] satisfies that test." Brief for United States as *Amicus Curiae* 11.

The Court states that, "at a minimum, limitations imposed pursuant to state water quality standards adopted pursuant to §303 are 'appropriate' requirements of state law" under §401(d). *Ante,* at 11.[2] A water quality standard promulgated pursuant to §303 must "consist of the designated uses of the navigable waters involved and the water quality criteria for such waters based upon such uses." 33 U. S. C. §1313(c)(2)(A). The Court asserts that this language "is most naturally read to require that a project be consistent with *both* components, namely the designated use *and* the water quality criteria." *Ante*, at 13. In the Court's view, then, the "use" of a body of water is independently enforceable through §401(d) without reference to the corresponding criteria. *Ante*, at 13–14.

The Court's reading strikes me as contrary to common sense. It is difficult to see how compliance with a "use" of a body of water could be enforced without reference to the corresponding criteria. In this case, for example, the applicable "use" is contained in the following regulation: "Characteristic uses shall include, but not be limited to . . . [s]almonid migration, rearing, spawning, and harvesting." Wash. Admin. Code (WAC) 173–201–045(1)(b)(iii) (1990). The corresponding criteria, by contrast, include measurable factors such as quantities of fecal coliform organisms and dissolved gases in the water. WAC 173-201-045(1)(c)(i) and (ii).[3] Although the Act does not further address (at least not expressly) the link between "uses" and "criteria," the regulations promulgated under §303 make clear that a "use" is an aspirational goal to be attained through compliance with corresponding "criteria." Those regulations suggest that "uses" are to be "achieved and protected," and that "water quality criteria" are to be adopted to "protect the designated use[s]." 40 CFR §§131.10(a), 131.11(a)(1) (1993).

The problematic consequences of decoupling "uses" and "criteria" become clear once the Court's interpretation of §303 is read in the context of §401. In the Court's view, a State may condition the §401 certification "upon *any limitations* necessary to ensure compliance" with the "uses of the water body." *Ante*, at 12, 13 (emphasis added). Under the Court's interpretation, then, state environmental agencies may pursue, through §401, their water goals in any way they choose; the conditions imposed on certifications need not relate to discharges, nor to water quality criteria, nor to any objective or quantifiable standard, so long as they tend to make the water more suitable for the uses the State has chosen. In short, once a State is allowed to impose conditions on §401 certifications to protect "uses" in the abstract, §401(d) is limitless.

To illustrate, while respondents in this case focused only on the "use" of the Dosewallips River as a fish habitat, this particular river has a number of other "[c]haracteristic uses," including "[r]ecreation (primary contact recreation, sport fishing, boating, and aesthetic enjoyment)." WAC 173-201-045(1)(b)(v). Under the Court's interpretation, respondents could have imposed any number of conditions related to recreation, including conditions that have little relation to water quality. In *Town of Summersville,* 60 FERC ¶61,291, p. 61,990 (1992), for instance, the state agency required the applicant to "construct . . . access roads and paths, low water stepping stone bridges, . . . a boat launching facility . . . , and a residence and storage building." These conditions presumably would be sustained under the approach the Court adopts today.[4] In the end, it is difficult to conceive of a condition that would fall outside a State's §401(d) authority under the Court's approach.

III

The Court's interpretation of §401 significantly disrupts the careful balance between state and federal interests that Congress struck in the Federal Power Act (FPA), 16 U. S. C. §791 *et seq*. Section 4(e) of the FPA authorizes the Federal Energy Regulatory Commission (FERC or Commission) to issue licenses for projects "necessary or convenient . . . for the development, transmission, and utilization of power across, along, from, or in any of the streams . . . over which Congress has jurisdiction." 16 U. S. C. §797(e). In the licensing process, FERC must balance a number of considerations: "[I]n addition to the power and development purposes for which licenses are issued, [FERC] shall give equal consideration to the purposes of energy conservation, the protection, mitigation of damage to, and enhancement of, fish and wildlife (including related spawning grounds and habitat), the protection of recreational opportunities, and the preservation of other aspects of environmental quality." *Ibid.* Section 10(a) empowers FERC to impose on a license such conditions, including minimum stream flow requirements, as it deems best suited for power development and other public uses of the waters. See 16 U. S. C. §803(a); *California* v. *FERC*, 495 U. S. 490, 494–495, 506 (1990).

In *California* v. *FERC,* the Court emphasized FERC's exclusive authority to set the stream flow levels to be maintained by federally licensed hydroelectric projects. California, in order "to protect [a] stream's fish," had imposed flow rates on a federally licensed project that were significantly higher than the flow rates established by FERC. *Id.*, at 493. In concluding that California lacked authority to impose such flow rates, we stated:

> "As Congress directed in FPA §10(a), FERC set the conditions of the [project] license, including the minimum stream flow, after considering which requirements would best protect wildlife and ensure that the project would be economically feasible, and thus further power development. Allowing California to impose significantly higher minimum stream flow requirements would disturb and conflict with the balance embodied in that considered federal agency determination. FERC has indicated that the California requirements interfere with its comprehensive planning authority, and we agree that

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[2] In the Court's view, §303 water quality standards come into play under §401(d) either as "appropriate" requirements of state law, or through §301 of the Act, which, according to the Court, "incorporates §303 by reference." *Ante*, at 11 (citations omitted). The Court notes that through §303, "the statute allows states to impose limitations to ensure compliance with §301 of the Act." *Ante*, at 11. Yet §301 makes unlawful only "the [unauthorized] *discharge* of any pollutant by any person." 33 U. S. C. §1311(a) (emphasis added); see also *supra*, at 5. Thus, the Court's reliance on §301 as a source of authority to impose conditions unrelated to discharges is misplaced.

[3] Respondents concede that petitioners' project "will likely not violate any of Washington's water quality criteria." Brief for Respondents 24.

[4] Indeed, as the §401 certification stated in this case, the flow levels imposed by respondents are "in excess of those required to maintain water quality in the bypass region," App. to Pet. for Cert. 83a, and therefore conditions not related to water quality must, in the Court's view, be permitted.

> allowing California to impose the challenged requirements would be contrary to congressional intent regarding the Commission's licensing authority and would constitute a veto of the project that was approved and licensed by FERC." *Id.*, at 506–507 (citations and internal quotation marks omitted).

California v. *FERC* reaffirmed our decision in *First Iowa Hydro-Electric Cooperative* v. *FPC*, 328 U. S. 152, 164 (1946), in which we warned against "vest[ing] in [state authorities] a veto power" over federal hydroelectric projects. Such authority, we concluded, could "destroy the effectiveness" of the FPA and "subordinate to the control of the State the 'comprehensive' planning" with which the administering federal agency (at that time the Federal Power Commission) was charged. *Ibid.*

Today, the Court gives the States precisely the veto power over hydroelectric projects that we determined in *California* v. *FERC* and *First Iowa* they did not possess. As the language of §401(d) expressly states, any condition placed in a §401 certification, including, in the Court's view, a stream flow requirement, "*shall* become a condition on any Federal license or permit." 33 U. S. C. §1341(d) (emphasis added). Any condition imposed by a State under §401(d) thus becomes a "ter[m] . . . of the license as a matter of law," *Department of Interior* v. *FERC*, 952 F. 2d 538, 548 (CADC 1992) (citation and internal quotation marks omitted), regardless of whether FERC favors the limitation. Because of §401(d)'s mandatory language, federal courts have uniformly held that FERC has no power to alter or review §401 conditions, and that the proper forum for review of those conditions is state court.[5] Section 401(d) conditions imposed by States are therefore binding on FERC. Under the Court's interpretation, then, it appears that the mistake of the State in *California* v. *FERC* was not that it had trespassed into territory exclusively reserved to FERC; rather, it simply had not hit upon the proper device—that is, the §401 certification—through which to achieve its objectives.

Although the Court notes in passing that "[t]he limitations included in the certification become a condition on any Federal license," *ante*, at 6, it does not acknowledge or discuss the shift of power from FERC to the States that is accomplished by its decision. Indeed, the Court merely notes that "any conflict with FERC's authority under the FPA" in this case is "hypothetical" at this stage, *ante*, at 21, because "FERC has not yet acted on petitioners' license application." *Ante*, at 20–21. We are assured that "it is quite possible . . . that any FERC license would contain the same conditions as the State §401 certification." *Ante*, at 21.

The Court's observations simply miss the point. Even if FERC might have no objection to the stream flow condition established by respondents *in this case*, such a happy coincidence will likely prove to be the exception, rather than the rule. In issuing licenses, FERC must balance the *Nation's* power needs together with the need for energy conservation, irrigation, flood control, fish and wildlife protection, and recreation. 16 U. S. C. §797(e). State environmental agencies, by contrast, need only consider parochial environmental interests. Cf., *e.g.*, Wash. Rev. Code §90.54.010(2) (1992) (goal of State's water policy is to "insure that waters of the state are protected and fully utilized for the greatest benefit to the people of the state of Washington"). As a result, it is likely that conflicts will arise between a FERC-established stream flow level and a state-imposed level.

Moreover, the Court ignores the fact that its decision nullifies the congressionally mandated process for resolving such state-federal disputes when they develop. Section 10(j)(1) of the FPA, 16 U. S. C. §803(j)(1), which was added as part of the Electric Consumers Protection Act of 1986 (ECPA), 100 Stat. 1244, provides that every FERC license must include conditions to "protect, mitigate damag[e] to, and enhance" fish and wildlife, including "related spawning grounds and habitat," and that such conditions "shall be based on recommendations" received from various agencies, including state fish and wildlife agencies. If FERC believes that a recommendation from a state agency is inconsistent with the FPA—that is, inconsistent with what FERC views as the proper balance between the Nation's power needs and environmental concerns—it must "attempt to resolve any such inconsistency, giving due weight to the recommendations, expertise, and statutory responsibilities" of the state agency. §803(j)(2). If, after such an attempt, FERC "does not adopt in whole or in part a recommendation of any [state] agency," it must publish its reasons for rejecting that recommendation. *Ibid.* After today's decision, these procedures are a dead letter with regard to stream flow levels, because a State's "recommendation" concerning stream flow "shall" be included in the license when it is imposed as a condition under §401(d).

More fundamentally, the 1986 amendments to the FPA simply make no sense in the stream flow context if, in fact, the States already possessed the authority to establish minimum stream flow levels under §401(d) of the CWA, which was enacted years before those amendments. Through the ECPA, Congress strengthened the role of the States in establishing FERC conditions, but it did not make that authority paramount. Indeed, although Congress could have vested in the States the final authority to set stream flow conditions, it instead left that authority with FERC. See *California* v. *FERC*, 495 U. S., at 499. As the Ninth Circuit observed in the course of rejecting California's effort to give *California* v. *FERC* a narrow reading, "[t]here would be no point in Congress requiring [FERC] to consider the state agency recommendations on environmental matters and make its own decisions about which to accept, if the state agencies had the power to impose the requirements themselves." *Sayles Hydro Associates* v. *Maughan*, 985 F. 2d 451, 456 (1993).

Given the connection between §401 and federal hydroelectric licensing, it is remarkable that the Court does not at least attempt to fit its interpretation of §401

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[5] See, *e.g.*, *Keating* v. *FERC*, 927 F. 2d 616, 622 (CADC 1991) (federal review inappropriate because a decision to grant or deny §401 certification "presumably turns on questions of substantive state environmental law—an area that Congress expressly intended to reserve to the states and concerning which federal agencies have little competence"); *Department of Interior* v. *FERC*, 952 F. 2d, at 548; *United States* v. *Marathon Development Corp.*, 867 F. 2d 96, 102 (CA1 1989); *Proffitt* v. *Rohm & Haas*, 850 F. 2d 1007, 1009 (CA3 1988). FERC has taken a similar position. See *Town of Summersville*, 60 FERC ¶61,291, p. 61,990 (1992) ("[S]ince pursuant to Section 401(d) . . . all of the conditions in the water quality certification must become conditions in the license, review of the appropriateness of the conditions is within the purview of state courts and not the Commission. The only alternatives available to the Commission are either to issue a license with the conditions included or to deny" the application altogether); accord *Central Maine Power Co.*, 52 FERC ¶61,033, pp. 61,172–61,173 (1990).

into the larger statutory framework governing the licensing process. At the very least, the significant impact the Court's ruling is likely to have on that process should compel the Court to undertake a closer examination of §401 to ensure that the result it reaches was mandated by Congress.

IV

Because the Court today fundamentally alters the federal-state balance Congress carefully crafted in the FPA, and because such a result is neither mandated nor supported by the text of §401, I respectfully dissent.

HOWARD E. SHAPIRO, Washington, D.C. (MICHAEL A. SWIGER, GARY D. BACHMAN, VAN NESS, FELDMAN & CURTIS P.C., ALBERT R. MALANCA, KENNETH G. KIEFFER, GORDON, THOMAS, HONEYWELL, MALANCA, PETERSON & DAHEIM, WILLIAM J. BARKER, Takoma, Wash. City Atty., and MARK L. BUBENIK, on the briefs) for petitioners; CHRISTINE O. GREGOIRE, Washington Attorney General (JAY J. MANNING, Sr. Asst. Atty. Gen., and WILLIAM C. FRYMIRE, Asst. Atty. Gen., on the briefs) for respondent; LAWRENCE G. WALLACE, Deputy Solicitor General (DREW S. DAYS III, Sol. Gen., LOIS J. SCHIFFER, Acting Asst. Atty. Gen., JAMES A. FELDMAN, Asst. to Sol. Gen., and ANNE S. ALMY and ALBERT M. FERLO JR., Dept. of Justice attys., on the briefs) for U.S. as amicus curiae supporting affirmance.

A scale to measure ecol. integrity: production rates ?

FISH BITES

• September 16 was the cutoff date for public comments on a proposed interim rule that would release certain activities such as fishery harvest, hatchery management, habitat restoration, and research from the Endangered Species Act "take" regulations on coho salmon in southern Oregon and northern California if the National Marine Fisheries Service (NMFS) agreed the activities were regulated consistently with the Oregon Coastal Salmon Restoration Initiative. An interim rule that aims to protect threatened coho salmon stocks during establishment of a final rule by NMFS went into effect 18 August. At press time, the agency planned to reconsider and possibly amend the rule after the comment period closed. For information call Garth Griffin, 503/231-2005.

• Three recent studies conclude that natural diversity by itself does not ensure healthy ecosystems. Scientists who studied ecological diversity in California, Sweden, and Minnesota found that it "often had little bearing on the performance of ecosystems—at least as measured by the growth and health of native plants," according to an article in *The Washington Post*. Oddly, the studies found that ecosystems with the broadest biological diversity were often the weakest in productivity and nutrient cycling. However, scientists agreed that in areas with the greatest species diversity such as rainforests broad species variation seems to be critical to the ecosystem's adaptability to environmental changes.

• At press time, leaders involved in the politics of salmon management were arriving in Seattle, Washington, for the 13 September Salmon Homecoming Forum to discuss U.S.-Canadian negotiations of the Pacific Salmon Treaty and other related issues. For information on materials emerging from the meeting, call For the Sake of the Salmon, 503/650-5447.

• Obtaining information about recreational-fishing-trip-related expenses, satisfaction, viewing sites, and attitudes toward resource management is among a new set of recommendations for the Atlantic Coastal Cooperative Statistics Program socioeconomic data collection program that is being proposed by the Committee on Economics and Social Sciences, Atlantic States Marine Fisheries Commission. Under the recommendations, separate socioeconomic data collection programs will be developed for commercial and recreational fisheries. The new programs aim to integrate human elements into fisheries management. For information contact Bob Beal, 202/289-6400, ext. 332.

• Tunas, sharks, and swordfish may be managed under a single fishery management plan, although billfish would continue to have its own management system, according to the National Marine Fisheries Service. The agency has until 11 October to alter all fisheries management plans to comply with standards outlined in the Sustainable Fisheries Act regarding overfishing, rebuilding stocks, and reducing bycatch.

• A report to Congress regarding ecosystem approaches to marine fisheries conservation will be completed by October 1998. A National Marine Fisheries Service's Ecosystem Principles Advisory Panel, a group of 20 experts, will examine how marine ecosystem research is conducted and advise the agency regarding how such findings "can and should be used to improve marine fisheries management," according to the National Center for Marine Conservation, which serves on the panel.

MEMBERS: Submit Fisheries News items to Kristin Merriman-Clarke, 301/897-8616, ext. 220, kclarke@fisheries.org.

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Essays

Biodiversity and Ecological Redundancy

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Abstract: *This paper addresses the problem of which biota to choose to best satisfy the conservation goals for a particular region in the face of inadequate resources. Biodiversity is taken to be the integration of biological variability across all scales, from the genetic, through species and ecosystems, to landscapes. Conserving biodiversity is a daunting task, and the paper asserts that focusing on species is not the best approach. The best way to minimize species loss is to maintain the integrity of ecosystem function. The important questions therefore concern the kinds of biodiversity that are significant to ecosystem functioning. To best focus our efforts we need to establish how much (or how little) redundancy there is in the biological composition of ecosystems. An approach is suggested, based on the use of functional groups of organisms defined according to ecosystem processes. Functional groups with little or no redundancy warrant priority conservation effort. Complementary species-based approaches for maximizing the inclusion of biodiversity within a set of conservation areas are compared to the functional-group approach.*

Resumen: *Este artículo trata el problema de que biota elegir a los efectos de maximizar los objetivos de conservación para una región particular cuando se hace frente a recursos inadecuados. La biodiversidad es considerada como la integración de variabilidad biológica a lo largo de todas las escalas, desde genética, pasando por especies y ecosistemas, hasta paisajes. La conservación de la diversidad es una empresa intimidatoria, y el artículo afirma que el enfocque a nivel de especies no es el camino correcto. La mejor forma de minimizar la pérdida de especies es mantener la integridad de la función del ecosistema. Por lo tanto, las preguntas importantes están relacionadas con los tipos de biodiversidad que son significativos para el funcionamiento de los ecosistemas. Para enfocar mejor nuestros esfuerzos necesitamos establecer cuanta redundancia hay en la composición biológica del ecosistema. Se sugiere un método para resolver el problema, basado en el uso de grupos funcionales de organismos, definidos de acuerdo a procesos ecosistémicos. Los grupos funcionales con poca o nula redundancia justifican un esfuerzo de conservación prioritario. Métodos complementarios, basados en especies, para maximizar la inclusión de biodiversidad dentro de una colección de áreas de conservación, son comparados con el método de grupos funcionales.*

Preface

This paper presents a functional approach to analyzing biological diversity, in the belief that this approach provides a more effective means of minimizing the decline in biodiversity brought about by human disturbance. Its take-home message is this: If scientists are to contribute usefully to the inevitable increase in management and political decisions relating to biodiversity, they need to address the issue of functional diversity and ecological redundancy in community composition. To do this requires development of a functional approach to describing biological composition, rather than sole reliance on the conventional taxonomic approach. Adherence to a policy that places equal emphasis on every species is ecologically unsound and tactically unachievable.

Paper submitted December 17, 1990; revised manuscript accepted April 19, 1991.

Introduction

The developing concern about human impact on the globe has focused attention on the issue of biodiversity and pushed it into prominence on many agendas. It is reflected in a number of new developments, such as the

IUCN international convention on biodiversity and the most recent programs adopted by the Scientific Committee on Problems of the Environment and the International Union of Biological Sciences, to name just a few. It will be a major agenda item for the 1992 United Nations Conference on Environment and Development.

Unfortunately, the rhetoric surrounding the debate is often confusing and superficial and could divert policies and activities into directions where desired goals won't be achieved. There are various interpretations of what is meant by "biodiversity," and its constant use and misuse in the media has induced a negative reaction to the term in some sections of the scientific community, leading to its rejection as a serious scientific topic. The popularization of declining biodiversity has unfortunately put it in the category of a "flavor-of-the-month" issue when in fact it is a serious and difficult problem that deserves long-term scientific consideration.

Decline in biodiversity includes all those changes that have to do with reducing or simplifying biological heterogeneity, from individuals to regions. Included are such phenomena as phenotypic plasticity; genetic variability within a population (allowing for a wide range of genotypic responses to environmental conditions); ecotypic variation (genetic variability between populations within a species); species richness (the number of species in a community); species (alpha) diversity (involving both the number of species and the relative numbers of individuals per species); functional diversity (the relative abundances of functionally different kinds of organisms); gradient (beta) diversity, which extends to diversity resulting from speciation of ecological equivalents (gamma or delta diversity—see Cowling et al. 1989); community diversity (the number, sizes, and spatial distribution of communities, sometimes referred to as patchiness); and even the diversity of the scales of patchiness (landscape diversity). Taken together, "ecological complexity" is a better term for all these aspects of biological heterogeneity.

A decline in any of these represents simplification and therefore loss of "biodiversity." The question we need to answer is "So what?"

I divide the reasons for maintaining biodiversity into two categories: ecological and "others." Norton (1988) puts these "other" concerns into three categories of values—commodity, amenity, and moral. I exclude here the moral or ethical arguments, not because they are unimportant, but because they are nonscientific. There are gray areas in all such distinctions, and arguments in favor of conserving pandas or koalas generally involve a mixture of moral concerns and scientific awareness of genetic uniqueness and rarity (to which I will return later). I am referring here to the genuinely moral arguments—which nevertheless are usually associated with "charismatic megavertebrates" rather than fungi or nematodes. The ethical implications of species loss is an important topic, but for a different essay. The amenity issues are generally rather vague, except for specific examples where values are attached to particular species. The commodity issues mostly seem to relate to future possible benefits from as-yet-unknown specific pharmacological properties, etc. Such issues can be grouped under the heading of option foreclosure; and while no one would argue against it, it is difficult to attach levels of probability and potential benefits in the absence of appropriate information.

The major reasons advanced for concerns about biodiversity are ecological. Each of the various aspects of ecological complexity described above, has been implicated to a greater or lesser degree in the ways in which ecosystems and communities function and (in particular) persist. Initially, there was uncritical acceptance of an assumed positive relationship between species richness and "stability," but this was brought into question by May (1972) and others, and the focus switched to the kinds of diversity. Based on both theoretical and empirical evidence it seems that it is diversity at the community level (patchiness), if anything, that is important in long-term stability. Nevertheless, it is species richness that is most commonly invoked in concerns about biodiversity, and the approach to the problem usually involves devising means (including political and legal) to prevent decline in biodiversity. In itself this is perfectly reasonable. From a conservation viewpoint efforts to prevent the loss of any species are laudable. However, the survival of particular target (favored) species can usually be assured by correct habitat management, control of exploitation, or both. This is not to say that correct habitat management is simple, and it should not be dismissed in a facile way. Its most difficult aspect is probably dealing with habitat or landscape fragmentation and its consequent denial of access to refugia at critical times (which reflects the importance of changes in landscape diversity). Resolving the overall problem of decline in biodiversity requires more than focusing on particular cases of species conservation. It requires understanding the relations between biodiversity and ecosystem function and applying this understanding.

Biodiversity and Ecosystem Function

Given that the objective is to minimize reduction in biodiversity (including the loss of species), the important questions in this debate concern the *kinds* of biodiversity that are most significant to the ways ecosystems function, because this is how to best focus our conservation efforts. Which kinds, and what amounts, of biological simplification lead most readily to significant or irreversible changes in the inherent structure and function of an ecosystem (i.e., to an unsustainable decline in its resilience)? Put another way, which aspects of diversity, and which kinds of species, are most important to ecosystem function?

Ecologically, all species are not created equal. At one extreme, some are determinants, or "drivers," of the ecosystem of which they form a part. At the other extreme are those that are "passengers." Removing the former causes a cascade effect, but loss of the passengers leads to little change in the rest of the ecosystem. Apparent passengers, at one time scale, may of course turn out to be infrequent determinants, and this distinction needs to be treated carefully. It raises the major legitimate argument against classifying species in terms of their contribution to ecosystem function. Nevertheless, attempting to deal with each species individually becomes impossible—consider, for example, just the number of invertebrate species in a hectare of tropical rain forest. Provided we deliberately and iteratively reexamine the guild composition, the advantages of a functional approach argue in its favor. This does not mean that we should ignore what we know about particular "keystone" or otherwise important species, but rather that we should include this knowledge in a more systematic and thorough analysis of ecosystem function.

Putting the problem another way, we need to ask how much, or rather, how *little*, redundancy there is in the biological composition of ecosystems. This question is at the heart of ecological science—the relations between structure and function of ecological communities—and as such should excite anyone who is interested in ecology.

Without knowing anything about ecological redundancy, how can we value a decline in biological diversity?

Contrast, for example, an ecosystem where a single, wide-ranging ant predator is prominent, with the situation involving the southeastern Australian jack-jumper ants (nominally *Myrmecia pilosula*), which were thought until recently to constitute such a species. "*M. pilosula*" is now known to include at least five sibling southeastern taxonomic species. They differ dramatically in chromosome numbers, but only slightly in morphology (Imai et al. 1988). Their collective distribution in suitable habitats runs from the Blue Mountains to Tasmania and parts of southern South Australia, and several species are very widespread. In some places only one species is found, but in others up to three may be sympatrically associated. None occupy the whole area, but the three most common species together cover virtually the full geographical range of the group (R. W. Taylor, personal communication). There are no apparent ecological distinctions between these entities, so that, although they are reproductively distinct gene pools, and clearly "good" species, they constitute in effect a single functional ecological unit. Although it is of great scientific interest to understand the nature and evolutionary history of their diversity, few would dispute that according all of these species the same priority (and therefore conservation effort and expenditure) as the single-species predator might be misdirected, under some circumstances.

Regrettable as it might be, it is most likely that global biodiversity concerns will ultimately reduce to a cost-benefit analysis. Without a knowledge of redundancy, or more broadly, the relationships between levels of biodiversity and ecosystem function, we cannot estimate either the costs or the benefits.

One adverse but absurd response to this assertion is that acknowledging that the loss of some species may not be as ecologically critical as the loss of some others is tantamount to advocating their removal. Critics invoke Ehrlich and Ehrlich's (1981) fable about rivet poppers on an aeroplane. What I am suggesting in no way supports any actions or policies that deliberately lead to a decline in biodiversity. What I do advocate is that the best way to succeed in our efforts to reduce the decline in biodiversity is to focus initial attention on the aspects of biodiversity that are critical for maintaining the resilience of the ecosystems concerned. Resilience in this context is taken to be the capacity of the ecosystem to maintain its characteristic patterns and rates of processes (such as primary productivity, allocation of photosynthate, surface hydrology, energy exchange, nutrient cycling, herbivory, etc.) in response to the variability inherent in its climatic regime. By maintaining the integrity of ecosystem function we minimize the chances of losing the many species we have not yet described and those of whose very existence we are as yet unaware.

If we consider the case of a decline in numbers of individuals within a species, the analogous issue is population viability analysis: What are the required conditions, and what is the critical number of interacting individuals, to maintain a population? Or, in a more general sense, what is the relationship between density and population viability, and what determines it? The problem involves both longer-term (e.g., genetic variability loss) and more immediate processes (effects of extreme events, density-dependent effects of competition, minimum breeding levels, dispersal and reinvasion rates, and so forth). At the multispecies level, the same issues remain a concern, but perhaps more important are the issues relating to species interactions and the ecosystem processes described above.

A Suggested Approach

How do we address the problem?

As implied earlier, a necessary step in analyzing the functional relationships between biological diversity and persistence in an ecosystem is to get away from a purely species-centered view of biodiversity, and to

consider it instead in terms of functionally different kinds of organisms. The appropriate basis for defining the species functional types (guilds) is the way the biota regulates ecosystem processes. Defining them in this way focuses attention on the processes that maintain ecosystem and community function, and on how changes in the relative or absolute abundances of the functional groups concerned, and in their patterns of distribution, will influence these processes.

Step one, therefore, is an iterative procedure involving analyses of ecosystem function (identifying the rate-limiting or otherwise relatively important processes in the system of concern) coupled to the development of appropriate corresponding functional classifications of the biota, through guild analyses of one sort or another. The objective should be to try to further subdivide the species in a guild on the basis of nontrivial functional attributes (nontrivial in the sense that they are related to limiting or dominant ecosystem processes for that ecosystem). If this cannot be done and there are still several different species in the group, then on the basis of current knowledge, there is some ecological redundancy within the guild concerned. An obvious problem in this regard is the time scale on which function is considered. The separate significance of a particular species may only become apparent under particular environmental conditions, and such time-dependent, episodic features of guild analysis constitute a difficulty that must be considered from the perspective of long-term ecosystem function.

Step two is to determine the number of species within each guild. Those represented by only a few or even a single species are clearly unable to withstand any loss of species and constitute an obvious, immediate conservation focus.

Step three is to further examine the interactions among the species in each guild. Complete functional redundancy only occurs if, following the removal of one species, there is density compensation among the remaining species. A complicating factor is that the different species in a guild, while all performing the same function, may respond differently to different environmental conditions. With the complete set of species, net guild abundance (or function) may remain relatively constant under a fluctuating environment. Loss of some species may well lead to an increase in abundance of others (i.e., density compensation occurs), but because the diversity of response to environmental conditions has been reduced, net guild abundance may then fluctuate more in response to environmental fluctuations. Once again, in the absence of adequate information, we need to adopt a successive approximation approach based on what we do know.

The final step is to consider the relative importance of the functional groups (the analogue to the question about species importance). The logical progression in ecological studies, from structure to function and then to the relations between them, indicates that the approach to this step is to examine how a change in abundance of a functional group directly affects ecosystem and community processes, and how such a change influences the net effect of the biota (through changes in the timing and overall rates of predation, dispersal, herbivory, decomposition, nutrient retention and uptake, biomass accumulation, etc.). In other words, all the issues involved in ecological stability analysis are considered, but using functional groups instead of taxonomic species. Achieving this step involves developing conceptual and analytical models using a combination of existing knowledge (see step one above) and a range of experiments specifically designed to examine these relations. It is a fruitful area for experimental ecologists and will most likely involve reciprocal experiments in which, on the one hand, functional groups are removed from an ecosystem and the effects on function are measured, and on the other, function is altered (changes in nutrient cycling, hydrological regime, etc.) and changes in functional group abundance or performance are measured. Functional groups considered (on the basis of present knowledge) to be the major drivers of the system warrant initial attention in this approach.

Complementary Species-based Approaches

Given the complexities of defining and establishing functional groups, particularly the extent of lumping or splitting, there is a danger that (as one reviewer of an early draft put it) we may replace one taxonomic approach with another, more confusing one. However, as indicated earlier, I do not advocate a complete switch. Too often in the development of ecology there has been a swing from one extreme to another (the "association" vs. the "continuum," equilibrium vs. disequilibrium, etc.) with the eventual realization that both approaches were valid and that the extent to which each was important depended on the nature of the system. No doubt, in the ensuing debate on how to maintain biodiversity, the use of both species and functional groups will turn out to be appropriate, at different scales.

One species-based approach, which perhaps best complements the functional approach, is concerned with weighting species (or other taxa) according to their taxonomic distinctness, and in this way identifying priority choices for conserving biodiversity. The approach has so far been most comprehensively dealt with be Vane-Wright and colleagues (Vane-Wright et al. 1991) and is encapsulated in May's (1990) account of the problem. The approach involves deriving some measure of taxonomic distinctness based on the topology of a hierarchical taxonomic classification. Using these weightings, Vane-Wright and colleagues have shown how the priority order for the minimum set of reserve areas needed to conserve the biodiversity in a particular taxonomic group differs markedly from the set derived by giving all species equal weight. May (1990) has indicated that the method used to derive the weightings needs further work, and Faith (in press) has developed a measure of phylogenetic diversity that resolves some of the difficulties. The significance of the measure in the context of this paper is that the value of a species is based on its contribution to overall feature diversity. Functional groups are also characterized by their different features, so that similar measures of feature diversity may be useful in placing relative importance values (functional as opposed to phylogenetic importance) on different functional groups.

The main difference between the functional group approach I have suggested and the taxonomic-distinctness approach of Vane-Wright et al. has to do with the scale of concern. Taxonomic distinctness is a valuable tool for helping to choose among many different areas to ensure that maximum biodiversity is included (for example, in a reserve network). The functional group approach focuses attention on which species are of major concern in managing, or identifying appropriate boundaries for, a particular area or region to minimize the loss of biodiversity. The two are therefore complementary in devising an overall conservation strategy.

Conclusion

In future political and economic tradeoffs that will decide how much nations are prepared to pay to maintain biodiversity (in terms of foregone production or direct restoration costs), ethical and commodity arguments will certainly play a role, but the weight of evidence will most likely come from the ecological side. The worrisome cost of decline in biodiversity, particularly to politicians who may be held accountable, is the threat of a collapse in the "stability" of ecosystems (whatever that means). This threat, however, will become progressively less an issue as the passage of time reveals scientists' inability to demonstrate it.

There will always be highly motivated conservation organizations that collectively take on the plight of some hundreds or even thousands of visible, identified species, but this is an immeasurably small part of the problem. If these species act as "umbrella" species, and enhancing them unwittingly helps the plight of others, then the efforts of such organizations are positively magnified. Such claims, however, are statements of faith and there is generally no effort to consider whether the actions taken to promote the welfare of elephants or lemurs, for example, are having a positive or negative effect on the welfare of loosely connected species, such as butterflies or soil-surface lichens. Identifying these focal species in the context of a functional analysis will permit an evaluation of their umbrella role and will also highlight appropriate (and inappropriate) conservation activities.

Five categories of species have been, and are, used to justify special conservation effort (Noss 1990). In summary they can be labeled as ecological indicator, keystone, umbrella, flagship (charismatic), and vulnerable species. If a strategy to enhance one or more such species turns out to have an overall negative effect on the viability of many other species in the ecosystem, then the arguments in favor of such a strategy obviously need to be questioned. Although many reserves were originally established around focal species and some are still intentionally managed to conserve just those species, conservation organizations responsible for managing an area generally avoid such a stance, and their actions constitute a genuine effort to enhance the welfare of all species. They are, unfortunately, confronted with the problem of not knowing enough about all these species to be confident of achieving their objective. Changing the focus from particular species to functional groups, and coupling this with an analysis of ecological redundancy, particularly in those functional groups that are on the "driver" side of the continuum, is a good start to improving the situation.

In terms of an overall approach to conserving biodiversity we need to resolve two issues: (1) how to choose the optimal set of bits of a region or of the world to maximize the biodiversity they include, and (2) how to manage any area or region to ensure the long-term persistence of all its biota (including species we don't yet know exist). The functional group approach addresses the latter issue.

What I have suggested here clearly raises more problems than it solves. But this is largely due to its stage of development. Thus far, the idea of functional groups has been restricted to very general or global classifications. Functional aspects of biodiversity have been discussed in general terms (e.g., Noss 1990), but the notion of functional groups has yet to be applied in a detailed way to particular ecosystems. Given the disappointing progress in achieving programs using individual species approaches to biodiversity, the analysis of ecological redundancy deserves serious attention.

Acknowledgments

This paper was greatly improved by comments and contributions from Alan Andersen, Dick Braithwaite, Francis Crome, Dan Faith, Graham Harrington, Chris Margules, Steve Morton, and John Woinarski (who suggested the "drivers" and "passengers" analogy). I also thank Bob May and an anonymous referee for their valuable suggestions.

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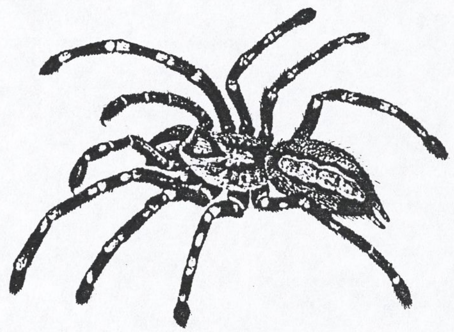

North American Journal of Fisheries Management 15:220–228, 1995
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Some Factors Affecting a Hatchery-Sustained Kokanee Population in a Fluctuating Colorado Reservoir

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Abstract.—The population of kokanees *Oncorhynchus nerka* in Lake Granby, Colorado, is expected to satisfy the competing demands of providing summer harvest for anglers, kokanee eggs for restocking, and prey for trophy lake trout *Salvelinus namaycush*. In the late 1970s, declines in numbers of kokanees harvested and kokanee eggs collected prompted investigations of the influences of stocking rates, reservoir fluctuations, competition with *Mysis relicta*, and lake trout predation. The kokanee population has been maintained mainly by annual stocking of fry (≤30 mm total length, TL) since 1951. When maturing spawners exceeded 367 mm TL, more than 50% of them were harvested in the summer recreational fishery, which reduced the number of kokanees in some fall spawning runs. However, when maturing year-classes were composed mainly of smaller kokanees, proportionately fewer were harvested, and the number of maturing kokanees entering the spawning run increased. Despite a trend of increased stocking from 1951 to 1978, mean kokanee spawner length varied inversely with the reservoir's water volume. In years of low reservoir volume, water temperatures were warmer. This facilitated *Daphnia* population development, which enhanced survival and growth of stocked kokanees. The colder water temperatures of high reservoir volumes were associated with later appearance of *Daphnia*, reduced kokanee recruitment, and smaller kokanees. Kokanee overstocking in the late 1970s resulted in stunting during the 1980s and shifted the predominant age of spawners from age 3 to age 4. Overpopulation also diminished angler perception of fishery quality and eliminated *Daphnia pulex*, the kokanees' primary food supply. The inverse relationship between reservoir volume and mean kokanee size has persisted despite *M. relicta* predation on *Daphnia* and lake trout predation on kokanees, which suggests that thermal and productivity trends in the reservoir will continue to exert a regulatory role in kokanee population dynamics.

Kokanees *Oncorhynchus nerka* represent a major fishery resource in the western USA and Canada (Wydoski and Bennett 1981; Rieman and Myers 1992). The species is especially well suited to life in fluctuating mountain reservoirs because the majority of its life is spent in pelagic environments where crustacean zooplankters, principally *Daphnia* spp., make up the bulk of its diet (Finnell and Reed 1969; Klein 1979). Although introduced kokanees often develop self-sustaining populations (Wydoski and Bennett 1981), many populations are augmented (Rieman and Myers 1992) or maintained entirely by stocking.

In Lake Granby, Colorado, kokanee reproduction appears limited by cold water temperature (for stream spawners) or by lack of suitable substrate (for shoreline spawners). Finnell (1959) documented that both naturally and artificially deposited kokanee eggs in Lake Granby inlet streams failed to hatch. This was attributed to stream temperatures less than 3.3°C, which is below the range of suitable temperatures reported by Combs (1965). Many kokanees collected from Lake Granby in winter retain eggs well after deterioration of their bodies has progressed, which suggests that substrates suitable for egg deposition are lacking. Furthermore, examination of nearly 4,000 kokanees for tetracycline marks in 1981–1986 revealed that 97% were stocked, which demonstrated that the population was not self-sustaining (Martinez and Wiltzius 1991).

Kokanees in Lake Granby historically supported one of Colorado's best reservoir fisheries, and have been the state's most reliable source for kokanee eggs, which are used to meet in-state and out-of-state stocking needs. In the late 1970s, declines in the numbers of kokanees harvested and kokanee eggs collected prompted further study of kokanee ecology and population dynamics in the reservoir (Martinez and Bergersen 1991). The establishment of *Mysis relicta* in the 1970s, reservoir storage trends, kokanee stocking manipulations, and an emphasis on a trophy lake trout *Salvelinus namaycush* fishery in the late 1980s have been implicated as major factors influencing the kokanee population. In this paper, we chronicle the history of kokanee management in Lake Granby and evaluate relationships between kokanee population characteristics, reservoir water level, and the establishment of lake trout and *M. relicta*.

Methods

Data used in our analyses included annual historical records of kokanee mean spawner length, stocking rates, eggs collected, and reservoir volume. Sporadic creel survey, kokanee spawner enumeration, water temperature, and crustacean zooplankton data were also used. These data did not allow testing of the relative importance among factors; rather, our analyses provide information and insight about the influences of each factor.

Lake Granby covers 2,938 ha at a maximum elevation of 2,524 m above sea level. It was constructed in 1949 primarily for irrigation; therefore, it is subject to large seasonal water level fluctuations (Martinez and Bergersen 1991). End-of-month records of reservoir water volume, obtained from the U.S. Bureau of Reclamation, were expressed as a percent of maximum reservoir volume. These data were regressed with mean kokanee spawner lengths and water temperatures. Water temperature data were obtained from Nelson (1971), Nelson (1982), Martinez (1986), Martinez and Bergersen (1991), and W. C. Lee (Colorado Cooperative Fish and Wildlife Research Unit, unpublished data).

Kokanees were introduced in Lake Granby in 1951 (Moore 1953) and have been stocked annually. Since 1954, kokanees have been stocked in the Colorado River at the location where kokanee eggs are collected (0.6–1.2 km upstream of the reservoir, depending on the water level) to ensure that young kokanees imprint and return to supply eggs. Until the mid-1970s, small portions of the annual stocking were released at a few sites around the reservoir to provide a snagging fishery when the fish matured. Through 1980, annual kokanee stocking consisted mainly of fry shorter than 30 mm (all lengths are total length) that were released in May or early June. In 1981–1985, kokanee harvest and spawning-run returns were evaluated from four length-groups: 25, 40, 55, 160 mm (Martinez and Wiltzius 1991). Kokanees stocked since 1985 have been 35–45 mm long.

Information on kokanee abundance and size was collected at the kokanee egg collection site on the Colorado River. Estimates of mean spawner length (in most years) and numbers of eggs collected have been recorded since 1954 and 1962, respectively. Kokanee numbers in annual spawning runs were estimated in 1975–1979 by using spawner sex ratios and body–egg relationships (Wiltzius, unpublished data) and in 1981–1986 by counting subsamples of spawners. Feed-administered oxytetracycline (OTC) was used to mark kokanees stocked in 1970 and in 1981–1985. Bone samples, usually vertebrae from behind the head, were examined under ultraviolet light to fluoresce the OTC bands (Martinez and Wiltzius 1991). In 1992, kokanee spawner ages were determined from otoliths as described by Parsons and Hubert (1988).

Creel surveys were performed in 1975–1979 (Sealing and Bennett 1980) and 1981–1986 (Martinez and Wiltzius 1991) with a stratified random system of counting and interviewing (Neuhold and Lu 1957). Shore anglers and boat anglers were interviewed to determine hours fished and numbers, sizes, and species of fish caught. Estimates of angling effort and harvest were derived as described by Powell (1975).

Crustacean zooplankton were collected with a Clarke-Bumpus metered plankton net (0.12-mm-aperture netting) and processed as described in Martinez and Bergersen (1991). The net was towed obliquely, and we present results for the depth range of 0–10 m, the zone of maximum crustacean zooplankton abundance (Martinez and Bergersen 1991). Mean lengths (in millimeters) of *Daphnia* in collections made in July or August are presented because they represented the period of peak or near-peak *Daphnia* density in Lake Granby (Nelson 1971; Martinez and Bergersen 1991).

Results and Discussion

Effects of Kokanee Stocking Rate

The annual kokanee stocking rate in Lake Granby varied greatly from 1951 to 1992 (Figure 1a). Kokanee stocking increased from 0.5–0.8 million in 1957–1968 to 1.1 million in 1969 due to concerns that reduced numbers of kokanees surviving to maturity (Finnell 1970) resulted in relatively small egg-takes in 1966–1967 (Finnell 1968; Figure 1b). The trend of stocking greater numbers peaked in 1977–1978, when nearly 2 million fry were stocked annually. These high stocking rates were in response to the record low egg-take of 1.8 million in 1976.

Mean lengths of kokanee spawners varied historically between large and small sizes, but in 1980–1986 they were as small as, or smaller than previously reported at Lake Granby (Figure 1c). In addition to being smaller in 1981–1984, kokanee spawners were numerous (Table 1), which contributed to large annual egg-takes of 10.2–16.3 million (Figure 1b). Further, spawning runs dominated by age-3 fish in the 1970s shifted to age-4 dominance in the 1980s and back to age-3 domi-

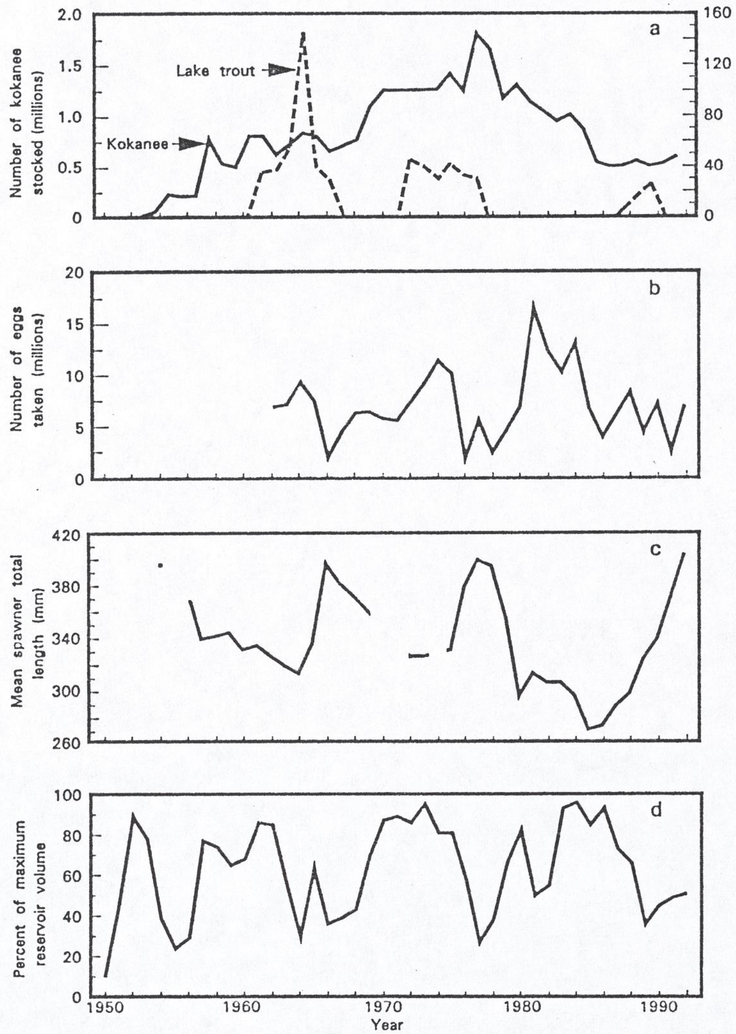

FIGURE 1.—Historic Lake Granby, Colorado, kokanee, lake trout, and reservoir capacity data: (a) number of kokanees and lake trout stocked; (b) number of kokanee eggs collected; (c) mean kokanee spawner length (gaps indicate missing data); and (d) 30 November reservoir volume (expressed as a percent of maximum reservoir volume).

nance in 1992 (Table 2), following several years of reduced stocking (Figure 1a). These phenomena, indicative of kokanee overabundance in the early 1980s, were apparently caused by the high stocking rates in 1977–1978.

Kokanee overpopulation also influenced angler perception of fishery quality. Despite high catches in the early 1980s (Table 1), anglers were dissatisfied with the small size of the kokanees. Although small kokanees continued to be harvested,

TABLE 1.—Creel survey summary and estimates of kokanee numbers harvested, used for supplying eggs, removed from the population, and mean kokanee length in the sport fishery and spawning run in Lake Granby, Colorado, 1975–1986.

Year	Duration of creel survey	Total hours of angling effort ($\times 10^3$)	Number of kokanees (thousands): Summer reservoir harvest	Used in egg-take operation	Fall snagging harvest	Removed from population	Mean total length (mm): Sport fishery creel	Fall spawning run
1975 (1976)	1 Apr–31 Mar	227.6	68.9	48.8	39.1	156.8	312	330
1976	1 Apr–31 Dec	171.1	44.6	6.9	21.8	73.3	320	379
1977 (1978)	1 May–31 Jan	131.2	43.0	16.7	13.5	73.2	343	399
1978	1 Apr–31 Dec	150.8	23.2	7.4	4.1	34.7	318	394
1979	1 May–31 Dec	130.4	20.8	19.6	12.7	53.1	295	356
1981 (1982)	1 May–24 Jan	125.7	16.1	83.0	21.1	120.2	267	312
1982 (1983)	17 May–14 Jan	141.2	39.1	79.4	55.0	173.5	259	306
1983	16 May–13 Nov	141.1	44.3	67.4	86.7	198.4	259	304
1984	14 May–25 Nov	135.0	24.2	100.0	49.0	173.2	279	295
1985	13 May–24 Nov	137.1	15.7	65.7	13.9	95.3	244	269
1986	12 May–28 Sep	99.0	5.0	28.5	8.5	42.0	234	272

they did not enter the summer harvest in proportion to their abundance. The percent of kokanees harvested during summer in 1975–1986 was positively related to mean spawner length (Figure 2). Mean spawner length is an index of kokanee length in the summer fishery ($r = 0.93$, $P < 0.01$, $N = 11$; Table 1). These relationships indicated that when kokanees were larger, a greater proportion of the maturing year-classes was harvested by anglers, which left proportionately fewer fish to mature and enter the spawning run. Conversely, when the maturing fraction of the population was smaller-sized, as in the early 1980s, a smaller percentage was harvested by anglers, which resulted in proportionately more kokanee reaching maturity. Maturing year-classes represent the largest individuals in the population, and these fish contribute most to the annual harvest (Klein 1979; Rieman and Myers 1990).

During the 1980s, it appeared that kokanee predation was the major factor affecting epilimnetic *Daphnia* populations (Martinez and Bergersen 1991), rather than predation by *M. relicta* as originally suspected by Sealing and Bennett (1980). Martinez and Bergersen (1991) believed the thermal refuge that prevented elimination of *Daphnia galeata mendotae* by *M. relicta* also provided refuge for the larger *D. pulex,* reported by Finnell and Reed (1969) to be the preferred food of kokanees in Lake Granby. Consequently, intense selective predation by overabundant kokanees was deemed responsible for the suppression and virtual disappearance of *D. pulex* throughout the 1980s. *Daphnia pulex* reappeared in Lake Granby in 1990 (Table 3), and we believe this resulted from reduced predation by lesser numbers of kokanees in the reservoir. Additionally, mean size of daphnids in 1991–1992 was markedly larger than previously recorded and was strongly correlated with mean spawner size ($r = 0.94$, $P < 0.01$, $N = 8$), not reservoir volume ($r = 0.17$, $P > 0.1$, $N = 8$). These findings suggest that low kokanee numbers in the early 1990s allowed *D. pulex* to recolonize and daphnids to grow to larger sizes.

Influence of Reservoir Volume

Comparison of mean kokanee spawner length with end-of-month reservoir volume revealed con-

TABLE 2.—Percent composition and mean total lengths (in parentheses) of age-classes in Lake Granby, Colorado, kokanee spawning runs, as determined from tetracycline-marked fish in 1973 and 1986, and from examination of otoliths in 1992.

Year	Number of fish examined	Percent composition of spawning run (mean total length, mm) at age: 2	3	4	5	Undetermined[a]
1973	93	11.8 (307)	85.0 (315)			3.2 (329)
1986	422	0.7 (249)	32.2 (254)	59.1 (262)	4.7 (320)	3.3 (334)
1992	102	11.8 (378)	76.4 (406)	11.8 (434)		

[a] Undetermined ages were known to be greater than age 3 in 1973 and greater than age 5 in 1986.

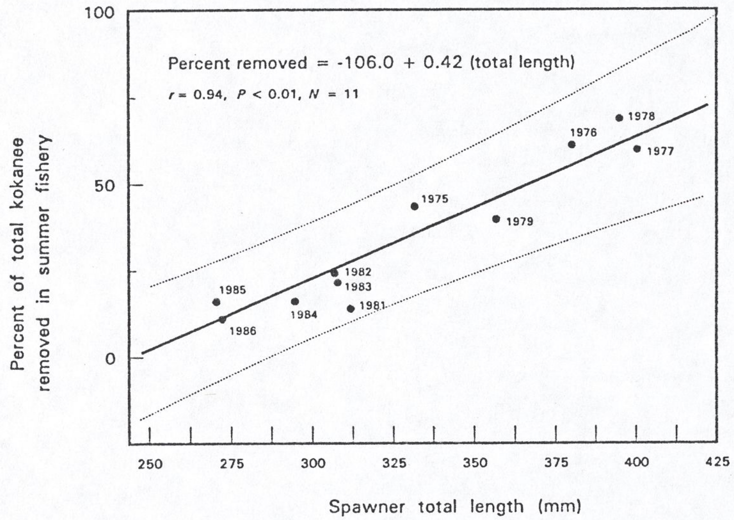

FIGURE 2.—Relation between angler harvest of kokanees and kokanee mean length in the spawning run, 1975–1986. Harvest percentages estimate that portion of the annual kokanee return removed during the kokanee fishing season, May–October, primarily by trolling. The dashed lines denote 95% confidence limits.

sistently negative correlations for all months. The 30 November reservoir volume was chosen as an index due to its high correlation with mean spawner length ($r = -0.66$, $P < 0.01$, $N = 34$) and coincidence with the spawning run. When reservoir volume was near maximum, mean spawner

TABLE 3.—Historic summertime occurrence and mean size of epilimnetic *Daphnia* species, mean kokanee spawner length, and 31 July reservoir volume for Lake Granby, Colorado.

Year	Date of zooplankton sampling	*Daphnia galeata mendotae*	*Daphnia pulex*	Mean length (mm): *Daphnia* spp.	Mean length (mm): Kokanee spawners	Reservoir volume (% of maximum)
1963	31 Jul	Present	Present	0.85[a]	318	68.2
1964	28 Jul	Present	Present	0.93[a]	312	49.3
1965	30 Jul	Present	Present	0.89[a]	335	64.9
1981[b]	23 Aug	Present	Absent	0.87	312	62.2
1982[b]	26 Jul	Present	Absent	0.78	305	57.9
1989[c]	4–7 Aug	Present	Absent	0.77	323	60.1
1991	7 Aug	Present	Present	1.20	371	59.8
1992	29 Aug	Present	Present	1.34	404	58.5

[a] Mean lengths for *Daphnia galeata mendotae* only (from Nelson 1971).
[b] From Martinez (1986).
[c] Unpublished data from G. Bennett and A. Martinez, Colorado Division of Wildlife.

length was consistently smaller than when the reservoir was low (Figure 1c, d). Therefore, the relationship between kokanee size and vulnerability to angling in the summer fishery and its implications for the fall spawning run appear to be linked to reservoir volume.

Trends in kokanee size suggest that kokanee growth and survival in Lake Granby were greater during periods of low reservoir volume. Mean water temperature (in the upper 40 m) was cooler when the reservoir was full, as in 1962, but was as much as 30% warmer when the reservoir held about half its maximum volume, as in 1990 (Table 4). In addition, the approximate depth of the 14°C isotherm, the threshold preventing *M. relicta* access to the epilimnion during its nighttime vertical migrations (Martinez and Bergersen 1991), occurred at greater depth when reservoir volume was low. These indicators of thermal conditions were strongly related to reservoir volume ($r = 0.95$, $P = 0.01$, $N = 5$, for mean water temperature and $r = 0.98$, $P < 0.01$, $N = 5$, for depth of the 14°C isotherm; Table 4). We theorize that a reduced water mass in Lake Granby warms earlier in the year, which facilitates development of *Daphnia* populations and results in more favorable conditions for kokanee survival and growth during the remainder of the year.

TABLE 4.—Comparison of 31 July reservoir volumes and mean water column temperatures (0–40 m) and approximate depths of the 14°C isotherm in mid to late July, Lake Granby, Colorado.

Variable	Reservoir volume (percent of maximum): 99.9	70.5	59.9	57.8	48.5
Temperature (°C)	9.5[a]	11.4[b]	11.5[c]	12.5[d]	13.7[e]
Depth (m) of 14°C isotherm	3	9	11	11	15

[a] 25 July 1962; from Nelson (1964).
[b] 14 July 1981; from Martinez (1986).
[c] 28 July 1992; P. J. Martinez, unpublished data.
[d] 18 July 1978; from W. C. Nelson, Colorado Division of Wildlife, unpublished data.
[e] 23 July 1990; from W. C. Lee, Colorado Cooperative Fish and Wildlife Research Unit, unpublished data.

Influence of Mysis and Lake Trout

Predation by lake trout and *M. relicta* competition for *Daphnia* have been shown to adversely affect kokanee populations (Beattie and Clancey 1991; Bowles et al. 1991; Spencer et al. 1991). Martinez and Bergersen (1991) concluded that although *M. relicta* delayed seasonal development of *Daphnia* populations in Lake Granby, it was not solely responsible for changes in the kokanee population. Although lake trout preyed on kokanees, they did not prevent kokanee overabundance during the early 1980s (Martinez and Wiltzius 1991).

Mean kokanee spawner length and 30 November reservoir volume were regressed for time periods before and after establishment of lake trout and after establishment of *M. relicta* (which also includes lake trout as a factor) in Lake Granby (Figure 3). These periods were lagged by 9 years following introduction of lake trout (1961) and *M. relicta* (1971) because passage of this length of time would be required before lake trout reached sizes to become predominantly piscivorous (Griest 1976) or *M. relicta* densities posed a competitive threat to kokanees (Nesler and Bergersen 1991). Tests for differences between regression slopes and intercepts followed the method of McCracken (1990).

All regressions were significant ($P < 0.05$), and their slopes were not significantly different ($P > 0.5$; Figure 3), which indicates that the inverse relationship between kokanee length and reservoir volume persisted during the three analysis periods. However, the intercept for the post-*Mysis*–lake trout period was significantly lower ($P \le 0.03$) than the intercepts of the other two regression lines (Figure 3), which indicates that kokanees were shorter following the establishment of *M. relicta*.

If lake trout predation on kokanees or *M. relicta* competition with juvenile kokanees for zooplankton, or both, caused significant mortality of ko-

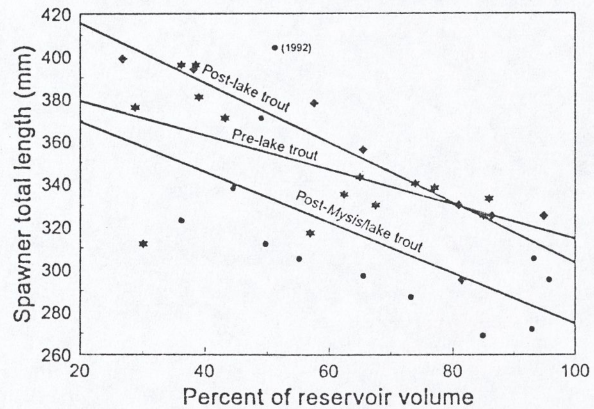

FIGURE 3.—Relation between mean kokanee spawner lengths and 30 November reservoir volume during pre-lake trout (1954–1970, denoted by stars; $r = -0.57$, $P = 0.03$, $N = 14$), post-lake trout (1971–1980, denoted by diamonds; $r = -0.91$, $P = 0.002$, $N = 8$), and post-*Mysis*–lake trout (1981–1992, denoted by dots; $r = -0.64$, $P = 0.03$, $N = 12$) predation periods. Testing for differences in slopes between the three periods showed no significant difference ($F_{2,28} = 0.62$, $P = 0.54$). Differences between intercepts were significant ($F_{2,30} = 5.22$, $P = 0.011$). Pair-wise comparisons for pre- and post-lake trout periods were not significantly different from each other ($P = 0.32$), but they differed significantly ($P = 0.03$ and $P = 0.004$, respectively) from the post-*Mysis*–lake trout period. The largest mean kokanee spawner length at Lake Granby, 404 mm, was recorded in 1992.

kanees, mean spawner length would be expected to increase (Beattie et al. 1988). If only age-0 kokanee survival declined due to *M. relicta* competition for zooplankton, mean spawner length would be expected to remain the same (Bowles et al. 1991). A decline in mean kokanee spawner size might result if *M. relicta* dramatically reduced cladoceran abundance (Morgan et al. 1978); however, *Daphnia* persisted in Lake Granby (Table 3).

The decline in mean spawner length observed at Lake Granby suggests kokanee overpopulation in the 1980s confounded the potentially adverse effects of both *M. relicta* and lake trout. However, mean kokanee spawner length was increasing in the late 1980s and early 1990s, and by 1992, spawners were the longest ever recorded at Lake Granby (Figure 1c). The abnormally large mean spawner length in 1992 (Figure 3), might have been caused by interaction of reservoir volume, reduced kokanee stocking, and enhanced lake trout management. Rieman and Myers (1990) cautioned that unusually large kokanees in a population is a sign that the population may have reached precariously low levels.

Management Implications

Reservoir Volume Fluctuations

The Lake Granby kokanee population appears to exhibit a density-dependent relationship with reservoir volume that is probably a result of variations in reservoir productivity. The initial appearance and duration of the kokanees' preferred food supply, *Daphnia,* also appears to be controlled by reservoir thermal conditions related to reservoir volume. Additionally, the extent of kokanee food competition with *M. relicta* would also be regulated by reservoir volume, which appeared to control the onset, depth, and duration of the thermal refuge where *Daphnia* was protected from predation by *M. relicta.* It is through this theorized cycle of comparatively rich food to comparatively limited food that reservoir volume and thermal conditions are believed to contribute to trends in *Daphnia* and kokanee population dynamics in Lake Granby.

If the *Daphnia* population develops earlier in years of low reservoir volume, then mean *Daphnia* size may be expected to increase in response to the longer growing period. However, kokanees' selectivity for the largest daphnids (Martinez and Bergersen 1991) apparently controls mean *Daphnia* size to a greater extent than do reservoir thermal conditions. When mean *Daphnia* size in the early 1960s was smaller (0.89 mm) than during the early 1990s (1.27 mm), reservoir volumes were nearly equal, 60 and 59%. Consequently, reservoir volume did not appear to be the factor controlling mean *Daphnia* size. The most likely explanation is that during the 1960s, more numerous kokanees (indicated by smaller mean spawner lengths) selectively cropped larger *Daphnia* more effectively than in the 1990s when kokanees appeared to be less abundant. The influence kokanees exert over *Daphnia* species and size composition through selective cropping of *D. pulex* and large *Daphnia* in general suggests that, despite the link between reservoir volume and trends in kokanee size and abundance, kokanees remain a dominant influence on *Daphnia* populations.

Kokanee Length and Density

Although reservoir volume appears to have an overriding effect on kokanee population dynamics in Lake Granby, the magnitude of kokanee stocking and survival can impose trade-offs for managers. Therefore, predictions of density-dependent relationships that influence kokanee growth, length, and fishery quality should influence management goals for population size (Rieman and Myers 1992) and must be taken into account to safeguard kokanee egg supplies.

Kokanee overpopulation and stunting diminishes fishery quality. Often, as kokanee density increases and size declines, catch rates and angler effort decline (Rieman and Myers 1990). Although many 200–250 mm kokanees were present in Lake Granby in the early 1980s, anglers experienced difficulty catching them. Conversely, kokanee populations exhibiting minimum densities and maximum growth may lack compensatory reserve and could be vulnerable to catastrophic events (Rieman and Myers 1992), which jeopardizes egg production for natural deposition or hatchery production.

Kokanee management goals should also consider lake productivity (Rieman and Myers 1992). Martinez and Wiltzius (1991) projected that Lake Granby's kokanee population historically yielded approximately 25,000 kg of kokanees from its maturing year-classes, including those harvested as immature in the summer fishery. Reservoir records indicate that Lake Granby's 30 November volume averaged 65% and 2,500 ha in size. Based on these averages, the reservoir produced about 10 kg/ha of maturing kokanees annually. This value is high relative to kokanee yields reported for 28 lakes and reservoirs in the northwestern USA and British Columbia by Rieman and Myers (1990).

Martinez and Wiltzius (1991) recommended targeting a mean spawner size of 330–340 mm at Lake Granby to provide fishery quality and yield for anglers and also ensure an adequate supply of kokanee eggs. Factors that contribute to reduced kokanee densities and result in larger kokanees should be avoided because overexploitation and excessive piscivory can destabilize even hatchery-sustained populations (Rieman and Myers 1990). For schooling species like kokanee, depensatory mortalities may limit population size to low levels or cause population collapse if piscivores continue to selectively prey upon them after their numbers have declined (Beattie et al. 1988; Bowles et al. 1991).

Lake Trout Management

Sealing and Bennett (1980) recommended that lake trout stocking in Lake Granby be discontinued because of the low lake trout harvest and their adverse effects on the kokanee fishery and egg-take. No lake trout were stocked in Lake Granby from 1978 to 1987, but stocking was resumed in 1988 because managers believed *M. relicta* had so damaged the kokanees' food supply (*Daphnia*) that future management of the reservoir should instead emphasize the lake trout fishery. However, before 1987, Lake Granby's kokanee population did not exhibit signs of collapse, which would have been characterized by unusually large and sparse fish (Rieman and Myers 1990); rather, it exhibited characteristics of overpopulation.

In the 1980s, several factors created a favorable environment for lake trout: high reservoir volume increased the environment available to lake trout and facilitated their reproduction (Martinez and Wiltzius 1991); *M. relicta* was probably peaking in density, which contributed to lake trout recruitment (Griest 1976); overabundant, small kokanees provided abundant prey; and protected-slot regulations for lake trout (508–812 mm in 1988–1989 and 558–864 mm in 1990–1992, both with a one-fish limit) were implemented. Martinez and Wiltzius (1991) recommended reduced kokanee stocking rates (which commenced in 1986) to alleviate kokanee overpopulation, enhance the kokanee fishery, and ensure sufficient egg numbers. However, enhanced lake trout management was not part of this recommendation. These reduced kokanee stocking rates, in concert with the intensive lake trout management, minimize the likelihood that the kokanee harvest will return to the high levels observed in 1975–1984.

Even increased stocking may not be sufficient to maintain or recover kokanees if low kokanee recruitment during periods of delayed *Daphnia* population development fails to saturate piscivores (Bowles et al. 1991). Lake trout stocking in Lake Granby was halted in 1992 (at least temporarily), and the protected slot was shifted to 660–915 mm (with a two-fish limit) to reduce the reservoir's lake trout population. Managing the kokanee population for a summer fishery and an egg source would probably best be served by the 1985–1987 lake trout minimum length limit of 508 mm that protected the mysid-consuming component of the population and encouraged harvest of the more piscivorous component. However, a 508-mm minimum length limit may reduce the number of trophy lake trout, which are highly valued by some anglers and attract both media and management attention. Despite flexibility in Lake Granby kokanee stocking rates, optimizing kokanee management to meet three conflicting demands—summer harvest, a substantial spawning run, and an ample lake trout prey base—appears far more complex than strictly managing for the summer kokanee fishery and egg supply.

Acknowledgments

T. Powell, D. Beauchamp, B. Johnson, D. Willis, and two anonymous reviewers provided valuable comments and criticism to improve this paper. D. Bowden assisted with statistical analyses and interpretation. We thank M. Jones and B. Weiler for their contributions to the data used in this report. A special thanks goes to V. Paragamian for encouraging publication of this study.

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North American Journal of Fisheries Management 15:229–237, 1995
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Kokanee Population Density and Resulting Fisheries

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Abstract.—Catch rate and effort for and yield of kokanee *Oncorhynchus nerka* in seven lakes and reservoirs in Idaho and Oregon were related to fish density. The relationships were not linear. As kokanee density increased from less than 10 to 30–50 fish/ha, values of all three fishery characteristics tended to increase. Little or no improvement occurred at higher densities, and yield appeared to decline at densities above 50 fish/ha. The domed shape of these relationships was explained by a model linking density-dependent length at age and size-dependent catchability: as density increases, anglers encounter kokanee more frequently, but fish length declines at high densities, reducing catchability; low densities should allow fast growth and high catchability, but reduced populations could be subjected to depensatory and potentially destabilizing mortality. This model and its empirical support indicate that management to increase the density of kokanees likely will not produce a proportional benefit for anglers, and the quality of a fishery may even decline.

Kokanee *Oncorhynchus nerka* represent an important fishery resource throughout much of the western United States and Canada (Wydoski and Bennett 1981; Rieman and Myers 1992). The species has been introduced to and become established in many large oligotrophic lakes and reservoirs. The fish communities of western lakes are generally simple, and kokanee populations often reach high densities in what may have been relatively unexploited niches. Kokanees are pelagic, schooling fish that forage almost exclusively on large zooplankton. Because their growth is density dependent and strongly mediated by productivity of the rearing environment (Rieman and Myers 1992), the size and number of fish available to anglers may vary substantially within and among waters.

Management of kokanee fisheries has been eclectic. Attempts to influence density and size of kokanees in Idaho have taken several forms: hatcheries and spawning channels have been used to stabilize or increase densities; introductions of predators, blocking of spawning habitat, and intentional exploitation of spawners have been used to limit or reduce numbers; and opossum shrimp *Mysis relicta* have been introduced as prey to enhance growth (Bowles et al. 1991). Management goals have seldom been consistent among kokanee waters and lack a strong quantitative basis. In Idaho, some systems are managed to produce low densities of very large fish in the creel as a bonus to trout fisheries; other stocking programs strive to maximize densities without causing a decrease in size of fish. Some lakes have produced very large fish but not without some risk. Priest Lake in Idaho produced world-record size kokanees (3.0 kg) in the mid 1970s shortly before the population collapsed irretrievably (Bowles et al. 1991). Flathead Lake in Montana supported a popular fishery on large (270–400-mm fork length) kokanees shortly before the fishery collapsed in 1986 (Hanzel 1984, 1987; Hanzel et al. 1988).

We undertook a study to compare kokanee fisheries and populations throughout Idaho to better define the relationships between fish density and the resulting fishery. Our objective was to define the trade-offs inherent in managing kokanee density. We hypothesized that fishery statistics would improve with increasing low to moderate kokanee densities but not in a linear fashion. We speculated that returns to a fishery would diminish at increasing high densities because of density-dependent reductions in growth and size-dependent changes in catchability. We used two approaches to examine our hypotheses. First, we related available empirical estimates of fishing success and effort to estimates of kokanee density. Second, we linked

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Optional, but very interesting

Refinement and Calibration of a Bioenergetics-Based Foraging Model for Kokanee (*Oncorhynchus nerka*)

Accepted CJFAS 2/26/97

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Abstract

Results from a mechanistic, bioenergetics-based foraging model for kokanee (*Oncorhynchus nerka*) were compared with results from a corroborated standard model. Daily growth estimates from the mechanistic model were 239% higher than estimates from the standard model at temperatures ≥ 12°C, and 42% lower at temperatures ≤ 8°C. The mechanistic model was then modified by incorporating a different respiration function and a new size- and temperature-dependent functional response. Although sensitive to prey and predator size, prey handling time, and feeding duration, results from the modified model were comparable to the standard model. Using observed vertical profiles of temperature and prey densities, model growth estimates for kokanee from Blue Mesa Reservoir, Colorado bounded observed growth under realistic ranges of model parameters. The model also made the following four predictions: seasonal and annual ontogenetic shifts in 1) foraging and 2) migration strategies; 3) very low prey handling times (0.33 $s \cdot$*Daphnia*$^{-1}$) for larger fish, suggesting that kokanee may be capable of gulp/filter feeding; and 4) higher daily maximum consumption rates for smaller kokanee than previously hypothesized. The revised model provides a mechanistic means to forecast anthropogenic and climatic thermal effects on fish behavior and growth.

Introduction

Bioenergetics models (Hewett 1989; Hewett and Johnson 1992) have proven to be an invaluable tool in fisheries ecology. The elegance of these models (collectively called the "Wisconsin" model; Ney 1990) has been their use of fundamental thermodynamics to uncover important ecological insights. For example, the Wisconsin model has been used to explicitly predict physiological effects of body size (e.g., Post 1990), behavioral thermoregulation with changes in body size and food availability (e.g., Crowder and Magnuson 1983), and contaminant accumulation and elimination dynamics (e.g., Madenjian et al. 1993). Overall, these models have defined constraints on growth via temperature, body size, and feeding rate (e.g., Rice et al. 1983; Luecke et al. 1996). The Wisconsin model has also been useful for management purposes including determination of stocking densities (e.g., Stewart et al. 1981) and harvest rates (e.g., Carline et al. 1984; Johnson et al. 1992). For a complete review of the Wisconsin model, see Trans. Am. Fish. Soc. 122(5).

Up to now, these models have performed well at predicting direct effects of environmental change on the consumption and growth of fishes. However, there are no explicit mechanisms for linking consumers with their prey (but see Madenjian et al. 1993). Feeding rate or growth is a required input to solve the energy budget. However, many environmental problems will affect predators indirectly through effects on their prey. For example, eutrophication, nutrient abatement, chemical pollution, thermal pollution, and climate change can affect production of lower trophic levels (e.g., Schindler et al. 1985; McQueen et al. 1986; Carpenter and Kitchell 1993; Porter et al. 1996, Zagarese et al. 1994). To predict the impact of these environmental effects, feeding rate needs to be an explicit, predicted function within the modeling framework.

Incorporation of an explicit feeding function is also important because studies of predator-prey relationships are making a transition from aggregated population level analyses of predator demand and prey supply (e.g., Stewart et al. 1981; Stewart and Ibarra 1991; Eby et al. 1995; Rand et al. 1995) to more detailed, spatially-explicit models of predator-prey interactions (e.g., Mason et al. 1995). These latter models scale up from individuals to populations while accounting for spatial heterogeneity in the biotic (e.g., prey distributions) and abiotic (e.g., temperature, light, and dissolved oxygen) environments.

In this paper, we refine and calibrate a spatially-explicit, bioenergetics-based foraging model for kokanee salmon (*Oncorhynchus nerka*) (Bevelhimer 1990; Bevelhimer and Adams 1993) by incorporating an explicit and improved feeding function to link predator dynamics to prey density. Kokanee are well suited for this type of modeling approach because 1) they are extremely selective in their diet (e.g., Vinyard et al. 1982), 2) their prey are usually vertically stratified (e.g., Lampert 1989), and 3) they exhibit strong diel vertical migrations through a range of temperatures (e.g., Finnell and Reed 1969). Our goal was to develop a realistic and predictive model that could be used to study possible climatic and anthropogenic thermal effects on growth and production of kokanee. In addition to its utility for applied issues, the model provides a framework for examining basic foraging ecology of kokanee and other planktivorous fishes.

Methods

We first describe the model of Bevelhimer and Adams (1993) and outline the comparison we make with the Wisconsin model. Results of this comparison are presented to introduce and justify the refinements to Bevelhimer and Adams' model. We then outline further comparisons between the modified model and the Wisconsin model, and a preliminary sensitivity analysis of the modified model. Finally, we describe parameterization and calibration of the modified model using field data.

General model description

We adopted the bioenergetics model for kokanee developed by Bevelhimer and Adams (1993), from here on referred to as the "B&A" model. The B&A model was originally developed to test the growth maximization hypothesis for kokanee (Bevelhimer and Adams 1993). This hypothesis predicts that kokanee undergo diel migrations to maximize their net energy assimilation by maximizing food consumption and minimizing metabolic costs. Alternatively, Eggers (1978; sockeye) and Johnston (1990; kokanee) suggest diel migration by juveniles is a result of predator avoidance, whereas Clark and Levy (1988; sockeye) propose that migration results from a trade-off between predation risk and energetic efficiency. Results from Bevelhimer and Adams (1993) support the growth maximization hypothesis when kokanee and their prey are thermally segregated - vertical migration can be energetically advantageous under these conditions.

The B&A model is based on the bioenergetics mass balance equation (Kitchell et al. 1977):

$$G = C-(R+F+U), \tag{1}$$

where G = specific growth rate ($g \cdot g^{-1} \cdot day^{-1}$), C = specific rate of consumption, R = specific rate of respiration (including basal and active metabolism, and specific dynamic action), F = specific rate of egestion, and U = specific rate of excretion. The B&A model differs from the Wisconsin model in four important features: the B&A model 1) is constructed to estimate growth from consumption, 2) models consumption as a type II functional response, modified by a temperature-dependent digestion function, 3) is rescaled for a 30-min time step, and 4) allows fish to vertically migrate. Data requirements for a 24-h simulation include vertical profiles of water temperature and prey density, initial fish mass, time fish spends in each depth stratum, feeding status (feeding or not feeding) during each 30-min time step, and mean prey size. A factorial combination of depths and feeding durations is used to examine resultant growth from a suite of possible migration strategies for each given set of environmental conditions.

Estimates of consumption and growth rates, and gross conversion efficiency from Bevelhimer and Adams (1993) were within the range expected for similarly sized kokanee feeding at high rations (Brett 1979). However, these model estimates have not been directly compared to field estimates or results from other models. For the more mechanistic B&A model to be applied to the same range of basic and applied questions that the Wisconsin model has proven useful, calibration and corroboration are critical next steps.

To run a simulation, a fish of a given size is placed in a particular depth stratum with a corresponding water temperature, prey density, and mean prey size. If the fish is feeding, the amount of food consumed is determined as a function of prey density at that depth. At the end of the first 30-min period, fish growth is determined by subtracting energetic losses from energy consumed (see Table 1 of Bevelhimer and Adams (1993) for model equations), and the fish moves (or stays) to the next depth stratum as indicated by model input. Any food remaining in the stomach at the end of the time step is carried over to the next 30-min time step. Food consumed during this next time step, dependent on feeding status and prey density at that depth, is added to any undigested food in the stomach. If the amount of food in the stomach would exceed the stomach capacity (Table 1; Bevelhimer and Adams 1993), then the fish is considered satiated, and consumption during the 30-min period is set at the stomach capacity. As a result, food intake during a 30-min time step can be lower than the amount determined by the functional response. The process of calculating growth is repeated for this and all subsequent time steps. At the end of 24 h, growth is summed over all time steps to provide an estimate of daily growth. Each 24-h simulation was run until a steady-state (ending stomach content mass equal to beginning stomach content mass) was reached (Bevelhimer and Adams 1993). Results from the steady-state runs were used in the analyses.

The Wisconsin model was also used to examine the bioenergetics of kokanee. This model has been corroborated with independently derived estimates of consumption and energy budgets for three populations of juvenile sockeye salmon (anadromous form of kokanee; Beauchamp et al. 1989). Therefore, we were interested in any departures of the B&A model results from the Wisconsin model results for a 24-h simulation, and we attempted to refine the B&A model to reconcile these differences.

We evaluated the B&A model by comparing the daily scope for growth (energy available to a fish after accounting for all energetic losses) and specific rates of consumption, respiration, egestion and excretion of a 500-g kokanee to the Wisconsin model. The standard simulation of Bevelhimer and Adams (1993) was initially used for the B&A model. Inputs to the model for the standard simulation include 1) feeding duration of 12 h, 2) feeding swimming speed of 20 $cm \cdot s^{-1}$, and 3) 2.25-mm prey (*Daphnia* sp). The model was run for 24 h over a range of temperatures (4-25°C).

Maximum scope for growth was estimated by setting prey density to a saturation level (10^6 *Daphnia*·m^{-3}) where the fish could feed at maximum rate (73 *Daphnia*·min^{-1} ; Hyatt 1980). For the Wisconsin model (Hewett and Johnson 1992), parameters were taken from Beauchamp et al. (1989), with proportion (P) of maximum consumption (C_{max}) set to 1.0. Growth and specific rates of consumption and losses were estimated over the same range of temperatures as the B&A model. The same *Daphnia* and kokanee caloric contents were used in each model (Table 1).

Results from the comparison of the two models showed a large discrepancy in daily scope for growth estimates. Daily scope for growth from the B&A model was an average of 42% lower than the Wisconsin model at temperatures ≤ 8°C, and an average of 239% higher at temperatures ≥ 12°C (Fig. 1a). The B&A model predicted positive growth across all temperatures (4-25°C), with an optimum growth of 4.03 g·day^{-1} at 16°C. The Wisconsin model predicted positive growth for temperatures ≤ 18°C, with an optimum growth of 3.17 g·day^{-1} at 8°C (Fig. 1a).

The discrepancy in growth estimates can be attributed to much lower active respiration rates in the B&A model (Fig. 1b,c). Across all temperatures examined, respiration estimates from the B&A model were, on average, 43% lower than estimates from the Wisconsin model. The B&A model also estimated higher consumption rates and showed a plateau in consumption at higher temperatures (Fig. 1b), whereas the Wisconsin model predicted lower consumption rates as well as a drop in consumption at temperatures > 18°C (Fig. 1c).

All other components of the energy budget used in the B&A model (egestion and excretion; Bevelhimer and Adams 1993) were the same functions used in the Wisconsin model (Beauchamp et al. 1989). We therefore modified the respiration and consumption functions of the B&A model to produce growth estimates comparable to the corroborated Wisconsin model.

Modified B&A model

Respiration - The respiration function of Beauchamp et al. (1989; from Hewett and Johnson 1992):

$$[2] \qquad R = 0.00143 \cdot M^{-0.209} \cdot e^{(0.086 \cdot T)} \cdot ACTIVITY \cdot oxycal \cdot \frac{t}{t_{day}} \,,$$

where R = respiration ($cal \cdot g^{-1} \cdot t^{-1}$), M = mass (g), T = temperature (°C), ACTIVITY = $e^{(0.0234 \cdot VEL)}$ and is the increment for active metabolism, VEL = $9.9 \cdot e^{(0.0405 \cdot T)} \cdot M^{0.13}$ and is the optimal swimming speed ($cm \cdot s^{-1}$), oxycal = oxycaloric conversion factor ($cal \cdot g^{-1}\ 0_2$), t = model time step (min), and t_{day} = length of day (min), was substituted into the B&A model (Table 1). Respiration was divided by 48 to convert from the daily time step of Beauchamp et al. (1989) to the 30-min time step of Bevelhimer and Adams (1993).

Functional response - Experiments have demonstrated that young sockeye from the Pacific northwest stop feeding as water temperature approaches their upper tolerance limit (≥ 23°C; Donaldson and Foster 1940; Brett 1952; Brett et al. 1969). We therefore concluded that the asymptote in consumption at the highest temperatures in the B&A model (Fig. 1b) was inappropriate for western North American stocks. To correct this, the amount of *Daphnia* biomass consumed in each time step was modified by Thornton and Lessem's (1978) temperature function (Beauchamp et al. 1989; Table 1). Application of the Thornton and Lessem function was scaled with reference to

10°C because the functional response used in the B&A model was derived at this temperature (Hyatt 1980; Bevelhimer and Adams 1993). Furthermore, the function was applied to the biomass of *Daphnia* consumed, and not the number consumed, because the function coefficients were derived using biomass measurements (Beauchamp et al. 1989).

Sensitivities of the Wisconsin model parameters are well known (Kitchell et al. 1977; Bartell et al. 1986). Therefore, we did not perform sensitivity analyses on the components of the modified B&A model shared with the Wisconsin model. However, we did perform a preliminary sensitivity analysis of the modified B&A model on the unshared components. The new model was run using two sizes of kokanee (100 and 500 g), three feeding durations (6, 12, and 18 h), and three prey sizes (1.75, 2.25, and 2.75 mm). Results were compared with the Wisconsin model across the same temperature range and maximum feeding rates used in the initial comparison.

Results from this comparison suggested one of two possibilities: either 1) there should be large differences in time spent foraging (~6 h) between 100 and 500-g fish, or 2) there are shortcomings in the consumption function. For the latter, consumption is the only plausible function to criticize as respiration, egestion, and excretion are identical in both models, and differences in SDA are both minimal and dependent on the amount of food consumed. Furthermore, the functional response used in the B&A model (Hyatt 1980) was derived from feeding experiments using a single size-class of kokanee (15 g) at 10°C, and did not include the possibility of size-dependence in foraging rate. Because work on other fishes suggests predator size can influence their functional response (Werner 1977; Miller et al. 1992, 1993; Walton et al. 1994), we pursued modification of the functional response.

We scaled the functional response to predator size through volume searched using the following form of a Holling type II functional response:

$$C = \frac{E \cdot Z}{1 + E \cdot Z \cdot h} \cdot 60 \quad , \qquad [3]$$

where C is consumption (*Daphnia*·min^{-1}), E is volume searched (m^{-3}), Z is *Daphnia* density (m^{-3}), and h is handling time (s·*Daphnia*$^{-1}$; Table 1). Volume searched, E, was taken from Gerritsen and Strickler (1977):

$$E = \frac{\pi \cdot R_d^2}{3} \cdot \frac{(3 \cdot v^2 + u^2)}{v} \quad , \qquad [4]$$

where R_d is the reaction distance of kokanee to their prey (m), v is kokanee swimming speed (m·s^{-1}), and u is *Daphnia* swimming speed (m·s^{-1}; Table 1). Kokanee swimming speed is size- and temperature-dependent and is determined from the VEL component of the respiration function (Eq. 2; Table 1). We assumed that during feeding 100% of the *Daphnia* encountered by kokanee are ingested (Hyatt 1980, Vinyard et al. 1982).

To calibrate the functional response, Equations 3 and 4 were used to predict consumption at the prey densities, fish size (15 g), and water temperature (10°C) used in the experiments of Hyatt (1980). Handling time was taken from the maximum consumption observed by Hyatt (≈ 50 *Daphnia*·min^{-1} or 1.2 s·*Daphnia*$^{-1}$). Predictions from Equations 3 and 4 under these conditions were then compared to the results of Hyatt (1980).

The new functional response scales for body size in two ways. First, increased body size increases swimming speed, thus directly influencing the volume searched E (Eq. 4). The second possible influence is handling time differences among fish size-classes. No handling time data were available so a range of values were used (Table 1). Reaction distance was assumed to be constant across the size-classes because the literature suggests reaction distances in other visually feeding planktivorous fishes increase greatly during very early development, but then diminish beyond a certain size - usually within the first year of life (e.g., Breck and Gitter 1983; Rahmann et al. 1989; Wahl et al. 1993). Therefore, the mean reaction distance of 15-g kokanee from Hyatt (1980) was assumed to represent the reaction distance of larger fish (Table 1). We examined the sensitivity of the functional response to changes in fish body size (i.e., volume searched) and handling time.

Model Parameterization and Simulations

Growth estimates from the modified model were dependent on model inputs (predator and prey sizes, feeding duration, handling time). As a result, various combinations of model inputs could be used to generate growth estimates similar to the Wisconsin model. We therefore compared estimates of growth from the modified B&A model with observed growth of age-1, -2, and -3 kokanee from Blue Mesa Reservoir, Gunnison, CO (Cudlip et al. 1987). Inputs to the model included observed vertical profiles of temperature and *Daphnia* densities from 1994, mean prey size from kokanee stomachs sampled in 1995, and observed masses of fish from 1995. Limnological data from 1994 were used because these data were collected at a finer spatial and temporal resolution than in 1995. However, much more fish growth data were available from 1995 than 1994. Because comparisons of temperature profiles, prey densities and distributions, and kokanee growth collected in both years showed similar patterns (Johnson et al. 1995, 1996), we assumed results would not be compromised by using input from the two different years.

For simulations of each age-class, a range of feeding durations and handling times were used. The goal was not necessarily to match modeled growth with observed - inputs can be adjusted to generate matching results. Rather, the goal was to bound the estimates using a more mechanistic approach than the more commonly used Wisconsin model. Incorporating feeding mechanisms should then clarify which factors are most important to understanding kokanee growth, and how these factors might direct future field and laboratory work.

Blue Mesa Reservoir (BMR) is a mesotrophic, 3 700 ha, 32 km long impoundment in southwestern Colorado with a storage capacity of 1.16×10^9 m^3. The fish community of BMR is relatively simple, consisting of primarily kokanee, rainbow trout (*Oncorhynchus mykiss*), brown trout (*Salmo trutta*), lake trout (*Salvelinus namaycush*), and longnose sucker (*Catostomus catostomus*). Kokanee is the dominant fish species. However, the population has been steadily declining over the past three years with a concomitant increase in the lake trout population (Sherman Hebein, Colorado Division of Wildlife, unpublished data).

Thermal profiles of BMR were obtained using a Yellow Springs Instruments Model 58 meter with a 60-m probe cable. Measurements were taken at 1-m intervals from 0 to 20 m and at 5-m intervals from 20 to 55 m, from May through September 1994.

Zooplankton were collected by oblique tows using a Wildco model 37-315 Clark-Bumpus plankton sampler with a 130-mm diameter opening and a 153-μm net. The flowmeter on the Clark-Bumpus sampler was calibrated using a Schwaffer water velocity meter. Two replicate samples were taken from each of 0-5, 5-10, 10-15, and 15-30-m strata on 21 May 1994. During June-September 1994 three replicate samples were collected every two to three weeks from each of 0-5, 5-10, and 10-15-m strata, and two replicates from the 15-30-m stratum. All samples were taken between the hours of 09:00 and 12:00, and preserved in 8% sugared, buffered formalin.

A 1-mL aliquot was taken from each sample using a Hensen-Stempel pipette. The aliquot was placed in a Sedgwick-Rafter cell where all *Daphnia* were identified to species and enumerated (Lind 1979; Soranno and Knight 1993) under a compound microscope. The first 24 individuals encountered in each sample were measured with an ocular micrometer to the nearest 0.01 mm. Two aliquots from each replicate sample were processed.

Densities of *Daphnia* ≥ 1.0 mm in each stratum (m^{-3}) were used as prey input to the model because 1) kokanee feed exclusively on *Daphnia* in BMR (97% *D. pulex* and 3% *D. galeata*; Johnson et al. 1995, 1996), and 2) the original functional response used by Bevelhimer and Adams (1993) was a function of the density of *Daphnia* ≥ 1.0 mm (Hyatt 1980).

Mean length of each age-class of kokanee in 1995 was estimated from otolith samples obtained on 8 June (age-1, n=11; age-2, n=20; age-3, n=8) and 26 July (age-1, n=22; age-2, n=33; age-3, n=16) from fish sampled in vertical gill nets and angler's creels (Martinez 1996). Mean length at the end of the growing season was estimated from backcalculations (age-1, n=123; age-2, n=54; Johnson et al. 1996) and from otoliths of fish in the spawning run (age-3, n=163; Martinez 1996). Wet masses were computed using a length-mass regression ($r^2 = 0.95$, n=228) developed from all fish sampled in vertical gill nets during June through September (Johnson et al. 1996). We computed the instantaneous daily growth rate (G) and interpolated masses (M) between fish sampling dates using the formula:

$$[5] \qquad M_1 = M_0 \cdot e^{Gt}$$

where M_1 = final mass (g), M_0 = initial mass, and t = number of days between sampling dates (for G) or number of days to the interpolated mass (for M). We estimated daily growth rates (DGR; $g \cdot d^{-1}$) on limnological sampling dates from the equation:

$$[6] \qquad DGR = M_0 \cdot e^{Gt} - M_0$$

where M_0 = mass at the start of the day, and t = 1 d.

Vertical profiles of temperature and *Daphnia* (≥1.0 mm) densities from a reference station in Sapinero Basin, the largest and most downstream basin of BMR, were used as inputs to the model (Table 1). Three dates were chosen from the 1994 sampling period to represent seasonal fluctuations in temperature and prey availability. Because mature BMR kokanee typically begin their spawning migration in September, we did not use September sampling dates for the simulations.

Temperature data on each limnological sampling date, t_{lim}, were averaged into seven depth strata: 0-5, 5-10, 10-15, 15-20, 20-25, 25-30, and 30-50 m. *Daphnia* densities from the zooplankton sampling were assigned to these strata accordingly. The observed densities from the 15-30-m strata were consistently low and were assigned to each of the 15-20, 20-25, 25-30, and 30-50-m strata. The 30-50-m stratum was used to allow kokanee access to deeper, colder water despite no routine zooplankton sampling at these depths. Few *Daphnia* were found in zooplankton samples collected from 40 and 50 m in July 1994 and 1996 (BMJ, unpublished data), indicating extrapolation of

Daphnia densities from the 15-30-m stratum to these depths is a reasonable assumption. Additionally, data from experimental vertical gill nets set in BMR in 1994 and 1995 show that kokanee do reside at these depths at times (Johnson et al. 1995, 1996).

Daphnia do not vertically migrate in BMR (Johnson et al. 1995). Therefore, the vertical distribution of *Daphnia* used as model input for each 24-h simulation was held stationary.

Fish were allowed to locate at two depths (feeding and non-feeding periods) in each 24-h simulation. Depths were the mid-points of the strata identified above (2.5, 7.5, 12.5, 17.5, 22.5, 27.5, and 40 m). All possible migration strategies were evaluated (7 depth strata = 28 different migration strategies). The migration strategy that maximized growth on each limnological sampling date (t_{lim}) was noted, and that growth was used in the comparison with the observed growth estimates on that date.

The mean size of *Daphnia* in the diets of BMR kokanee in 1995 (1.68 mm; Johnson et al. 1996) was used to convert consumption from numbers to biomass (Table 1). Mean size consumed did not differ across the season or age-classes (BMJ, unpublished data). Initial masses of each kokanee age-class were determined for day t_{lim}-1 using Equation 5. Very little information on kokanee feeding duration and prey handling times was available in the literature, but initial growth estimates from the model appeared to be sensitive to these parameters. We performed simulations at seven different feeding durations (4, 6, 8, 10, 12, 14, and 16 h) and five different handling times (0.33, 0.5, 0.67, 1.0, and 1.2 s·*Daphnia*$^{-1}$) to evaluate the sensitivity of the modified model to these parameters. We used observed growth ± 20% as our criteria for determining which combinations of feeding durations and handling times were realistic.

Results

Modified B&A model

For a 500-g kokanee under standard simulation conditions, application of the respiration function of Beauchamp et al. (1989) and the Thornton and Lessem (1978) temperature function greatly improved the performance of the B&A model when compared to the Wisconsin model. The combination of higher respiration rates (identical to the Wisconsin model) and the decline in consumption at higher temperatures (Fig. 1d) brought estimates of scope for growth in line with estimates from the Wisconsin model for temperatures > 10°C (Fig. 1a). Growth estimates at low temperatures were still less than the Wisconsin model - a result of lower consumption in the modified B&A model at these temperatures (Fig. 1d).

Scope for growth varied considerably with fish size and feeding duration when prey size (2.25-mm *Daphnia*) was held constant (Fig. 2a,b). For a 500-g kokanee, a 12-h feeding duration best fit growth estimates from the Wisconsin model (mean squared error, MSE = 0.82; Fig. 2a). A 6-h feeding period resulted in lower estimates across the entire temperature range (MSE = 3.97), while an 18-h feeding period resulted in higher estimates (MSE = 5.85; Fig. 2a). Temperature for optimum growth also shifted with changes in feeding duration. The more feeding duration was restricted, the lower the optimum temperature (Fig. 2a). This is expected from the B&A model - as food becomes limited, simulated fish minimize energy costs by using colder water (Bevelhimer and Adams 1993). This has also been demonstrated empirically (Crowder and Magnuson 1983). For the 100-g kokanee, a 6-h feeding duration best matched growth estimates from the Wisconsin model (MSE = 0.10; Fig. 2b). Feeding periods of 12 and 18 h both overestimated scope for growth (MSE = 1.27 and 4.27, respectively). Again, a decrease in optimum temperature for growth occurred with decreasing feeding durations (Fig. 2b).

When prey size and feeding duration were varied simultaneously, and fish were held at their optimum temperature for growth, results differed for the two fish sizes. Increasing prey size from 1.75 to 2.75 mm (an increase in *Daphnia* mass of nearly 400%) for the 100-g fish resulted in relatively small increases in growth (average across feeding durations = 12%; Fig. 2d). Much larger increases occurred when feeding time was increased from 6 to 18 h (average across prey sizes = 218% increase). For the 500-g fish, an increase in prey size from 1.75 to 2.75 mm translated to an average increase in growth of 458% (Fig. 2c). Increasing feeding duration for the larger fish also increased growth rates by over one order of magnitude (average of 1033%; Fig. 2c).

Estimates of consumption (*Daphnia*$\cdot$min^{-1}) from the functional response using Equations 3 and 4 for a 15-g kokanee, feeding at 10°C with a handling time of 1.2 s$\cdot$*Daphnia*$^{-1}$, fell within the 95% confidence intervals of the experimental data of Hyatt (1980; Fig. 3a). Consequently, we assumed that the new functional response (Eqs. 3 and 4) was adequate to describe foraging of a 15-g kokanee under these conditions, and that it could then be scaled for body size effects via size-dependent search volume. A complete list of equations used in the modified B&A model is listed in Table 1.

Consumption rate estimates from the new functional response were much more sensitive to handling time than fish body size (Fig. 3b). The asymptote of consumption rate decreased by 70% (from 166 to 49 *Daphnia*$\cdot$min^{-1}) when handling time was increased 260% (from 0.33 to 1.2 s$\cdot$*Daphnia*$^{-1}$), whereas there was very little difference in consumption rate with a 90% reduction in body size (from 573 to 59 g; Fig. 3b).

Model Calibration

Surface temperatures in Sapinero Basin in 1994 ranged from a low of 13 °C on 21 May to a high of 20 °C on 18 August (Fig. 4). Hypolimnetic temperatures generally stayed near 5 °C throughout the season. Despite these vertical gradients, a strong thermocline was not apparent on any of the sampling dates (Fig. 4).

The abundance of *Daphnia* ≥ 1.0 mm in the upper 10-m of the water column remained high throughout the season, accounting for 91% of all *Daphnia* in this size-class in the water column (Fig. 4). Maximum densities never fell below 9 100 m^{-3} (21 May), while the highest recorded density exceeded 17 300 m^{-3} (21 July; Fig. 4). These maximum densities were well above densities required to saturate the functional response for each handling time (Fig. 3).

Growth rates of kokanee collected from BMR in 1994 and 1995 were relatively high. Mean length of BMR kokanee at age-1 (170 mm; Johnson et al. 1996) was greater than backcalculated length at age-1 reported in other lakes throughout the western United States (range = 78-156 mm, n = 8: Bjornn 1961; Bowler 1976; Bowler 1979; Cordone et al. 1971; Clark and Traynor 1972; Hanzel 1974*a*,*b*). Age-2 and -3 BMR kokanee each had the second largest length at age (264 and 335 mm, respectively; Johnson et al. 1996) when compared to similarly aged fish throughout the west (age-2, range = 154-319 mm, n = 8; age-3, range = 209 - 362 mm, n = 7: Bjornn 1961; Bowler 1976; Bowler 1979; Cordone et al. 1972; Clark and Traynor 1972; Hanzel 1974*a*,*b*). Daily growth estimates of BMR kokanee ranged from 0.41 to 1.39 $g \cdot day^{-1}$ for age-1 fish, 0.52 to 2.66 $g \cdot day^{-1}$ for age-2 fish, and 1.85 to 2.40 g·day^{-1} for age-3 fish (Fig. 5). All three age-classes showed a drop in daily growth over the second half of the field season (Fig. 5).

Simulations using the modified model (Table 1) and observed data from BMR (Figs. 4 and 5) corroborated results from earlier evaluations (Figs. 2 and 3). Daily growth estimates from the model indicated that different foraging strategies should be employed by different age-classes, but that these optimal strategies change seasonally with changes in prey and temperature distributions and fish body size.

Early in the growing season (10 June), daily growth estimates of age-1 kokanee were more sensitive to changes in feeding duration than to changes in handling times (Fig. 6a). Using the mean growth rate across all handling times for each of the 4 (0.66 g·d^{-1}) and 16-h (1.69 g·d^{1}) feeding durations (Fig. 6a), the range in daily growth estimates was 163% of the observed growth (0.80 g·d^{-1}). Using the mean growth rate across all feeding durations for each of the 1.2 s·*Daphnia*$^{-1}$ (1.22 g·d^{-1}) and 0.33 s·*Daphnia*$^{-1}$ (1.39 g·d^{-1}) handling times, the range in daily growth estimates was only 21% of the observed growth. Similar comparisons for age-2 and -3 kokanee showed that modeled growth of age-2 fish was also more sensitive to feeding duration than to handling time (90 versus 36%, respectively; Fig. 6b), whereas modeled growth of age-3 fish was more sensitive to handling time than to feeding duration (151 versus 127%, respectively; Fig. 6c). Based on observed daily growth estimates (± 20%), model simulations for 10 June suggest that age-1 kokanee should feed between 4 and 6 h·d^{-1}, age-2 between 12 and 16 h·d^{1}, and age-3 between 8 and 16 h·d^{1} , depending on the handling time (Fig. 6).

The model also indicated a progression in kokanee migration strategies for 10 June. Age-1 fish were predicted to feed at the surface and migrate the least, age-2 fish were predicted to feed at or near the surface and migrate slightly deeper than age-1 fish, and age-3 fish were predicted to feed below the surface and migrate the deepest (Fig. 6). Within each age-class, foraging occurs higher in the water column and migration distances decrease with increases in feeding durations and/or decreases in handling times (Fig. 6).

Daily growth estimates from the modified B&A model for age-1 kokanee during the middle of the growing season (21 July) were again more sensitive to feeding duration than to handling time. Increasing feeding duration from 4 to 16 h changed daily growth by 135% compared to observed growth, whereas decreasing handling time from 1.2 to 0.33 $s \cdot \textit{Daphnia}^{-1}$ changed daily growth by 47% (Fig. 7a). Results (not shown) from simulations using the starting mass for age-1 fish on 10 June (60 g) for the 21 July input data (Fig. 4) were qualitatively similar to growth estimates from 10 June. This indicates that the increasing (decreasing) sensitivity of growth rates to handling time (feeding duration) for age-1 fish is a result of increased body size rather than differences in the prey and temperature distributions on the two dates. Model growth rate estimates for age-2 fish on 21 July were nearly equally sensitive to changes in feeding duration and handling time (71 versus 61%, respectively; Fig. 7b). Age-3 fish were more sensitive to handling time than to feeding duration (140 versus 96%, respectively; Fig. 7c), similar to simulation results for 10 June (Fig. 6c).

Comparisons of modeled growth estimates with observed estimates (± 20%) on 21 July show that an increase in the amount of time spent feeding (compared to 10 June) was necessary for all age-classes to bound observed growth (Fig. 7). Age-1 fish needed to feed 6 to 12 $h \cdot d^{-1}$ to grow the observed 1.39 ± 0.28 $g \cdot d^{-1}$, age-2 fish 14 to 16 $h \cdot d^{-1}$ to grow 2.66 ± 0.53 $g \cdot d^{-1}$, and age-3 fish 10 to

16 $h \cdot d^{-1}$ to grow 2.4 ± 0.48 $g \cdot d^{1}$ (Fig. 7). If the handling time of age-3 fish was restricted to ≥ 0.5 s·*Daphnia*$^{-1}$, their modeled growth would only approach the observed estimate if they fed for 16 $h \cdot d^{-1}$, demonstrating the importance of an accurate handling time estimate for larger fish (Fig. 7c). Furthermore, simulations using the Wisconsin model for age-1 and -2 kokanee on this date show that these fish could not reach their observed growth when allowed to feed at maximum consumption (P = 1.0) at their optimum temperature (Fig. 7a, b).

In general, results from the modified B&A model also show that age-1 fish should forage at and migrate to deeper depths on 21 July than on 10 June. Age-1 fish will also feed closer to the surface and migrate less with increased feeding durations and/or decreased handling times. The migration strategy of age-2 fish was to feed and migrate deeper than on 10 June. However, their migration strategy generally remained unchanged on 21 July regardless of feeding duration or handling time (Fig. 7b). The migration strategy of age-3 fish on 21 July remained unchanged with feeding duration, but changed drastically with different handling times. For example, these fish migrated from 7.5 to 40 m with a handling time of 0.33 s·*Daphnia*$^{-1}$. At the highest handling times, they did not migrate, remaining at 40 m depth (Fig. 7c).

Results from model simulations for 18 August show that growth of age-1 fish was still more sensitive to feeding duration than to handling time (442% versus 212%, respectively; Fig. 8a), but that the difference was smaller than previous dates. Model growth of age-2 and -3 fish was more sensitive to changes in handling time than to changes in feeding duration (398% versus 336%, respectively, for age-2; 142% versus 24%, respectively, for age-3; Fig. 8b, c). Depending on handling time, age-1 kokanee needed to feed between 6 and 14 $h \cdot d^{-1}$ to bound the observed growth rate, age-2 between 6 and 16 $h \cdot d^{-1}$, and age-3 between 12 and 16 $h \cdot d^{-1}$ (Fig. 8). The required feeding duration of age-2 fish dropped dramatically - a result of the substantial drop in the observed growth rates (from > 2.5 to < 1.0 $g \cdot d^{-1}$; Fig. 5b).

Optimal migration strategies for 18 August, when surface water temperature was highest, show that age-1 fish will feed at and migrate to deeper depths than on 21 July. However, migration strategies within this age-class did not change very much with feeding duration or handling time (Fig. 8a). Migration strategies for age-2 and -3 fish are similar to their respective migration patterns on 21 July (Fig. 8b,c).

Discussion

In this study, we have modified the original B&A model to provide comparable results to the corroborated Wisconsin model, and to calibrate the new model using field observations. The process of evaluating the sensitivity of the model and identifying combinations of inputs that bounded observed growth uncovered some interesting predictions about the foraging ecology of kokanee. First, the model predicted an ontogenetic shift in foraging strategy when kokanee reached approximately 300 g. Foraging strategies of kokanee < 300 g should be to increase their feeding time, while strategies for fish > 300 g should be to reduce their handling times. This shift in feeding strategy is a result of changing stomach capacities of the fish. If we assume that consumption of larger prey is equivalent to more efficient consumption of smaller prey, then the preliminary sensitivity analysis (Fig. 2c, d) demonstrates the relationship between stomach capacity and foraging strategy. While feeding on the smallest prey sizes (1.75 mm), the stomach capacity of smaller fish was reached quickly while consuming at maximum rates. The only way to increase consumption (i.e., growth) is to spend more time feeding. Conversely, larger fish were not limited by stomach capacity while feeding on 1.75-mm *Daphnia*. Therefore, increasing prey size to 2.25 mm (or increasing the rate at which 1.75-mm *Daphnia* are consumed) resulted in a much larger increase in growth.

Second, the model results suggested that age-3 kokanee required very short handling times (0.33 s·*Daphnia*$^{-1}$) to allow sufficient consumption rates to match their observed daily growth later in the season. Laboratory observations made by Hyatt (1980) demonstrated that age-0 kokanee are particulate feeders. However, it is difficult to accept that kokanee could feed on 3 *Daphnia*·s^{-1} with this feeding mode. Such a short handling time suggests the ability to forage by gulping and/or filtering, and simple calculations show that this hypothesis is tenable. Mouth gape area measurements made on adult kokanee (mean mass 511.2 g) collected from BMR averaged 0.0004 m^2 (JDS, unpublished data). At 10°C, these fish have an optimum swimming speed of 0.33 m·s^{-1} (Beauchamp et al. 1989, Table 1). Using mean prey density of 17 500 *Daphnia*·m^{-3} (maximum observed densities in BMR; Fig. 4), and the equation

$$[4] \qquad \mathit{HandlingTime} = \frac{1}{\mathit{MouthArea} \cdot \mathit{SwimmingSpeed} \cdot \mathit{PreyDensity}},$$

potential *in situ* handling time is estimated to be 0.43 s·*Daphnia*$^{-1}$. Given the integrated nature of zooplankton samples collected by the Clarke-Bumpus, it is likely that kokanee can experience much higher densities than 17 500 *Daphnia*·m^{-3} in BMR. Consequently, handling time could easily reach 0.33 s·*Daphnia*$^{-1}$.

While Hyatt (1980) did not observe filter feeding in kokanee during feeding experiments using

Daphnia spp., maximum prey densities used in his experiments were 2 000 m^{-3}, compared to epilimnetic densities of 9 000 to 17 500 m^{-3} in BMR. We are not aware of any other studies that have specifically examined the foraging behavior of kokanee at such high zooplankton densities. Some studies have indicated that prey intake by other planktivorous fishes can be maximized by switching from particulate to filter feeding when prey concentrations exceed some critical threshold (e.g., Gibson and Ezzi 1992).

Third, when allowed to feed for 16 h (midsummer day length) in the modified model, age-1 BMR kokanee were predicted to have maximum growth rates nearly double the maximum scope for growth estimate (at the optimum temperature) from the Wisconsin model (Figs. 6a-8a). In this case, only a small portion of the difference (~10%) can be attributed to the energetic efficiency of vertical migration - smaller fish are more tolerant of warmer water and therefore not as restricted in their upper thermal range compared to larger fish. Rather, the differences in predicted growth rates are a result of the differences in maximum consumption rate in each model.

The discrepancy points out the need to accurately extrapolate from laboratory feeding experiments to feeding behavior in the field. This is an important issue given the exciting technological advances in spatially-explicit modeling of predator-prey interactions (Brandt et al. 1992; Mason and Patrick 1993, Mason et al. 1995). We suspect that feeding rate predictions differ due to different time scales used in each model. In the modified B&A model, fish feed in 30-min time steps. Maximum consumption over 24 h is determined by feeding duration, stomach capacity, and gastric evacuation rate. Additionally, the functional response was derived at a 1-min time scale with fasted fish, and therefore motivation to feed is maximal in the model as long as there is any unfilled stomach volume. Because satiation does not enter directly into the calculation of *in situ* feeding rate, long feeding durations may predict unrealistic daily consumption rates in the modified model. However, Godin (1981) experimentally demonstrated that feeding rates of juvenile pink salmon (*O. gorbuscha*), after satiation, were approximately equal to their gastric evacuation rate. More work is needed to determine the importance of satiation on the functional response of age-1 and older kokanee .

In the Wisconsin model, maximum daily consumption rate was derived from feeding experiments where fish were fed excess rations three times a day (Brett et al. 1969, Brett 1971). It is not clear how scaling three distinct feeding bouts to 24 h might affect maximum daily consumption estimates, compared to a more continuous feeding regime typical of a pelagic planktivore. Furthermore, results of feeding experiments using pelleted food may not be applicable to fish in the wild (Beauchamp et al. 1989). Beauchamp et al. (1989) state that their model of maximum consumption should be considered an hypothesis. In light of our results, we hypothesize that maximum consumption rates of age-1 kokanee (< 150 g) can be considerably higher than previously predicted by the Wisconsin model.

Alternatively, Luecke and Brandt (1993) found that rainbow trout increased the mass of *Daphnia* in their stomachs by reducing (squeezing out) the water content of their prey. This effectively doubled the energy density of the *Daphnia*. If kokanee are capable of this, then our model would overestimate the feeding durations and/or underestimate the prey handling times required to bound observed growth. It would also explain why growth estimates from the Wisconsin model required a P > 1.0 to approach observed growth of age-1 and -2 kokanee in July. However, even doubling growth estimates from our modified model for age-3 kokanee in August would still require a feeding rate of 3 *Daphnia*·s^{-1} to approach observed growth.

Finally, the model predicted ontogenetic shifts in migration strategies at both seasonal and annual time scales - consistent with expectations from the bioenergetics principle that thermal optima are mass-dependent. As the growing season progressed, age-1 fish in the modified model fed at greater depths and migrated longer distances. Age-2 and -3 fish showed similar but weaker patterns for the first half of the growing season. Across age-classes, the model demonstrated that older fish tend to feed at and migrate to greater depths at any given point in time.

For all simulations, we kept kokanee reaction distance constant (0.08 m) regardless of feeding depth. This is an unlikely assumption given the changes in light level with depth at both diurnal and seasonal time scales. Based on secchi depths for Blue Mesa Reservoir on the three simulation dates (2.9, 3.9, and 5.6 m for June, July, and August, respectively; BMJ, unpublished data), calculated changes in percentage transmission of surface light from a depth of 2.5 to 12.5 m as a function of secchi depth (Wetzel 1983), and measured reaction distances of several fish species over a range of light intensities (O'Brien 1979), we reduced kokanee reaction distance to 0.04 m and ran several simulations across the three simulation dates. Decreased reaction distance did not affect model growth rates of smaller kokanee because their smaller stomach capacities were saturated at the high prey densities. However, model growth rates of fish that were predicted to maximize growth by feeding at 12.5-m depth (age-2 kokanee in August, and age-3 model kokanee in July and August) were reduced two to five times. Consequently, the optimum migration strategies in these cases shifted to feeding depths of < 10 m, where light levels and reaction distances would be presumably greater. However, growth rates would be lower than initial simulations (reaction distance 0.08 m) because of warmer temperatures at these feeding depths. This is particularly important to note for age-3 fish in August, where the gap between observed and model growth would widen, enforcing the notion that these fish might have to feed at a greater rate and/or for longer periods of time. Future modifications to the functional response to include the effects of light levels on reaction distance would add another level of sophistication to the model, and might provide more insights into the foraging ecology of kokanee.

We have been sampling kokanee with both experimental vertical gill nets and sonar since 1993 to examine diets and to estimate population abundances. The sampling designs employed do not provide adequate temporal resolution and coverage to appropriately test our model predictions of migratory behavior. Other studies have found similar differences between day and night vertical distributions of kokanee (e.g., Finnell and Reed 1969; Maiolie and Elam 1996), although these patterns are not ubiquitous and may even be reversed (e.g., Chapman and Fortune 1963; Levy 1991). A comprehensive series of diel surveys in BMR is planned for the 1997 field season to corroborate model predictions.

The model predictions, while not fully tested in this study, demonstrate the predictive capabilities that are possible by adding more ecological realism to the bioenergetics framework. Despite enjoying wide use, application, and in a few cases corroboration (Hanson et al. 1993; Ney 1993), the Wisconsin model lacks some of this ecological realism. Ecosystem managers need predictive models to forecast individual responses and community and ecosystem consequences of natural and anthropogenic environmental change. In reservoirs, climate and water management interact to determine stratification patterns, with obvious implications for lentic biota. In response to the increasing demand on reservoir water in the western United States to serve an expanding range of purposes, traditional reservoir operation schedules are being changed. Large releases to simulate natural floods for downstream habitat restoration (Wuethrich 1996), periodic releases to help transport salmon smolts to the ocean (Berggren and Filardo 1993), and spring releases to mimic a natural snowmelt hydrograph and improve spawning conditions for endangered Colorado River fishes (Tyus 1992) all are significant departures from historic operations. Few, if any studies have addressed the upstream (reservoir) effects of these new operation strategies.

Our intent in further developing the B&A approach was to generate a modeling framework that was sufficiently realistic and accurate to predict effects of seasonal variation in vertical gradients of temperature and prey density on kokanee growth, behavioral response, and population consumption demand. It is reasonable to hypothesize that changing reservoir operations could alter temperature and prey stratification, imposing constraints on kokanee depth distribution, especially in reservoirs such as BMR that are near the upper thermal limit for kokanee. Consequences might include reduced access to predominately epilimnial zooplankton resources, reduced scope for growth, and increased spatial and temporal overlap with, and hence, predation risk from the primary piscine predator, the lake trout (e.g., Martinez and Wiltzius 1995). The modeling framework further developed here provides the means to predict the effects of reservoir stratification scenarios on fish behavior and growth, and as such, could be a powerful tool for understanding the ecological effects of anthropogenic environmental change.

Acknowledgments

Mark Bevelhimer graciously provided a copy of his spreadsheet kokanee model. Krista Bonfantine, Blake Byall, Cory Counard, Derrek Faber, Brian Herwig, Glenn Szerlong, Mike Wise, and a host of other excellent student helpers collected and/or processed the data for Blue Mesa Reservoir. Patrick Martinez of the Colorado Division of Wildlife provided field assistance, and supplied kokanee growth data. Rick Harris (NPS), Steve Hiebert (USBR), and Gordon Mueller (USGS-BRD) provided logistical support in the field. Comments by Dave Beauchamp, Mark Bevelhimer, Jim Kitchell, Patrick Martinez, Doran Mason and an anonymous reviewer greatly improved earlier versions of this manuscript. This study was supported by funds from the U.S. Bureau of Reclamation, Grand Junction Projects Office, Colorado.

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List of Figures

Figure 1. Comparison of estimates from the B&A, modified B&A, and Wisconsin bioenergetics models for a 500-g kokanee under standard simulation conditions (see text). (A) Scope for growth estimates as a function of temperature for all three models. (B) The energy budget from the B&A model as a function of temperature. Scope for growth is represented by area between total respiration (R) and consumption (C) minus losses curves. (C) and (D) Same as (B) but for the Wisconsin and the modified B&A models, respectively.

Figure 2. (A) Scope for growth estimates for a 500-g kokanee as a function of temperature and feeding duration for the modified B&A model. Scope for growth estimates from the Wisconsin model are also shown. (B) Same as (A) but for a 100-g kokanee. (C) Scope for growth estimates for a 500-g kokanee as a function of feeding duration and prey size for the modified B&A model. (D) same as (C) but for a 100-g kokanee.

Figure 3. (A) Comparison of original (Hyatt 1980) and modified functional responses. Hyatt's (1980) functional response was determined using lab experiments with 15-g kokanee at 10°C. The solid line

describes the functional response by C=Z/(0.0138·Z+11.5), where C is consumption (*Daphnia*·min^{-1}) and Z is *Daphnia* density (m^{-3}). The dotted line indicates the modified functional response (see Table 1), using a 15-g kokanee at 10°C, with a handling time of 1.2 s·*Daphnia*$^{-1}$. (B) Sensitivity of the modified functional response when fish body size and handling times are varied.

Figure 4. Vertical profiles of temperature and densities of *Daphnia* ≥ 1.0 mm in Sapinero Basin, Blue Mesa Reservoir, 1994. Asterisks indicate data used as inputs to the modified B&A model for comparison of model growth estimates with field observations.

Figure 5. Observed masses and daily growth estimates of (A) age-1, (B) age-2, and (C) age-3 kokanee from Blue Mesa Reservoir, 1995. Exponential growth was used to generate daily growth estimates (see text). Daily observed growth is plotted on limnological sampling dates (Fig. 4) to compare with estimates generated by the modified B&A model.

Figure 6. Daily growth estimates from the modified B&A model for (A) age-1, (B) age-2, and (C) age-3 kokanee, using limnological data from 10 June 1994. Starting masses of kokanee for model simulations, as determined from field observations, were 59.79 g for age-1, 222.87 g for age-2, and 575.07 g for age-3. The horizontal dotted lines represent daily growth from field observations for the same date, while the horizontal dashed lines indicate maximum scope for growth at optimum temperature as predicted by the Wisconsin model. Solid squares connected by vertical lines indicate depths of migration strategies from the modified B&A model that maximized growth for the given

feeding duration and handling time.

Figure 7. Same as Figure 6, but for limnological sampling date 21 July 1994. Starting kokanee masses for simulations were 103.38 g for age-1, 314.70 g for age-2, and 666.46 g for age-3. Single solid square for a given feeding duration and handling time indicates migration strategy that maximized growth was to remain at the indicated constant depth for the entire 24-h simulaton.

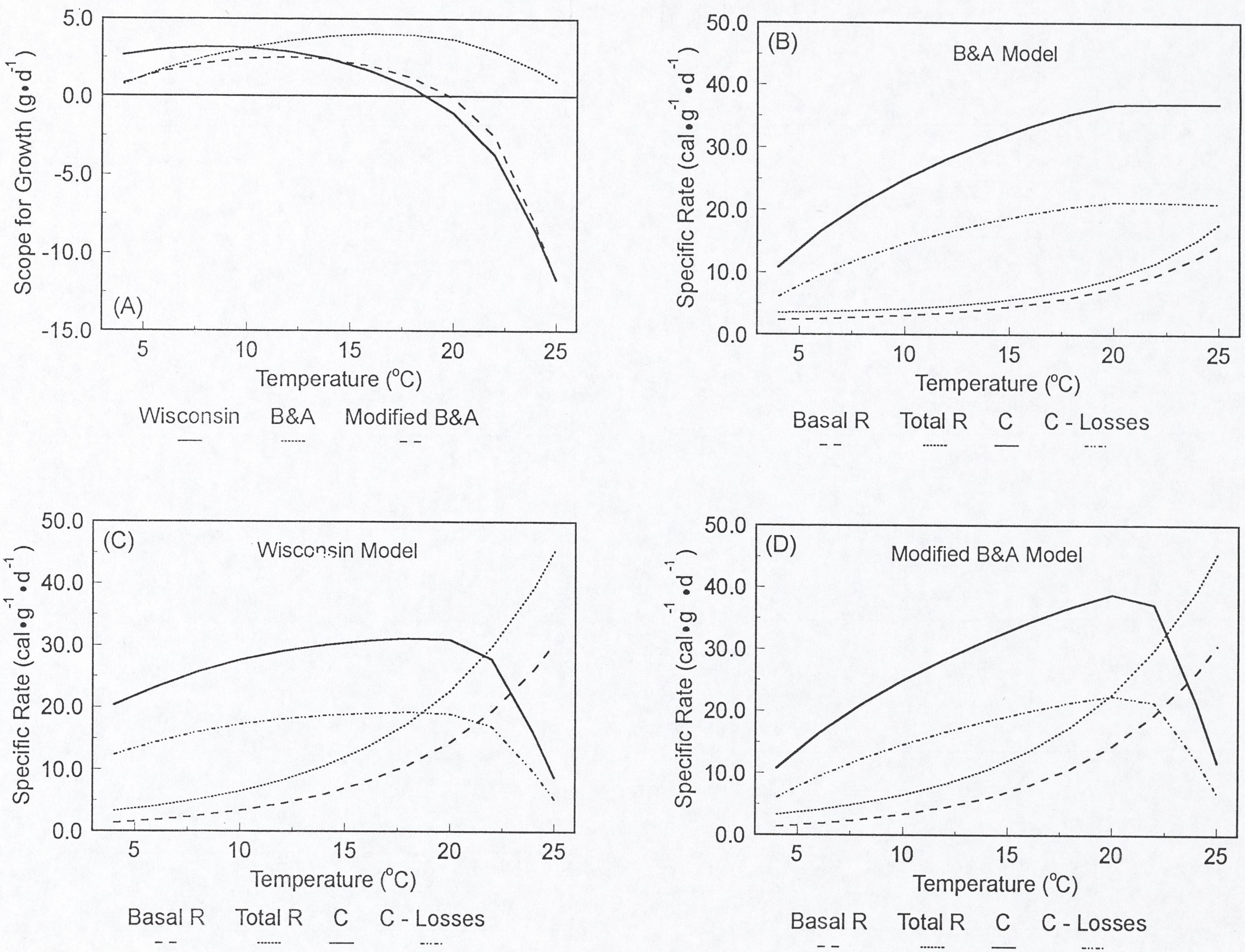
Figure 8. Same as Figure 7, but for limnological sampling date 18 August 1994. Starting kokanee masses for simulations were 121.15 g for age-1, 342.45 g for age-2, and 722.34 g for age-3.

Table 1. The modified B&A model as developed from Bevelhimer (1990) and Bevelhimer and Adams (1993). Sources are as follows: 1) Gerritsen and Strickler (1977), 2) Thornton and Lessem (1978), 3) Beauchamp et al. (1989), 4) Hyatt (1980), 5) Brett (1971), 6) Dumont et al. (1975), 7) Elliott and Persson (1978), 8) Brett and Higgs (1970), 9) Bevelhimer and Adams (1993), 10) Hewett and Johnson (1992), 11) Brett and Groves (1979), 12) Richman (1958). Note that 1 cal = 4.184 J.

Parameter	Value	Source
Consumption (C)		
C (*Daphnia*·min^{-1})	$[E \cdot Z]/[(1+(E \cdot Z \cdot h)] \cdot TL \cdot 60$	
E, volume searched (m^3)	$(\pi \cdot R_d^2)/3 \cdot (3 \cdot v^2+u^2)/v$	1
TL, Thornton-Lessem function	$[(0.58 \cdot e^{(0.21 \cdot (T-3))})/(1+0.58 \cdot (e^{(0.21 \cdot (T-3))}-1))] \cdot [(0.5 \cdot e^{(0.97 \cdot (24-T))})/(1+0.5 \cdot (e^{(0.97 \cdot (24-T))}-1))]$	2,3
R_d, reaction distance (m)	0.08	4
v, kokanee swimming speed (cm·s^{-1})	$9.9 \cdot e^{(0.0405 \cdot T)} \cdot M^{0.13}$	3
u, *Daphnia* swimming speed (cm·s^{-1})	0	
Z, prey density (*Daphnia*·m^{-3})		
h, handling time (s·*Daphnia*$^{-1}$)	0.33-1.2	
T, temperature (°C)		
M, kokanee mass (wet g)		
stomach capacity (wet g)	$[14.1-4.95 \cdot \log_{10}(M)]/100$ for $M < 253.5$ g; $0.022 \cdot M$ for $M \geq 253.5$ g	5

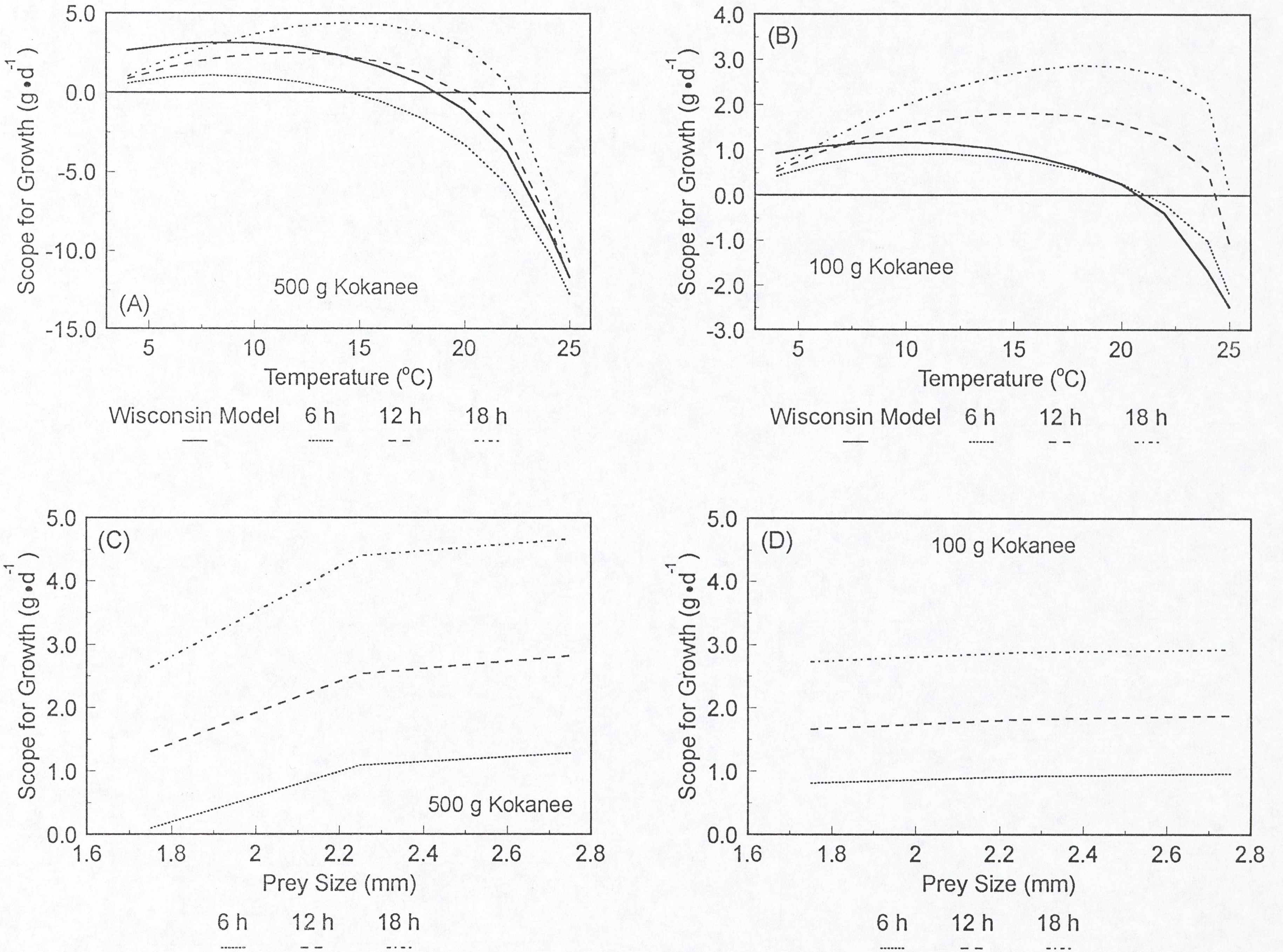
m, *Daphnia* mass (wet mg)	$0.052 \cdot L_d^{3.012}$	6
L_d, *Daphnia* length (mm)		
Digestion (D)		
D ($cal \cdot t^{-1}$)	$[((C \cdot m - M_0/r) \cdot (1-e^{-rt})) + (C \cdot m \cdot t)] \cdot E_{dap}$	7
r, digestion coefficient	$0.0140 \cdot T - 0.0154$	8
M_0, initial stomach content mass (wet g)		
t, model time step (min)	30	9
Respiration (R)		
R ($cal \cdot g^{-1} \cdot t^{-1}$)	$0.00143 \cdot M^{-0.209} \cdot e^{(0.086 \cdot T)} \cdot ACTIVITY \cdot oxycal \cdot t/t_{day}$	3
ACTIVITY	$e^{(0.0234 \cdot VEL)}$	3
VEL	$9.9 \cdot e^{(0.0405 \cdot T)} \cdot M^{0.13}$	3
oxycal, oxycaloric conversion factor ($cal \cdot g^{-1}$ O_2)	3241	
t_{day}, length of day (min)	1440	
Egestion (F)		
F ($cal \cdot t^{-1}$)	$0.455 \cdot T^{-0.222} \cdot D$	10
Excretion (U)		
U ($cal \cdot t^{-1}$)	$0.0233 \cdot T^{0.580} \cdot (D-F)$	10
Specific Dynamic Action (SDA)		

0	SDA ($cal \cdot t^{-1}$)	$0.14 \cdot (D-F)$	11
	Energy Density		
	E_{dap} ($cal \cdot$ wet g^{-1} *Daphnia*)	586	12
	E_{kok} ($cal \cdot$wet g^{-1} kokanee)	$1.851 \cdot M+1250$ for $M \leq 196$ g; $0.1254 \cdot M+1588$ for $M > 196$ g	10



(A)
Scope for Growth (g•d^-1)
5.0
0.0
-5.0
-10.0
-15.0
5
10
15
20
25
Temperature (°C)
Wisconsin
B&A
Modified B&A
(B)
B&A Model
Specific Rate (cal•g^-1•d^-1)
50.0
40.0
30.0
20.0
10.0
0.0
Basal R
Total R
C
C - Losses
(C)
Wisconsin Model
(D)
Modified B&A Model

Fig. 1



(A)
500 g Kokanee
Scope for Growth (g•d⁻¹)
Temperature (°C)
Wisconsin Model 6 h 12 h 18 h
(B)
100 g Kokanee
Scope for Growth (g•d⁻¹)
Temperature (°C)
Wisconsin Model 6 h 12 h 18 h
(C)
500 g Kokanee
Scope for Growth (g•d⁻¹)
Prey Size (mm)
6 h 12 h 18 h
(D)
100 g Kokanee
Scope for Growth (g•d⁻¹)
Prey Size (mm)
6 h 12 h 18 h

Fig. 2

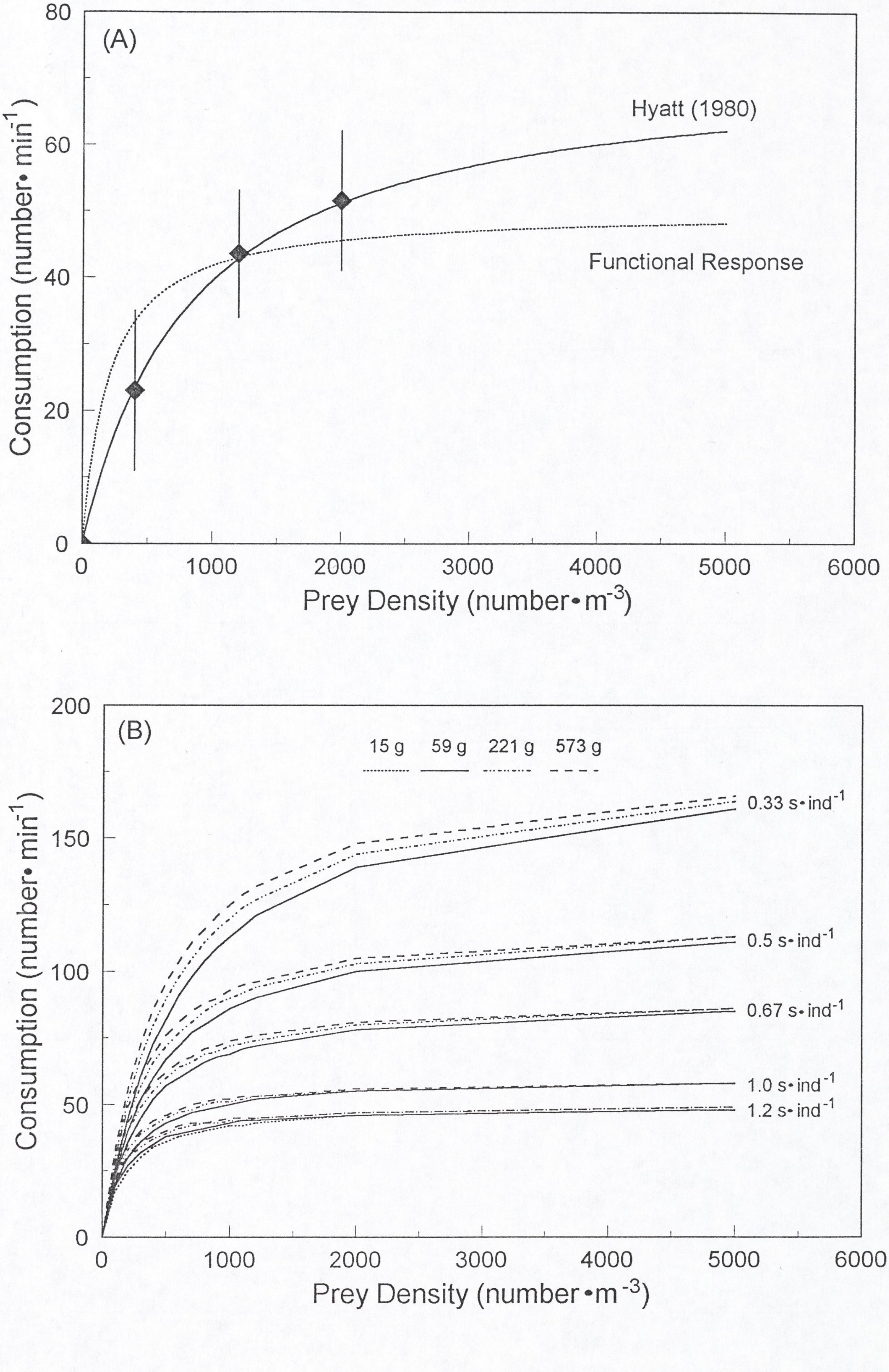
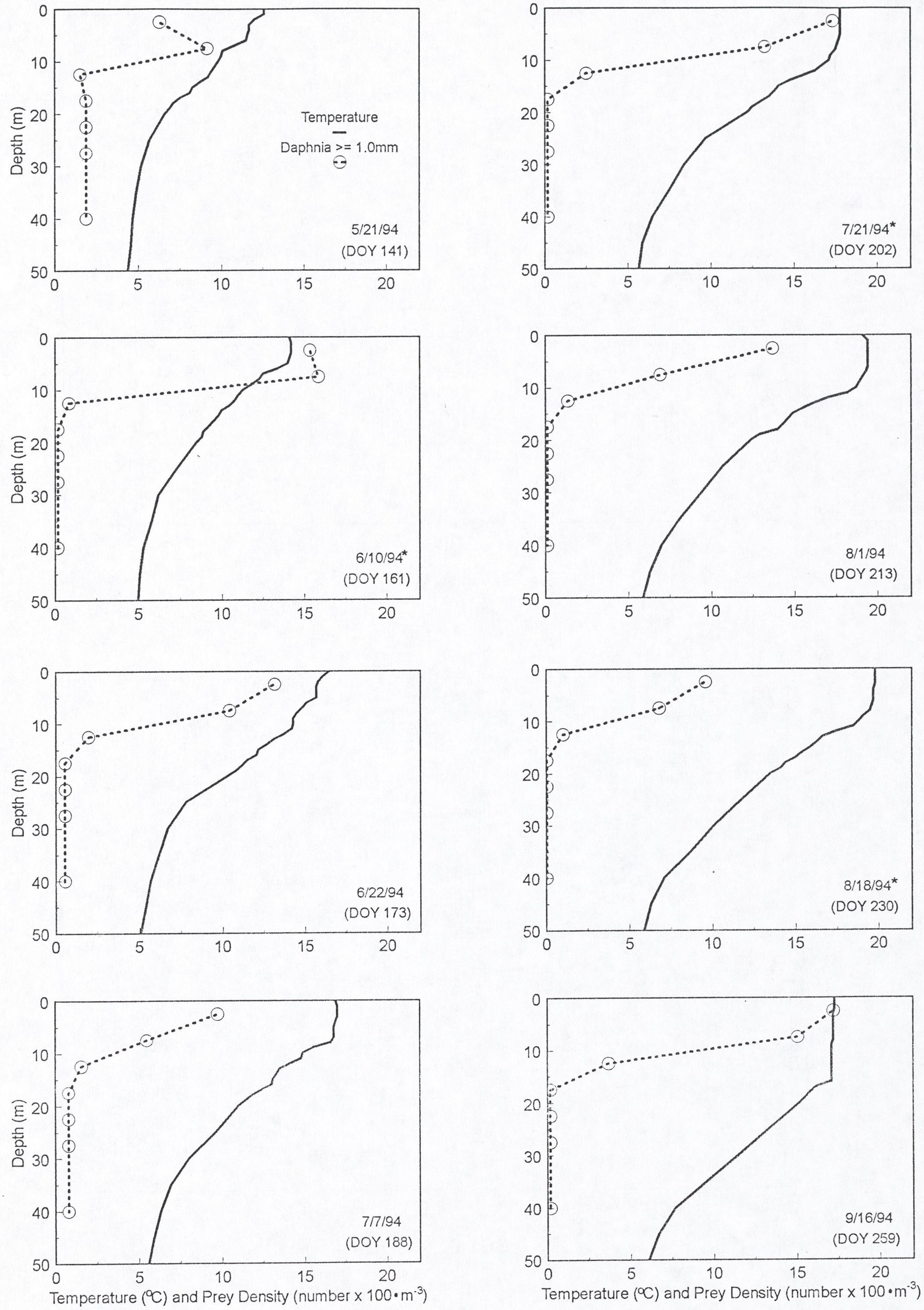

(A)
Consumption (number• min-1)
Hyatt (1980)
Functional Response
Prey Density (number• m-3)
(B)
15 g
59 g
221 g
573 g
0.33 s• ind-1
0.5 s• ind-1
0.67 s• ind-1
1.0 s• ind-1
1.2 s• ind-1
Consumption (number• min-1)
Prey Density (number •m-3)

Fig. 3



Temperature
Daphnia >= 1.0mm
Depth (m)
5/21/94
(DOY 141)
7/21/94*
(DOY 202)
6/10/94*
(DOY 161)
8/1/94
(DOY 213)
6/22/94
(DOY 173)
8/18/94*
(DOY 230)
7/7/94
(DOY 188)
9/16/94
(DOY 259)
Temperature (°C) and Prey Density (number x 100•m^{-3})

Fig. 4

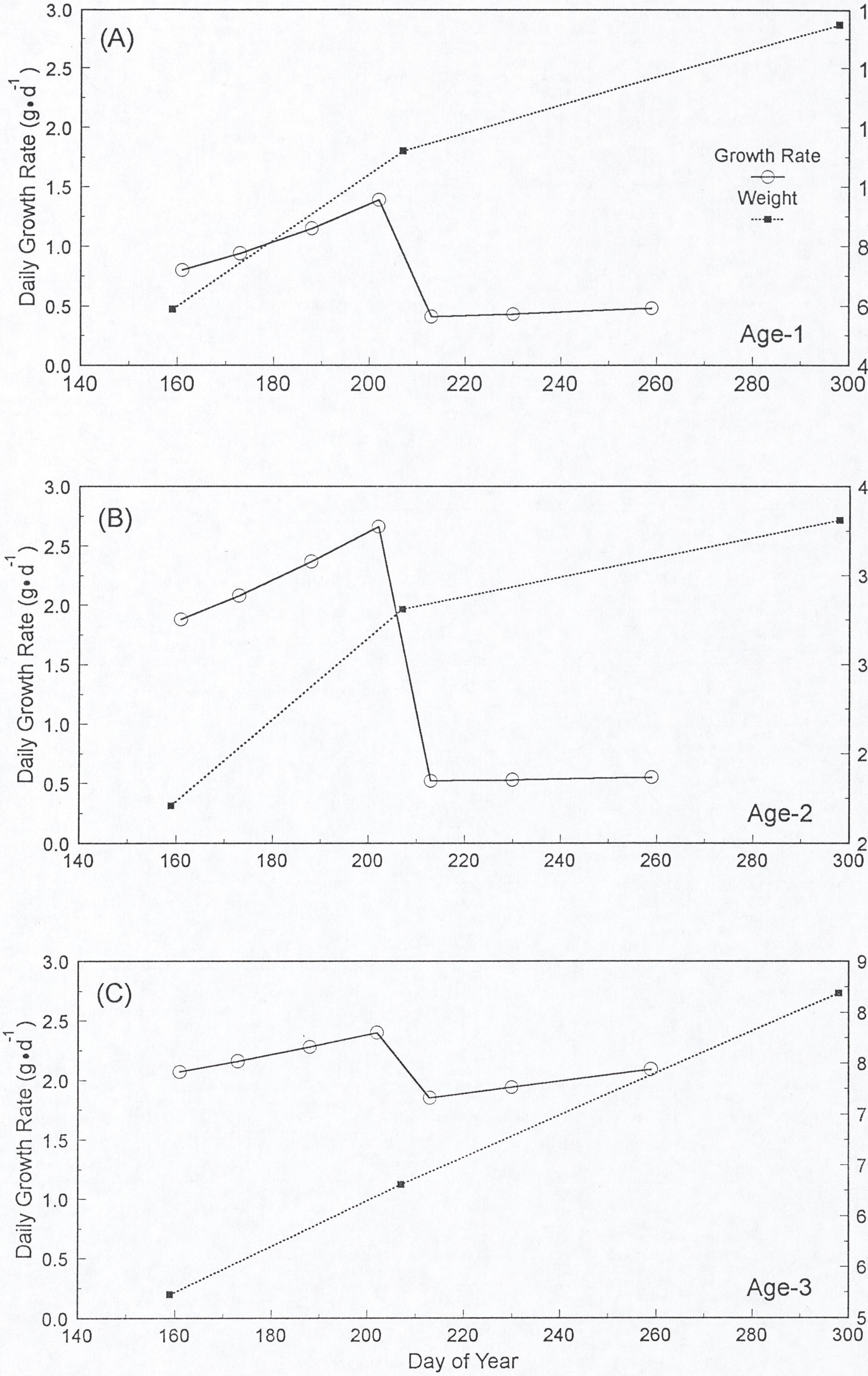
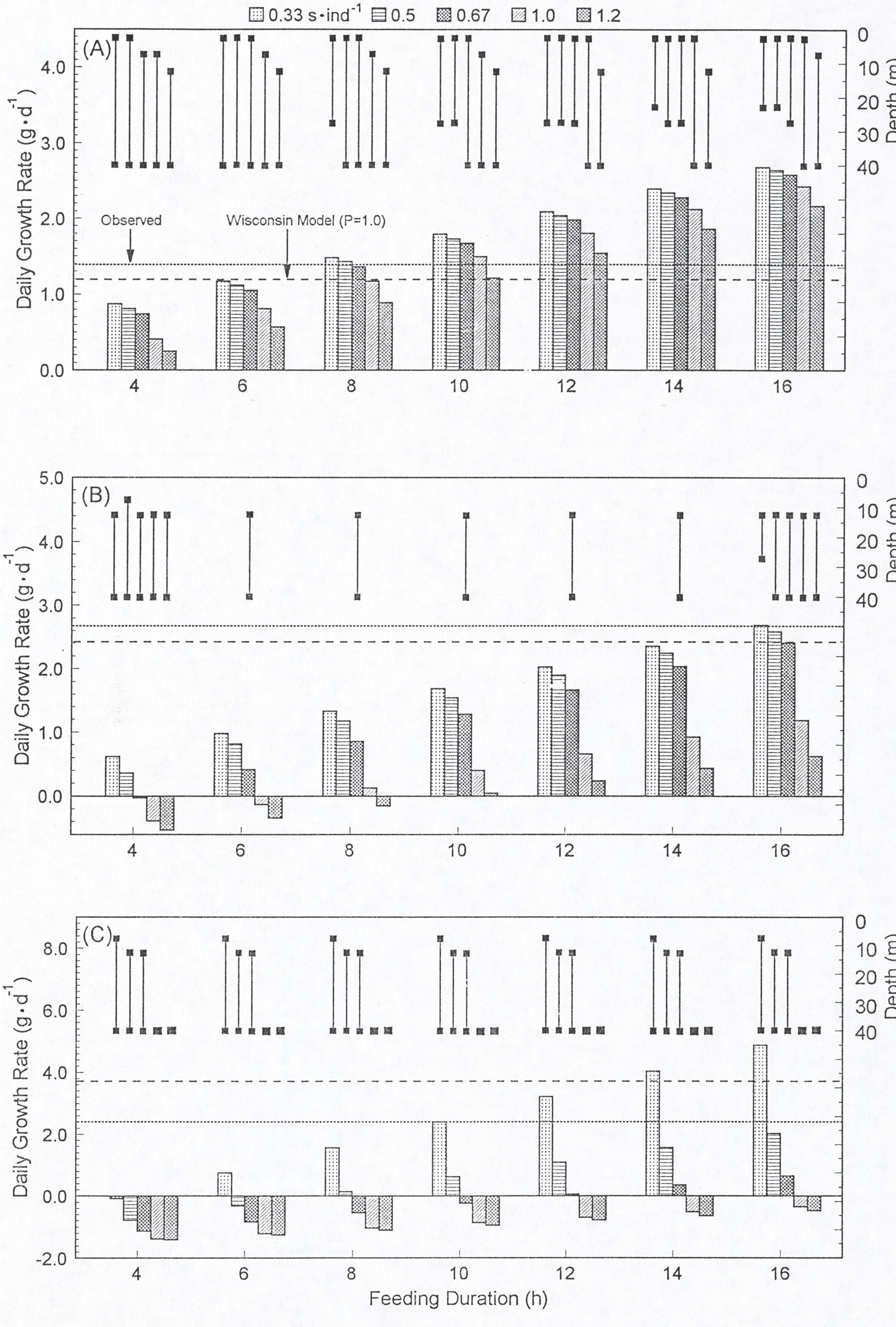
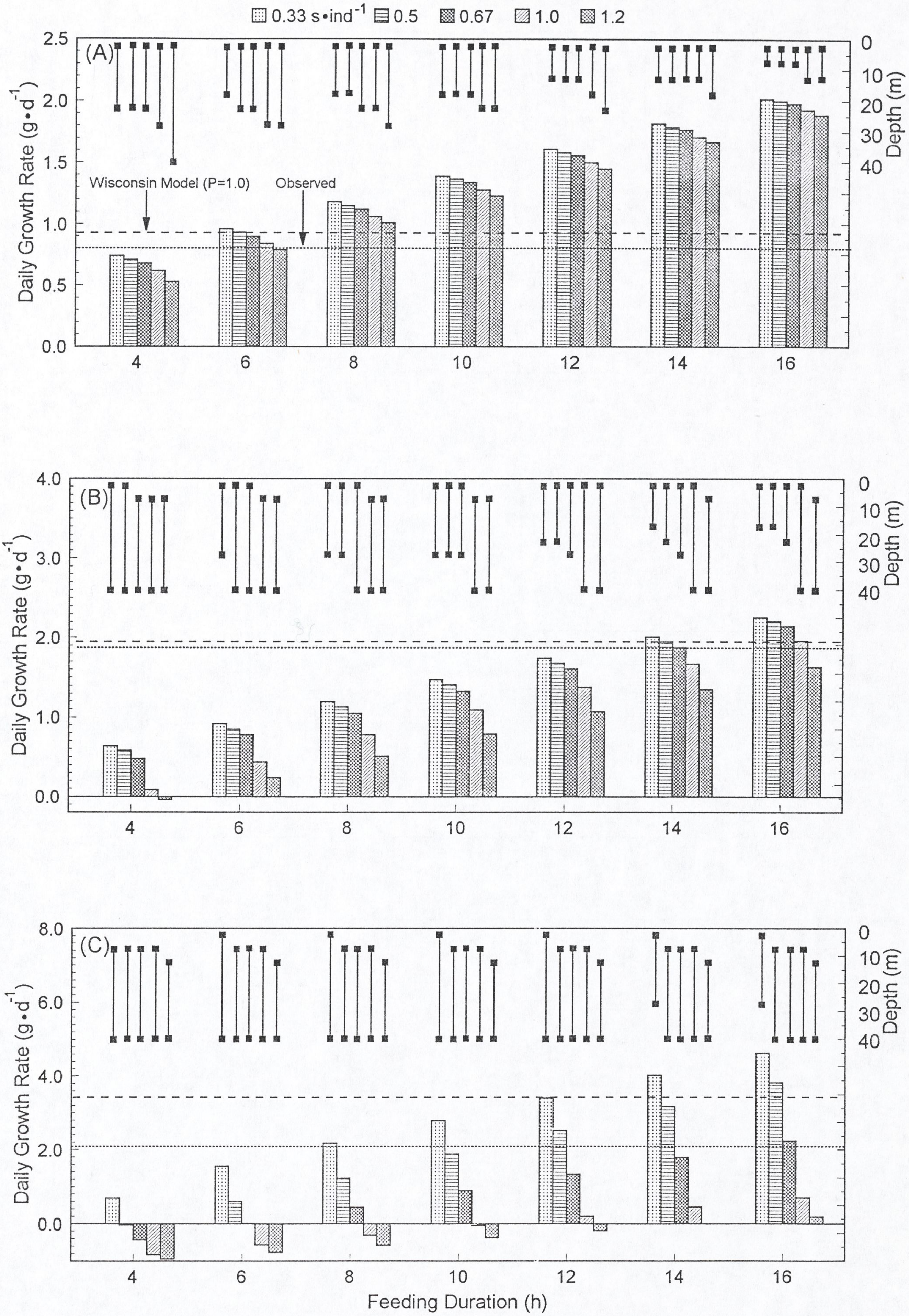

(A)
Growth Rate
Weight
Age-1
(B)
Age-2
(C)
Age-3
Daily Growth Rate (g•d^{-1})
Mass (g)
Day of Year

Fig. 5



0.33 s•ind^{-1}
0.5
0.67
1.0
1.2
(A)
(B)
(C)
Observed
Wisconsin Model (P=1.0)
Daily Growth Rate (g•d^{-1})
Depth (m)
Feeding Duration (h)

Fig. 6



0.33 s•ind⁻¹ 0.5 0.67 1.0 1.2
(A)
Wisconsin Model (P=1.0)
Observed
(B)
(C)
Daily Growth Rate (g•d⁻¹)
Depth (m)
Feeding Duration (h)

Fig. 7

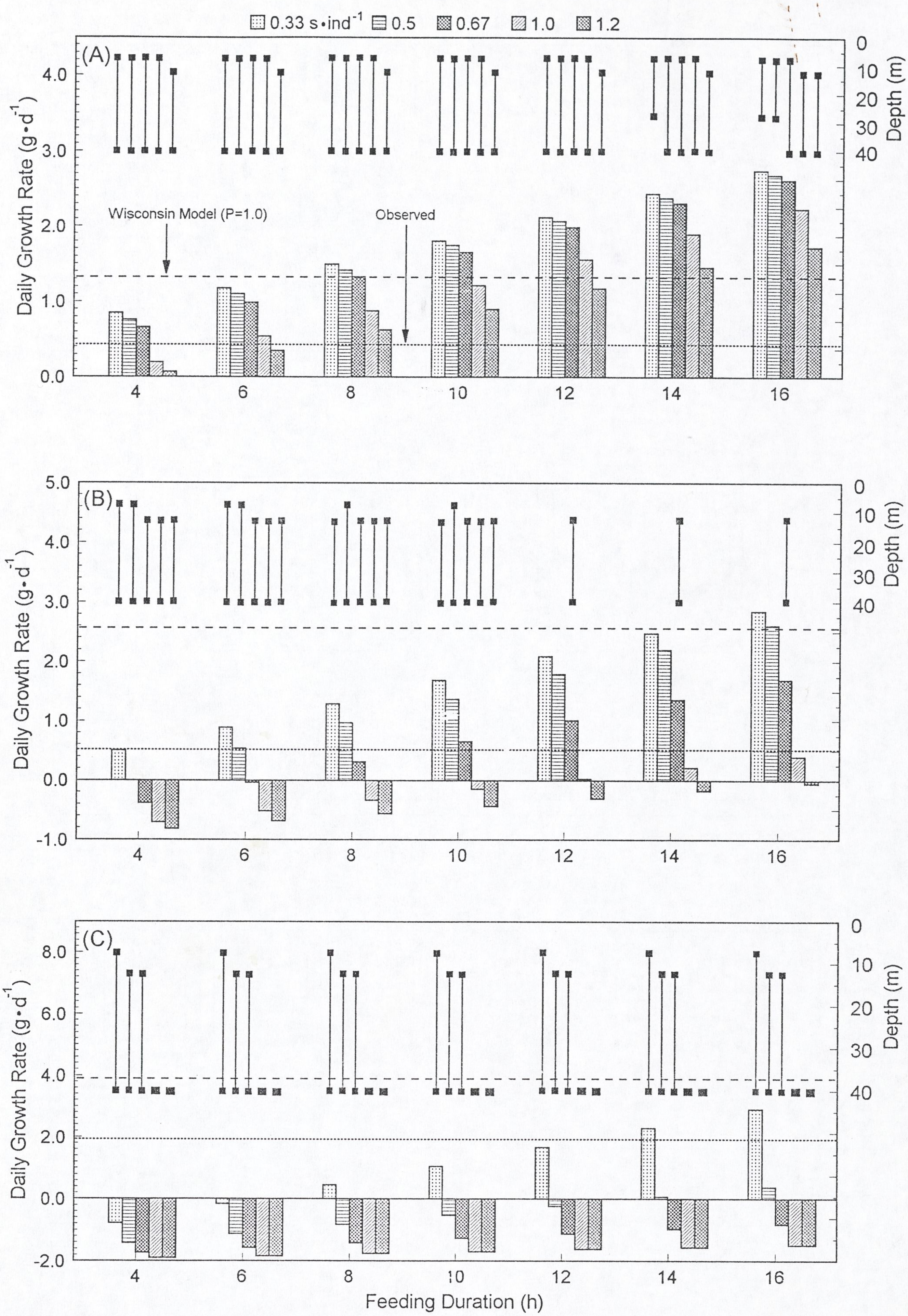

0.33 s•ind⁻¹ 0.5 0.67 1.0 1.2
(A)
(B)
(C)
Wisconsin Model (P=1.0)
Observed
Daily Growth Rate (g•d⁻¹)
Depth (m)
Feeding Duration (h)

Fig. 8

Copy 2

Experimental Flooding in Grand Canyon

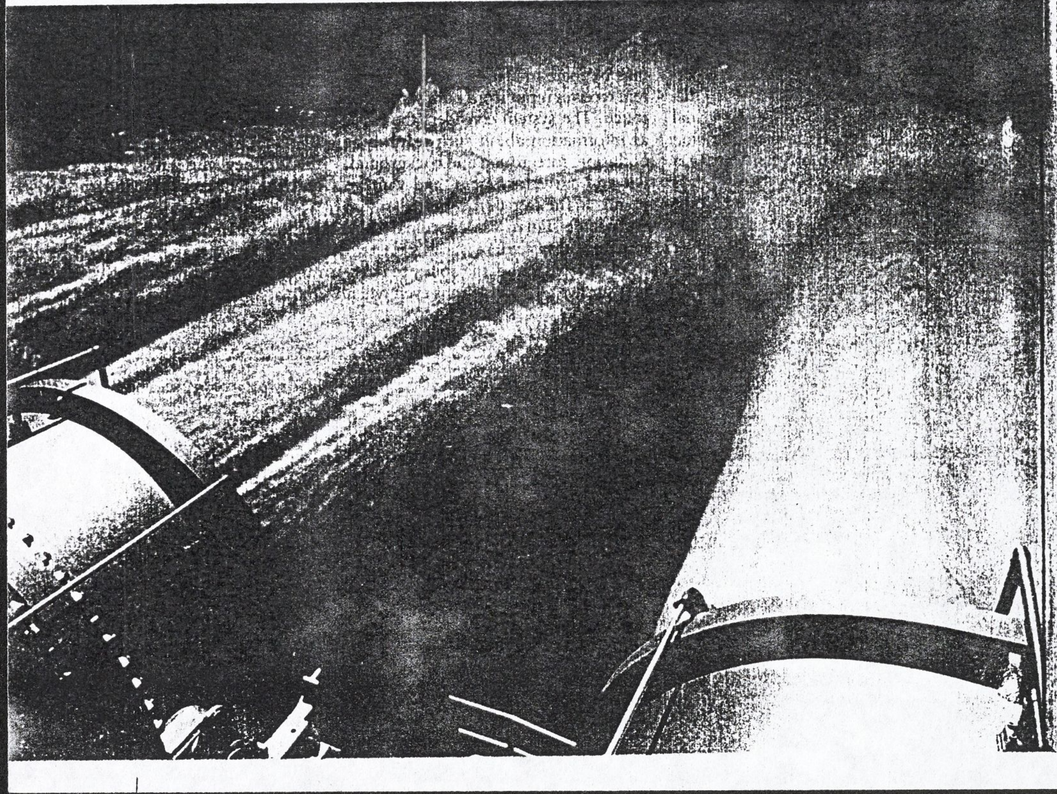
Scientists monitor a controlled deluge that was staged in the early spring of 1996 solely for the benefit of the environment in and around the Colorado River

by Michael P. Collier, Robert H. Webb and Edmund D. Andrews

For more than three decades, Glen Canyon Dam has impounded the flow of the Colorado River above Grand Canyon, the vast winding chasm in America's southwestern desert that ranks as one of the wonders of the natural world. Although many people recognized that damming the flow would destroy the river upstream, few anticipated that there might be serious environmental consequences downstream. But over the years, scientists, government officials and professional river guides have become increasingly aware of troubling changes within Grand Canyon.

These alterations have occurred because the dam replaced the Colorado's natural pattern of forceful summer flooding with a gentle daily ebb and flow dictated entirely by the electrical power demands of distant cities. The dam thus eliminated the normal seasonal variation in river flow and ended the immense floods that had annually washed through the canyon. Although these floods had lasted only a few weeks of the year, they had been the principal force sculpting the river corridor. The floodwaters routinely stripped all but the highest vegetation from the channel banks, deposited sandbars and plucked boulders out of rapids. After Glen Canyon Dam went into service, exotic flora encroached, sandbars disappeared and boulder piles clogged the main channel.

So as dozens of scientific observers (including the three of us) made ready, the secretary of the interior, Bruce Babbitt, launched a bold experiment in environmental restoration at 6:20 A.M. on March 26, 1996, opening the first of four giant "jet tubes" at Glen Canyon Dam. Over the next nine hours, the other three tubes and the eight hydroelectric turbines added to the torrent, which grew to 1,270 cubic meters per second—a discharge 50 percent greater than the maximum flow through the turbines alone. As the surge of water mounted, the surface of the river rose five meters higher than usual. In all, 900 million cubic meters of water coursed through the canyon during the weeklong experiment. Never before had an intentional flood been released specifically for environmental benefit, and we were eager to help assess the results.



MICHAEL P. COLLIER

A Changed River

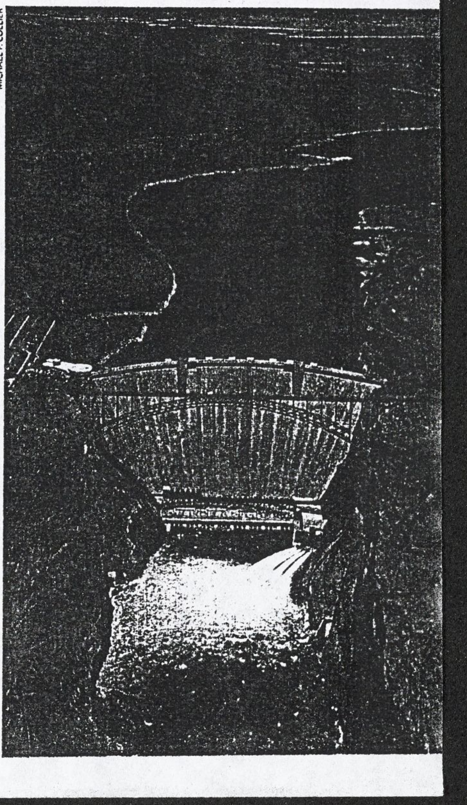
Along with many other scientists who monitored the experimental flooding, we have been aware that conditions in the canyon had been evolving dramatically since Glen Canyon Dam began operations in 1963. After construction of the dam, virtually all sediment coming from upstream was trapped above the dam, in the newly created Lake Powell, and most sandy beaches in Grand Canyon began slowly but steadily to vanish. By the time the test flood was planned, some rapids in the river had become so obstructed by coarse debris swept down from side canyons that particular stretches had become extremely difficult to navigate. The bridled river did not have sufficient power to clear away the boulder-filled deposits. Many people familiar with the canyon had also observed dramatic alterations to the vegetation since the dam was built. Native coyote willow, as well as exotic tamarisk, camelthorn and even bermuda grass, took root on beaches that had previously been bare. Mature mesquite trees growing at the old high waterline began to die.

But not all changes brought about by the damming of the river were obviously undesirable. Trout—which did not live there before in the relatively warm, turbid waters of the free-running river—flourished in the cold, clear water below the dam. Stabilization of flow favored trees and shrubs on the riverside, which provided new homes for some endangered birds. The green ribbon of new vegetation made the once barren canyon appear more hospitable to other kinds of wildlife as well—and to countless campers who traveled the river for recreation.

Indeed, the many beneficial changes to the canyon ecosystem may have diverted attention from some of the more disturbing trends. It was not until 1983 that many scientists and environmentalists took full notice of the important role that floods originally played in shaping the canyon. In June of that year, a sudden melting of the winter snowpack rapidly filled Lake Powell and forced the operators of Glen Canyon Dam to release water at a rate of 2,750 cubic meters per second. This flow was far smaller than some recorded flood episodes, but it still constituted a momentous event.

This emergency release in 1983 required the first use of the "spillways"—giant drain tunnels carved into the walls of Glen Canyon alongside the dam. The operators of the dam had at first been dismayed—and then gravely concerned—to see the outflow turn red as swiftly moving water plucked first concrete and then great blocks of sandstone from the spillway tunnels. Some feared that destruction of the spillways could catastrophically undermine the dam. Fortunately, the crisis passed, and engineers were able to redesign the spillways to minimize "cavitation." This phenomenon (formation of a partial vacuum within a moving liquid) had sucked material from the tunnel walls and caused them to erode with startling speed.

The downstream effects of the 1983 flood also took others by surprise. When the waters receded from the flooded banks, scientists and guides familiar with the river were stunned to see many of the formerly shrunken beaches blanketed with fresh sand. The flood had killed some exotic vegetation that had grown artificially lush and had also partially restored riverine animal habitats in many spots. Had several years of ordinary dam operations followed, many people would have hailed the 1983 flood for improving conditions in the canyon. Instead runoff in the Colorado River basin during the next three years remained quite high, and the operators of Glen Canyon Dam were forced to release huge amounts—an average of 23 billion cubic meters of water every year. Flows commonly reached 1,270 cubic meters per second, for at least brief periods, each



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JETS OF WATER (*opposite page*) emerge during the experimental flood from four steel drainpipes built into the base of Glen Canyon Dam (*right*). The water stored in the adjacent reservoir, Lake Powell, can also flow through the hydroelectric turbines situated underneath the dam or, if there is urgent need to lower the lake, through the two "spillway tunnels" carved into the canyon walls (*visible at right, below the dam*).

year through 1986. The beaches that had been built up in 1983 soon washed away. A single flood, it seemed, could create beaches; frequently repeated floods could destroy them.

Time for Another Flood?

As scientists learned more about risks and benefits of flooding in the canyon, many of those interested in the fate of the river began to recognize the need to restore flooding of some type. Most geologists who had studied the movement of sediment by the Colorado River were convinced that an artificial flood would benefit the canyon, and they began championing that idea within the scientific community in 1991. But during discussions, some biologists worried aloud that a flood would jeopardize the gains that had been made within the canyon by several endangered species. A few geologists, too, were concerned that the beaches nearest Glen Canyon Dam might be inadvertently washed away. And anthropologists working in the canyon expressed concern that new flooding would accelerate erosion and threaten the integrity of archaeological sites next to the river.

Yet the overall sentiment was that purposeful flooding would be more beneficial than harmful and should be arranged. By 1993 the murmurs in favor of a flood had turned to shouts. Some of the loudest voices came from river guides who were being forced to find camping sites on smaller and smaller beaches—despite the fact that millions of metric tons of sand were reaching the Colorado every year by way of its two main tributaries below the dam, the Paria and Little Colorado rivers. Under the normal operating regime of Glen Canyon Dam, only 450,000 metric tons of this sand wash downstream and out of Grand Canyon. So sand was filling the canyon, but it was not accumulating on the banks. Rather it was settling out of sight on the bottom of the river.

Along with others at the U.S. Geological Survey (USGS) and the Bureau of Reclamation's Glen Canyon Environmental Studies program, we were certain that a flood would stir up these deposits and drape them along the banks, just as the river had done before the dam had reined it in. But what sort of flood would be most appropriate? The people debating that question agreed that the best time of year for an initial test would be during a narrow window in late March, when fish were least likely to be spawning and troublesome tamarisk plants would not yet be able to germinate. A date at that time would also assure that most bald eagles and waterfowl that had wintered in the canyon would have already left. Still, the optimum choice for the size of the flood remained elusive.

One reason for that difficulty was that the quantity of sand moved by a river varies quite strongly with the rate of discharge: when the discharge rate doubles, the flux of sand increases eightfold. Consequently, for a given flood volume, more sand will be stirred up and deposited on the banks by a large flood that runs for a short time than by a lesser flood of longer duration. One of us (Andrews) argued for a release at the rate of 1,500 cubic meters per second, which would have been close to two thirds the size of the typical annual flood before the dam was built. After all, if the goal was to restore a critical natural process, why not try roughly to approximate that level?

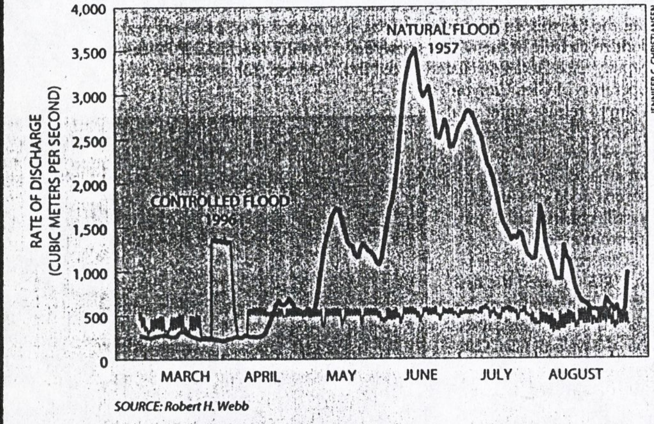
But there was an important logistical constraint: flows greater than 1,270 cubic meters per second through the dam would require the use of the spillways. Despite having made repairs and improvements, officials at the Bureau of Reclamation were reluctant to risk repetition of the frightening experience of 1983. Restricting the flood to 1,270 cubic meters per second would also minimize the threat to an endangered species of snail that lived near the dam. Most proponents of flooding felt that this level was a reasonable compromise. They agreed that the flood would last one week—enough time to redistribute a considerable amount of sand but not so long as to deplete all sand reserves at the bottom of the river.

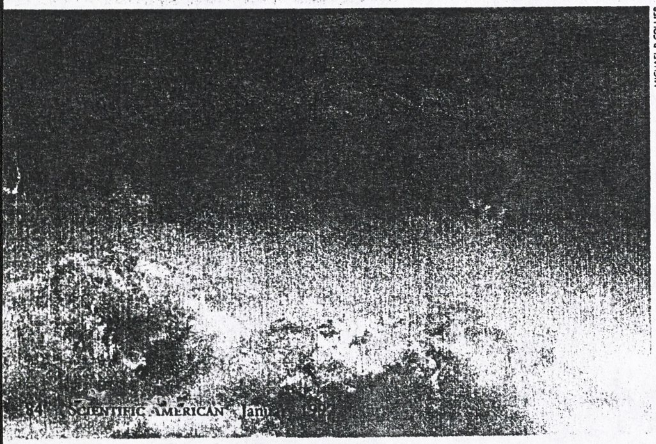
On the eve of the test, our biggest fear was that the water would not have the power needed to build sizable beaches. But John C. Schmidt, a geologist at Utah State University who had also favored the flooding experiment, had a bigger concern. He worried that something might unexpectedly go wrong: Would scientists in their arrogance ruin what was left of the heart of Grand Canyon?

On a Rising Tide

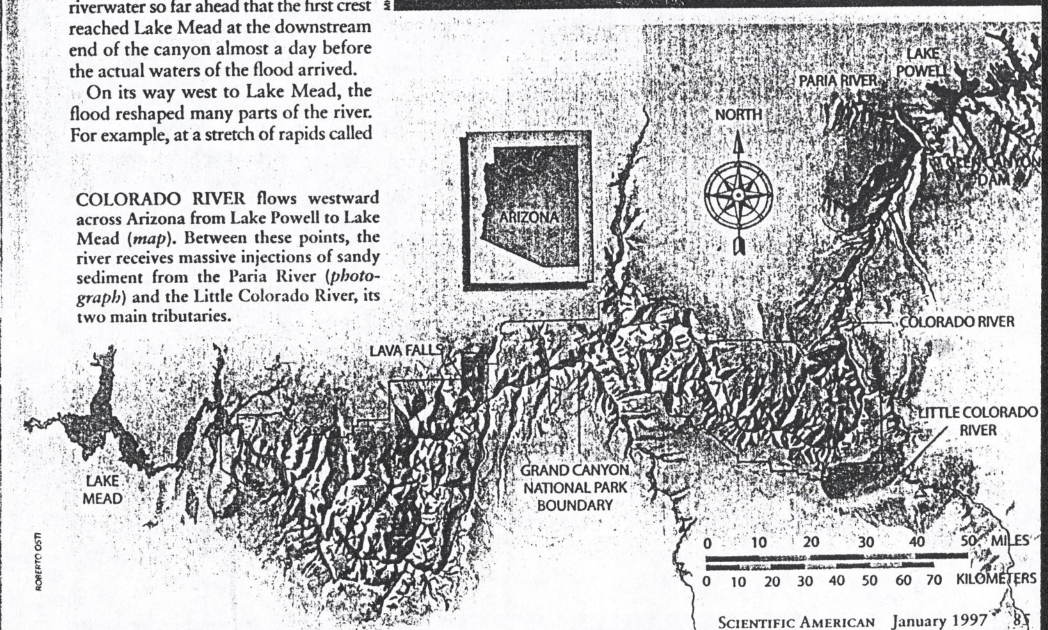
On March 26 the flood began on schedule. The waters of the river rose and raced down the canyon. On signal, scientists from the USGS released 30 kilograms of a nontoxic fluorescent dye into the river a short distance downstream from the dam. They used the chemical to track the velocity of the water by measuring the arrival of this dye at six sites spaced throughout the canyon, where they had placed sensitive fluorometers. A numerical model developed by researchers at the USGS accurately predicted the progress of the flood. The model and measurements showed that the floodwaters accelerated as they ran through the canyon, pushing riverwater so far ahead that the first crest reached Lake Mead at the downstream end of the canyon almost a day before the actual waters of the flood arrived.

On its way west to Lake Mead, the flood reshaped many parts of the river. For example, at a stretch of rapids called

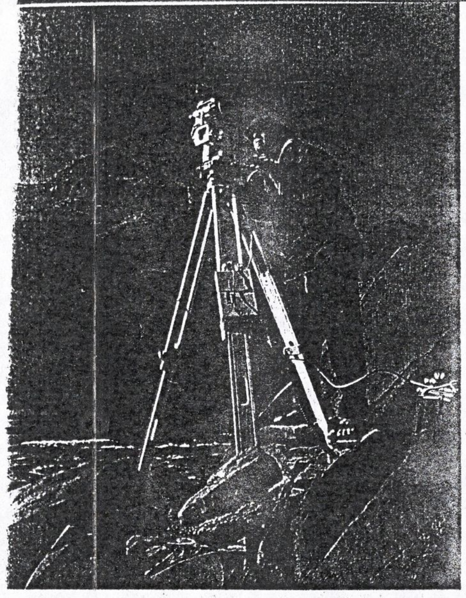


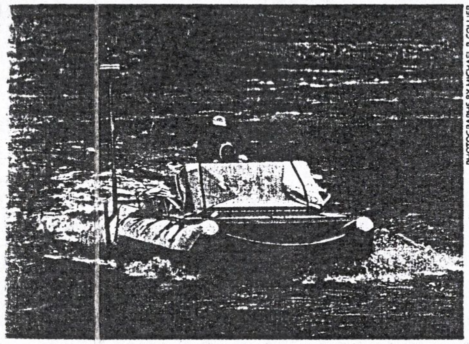


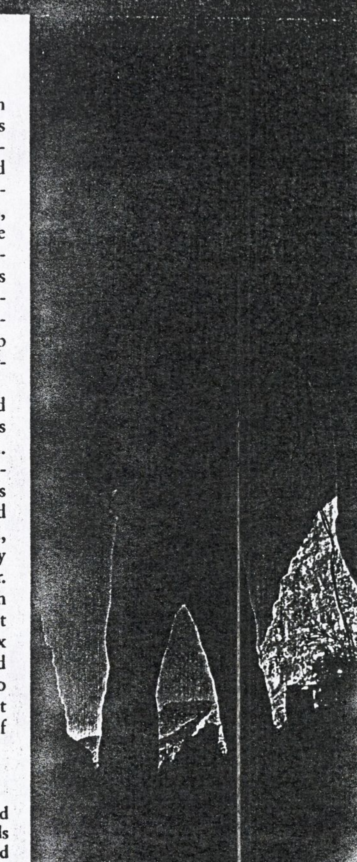
DISCHARGE of water during the experimental flood of 1996 may have appeared extremely powerful (*photograph*), but the flow maintained for that one week is dwarfed by natural events of the past, such as the flood of 1957 (*chart*), which endured for much of the spring and summer.



COLORADO RIVER flows westward across Arizona from Lake Powell to Lake Mead (*map*). Between these points, the river receives massive injections of sandy sediment from the Paria River (*photograph*) and the Little Colorado River, its two main tributaries.







PHOTOGRAPHS BY MICHAEL P. COLLIER

Lava Falls, about 300 kilometers below the dam, the river rose against a fan-shaped bank of loose mud and boulders that had been formed one year earlier after a debris flow roared down a small side canyon. The material deposited by that cascade of rock and mud had narrowed the Colorado—normally 50 meters wide there—by almost 20 meters. Although some geologists had previously concluded that very large floods would be required to clean out such constrictions, we believed this flood would be sufficient to do the job.

And so we were quite pleased to see just how effective the experimental flood proved. As discharge of the river surpassed 850 cubic meters per second at Lava Falls on March 27, the energized water quickly cut through the new debris fan, reducing its size by one third. We studied that event by placing radio transmitters in 10 large stones positioned originally near the top of the rapids. Despite their considerable size (up to 0.75 meter across), all 10 rocks traveled downstream during the flood. Using directional antennas, we subsequently located eight of the boulders. The great stones had moved, on average, 230 meters.

Besides tracking boulders at Lava Falls, we worked with several colleagues to measure the deposition of sand at some other key locales. For those studies, we chose five eddies—places where the river widens abruptly, and water swirls upstream near the banks. Employing laser tracking equipment and a small boat equipped with a sonar depth finder, we charted the sandy bottom during the flood. The results were quite surprising. We found that a great deal of sand accumulated in the first 36 to 48 hours. But as the influx of sand slowed, the bottom of the eddy began to lose sand back into the main channel.

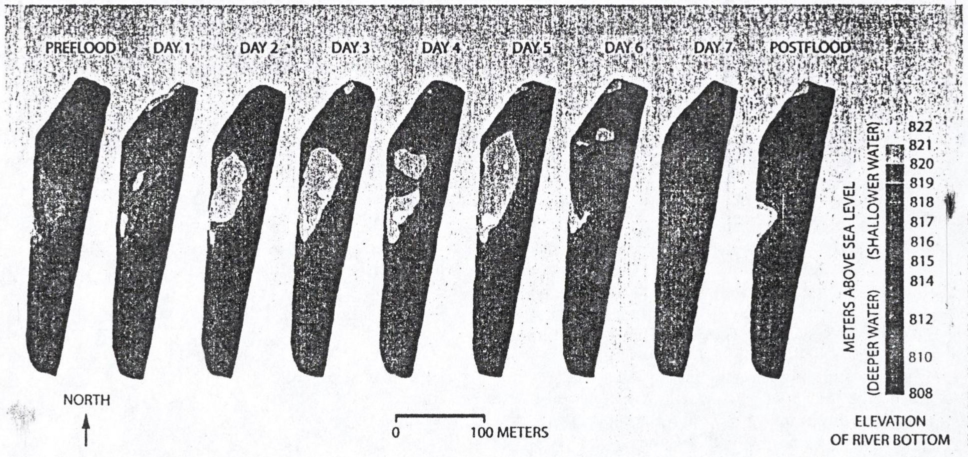
This behavior initially puzzled us, but after we examined the measurements more carefully, we realized that much of the sediment had originally settled above its so-called angle of repose, an unstable configuration that resulted in some newly deposited sand slumping back into the main channel. Still, we found that the overall amount of sand after the flood had increased in all five places we mapped.

Many other scientists made important observations during the course of the flood. Near the lower end of Grand Canyon, our colleague J. Dungan Smith measured the velocity of the river and concentration of sediment held in suspension by the turbulent water. His goal is to compare the quantity of sediment washed out of the canyon during the flood with the amount normally delivered into the canyon by the Paria and Little Colorado rivers. Smith is still analyzing his data, but he should soon be able to predict how often floods could be staged without depleting the existing sand reserve.

Several other scientists took special interest in the movement of sand. Using optical sensors and sonar equipment borrowed from his oceanographer colleagues at the USGS, David M. Rubin studied the sediment concentration of water entering an eddy and characterized the fine-scale patterns in the deposition of this sand. Working at the same site, Jon M. Nelson documented the curious behavior of swirling vortices that form in a line where the main downstream current rushes past a slower, upstream-flowing eddy. Nelson observed that as the main current pushes these vortices downstream, the vortices tip over, because flow is slowed near the channel bottom where friction is greatest. In this canted position, he reasoned, the vortices should then act to sweep sediment out of the main current and into the eddy.

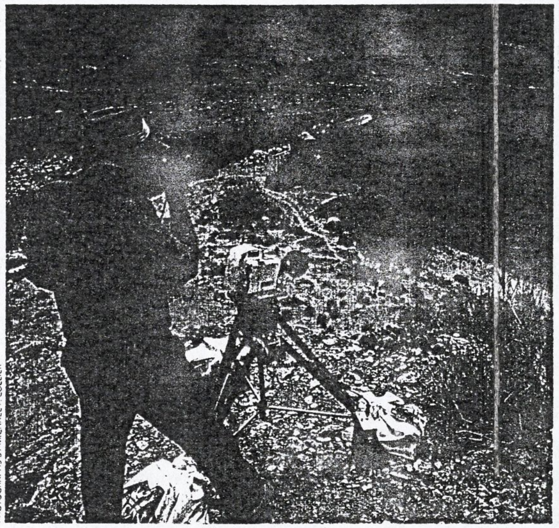
But sediment came and went within the eddy at rates far greater than anticipated. With a sinking feeling, Rubin and Nelson watched as $70,000 worth of borrowed equipment was first buried, then excavated and finally carried away by the water. They were fortunate enough to have collected sufficient data to show that the vortex "sediment pump" operated as they had predicted. So their ideas withstood the test flood, even though much of their equipment did not.

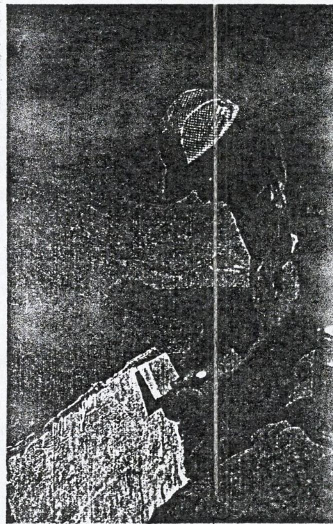
SAND DEPOSITION within an eddy, a place where water swirls in the upstream direction near the banks, raised the bed of the river along one margin (*tan areas in diagrams*) in the first days of the flood. Later during the flood, much of that sand escaped back into the main channel (*blue areas in diagrams*). To collect this record of sediment accumulation and removal, a boat fitted with an acoustic echo sounder (*photograph at left*) measured the depth of the water, and surveying equipment on land tracked the position of the boat (*photograph at top*).



JENNIFER C. CHRISTIANSEN; SOURCE: CHRISTOPHER E. JOHNSTON

SCIENTIFIC STUDIES carried out during the experimental flood included documentation of fine-scale patterns of sand deposition using plaster molds (*bottom right*), time-lapse videography of the floodwaters (*bottom left*) and measurement, by means of a directional antenna (*top right*), of the displacement of boulders that were fitted with radio transmitters.





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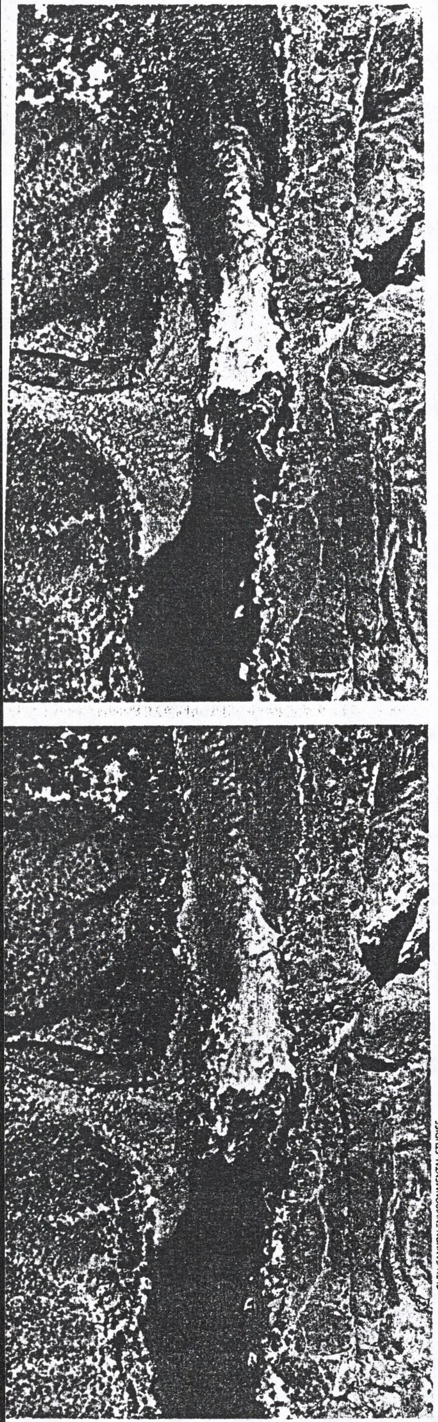


GLEN CANYON ENVIRONMENTAL STUDIES

As expected, a good deal of the newly deposited sand quickly eroded, but months later much of it still remained at those sites monitored by scientists—and at many other places as well. During the summer of 1996, many longtime observers believed the Colorado River had taken on something of its original appearance. Those impressions echoed the more careful assessment of Lisa H. Kearsley, a biologist working for the Bureau of Reclamation. She tracked the fate of almost 100 beaches throughout the canyon and concluded that 10 percent of them were diminished by the flood, whereas 50 percent were augmented, and the remainder were unaffected. Six months after the flood, she found that much sand had slipped back into the river, but there was still more beach area than before.

The expanded beaches should please campers in years to come, but scientists are also anxious to know how the flood might have affected many less vocal residents of the canyon. Because the earlier unintentional flood of 1983 had hurt the trout fishery, some biologists were particularly concerned that the experimental flood of 1996 would wash many fish far downstream. To find out, biologists stationed below Lava Falls during the experimental flood placed nets in the river. These scientists captured a few more trout than they would have otherwise done, but their tests did not show any flushing of native fishes, whose ancestors had, after all, survived many larger natural floods. The biologists surmised that the native species (and most of the trout) must have quickly retreated to protected areas along the riverbank. Other investigators determined that the floodwaters had hardly disturbed the ubiquitous cladophora algae and associated invertebrates, which constitute an important source of food for fish.

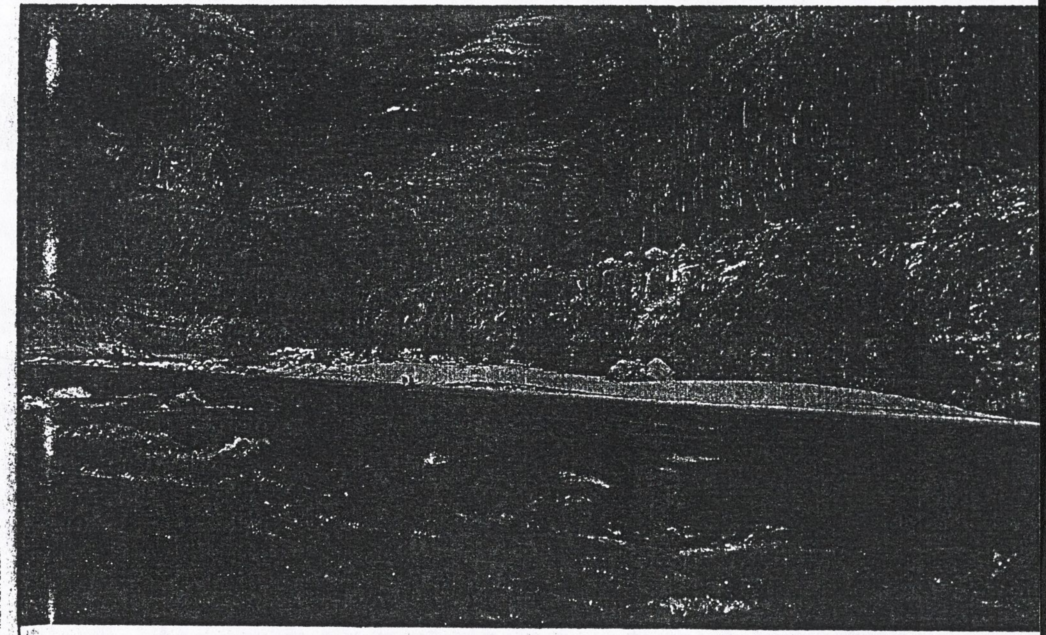
But the effects on other components of the local biota are still a matter of intense debate. Lawrence E. Stevens, a biologist with the Bureau of Reclamation, has studied the river for 25 years as an entire suite of animals—some endangered—migrated into the canyon and survived in the artificial environment created by Glen Canyon Dam. He is concerned that intentional flooding may threaten the existence of some species protected by the Endangered Species Act, such as the humpback chub (a fish), the southwestern Willow Flycatcher (a bird) or the Kanab ambersnail. But we would argue that floods were part of the natural cycle of the Colorado River in the past, and many species, both common and endangered, have adapted to this process as long as there has been a Grand Canyon—for about five million years. Restoration of flooding may be detrimental to some organisms, but we and many of our colleagues hypothesize that in the long run a collection more resembling the native fauna will return.

Epilogue

Did the flood work? It deposited significant amounts of sand above the normal high-water line and rejuvenated some backwater habitats important to spawning fish. The flood widened the two largest rapids on the river. Archaeological sites along the edge of the river were neither helped nor hurt by the high water; most of the encroaching vegetation was similarly unaffected.

So in our view the environmental benefits outweighed any damage. But one needs to consider other costs as well. Five months after the flood, David A. Harpman, an economist with the Bureau of Reclamation, was analyzing factors that bear on the final price tag. Because power had been continuously generated during the flood even at times when demand was low, and because the huge quantity of water sent through jet tubes produced no electricity at all, he

LAVA FALLS, a stretch of rapids in the Colorado, was narrowed by coarse, rocky material that had washed down a side canyon and spread into a fan-shaped deposit. An aerial photograph taken before the flood (*top left*) shows an obvious constriction in the river. A matching photograph taken after the flood (*bottom left*) reveals that much of the debris has been cleared away.



MICHAEL P. COLLIER

REJUVENATED BEACHES, such as the one enjoyed by these kayakers, signal that the flood restored habitats along the river's edge to a more natural configuration. Such changes should, for example, benefit native fish, which spawn in the shallows.

estimates that the Bureau of Reclamation has foregone about $1.8 million in lost revenue (about 1 percent of the total yearly income from the sale of electricity). Add to this expense the price of the scientific studies, and the total cost of the experiment almost doubles.

Because similar expenditures will be incurred during future floods, the Bureau of Reclamation will want to know precisely how big and how often floods will be needed to support the environment. The answers are far from clear. All scientists involved agree that a future flood need not last seven days. Smith believes Grand Canyon beaches can be improved by floods staged perhaps every year, as long as incoming sediment from the Paria and Little Colorado rivers is at least as great as the amount of sediment carried out of the canyon during a flood. One of us (Webb) argues for an initial release of as much as 2,800 cubic meters per second to scour debris fans, followed by an immediate drop to more moderate beach-building levels. Andrews emphasizes that under any scenario, artificial floods should be made to vary in magnitude from year to year, the better to mimic natural variability.

Will there be more floods? Probably—both in Grand Canyon and elsewhere. We have studied several other American rivers controlled by dams, and they, too, would benefit from periodic floods. So the ideas and instrumentation developed by scientists working within Grand Canyon during the 1996 experimental flood could soon help restore natural conditions within and around many other rivers across the nation and, perhaps, throughout the world.

The Authors

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MICHAEL P. COLLIER, ROBERT H. WEBB and EDMUND D. ANDREWS have long cherished the splendor of Grand Canyon. Collier, who considers himself a writer and photographer rather than a true scientist, also maintains an active medical practice in Flagstaff, Ariz. He earned a master's degree in geology from Stanford University in 1978 and worked for six years as a river guide in Grand Canyon before he began collaborating with U.S. Geological Survey scientists. Webb received a doctorate from the University of Arizona in 1985 and then joined the staff of the USGS as a hydrologist. Since 1989 he has also taught at the University of Arizona. Andrews worked as a river guide in Grand Canyon from 1969 to 1974. Three years later he earned a doctorate from the University of California, Berkeley, and has since done research for the USGS in its water resources division. Andrews also maintains an ongoing affiliation with the University of Colorado at Boulder.

Further Reading

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A Recipe for River Recovery?

River ecologists are advocating a broader approach to rescuing damaged rivers, betting that restoring the physical processes that shape a river's habitats will bring back ailing fisheries

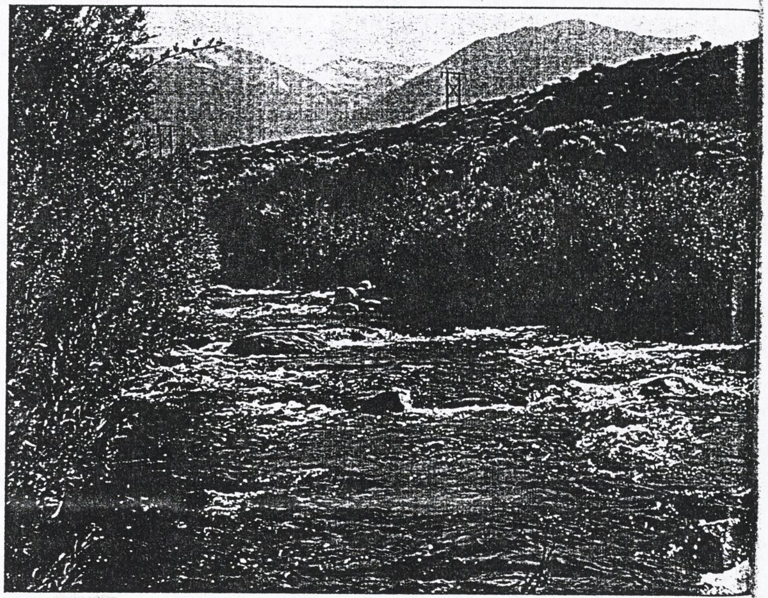
Look at the Trinity River as it flows through the heavily forested hills of Northern California's Trinity County, and at many spots you will see what appears to be an idyllic natural scene: flashing water coursing between wooded banks. But to the trained eye of a river ecologist, the sight is not so pretty. Those willows and alders along the riverbanks confine the river to a fixed, rectangular channel—a far cry from the shallow and shifting banks typical of a healthy river. And that is only the most outward sign of the transformation that has occurred on the Trinity since a dam completed in 1963 robbed the river of the winter and spring floods that could send as much as 3000 cubic meters of water per second (m^3/s) churning through the channel. For 20 years after the dam was built, the Trinity lived year-round on a comparative trickle, an unvarying 4 m^3/s released from the dam.

Without those annual floodwaters to move sediments down the channel, sweep away encroaching plants, and shift the river's banks, the Trinity's ecology changed dramatically and rapidly. In the mid-1960s biologists with California's Department of Fish and Game already noted vegetation encroaching on the riverbanks. Habitats for frogs, turtles, aquatic insects, and fish that favor the river's warm, shallow edge waters disappeared. Gravel spawning beds used by salmon filled with sand, and the local Hoopa Valley Indian tribe saw a precipitous decline in its traditional salmon fishery.

The Trinity's plight is all too common. Countless rivers and streams in the water-poor West have suffered intense damage from dam projects built in the first half of this century. Fisheries were devastated, and several species of salmon and other commercially important fish hit the endangered list. "The way the dams were built was at best incredibly naïve," says San Francisco–based consulting hydrologist Philip Williams. "[They] were planned ignoring ecologic impacts."

But the Trinity is more than an example of a damaged river. It has become a test case for a new, albeit controversial, approach to river restoration that takes a broader perspective than has been previously taken, focusing not on single fish species but on the whole river system. The approach reflects a growing awareness that habitat modification efforts must take into account all the varied processes that shape an ecosystem (*Science*, 13 September, pp. 1518, 1555, and 1558).

Until recently, restoration efforts on rivers like the Trinity were typically led by fisheries biologists, who generally leaned heavily on a physical habitat simulation model, which goes by the catchy acronym PHABSIM. Developed by the Fish and Wildlife Service in the 1970s, the model focuses on optimizing habitats for a single important species of fish, such as salmon. Now, says Williams, "there is another group of ecologists who see restoring natural processes as a key."



Williams is referring to the natural physical processes that help a river shape its banks and bottom. These processes are best restored, according to river morphologist Luna Leopold of the University of California, Berkeley, by mimicking the seasonal variability in water flow, including occasional torrential floods like the experimental flood released last year on the Colorado River (*Science*, 19 April, p. 344). The effect is to make the rivers smaller versions of what they were before they were dammed. That "doesn't mean you can't use the water," says Leopold—indeed, half or even more of a river's natural flow may be diverted. But the remaining water must be used "to keep the river in some kind of equilibrium which depends on both high and low flows."

A hot political issue

Like all water issues in the parched West, however, this approach is fiercely controversial because higher flows would take water away from agriculture and from slaking the thirst of cities like Los Angeles. And even ecologists are not in total accord on the idea. Proponents of restoring more natural river processes believe, for example, that the approach is not only better for river ecology in general but will also produce the greatest numbers of healthy fish. But they don't yet have the numbers to prove that true, and critics argue that the impact on fisheries is far from certain. "It will make a great river," says Andrew Hamilton, a biologist with the Fish and Wildlife Service. But how much it will improve fish numbers, he says, is "just a wild guess."

These arguments will be played out publicly over the next year, in two cases. At the end of this month, the Fish and Wildlife Service will release its proposal for restoring the Trinity River, and a similar restoration plan released last February for the streams that feed Mono Lake on the east side of California's Sierra Nevada—which were dried up in 1941 by water diversions to Los Angeles—will undergo public hearings sometime within the next year.

What happens in these cases is being closely watched by river experts concerned with the conflict between water demands and efforts to maintain or restore healthy rivers. "There is a full court press to get all the [restoration] done that we can," says Kirk Rodgers, deputy regional director at the Bureau of Reclamation for the mid-Pacific region, "because many people are visionary enough to see that other [water] demands are picking up. They are trying to re-establish what [habitats] they can and put a protective cloak around them."

In an early effort to provide guidance for trying to improve prospects of river fisheries, in the 1970s the Fish and Wildlife Service developed a system of models for predicting how water-flow changes in a river would influence the capacity of the river to produce fish. At the core of this approach was PHABSIM, which predicts the depths and speeds of water that correspond to different levels of flow in a river and matches them with the known habitat preferences of fish. Water flows can then be adjusted to maximize those preferred habitats.

But many fisheries biologists say that PHABSIM presents a distorted view of what is best for a river, because it focuses too narrowly on the needs of one species of fish, and generally on just one critical life phase. For example, it might focus on ideal conditions for the rearing of juvenile Chinook salmon, which typically prefer "slow, relatively shallow water," says Sam Williamson, a research ecologist with the National Biological Service in Fort Collins, Colorado. If you only take that information into account, he notes, it might lead to a recommendation that a lot of water can be diverted with no harm to the fish. But it would ignore other needs of the salmon, such as for faster, deeper water to bring them food and keep the water temperature cool, and would also disregard the effects of such low flows on the shape of the river channel.

PHOTOS BY G. SMITH

Restoration target. The left photo shows Rush Creek, one of the five streams that feed Mono Lake, at a site above the water-diversion facility, and the right photo shows a reconstructed gravel spawning bed on the lower part of the creek.

Williamson and others maintain that the model is not supposed to be applied that way; a complete analysis should also include factors such as how different water flows would alter the river channels. But many ecologists complain that these more complex aspects tend to get overlooked by agencies and consultants who are seduced by the numbers generated by PHABSIM and who often recommend low water flows as a result. "Whether [PHABSIM] is science or not ... boy, it looks great," says Gary Smith, a fisheries biologist with the California Department of Fish and Game.

That was the case, for example, in the late 1970s when the Fish and Wildlife Service applied the analysis to the Trinity River. It recommended that the river's water allotment be roughly doubled to tripled, depending on the wetness of the year. Cecil Andrus, secretary of the interior at the time, implemented that increase, but also called for a 12-year study of the Trinity to determine whether other changes in its management were needed.

PHABSIM falls short

That study began in 1984, but by 1990 Robert Franklin, chief of the water division of the Hoopa Valley Tribe's fisheries department, was unhappy with how it was progressing. He felt the analysis relied too heavily on a narrow PHABSIM approach that would not recommend the variation in flows necessary to restore the natural processes of the river: "The tribe's position is that a healthy river is what you are striving for, and it will produce fish."

Franklin hired Arcata, California–based river-ecology consultants William Trush and Scott McBain to study the processes that create and maintain the river channel, including high flows. The need for these flows, known in the business as channel-maintenance flows, comes from a growing consensus about what is necessary for the health of an alluvial river—a river that has the potential to move its banks and bottom. One key standard, says Trush, is the ability to move the so-called "bed"—the full complement of sediments, from fine sands to boulders—down the river channel. This is essential for many river processes, such as the formation of transient gravel bars that provide river habitats, and maintenance of the gravel beds that fish use for spawning. "If you don't mobilize the bed, the fine particles intrude into the bed, fill up the interstitial areas, remove the habitat for invertebrates, and it destroys the spawning quality," Trush says.

To determine how much the bed needs to move, and how much water it takes to move the larger rocks in the bed, river morphologists study streams that haven't been altered or dammed, mark rocks, and see how often and at what flow levels they move. They have even devised elaborate trapdoor systems in the bottom of one Montana stream to sample rocks and sediments that are moving downriver, says Larry Schmidt of the U.S. Forest Service in Fort Collins. The conclusion from studies carried out over the past few decades: "You have to mobilize the channel bed on the average every other year," says Trush.

Since 1991, floods lasting several days each have been released each year on the Trinity. Because flows on the river must be limited to a maximum of about 170 m^3/s to avoid threatening homes built on the river's banks, the torrent was not sufficient to rip out vegetation that had been growing there for more than 30 years. But prior to the floods the study group had created several experimental sites, removing the invading vegetation with bulldozers and restoring the banks to a more natural shape.

Those physical changes, combined with the experimental flows, produced encouraging results. "The sites where they skimmed off the banks are narrowing on themselves," says Trush. "They are creating a morphology that is typical of alluvial rivers," such as shifting gravel bars in the river channel. Moreover, the researchers could see that fish preferred some of the renewed habitats. Some sites, especially those that had shallow banks, slow water, and gravel and cobble bottoms, had "extremely good use by [salmon] fry," says fisheries biologist Mark Hampton, who worked with the Fish and Wildlife Service on the Trinity project.

A modeling study the team did to analyze the effects of water levels on river temperatures also argued in favor of floods. In the spring, when the young Chinook salmon are migrating to the sea, they are very sensitive to water temperature. A river that doesn't get its normal allotment of snow melt will flow slowly, warming up more than the fish can tolerate. But the temperature model showed that flows of about 55 m^3/s could carry the young fish downstream quickly in a surge of hospitably cold water.

Buoyed by results such as these, the flow study group will recommend in its report, due out on 30 September, that the Trinity's water allotments should be increased. In the driest years, they would be only a little higher than the present allotment, but in wetter years when there is more water available, the annual volume of water coursing down the river would more than double. The majority of the extra water would surge down the river in the spring, when high flows are important not only to keep the temperature cool for migrating fish, but to move sand and gravel downstream and prevent seedlings from germinating and taking hold on the river banks. Those high flows would be punctuated with floods once every year or so to help maintain the river channel.

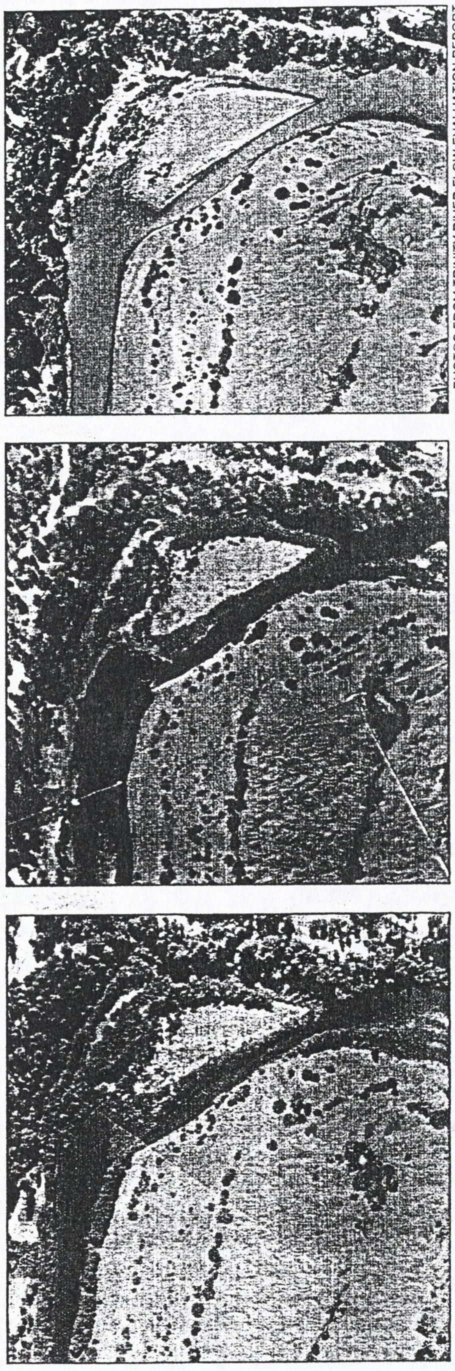
The flow study on the Trinity represents one of the most intensive studies of any U.S. river. "There is certainly a lot of science in the data collected that the recommendation is based on," says Hampton. But while the data suggest that fish will do better in the renewed habitats, it is impossible to quantify the expected improvement in terms of numbers of fish. "The underlying assumption ... is that you have to believe that restoring those natural processes will be good for the fishery."

But before the Trinity recommendations are implemented, the Bureau of Reclamation will take comments from water-user groups who may not be so willing to accept that assumption. "The whole channel-maintenance approach will come under intense scrutiny by water users," predicts Berkeley-based river ecologist Frank Ligon. Diverted Trinity river water travels through several power-generating stations on its way to the Sacramento River, and meeting the flow-study requirements would mean a reduction in power equivalent to what could sustain a community of 100,000 people, says Rodgers of the Bureau of Reclamation: "The power community is very concerned already." Likewise, the potential reduction has raised concern among municipal and agricultural users, says Jason Peltier, manager of the Central Valley Project Water Association, a consortium of water users.

Water users have become more environmentally enlightened, says Peltier, and recognize that to guarantee a stable future water supply they must "address and resolve" fishery problems. But nevertheless they will want to know what their sacrifice will produce in terms of fish. The users can "tell you in dollars and cents how it is going to affect them," says Rodgers, but "you cannot [tell] them what they are going to get in terms of pounds of fish or quantity of fish."

"The biggest challenge for the policy folks is how do you assess this now?" says Serg Birk, a biologist who worked on the Trinity project for the Bureau of Reclamation. "Do you assess it by how many fish return, or by how much habitat you create, or by measuring the parameters that the geomorphologists say indicate a healthy system because it mimics historic flows?" The assessment must consider more than just numbers of fish, says Hampton. "There are many ways to restore a fishery," he says. "You could build a hatchery and restore the fishery. But the Fish and Wildlife Service is in charge of protecting the fish and wildlife resources of the country for the benefit of the public trust. And building a hatchery doesn't necessarily do that."

Even the way that flow management will restore the overall environment requires more study, and the way to do that, says Trush, is through an approach called "adaptive management." This turns the management of a stream or river into an experiment in itself: Hypotheses are formulated, flows are manipulated to answer them, and the management of the river is adjusted accordingly. But to be done properly, adaptive management requires enough water to enable researchers to set up experiments, carry them out, and then alter the program based on their results. And researchers studying the river worry that the amount of water necessary for high-quality adaptive management may not be allotted to the Trinity in the end.



PHOTOS FROM TRINITY RIVER FLOW EVALUATION REPORT

Trees march in. These aerial photos from 1961, 1970, and 1974 *(top to bottom)* show a gravel bar in the predam Trinity that became colonized by trees and shrubs when the dam eliminated floods.

One ideal candidate for adaptive management is another project that Trush has been involved in, the restoration of the five feeder streams for Mono Lake. The lake's volume had been halved and salinity doubled as a result of the water diversions to Los Angeles. Various lawsuits in the 1980s resulted in a requirement that the city reduce by more than 90% the amount of water it takes from those streams until Mono Lake is returned to a healthier level. And in 1990 a Court of Appeals decision added the requirement that the streams be restored to a condition that can maintain fish. It will take at least 20 years for the lake to reach the required level, during which time the increased flows can be used to answer countless questions about what it takes to restore and maintain a stream and its fish population.

While Mono Lake and the Trinity may be two of the most visible cases of the new approach to river restoration, "you will see the same thing on some other rivers in California too," says hydrologist Williams, "as these ideas of ecosystem management permeate the agencies and there is a push to incorporate them into standard operations."

But while channel-maintaining flows may be catching on in California, their future seems less certain in other states. In Colorado, the U.S. Forest Service recently failed to convince a judge to limit future water diversions and guarantee the Forest Service the water necessary for maintenance flows on the South Platte River. Another important case, involving water-rights assignment for the Snake River and all of its tributaries, a water system that covers 80% of the state of Idaho, has yet to be decided. But the Forest Service hopes to learn from its setback in Colorado, as well as from the work going on in California, and present a case for the importance of high flows, channel maintenance, and adaptive management in the Snake River system, says K. Jack Haugrud, an attorney working on the case for the U.S. Department of Justice. "High flows are very important for maintaining stream channels," says Haugrud. "We intend, if we have to, to prove that in court."

It could be a tough sell. "We are in the water-poor portion of the world here," says Williamson of the National Biological Service. "It is easier to say what the minimum flow should be on a stream and divert everything else than it is to spend time trying to figure out what a stream really needs." Adaptive management, says Peltier of the Central Valley Project Water Association, "is a good concept." But it requires not only good science, he adds, but also "risk-taking, which government agencies are totally averse to doing." It will soon be seen whether the public and the water users can be convinced to take a risk on rivers like the Trinity.

–Marcia Barinaga

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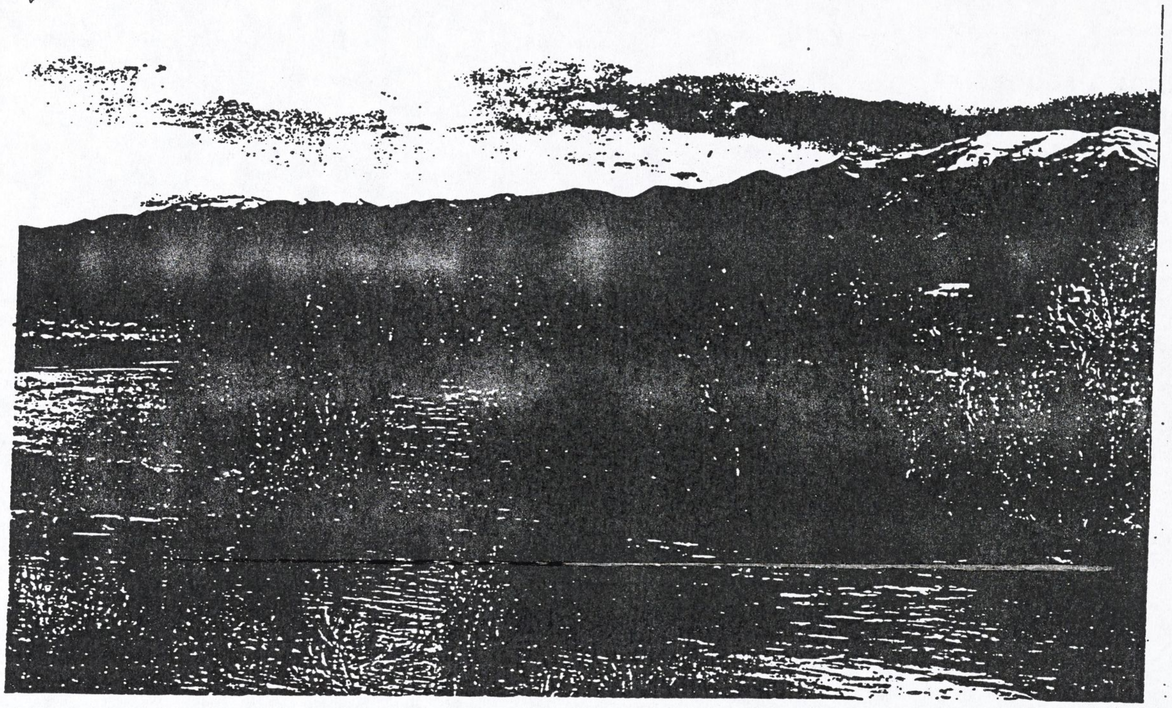
Instream Flows and the Restoration of Riparian Cottonwoods Along the Lower Truckee River, Nevada

Project Task #2: The Assessment of Recent Cottonwood Recruitment Along the Truckee River



(photo: Fremont cottonwoods along the lower Truckee River near Nixon, NV)

March 1996

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This report consists of a draft for the following manuscript which will be submitted for publication in a refereed journal:

Instream Flows For Cottonwood Seedling Recruitment:

A Case Study of the Lower Truckee River, Nevada

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ABSTRACT: The Truckee River drains Lake Tahoe, CA, and flows east and then north into Pyramid Lake, NV. A sequence of dams exist along the Truckee River → Tributaries and substantial flow is diverted offstream for irrigation, domestic and industrial use. Due to historically severe stream flow alteration, cottonwood seedling replenishment has been almost absent during most of the 1900's. Following the designation of the indigenous cui-ui sucker fish as an endangered species, alterations to stream flow patterns have been imposed to promote spawning of this fish, through increased stream flows in the late spring. Subsequently, an extensive cottonwood recruitment event occurred that resulted in a dense but narrow band of uniformly-sized cottonwood saplings, lining most the final 50 km river reach. Saplings were cut down and ring counts of basal discs revealed that establishment had occurred in 1987, a year with moderate stream flow at the onset of cottonwood seed release followed by a consistently gradual stream stage decline of about 2.5 cm per day. This event (1) demonstrates that it is possible to artificially create a cottonwood seedling recruitment event and (2) validates a current model that defines the stream stage pattern essential for cottonwood seedling establishment. This event provides an optimistic case study relative to prospects for the restoration of degraded riparian cottonwood forests along streams in semi-arid regions of western North America.

KEY WORDS: ecosystem restoration, Fremont cottonwood, instream flows, *Populus fremontii*, riparian vegetation, river stage, seedling recruitment

INTRODUCTION

In many semi-arid regions of North America, native trees are restricted to riparian areas, river valley flood plains. Here, the landscape is shaped by the flowing river and the vegetation is dependent on the riparian water table that is recharged with water originating from the adjacent river. Cottonwoods, various *Populus* species, are well adapted to these dynamic riparian zones and are the principal and often exclusive trees along many rivers of western North America. The cottonwoods provide a foundation for riparian forest ecosystems that provide welcome environmental, aesthetic and recreational relief and provide the richest wildlife habitats in these regions (Finch and Ruggiero 1993).

Riparian cottonwoods have declined dramatically across western North America; it is estimated that three-quarters of the riparian forests in the southwestern United States have already been lost (Johnson and Haight 1984). Along the lower Truckee River in western Nevada, cottonwood decline has already occurred, apparently due to impacts of livestock and from river flow reduction (Lang et al. 1990). Fortunately, many trees still survive along the Truckee and considerable river flows are still passed. Thus, the Truckee River provides a candidate stream for restoration efforts.

Recent studies of the Fremont cottonwoods (*Populus fremontii*) along the lower Truckee River are in agreement with respect to historical patterns and present conditions (Caicco et al. 1993; Lang et al. 1990). Existing cottonwood groves are decrepit since few replacement trees were established over the past century. Seedling recruitment has been limited to low elevation zones adjacent to the stream. Thus, a key problem is the deficiency of seedling recruitment at higher elevations along the stream banks (Lang et al 1990).

Following the designation of the indigenous cui-ui sucker as an endangered species, alterations to Truckee River flow patterns have been imposed to promote spawning of this fish, particularly through increased stream flows in the late spring. Following the imposition of the artificial spawning flows, an extensive cottonwood recruitment event occurred. The present study was conducted to investigate the hydrological conditions that enabled the cottonwood seedling recruitment. An understanding of this event is relevant to the development of a stream flow strategy for the restoration of riparian cottonwoods along the lower Truckee River and is also of broader interest since it presents a case study to investigate the validity of a general model that describes the instream flow patterns required for successful cottonwood seedling recruitment.

MATERIAL AND METHODS

The study involved the lower Truckee River, east of Reno, Nevada, along the reach between Wadsworth and Nixon, NV, in the Pyramid Lake Indian Reservation.

Regular field visits occurred during 1993 through 1995 and included visits to six specific sites where permanent study transects were established in 1994 to monitor vegetation and hydrology. Visits to numerous other sites along the river occurred and canoe-based float trips along the entire reach were conducted April 30, 1995, at a flow that just submerged the base of the sapling band, and in July, 1995, when extensive areas of cottonwood seedlings occurred due to an artificial cottonwood seedling recruitment flow pattern presented in 1995 (to be described in future reports).

Field visits to determine sapling elevations and distributions and to harvest stem discs were conducted Oct. 7 through 9, 1994; April 29 through May 1, 1995; and Sept. 27 and 28, 1995. Sapling stem discs were sampled by cutting at the substrate surface or after excavation to expose the root crown. A cross section of each disc was shaved with a single-sided razor blade and the number of annual rings were counted to determine sapling age. A total of 87 saplings were harvested and basal stem segments were analyzed along with measurements of sapling heights and basal stem diameters.

The position of the sapling band was determined relative to distance from and elevation above the adjacent stream position. The consistency of the sapling position relative to stream stage was further assessed during the April 30, 1995 canoe trip.

Stream stage versus discharge ratings curves were obtained for three United States Dept. of Interior - Geological Survey Water Resources Division hydrometric gauging stations along the Lower Truckee River (310351700 Nixon; #10351650 Wadsworth; #10351600 Derby Dam). Further stream bank elevation profiles were determined along with discharge estimates as measured by flow velocity and depth measurements. The various stage versus discharge ratings curves were compared and the function that appeared most universal (the rating curve for the Nixon hydrometric gauge) was selected for subsequent conversions. Daily hydrographs for the period from 1958 through 1994 were obtained and the Nixon stage versus discharge conversion was used to provide stream stage hydrographs and to calculate daily stage change rates.

The extent of the cottonwood sapling band along the river reach was determined from air photos taken. A lineal ticking method was determined to be suitable since the sapling were restricted to narrow bands paralleling the stream (Rood and Heinze-Milne 1986; Rood et al. 1995). For this, transparent acetate sheets were placed over the air photos and the stream was traced. The stream line was divided into 1 mm segments and the occurrence of cottonwoods along either or both banks was rated for each segment with a positive value indicating the occurrence of saplings along most of the 1 mm segment for a given bank side. This analysis reduced the spatial distribution to a one-dimensional estimation with no consideration for the breadth or subsequent area of the band. The analysis provided a score of 0, 1 or 2 for each 1 mm segment, representing no cottonwoods, or cottonwoods dominant along one or both banks, respectively. The analysis was conducted for the reach from the Wadsworth to the Nixon bridges and included river segments which were historically densely occupied by cottonwoods as well as a segment downstream from Dead Ox Wash, which was historically deficient of cottonwoods, possibly due to the natural occurrence of saline seeps. The analysis thus included a measurement of the entire reach rather than a subsampling estimation. Consequently, analysis involving statistical extrapolation to a broader population is neither appropriate nor required.

RESULTS AND DISCUSSION

Field visits in October, 1994 confirmed the previous reports (Caicco et al. 1993; Lang et al. 1990). Groves of mature trees were sparse and decrepit (Figure 1). Few intermediate-sized trees occurred. Conversely, dense bands of 1 to 2.5 inch (2 to 6 cm) basal diameter saplings paralleled the stream (Figure 2 and cover photo show the saplings and the elevation of the sapling band is described in Figure 3). As determined by counting rings, the saplings were primarily established in 1987. The distribution of saplings and apparent recruitment in 1987 are consistent with a preliminary suggestion (Lang et al. 1990). Analyses of annual hydrographs can provide insight into the age and distribution of seedlings (Figure 4). For such analyses, stream stage (water surface elevation) rather than discharge (flow rate) should be considered.

In semi-arid areas, 'losing' streams occur in which water moves from the river into the adjacent riparian water table. The riparian water table is thus closely coordinated with the stream stage and in the seedling recruitment zone, within about 25 m (80 ft) of the river's edge, the water table surface is probably at an elevation similar to the river stage (Rood et al. 1995). how does this match w/ Jen's work

A common model describing the hydrological pattern necessary for successful seedling establishment has been independently derived (Mahoney and Rood 1990, 1993; Scott et al. 1993). The stream flow conditions that combine to permit successful cottonwood seedling recruitment (Figure 4) occur occasionally under natural conditions and even more rarely along many dammed streams (Rood and Mahoney, 1990).

FIGURE 1. A typical view along the lower Truckee River valley. The riparian woodland consists of scattered large Fremont cottonwoods with few smaller trees. This present landscape contrasts with historical reports such as those by explorer Fremont (for whom the cottonwood species is named), who described extensive and dense stands of cottonwood and willow along the lower Truckee River.

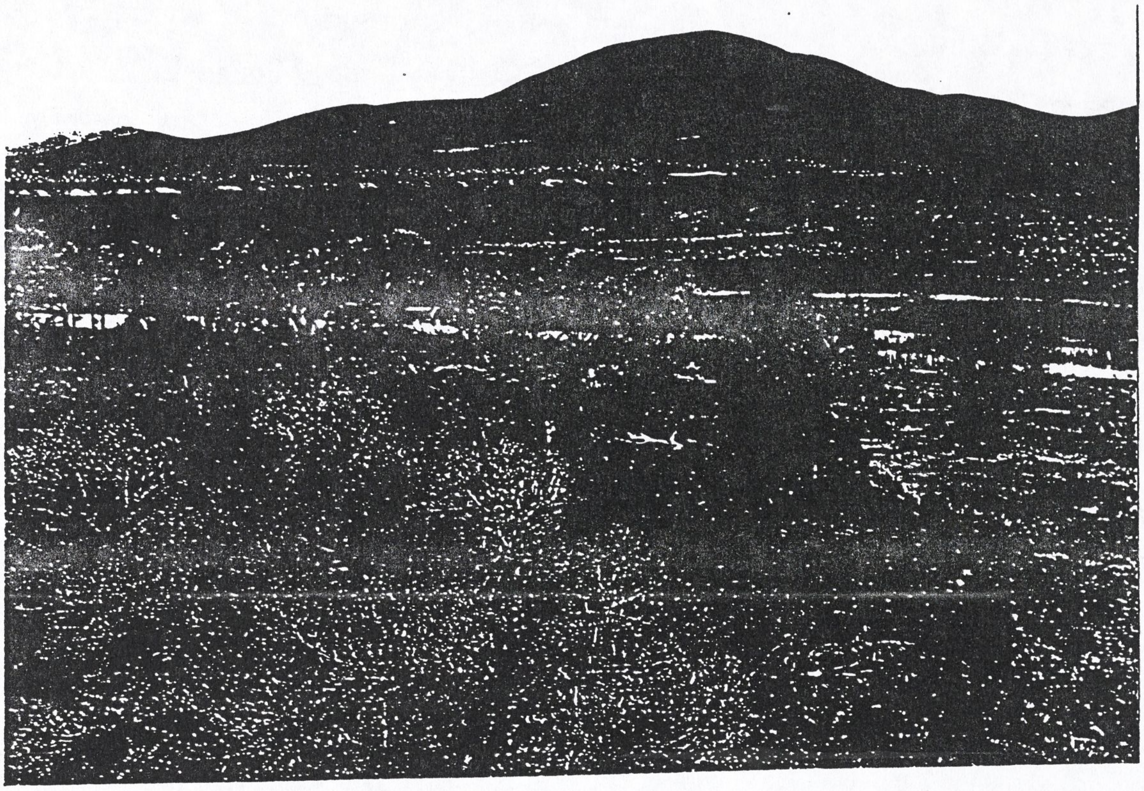


FIGURE 2. Dense bands of 8 year-old cottonwood saplings lining the lower Truckee River. The photo was taken May 1, 1995, when stream flows had risen to submerge the base of saplings. At lower flows, the stream is limited to the deeper channel which is located in between the two sapling bands.

FIGURE 3. Three short transects demonstrating the distribution of cottonwood saplings along the lower Truckee River. The saplings are restricted to narrow zones ranging from about 3 to 15 m (10 to 50 ft) from the river's edge and at elevations from about 40 to 70 cm (1.3 to 2.3 ft) above the late summer water line. This recruitment zone is narrow and low, and probably insufficient to replenish the aging cottonwood groves.

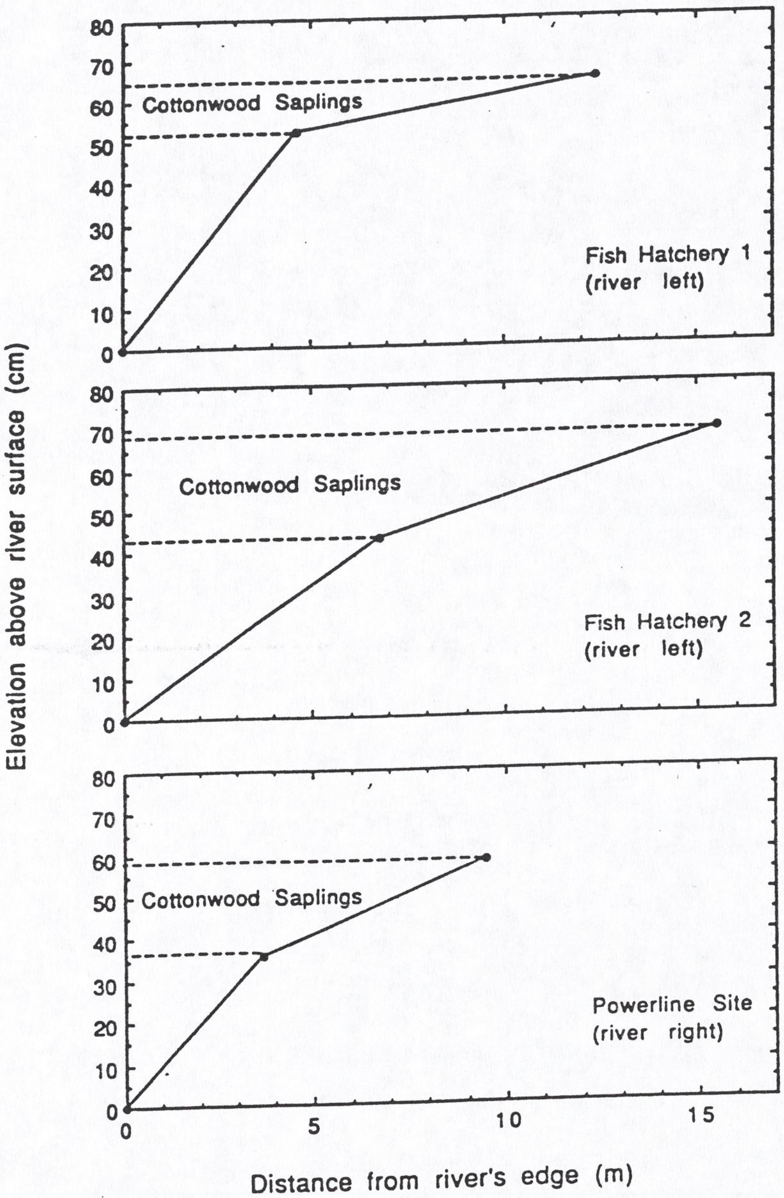
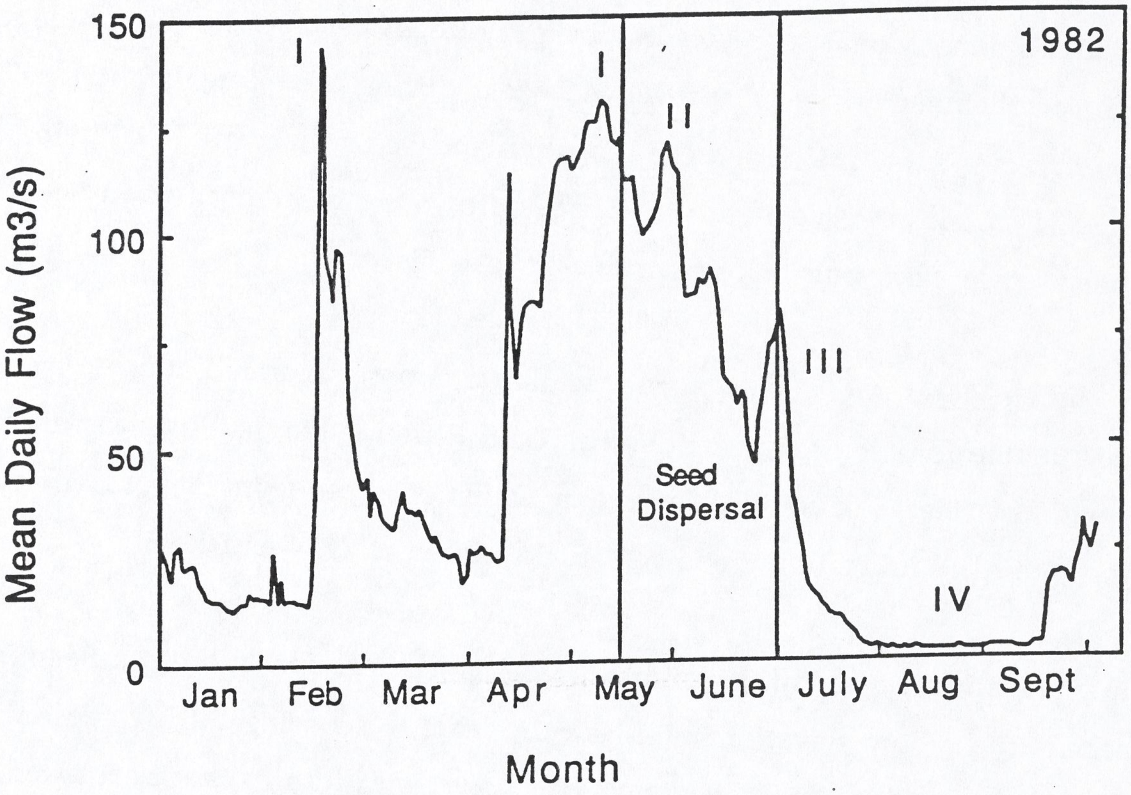


FIGURE 4. A typical annual hydrograph for the lower Truckee River (1982) demonstrating flow features essential for cottonwood seedling recruitment.

Numerals refer to hydrograph characteristics that are important for cottonwood seedling recruitment. Those characteristics are described in the following text.



I. Peak Flows - are required to drive the geomorphological processes associated with dynamic river meandering and the creation of recruitment zones, principally point bars on meander lobes.

Flood flows persist along the Truckee River, such as those in 1983 and 1986 (Lang et al. 1990). Winter storms produce short duration but potentially severe flood events (Figure 4 - I in Feb.). These winter floods drive stream meandering and erosional and depositional processes but are not directly responsible for cottonwood seedling establishment since no viable seed occur during the winter months. High flows from Sierra snow melt are more sustained and occur more predictably in May and June (I in May). The snow melt peak flows enable cottonwood seedling recruitment since they occur prior to or during seed dispersal.

II. Declining Flows After Peaks - are essential to expose saturated and barren sites that are suitable for seed germination. The critical period for seedling recruitment begins with the release of cottonwood seeds, which occurred from late-May through June and into early July along the lower Truckee River in 1994 and 1995.

The elevation of seedling establishment is critical for success. Seedlings established at very low elevations will be vulnerable to scouring during subsequent high flow events and will therefore not generally contribute to the areal extent of cottonwood recruitment. Seedlings established at excessively high elevations will succumb to drought stress as the declining water table drops out of the seedling root zone.

The suitable elevation for cottonwood recruitment has been determined by: (i) direct measurements of the recruitment zones along various rivers, (ii) excavation of seedlings to determine root growth capability, and (iii) experiments with artificial systems in which water table depth was varied. It has consequently been determined that the successful seedling recruitment zone extends from about 60 to 150 cm (2 to 5 ft) above the late summer river stage (Mahoney and Rood 1993). The elevation of successful recruitment is dependent on seedling growth capabilities and is thus generally similar for small streams and large rivers.

Based on the Nixon gauge ratings curve, the discharge required to reach the recruitment zone (60 to 150 cm or 2 to 5 ft above the late summer stage of about 30 cm) was determined as ranging from 20 to 115 m^3/s (Figure 5). These values are generally consistent with other generalized flow/depth relationships for the lower Truckee River (Lang et al. 1990).

III. <u>Gradual Flow Decline</u> - Although initial seedling establishment is usually abundant, seedling survival is generally very low. Survival requires that the rate of river stage decline be gradual enough that root growth can maintain contact with the receding riparian water table. For cottonwood seedlings, the maximum survivable rate of water table decline is about 2.5 cm/day (1 inch/day) (Mahoney and Rood 1991; McBride et al. 1988; Segelquist et al. 1993). Discharge changes producing a 2.5 cm stage decline can be estimated for the Truckee River (Table 1).

This suggests that the decline from 85 to 50 m^3/s should take place over 10 days (3 $m^3/s/day$) and the subsequent flow decline from 50 to 25 m^3/s should be presented over two weeks. Slightly more gradual flow decline rates should occur below 25 m^3/s.

FIGURE 5. A typical stage versus discharge ratings curve for the lower Truckee River, based on data from the Nixon hydrometric gauging station. The rating curve at that hydrometric station was intermediate between the curves for two other lower Truckee River gauging stations. The successful cottonwood seedling recruitment zone is typically 60 to 150 cm above the late summer stream stage which is about 30 cm on the adjusted stage graph (vertical line to the right of the 0 discharge plot frame axis). The two horizontal dashed lines represent the top and bottom of the recruitment zone and corresponding discharges are determined by the vertical lines from the ratings curve intercepts.

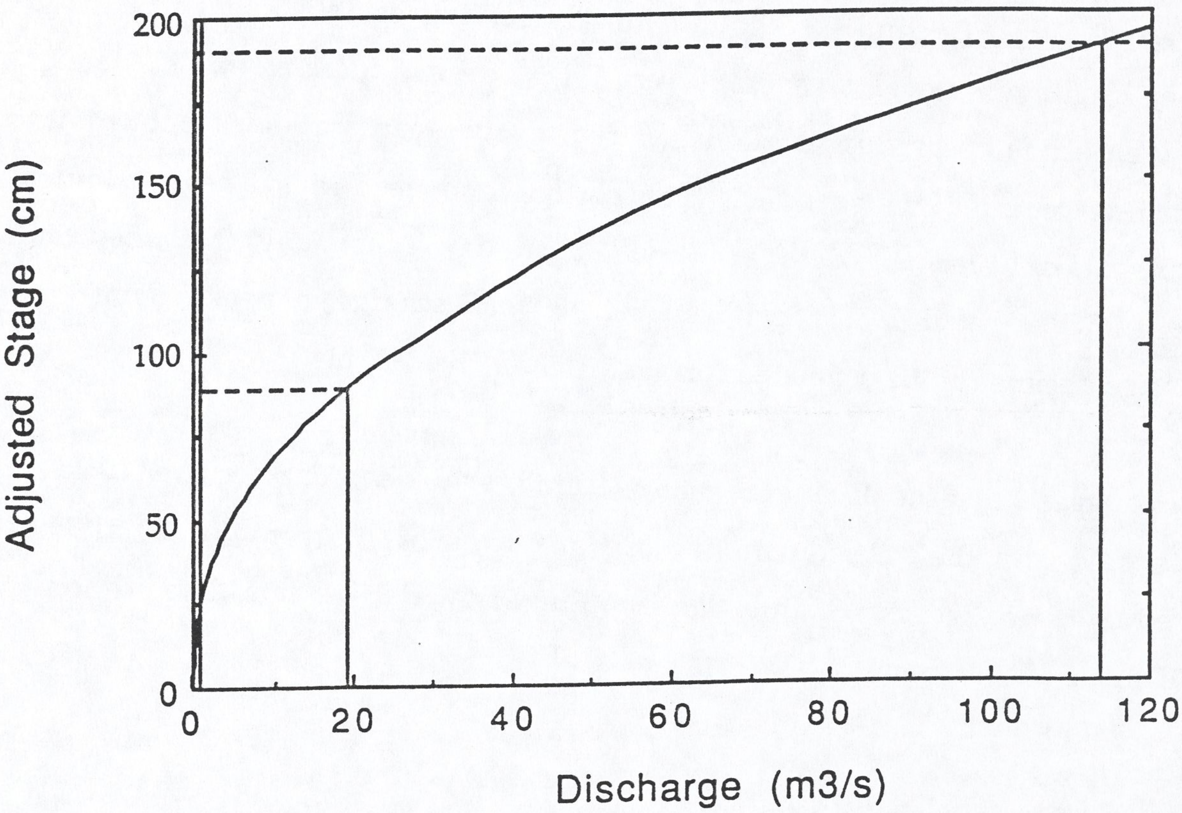


Table I. Approximate rates of stream flow reduction (discharge change rate) that will result in stream stage decline of about 2.5 cm/day (1 inch/day).

Discharge Range	Discharge Change Rate to Reduce Stage by 2.5 cm/day
85 to 56 m^3/s	2.8 $m^3/s/day$
56 to 28 m^3/s	2 $m^3/s/day$
28 to 14 m^3/s	1.4 $m^3/s/day$

IV. Sufficient Minimum Flows - should be presented through the hot, dry period of summer. Analyses of historical hydrographs indicate that flows in July and August were often less than 1.5 m^3/s in the 1980's and 1990's. These low flows are probably unfavorable for either new seedlings or established trees. Visible symptoms of drought stress would include senescence (yellowing) of leaves and branch mortality.

Analyses of Recent Historical Flows Along the Truckee River

The preceding model can be used to evaluate flow patterns along the Truckee River that occurred in the 1980's. The analysis first converts annual hydrograph data from discharges to stages, providing an annual profile of the water level. Secondly, rates of stage change are determined. Hydrographs that satisfy the instream flow needs for cottonwood recruitment are identified as those years in which:

(i) flows in late-May or June were between 28 and 115 m^3/s, and

(ii) stage decline rates only briefly exceeded 2.5 cm/day (Table 2).

This analysis indicates that recruitment was probable in 1981 and 1987 although mid-summer flows in both years were less than 1.5 m^3/s and this probably reduced seedling survival. Field observations confirmed that low elevation seedling recruitment had occurred in 1987 ((4) and Figure 3) supporting the validity of the model for the Truckee River.

Thus, sufficient flow frequently occurred to establish seedlings at favorable elevations. However, abrupt stage declines in early summer were probably lethal for the seedlings in the higher areas of the recruitment zone. These analyses suggest that relatively minor adjustments to flow regulation patterns could have had substantial benefits for cottonwood recruitment in the 1980's.

For sample comparisons, Figures 6 and 7 versus 8 and 9 are presented for 1987, a successful recruitment year, and 1986, a less successful year despite exceptionally high winter flows.

Table 2. Analyses of recent annual flows along the lower Truckee River with respect to instream flow needs for cottonwood seedling recruitment.

Year	Sufficient Spring Flow (& cfs*)	Gradual Stage Decline	Sufficient Instream Flow Pattern for Recruitment
1980	yes (2100)	no	
1981	yes (1700)	yes	yes
1982	yes (4000)	no	
1983	yes (6500)	no	
1984	yes (2600)	no	
1985	yes (1100)	no	
1986	yes (3000)	no	
1987	yes (1500)	yes	yes
1988	no		
1989	no		
1990	no		

* ($35.3\ ft^3/s = 1\ m^3/s$)

FIGURE 6. The daily river stage of the lower Truckee River in 1987. Successful cottonwood seedling recruitment in 1987 probably resulted from favorable stream stage (elevation) conditions that satisfied the hydrograph requirements already described. A moderate discharge and corresponding stage saturated the stream bank during the period of seed dispersal. Subsequently, the stream stage decline after initial seedling establisment was gradual, being about 2.5 cm/day (1 inch/)day (shown by the dashed line). The gradual flow and stage recession allowed root growth to maintain contact with the receding moisture zone.

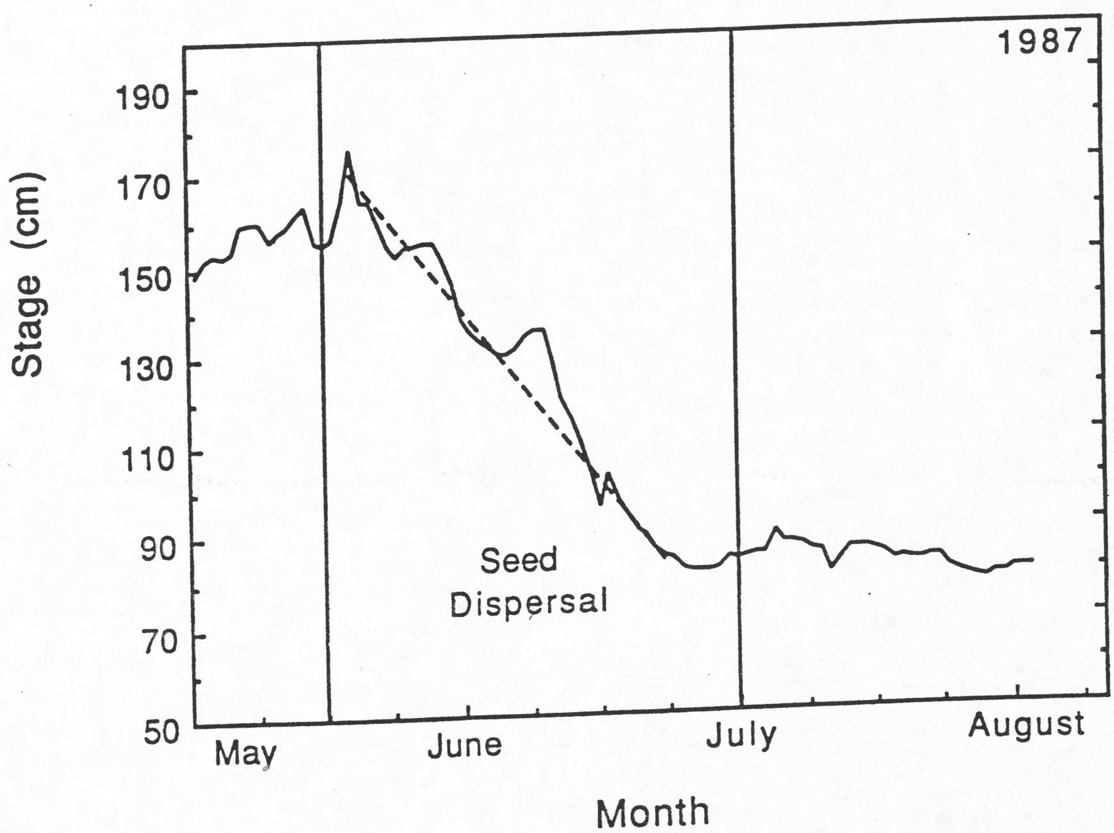


FIGURE 7. The daily rate of stage decline in 1987 for the lower Truckee River. The stage only exceeded 2.5 cm (1 in)/day for a few days and barely exceeded 5 cm/day. This gradual stage decline would permit cottonwood seedling survival.

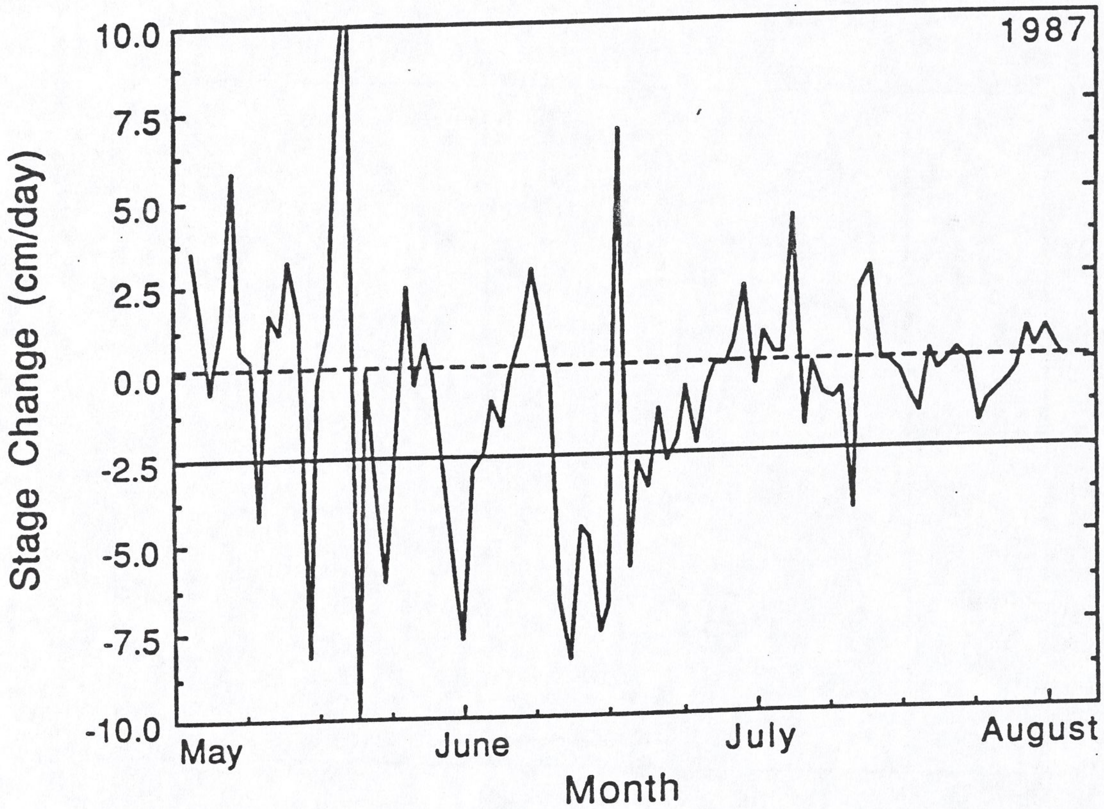


FIGURE 8. The daily river stage of the lower Truckee River in 1986. Although 1986 was a high flow year with massive winter flooding, seedling recruitment probably failed due to abrupt river decline in June. In contrast to the favorable stream stage pattern of 1987, the decline rate often exceeded 2.5 cm/day (1 inch/day) (dashed line).

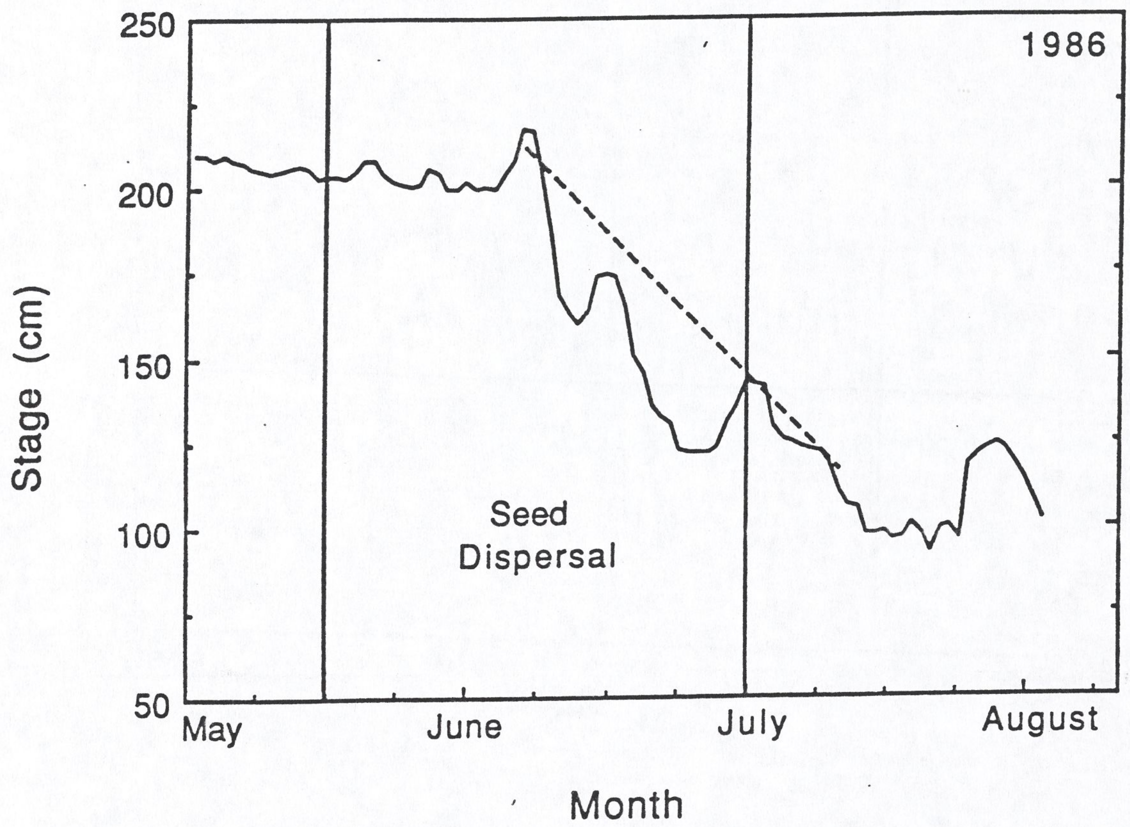
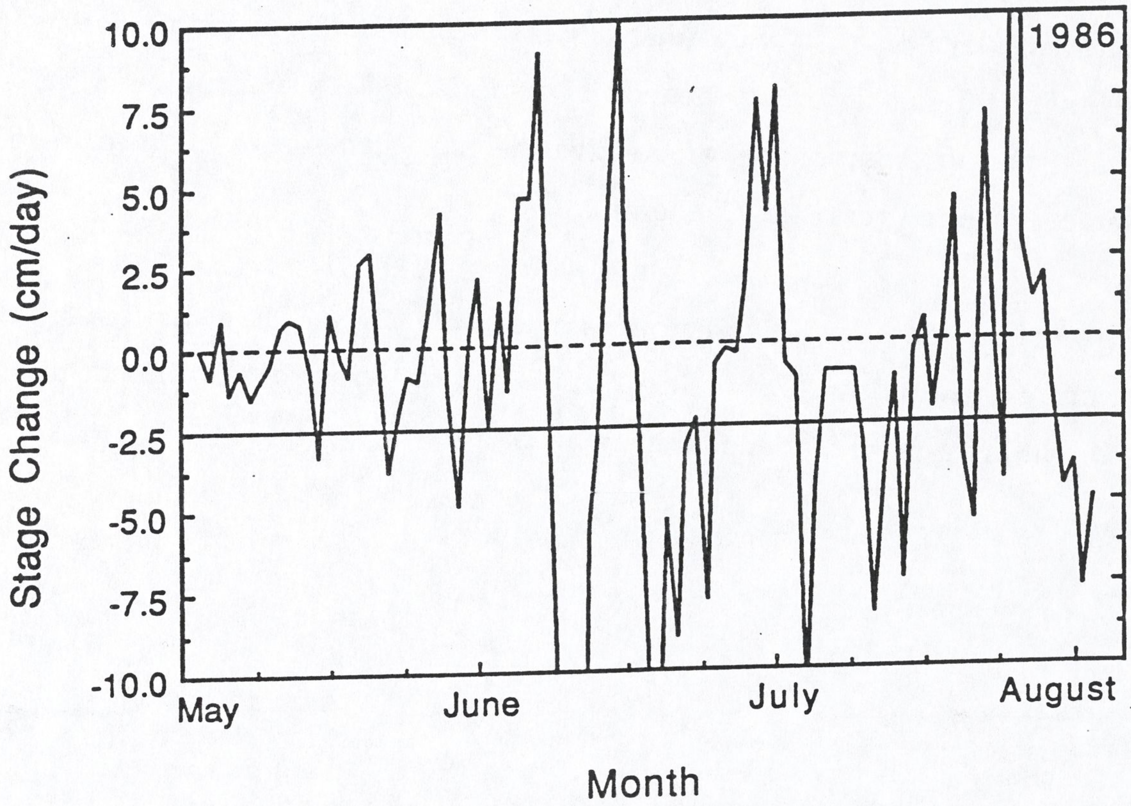


FIGURE 9. The daily rate of stage decline in 1986 for the lower Truckee River. The stream stage decline frequently exceeded 5 cm/day, and even exceeded 15 cm/day in early-June (bottom). These decline rates exceed the growth potential of cottonwood seedling roots and would thus leave the cottonwood seedlings, 'high and dry', resulting in drought-induced mortality



Environmental Management

It must be recognized that other factors also impact cottonwood growth and survival. Thus, livestock grazing and other influences must also considered for the successful restoration of the Truckee River cottonwoods.

The commitment of water for the benefit of riparian vegetation represents an allocation that is sympathetic with other environmental and recreational uses. For example, instream flows for the benefit of fisheries will also promote riparian ecosystems - various components of the riverine ecosystems have evolved to rely on the same dynamic stream flow patterns.

Finally, cottonwood seedling recruitment is naturally an irregular event that does not occur in low flow years. Stream flow for cottonwood recruitment might only be sought in years with abundant snow packs.

SUMMARY

A General Flow Prescription For Cottonwood Seedling Recruitment Along the Lower Truckee River

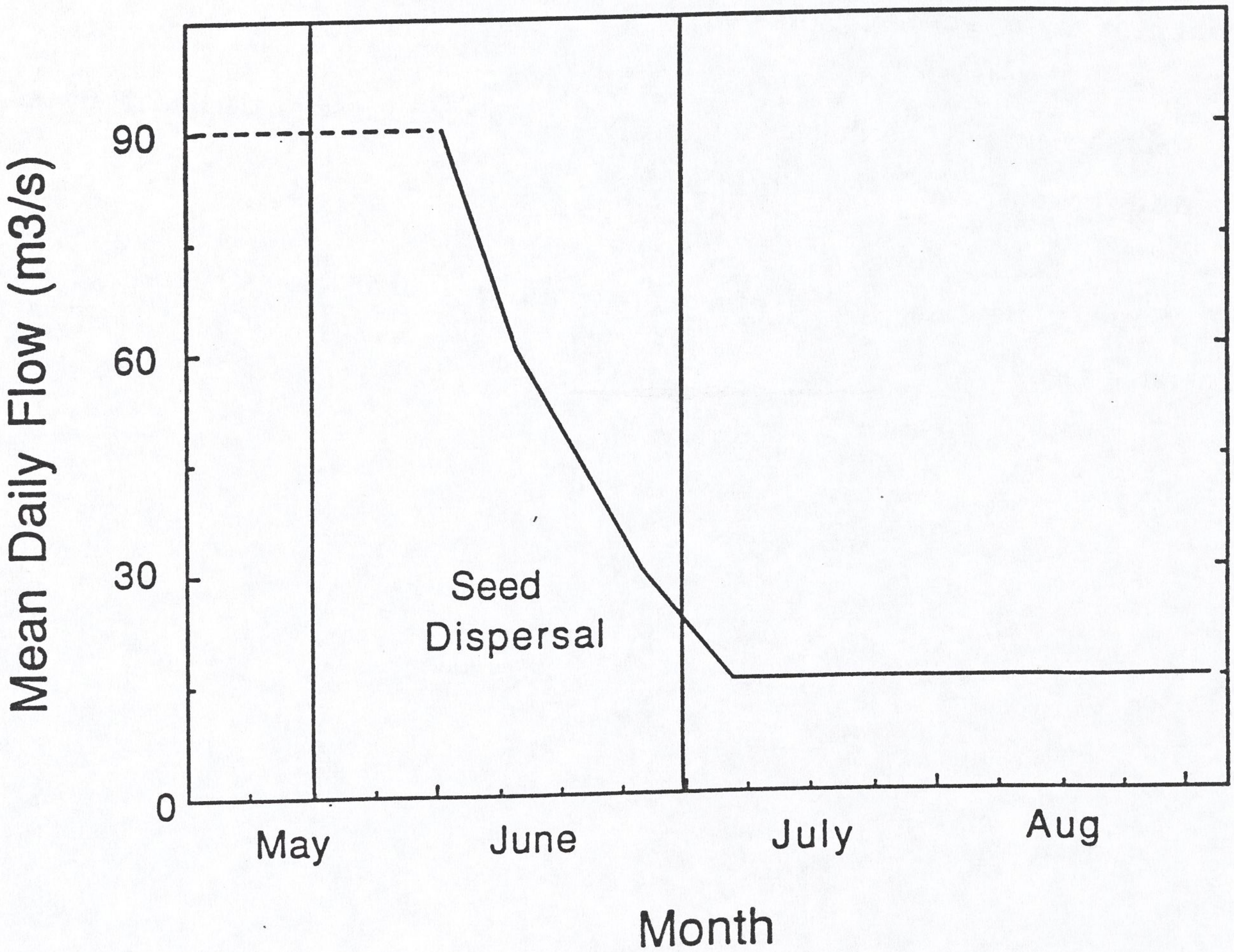
General flow recommendations to promote cottonwood seedling establishment along the lower Truckee River were produced (Figure 10). In recruitment (moderate or high flow) years:

(i) Flow at some point from mid-May through June should be from 40 to 115 m^3/s (1500 to 4000 ft^3/s) (higher initial flows are favorable since this will permit recruitment at a broader range of elevations),

(ii) Subsequent flow decline should be gradual, to produce stage decline that does not greatly or consistently exceed 1 inch/day, and

(iii) Summer flow should be sufficient to prevent lethal drought stress of the vulnerable seedlings.

FIGURE 10. An ideal flow pattern for cottonwood seedling recruitment along the lower Truckee River. The initial flow would be between 40 and 115 m^3/s (1500 and 4000 cfs), with higher starting flows increasing the height and extent of the recruitment zone. Flow decline should be gradual enough to maintain root contact and finally, sufficient summer flows should be presented. A hydrograph following this general pattern was artificially delivered in the summer of 1995 and resulted in extensive cottonwood seedling recruitment. July and August conditions were, however, exceptionally hot and dry, imposing high evapotranspirational demand and subsequent drought stress and drought-induced mortality. Some seedlings did survive through 1995 and their subsequent fate is presently under investigation and will be described in subsequent reports.



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R. B.

Effects of pollutants on freshwater organisms

Scott Hall, Jim Chamberlain,
Erika Godwin-Saad

A myriad of "pollutants" enter freshwaters from innumerable sources, and their effects on aquatic life are exhibited from the cellular to ecosystem levels. Much research has been published in these areas. This paper reviews some of the published research on the effects of chemicals on freshwater organisms.

METALS

Both growth inhibition and bioaccumulation of aluminum in the green alga *Chlorella pyrenoidosa* was studied by Parent and Campbell (1994) in soft water media. The results of these studies showed that aluminum bioavailability was predictably a function of the free aluminum ion in systems containing only inorganic monomeric aluminum, and the effect of aluminum on algal growth is highly pH dependent. *Hydrilla verticillata* was used to evaluate the usefulness of peroxidase activity as an indicator of rooted plant exposure to metabolic and organic contaminants (Byl *et al.*, 1994). Significant increases in this endpoint were observed as a result of exposure to 0.01 mg/L cadmium, copper, and chromium; 0.1 mg/L selenium; and 1.0 mg/L manganese. Tubbing *et al.* (1994) tested the hypothesis that the concentration of free copper metal ions is the main determinant of metal toxicity by adding different concentrations of copper to water from the River Rhine and measuring the effect on the photosynthetic rate of the alga *Selenastrum capricornutum.* Addition of 5 μM copper to the medium with 5 or 10 μm of EDTA inhibited algal photosynthesis, although copper was not voltametrically detectable (<0.005 μM). *Lemna minor* (duckweed) was grown in treated domestic wastewater containing added copper to study the relationship between complexation and bioavailability of copper (Buckley, 1994a). Measurement of the copper Complexing Capacity (CC) of the wastewater gave values of 0.26 to 0.29 mg/L. Growth was not inhibited until total copper exceeded 0.079 to 0.119 mg/L. Effective Concentrations (ECs) based on tissue concentration of copper rather than solution concentration are more sensitive and have been proposed as an alternative for work in complex solutions like wastewater. A particular effect of copper on duckweed was observed by Buckley (1994b) in the activity inhibition of the enzyme superoxide dismutase (SOD) in *Lemna minor* containing 408 μg Cu/g (dry wt) but not in plants containing 215 μg Cu/g (dry wt) or less. The presence of copper in a planktonic community caused a reduction in the dry-weight biomass of zooplankton, ciliates, flagellates, and phytoplankton (Havens, 1994a). Copper also reduced the effectiveness of the food web in transporting carbon to the surviving zooplankton.

Water hyacinths exposed to water containing 2μg Cd^{2+}/mL bioconcentrated the element mainly in the roots and in proportion to the increase of the thiol group content (Ding *et al.*, 1994). This suggests the possibility of using the thiol group content to assess the bioconcentration of heavy metal ions in water hyacinths and as a general parameter for monitoring heavy metal pollution. Dirilgen and Inel (1994) investigated the effects of combined zinc and copper concentrations on the growth and degree of metal accumulation in duckweed, *Lemna minor,* under laboratory conditions. Duckweed was selected for study because of its rapid growth and ability to adapt to aquatic conditions. The effects of increased concentrations of zinc and copper in combination were correlated with the corresponding relative growth rates (RGR), dry to fresh weight ratios (DFR), and concentrations of metal accumulated by the duckweed. The level of zinc accumulated in the plant was higher than the copper concentration accumulated in every concentration tested. At the concentrations of 0.10 to 2.00 ppm, zinc suppressed the inhibitory effect of copper. Macfie *et al.* (1994) studied the effects of cadmium, cobalt, copper and nickel on two strains of the green alga *Chlamydomonas reinhardtii.* The researchers evaluated the influences of the cell wall and pH in relation to metal toxicity. Their results showed that the wall-less strain was consistently more sensitive to all four metals than the walled strain. The authors suggested that the cell wall plays a role in conferring metal tolerance. They also noted that for both strains of green algae, metals were less toxic at pH 5.0 than pH 7.0 s.u. Williams *et al.* (1994) evaluated the effects of sulfate on selenite uptake and toxicity in the green alga *Selenastrum capricornutum.* Sulfate and selenite compete for active transport across the cell membrane through a common permease. These effects were investigated using two sulfate levels (3.3 and 33 mg/L) and two selenite levels (10 and 100 μg/L). Selenium uptake and toxicity analyses demonstrated antagonism between the two anions. Increasing sulfate resulted in significantly reduced selenite uptake and increased algal growth.

The acute toxicity of copper, cadmium, and zinc to the water flea, *Moina irrasa* was investigated (Zou and Bu, 1994). This water flea is commonly found in the freshwaters of the Yangtze Delta in China. The results demonstrated that metal toxicity to this cladoceran increased with increasing exposure time and that this particular species was more sensitive to the evaluated metals than many other species of cladocerans, including *Ceriodaphnia dubia* and *Daphnia magna.* The effects of three diets on the health and robustness of *Ceriodaphnia dubia* were evaluated for 19 generations by LaRocca *et al.* (1994). The results suggest that a diet including multiple species of algae is nutritionally superior and provides greater protection against copper toxicity than a diet including a single species of algae. Chronic toxicity tests were used to determine effects on *Daphnia magna* life-table data as a result of algal food concentrations in tests with cadmium at concentrations ranging from 0.5 to 5 μg/L (Kluttgen and Ratte, 1994). Results of these studies indicated that the development of juveniles was inhibited by cadmium at low food (*Chlorella saccharophila*) doses, whereas body length and reproduction were strongly affected at higher food doses. The intrinsic rate of natural increase was generally reduced by cadmium regardless of food concentrations. The effects of acclimation and exposure temperature on the acute toxicity of cadmium to the freshwater snail (*Potamopyrgus antipodarum*) were evaluated by Moller *et al.* (1994) using 48-hour toxicity tests. Results of these studies indicated that regardless of acclimation temperature, mortality increased with increased test temperature, and at all exposure temperatures snails acclimated at 15°C were most sensitive to cadmium. Cadmium LC50 values ranged from 1 to 4 mg/L. Effects of species and sex on metal residues in freshwater mussels collected from the St. Lawrence River were evaluated by Metcalf-Smith (1994). Study results indicated that *Elliptio complanata* demonstrated a broader response range to most of the 12 metals evaluated as compared to other species. Differences in metal uptake between sexes were less pronounced, but male organisms demonstrated less variability in metal uptake as compared to females. The effects of zinc on the structure of natural benthic assemblages from a third-versus a fourth-order stream were studied by Kiffney and Clements (1994) using artificial streams and 7 day exposures. Significant effects were observed at the community and population level due to zinc exposures of 130 μg/L, but the magnitude of response, especially for mayflies, differed between organisms from the different stream orders. Clements and Kiffney (1994) also evaluated laboratory and field approaches to determining the effects of metals on stream macroinvertebrates. Endpoints considered included benthos metal bioaccumulation, chronic toxicity to a water flea, and benthic community structure. An integrated approach was recommended given that different information was produced by each approach individually. With the decrease of heavy metal loadings into the South Fork and mainstem of the Coeur d'Alene River in Idaho, macroinvertebrate populations have risen both in number and diversity (Hoiland *et al.,* 1994). Seven years of close monitoring (1968 to 71, 1987 to 91) have showed large increases in taxonomic richness (0 to 18), Ephemeroptera-Plecoptera-Trichoptera index (0 to 8), and species diversity (0 to 1.8). Typical riparian vegetation, such as cedar, hemlock, and willow, were almost completely eliminated by heavy zinc, cadmium and copper concentrations. Reductions in the feeding rate of *Gammarus pulex* were shown by Maltby and Crane (1994) to be a sensitive indicator of the impact of complex metalliferous effluents on receiving water quality. Two metals, iron and manganese, were identified as the probable toxic agents. Exposure to sublethal concentrations of cadmium resulted in a significant increase in the frequency and degree of damage to the anal papillae of the larvae of two species-*Hydropsyche contubernalis* and *Hydropsyche siltalai* (Vuori, 1994). Collyard *et al.* (1994) investigated the influence of age on the relative sensitivity of *Hyallella azteca* to diazinon, alkylphenol ethoxylates, copper, cadmium, and zinc. The objective of the study was to investigate age-specific differences in sensitivity of the amphipod to contaminants with varying toxic modes of action. Overall, the results suggested that age-specific differences were relatively small. The 96-hour LC_{50} values varied by 50% or less among the different ages classes (between 1 to 26 days). In conclusion, no particular age class consistently was the most sensitive to any given toxicant. Cope *et al.* (1994) determined that nonthionein cytosolic cadmium was the most sensitive indicator of cadmium exposure in bluegills studied in bioaccumulation studies evaluating metal binding proteins as indicators of metal exposure.

PESTICIDES

Kirby and Sheahan (1994) studied the toxicity of three herbicides, atrazine, isoproturon, and mecoprop to the duckweed (*Lemna minor*) and the alga *Scenedesmus subspicatus.* Their results indicated that of the three herbicides, isoproturon was most toxic to duckweed. The 10-day EC_{50} values for effects on total chlorophyll concentration in duckweed by atrazine, isoproturon, and mecoprop were 62, 31, and 6 223 μg/L, respectively. Atrazine and isoproturon affected the cell production of *S. subspicatus* at similar concentrations (96-hr EC_{50} values were 21 μg/L). Mecoprop was far less toxic to *S. subspicatus* with a 96-hr EC_{50} value of 102 660 μg/L. The effects of the pyrethroid insecticide fenvalerate on riffle insect assemblages in stream microcosms was evaluated for a 30 day period by Breneman and Pontasch (1994). Initial exposure of the insect communities to 1.0 to 10.0 μg/L fenvalerate resulted in significant increases in drift. After 30 days, density and species richness significantly decreased for most taxa when exposed to 0.1 μg/L fenvalerate. The most severely impacted organisms included mayflies, stoneflies, riffle beetles, caddisflies, and some chironomids. Harrahy *et al.* (1994) exposed mayflies and stoneflies to Dimilin®. Mayflies were found to be sensitive to Dimilin® at concentrations of 0.6 μg/L, whereas stoneflies were found to be less sensitive to this insect growth regulator. Abdullah *et al.* (1994) investigated the effects of the organophosphate insecticide profenofos on the acetlycholinestrase (AChE) activity of the freshwater Australian shrimp *Paratya australiensis* in 21 day exposures. Profenofos significantly inhibited AChE activity at concentrations of 0.1 to 1.0 μg/L. Intermittent acute (24 hour) exposures were more harmful to the shrimp as compared to continuous acute exposures as evaluated by recovery in profenofos-free water. The effects of a common algalcide, copper sulfate, and an insecticide, Carbaryl, on freshwater zooplankton were studied by Havens (1994b). Across the gradients of increasing copper or Carbaryl doses, cladocerans were greatly reduced and copepods became dominant. A study was undertaken to determine whether deposits of fenitrothion (used for forrest spraying) in two small ponds within operational spray blocks was sufficient to be acutely toxic (lethal) to rainbow trout, *Oncorhynchus mykiss* and *Daphnia magna* (Ernst *et al.*, (1994). No mortality was observed to either test species in one pond. However, in another pond, approximately 30% mortality occurred with rainbow trout within 96 hours and greater than 50% mortality occurred to *Daphnia magna* within 48 hours.

Berrill *et al.* (1994) studied the effects of the forest-use pesticides fenitrothion, triclopyr, and hexazinone on three species of frog embryos and tadpoles as indicated by hatching success, ability to swim, avoidance, and mortality. Results of these studies indicated that hexazinone had no effects on frogs at environmentally unrealistic concentrations, and hatching success and subsequent avoidance were unaffected in all frog species by exposure to fenitrothion and triclopyr. However, newly hatched species of tadpoles were killed or paralyzed by concentrations of triclopyr and fenitrothion at concentrations of 8 μg/L and less. Beyers and Sikoski (1994) documented inhibition of acetylcholinesterase in the endangered Colorado squawfish as a result of exposure to technical grade carbaryl and malathion. Threshold concentrations of 7.4 μg/L carbaryl and 150 μg/L malathion were determined using a linear-plateau regression model. Effects as determined in 32-day early life cycle tests evaluating growth and survival also indicated that the Colorado squawfish was much more sensitive to carbaryl as compared to malathion. Overall, the biochemical indicator was a more sensitive determinant of toxicity as compared to the endpoints of growth and survival. Davies *et al.* (1994) evaluated the toxicity of seven pesticides to several species of Australian freshwater fish and crustaceans as determined by sublethal biochemical indicators. Decapod crustaceans were extremely sensitive to organophosphates. Sublethal indicators in fish were not protective of other effects in other fish species. Maximum Allowable Toxicant Concentrations (MATC) were also developed. Sunderam *et al.* (1994) determined the acute and chronic toxicity of Endosulfan to two Australian cladocerans and related their findings to deriving water quality criteria. For *Ceriodaphnia dubia,* the 48-hr EC_{50} (immobilization) was 490 μg/L and the chronic NOEC for reproductive impairment was 10 μg/L. For *Moinodaphnia macleayi,* the 48-hr EC_{50} was 215 μg/L and the chronic NOEC was 20 μg/L. The authors suggested that the concentration of endosulfan for Australian waters should be less than that currently specified by the Australian Water Quality Guidelines (10 ng/L). The lethal and sub-lethal toxicity of lindane to the fathead minnow (*Pimephales promelas*) and *Ceriodaphnia dubia* was reviewed (Constable and Orr, 1994). Lindane is frequently detected at levels of 0.001 to 0.02 μg/L in some Canadian rivers. The authors suggest that this low, but continuous level of contamination may pose a sub-lethal toxic threat to aquatic life. The reproductive NOEC values determined by their study for fathead minnows and *Ceriodaphnia dubia* were 21 and 6.6 μg/L, respectively.

DIOXINS/FURANS, PCBs

Walker and Peterson (1994) documented mortality in early life stage brook trout exposed to 101 to 470 pg/g 2,3,7,8-TCDD. These trout had been exposed to 2,3,7,8-TCDD as newly fertilized eggs then transferred to contaminant-free waters to develop. Other effects noted included yolk-sac edema, hemorrhages, and arrested development in sac-fry. Accumulation of PCDDs and PCDFs in white sucker muscle and liver were evaluated for fish collected from near pulp mill discharges (Servos *et al.,* 1994). PCDD/PCDF concentrations were much higher in liver as compared to muscle, but these differences could be accounted for by lipid normalization. Toxic equivalent concentrations were evaluated with regards to effects on mixed function oxidase (MFO) activity and positive correlations were observed. However, site-specific findings and findings that MFO activity is rapidly cleared in pulp-mill-exposed fish casted doubts on the causal relationship to PCDDs and PCDFs. The bioaccumulation of 40 PCB congeners in three unialgal species (*Selenastrum capricornutum, Anabaena sp.,* and *Synedra sp.*) was investigated over a 40 day period by Stange and Swackhammer (1994). For all species, initial PCB partitioning to algae was rapid, followed by slower partitioning of PCBs to algae. Partitioning of PCBs to algae was predictable for PCBs with log octanol-water partition coefficients of less than 6.0.

OTHER ORGANICS

Gala and Giesy (1994) documented photoinduced toxicity of the PAH anthracene to the green alga *Selenastrum capricornutum.* The stress index (SI) proved to be a useful indicator of photoinduced toxicity, demonstrating effects in 28 hour tests at anthracene concentrations as low as 8.3 μg/L. The rooted aquatic macrophyte *Hydrilla verticillata* was used to evaluate the usefulness of peroxidase activity as an indicator of exposure to anthracene (Byl *et al.,* 1994). Significant increases in peroxidase activity were noted as a result of exposure to 0.01 mg/L anthracene. The removal of phenols in the presence of copper and zinc by the aquatic weed, *Eichhornia crassipes,* was investigated by Nor (1994) in order to assess its ability to clean up industrial wastewater. The presence of copper or zinc resulted in decreased phenol uptake during the first 0.5 day, while the presence of copper and zinc in combination resulted in higher phenol uptake. After a one day exposure, however, little or no differences could be discerned.

Bioconcentration of a polynuclear aromatic compound, pyrene, was studied by Wildi (1994) at pH 4, 6, and 8 s.u. with larval stages of the chronomid midge, *Chironomid riparius.* The results revealed a greater bioconcentration rate (K_1) at higher pH than at lower pH. The reduced rate at low pH was likely the result of increased mucus production of the salivary glands and accelerated build-up of larval tubes in the acidified environment. The toxicity of 2,3,4,6-tetrachlorophenol (TeCP) and pentachlorophenol (PCP) was determined following standardized acute and chronic toxicity test protocols for *Daphnia* and rotifers

(Liber and Solomon, 1994). For *D. magna,* 48-hour LC_{50} estimates indicated that PCP was more toxic than TeCP. The commercial TeCP formulation DIATOX®, which contains a 6.5:1 ratio of TeCP:PCP, exhibited intermediate toxicity. Mean LC_{50} values were 1.2, 2.7, and 2.1 mg/L, respectively. *D. galeata* was more sensitive to TeCP than *D. magna* with a 48-hour LC_{50} value of 0.58 mg/L. No reproductive effects on surviving *Daphnia* were observed for either species. Rotifer tests were conducted with *Brachionus calyciflorus* and *Keratella cochlearis.* These tests also indicated that PCP was more acutely toxic to rotifers than TeCP. For example, the range of 24-hour LC_{50} values to *B. calyciflorus* was 2.09 to 7.76 mg/L for PCP and 2.31 to greater than 16 mg/L for TeCP. The accumulation of PAHs in mirror carp was studied by van der Weiden *et al.* (1994) while determining temporal induction of cytochrome P450 in this organism. From these studies, it was determined that up to 25% of the administered dose of PAHs was accumulated in the liver of the test species. High inductions of cytochrome P450 were also associated with the administration of PAHs. Fent and Meier (1994) investigated the effects of triphenylin chloride (TPT) on hatching, survival and morphology in the early life stages of European minnows, *Phoxinus phoxinus.* TPT compounds are used as a cotoxicant to tributyltin in antifouling paints. The authors reported that greater mortality was observed at higher temperatures in fish exposed to triphenylin. Hatching was delayed and hatching success was decreased at a level of 15.9 µg/L triphenylin. The investigators observed that the toxicity of TPT was similar to that of tributyltin.

CONVENTIONAL POLLUTANTS AND EFFLUENTS

Borgmann (1994) showed that ammonia exposure resulted in the continuous mortality of the amphipod *Hyalella azteca* for up to 10 weeks with similar mortality rates for adults and young. Tests demonstrated that ammonia toxicity to *H. azteca* is best defined on a total ammonia basis. Hickley and Vickers (1994) presented data on the toxicity of ammonia to nine native New Zealand freshwater invertebrate species. At a water temperature of 15°C and pH 7.6 and 8.2 s.u., the 96-hour EC_{50} concentrations ranged from 0.18 to greater than 0.8 g/m^3. The rank of species sensitivity was: shrimp (*Paratya curvirostris*) = mayfly (*Zephlebia dentata*) = stonefly (*Zealandobius furcillatus*) < Oligochaeta (*Lumbriculus variegatus*) < fingernail clam (*Sphaerium novaezelandiae*) < mayfly (*Deleatidium spp.*) < snail (*Potamopyrgus antipodarum*) < caddisfly (*Pycnocentria evecta*) < crustacean (*Paracalliope fluviatilis*). The authors conclude that the USEPA criteria may not provide adequate protection for New Zealand species.

Fathead minnows were exposed to thiocyanate in 124-day tests (Lanno and Dixon, 1994) evaluating effects on growth, physiological, reproductive, and histological parameters. Histological changes in thyroidal tissue were the most sensitive indicators of toxicity, indicating effects at concentrations of 1.1 mg/L. Other effects were observed at thiocyanate concentrations of above 15 mg/L. Nitrite was found to effect the survival of Grass Carp, *Ctenopharyngodon idella,* in relation with chloride (Alcaraz and Espina, 1994). The toxicity of nitrite to *C. idella* decreased in groups of fish exposed to the nitrite 96-hr LC_{50} value of 1.71 mg/L (plus higher concentrations) with increasing chloride concentrations of 5 to 6.5 mg/L. Through the use of GIS, Richards and Host (1994) found strong correlations between substrate characterization/coarse woody debris and macroinvertebrate assemblage richness and composition. Substrate characteristics were then tied to agricultural and urban land use, suggesting primary relationships between land use and stream habitat quality. The fine particle fraction of sediments collected near bulkheads made of chromated copper arsenate (CCA)-treated wood had elevated concentrations of the three chemicals (Weis and Weis, 1994). Concentrations of these chemicals decreased with distance from the bulkhead. Elevated concentrations of these contaminants were also detected in benthic organisms adjacent to the bulkheads. However, toxicity tests with the corresponding sediments did not reveal consistent toxicity. Analyses of the benthic community around the bulkheads did reveal reduced species richness, total numbers of organisms, and diversity compared with reference sediments with lower metal concentrations. The effects of chlorine on valve movement in the Asiatic Clam *Corbicula fluminea* was evaluated by Ham and Peterson (1994) using automated technologies. Significant reductions in valve closure were observed as a result of exposure to 0.02 to 0.07 mg/L total residual chlorine. Fu *et al.* (1994) compared the acute (92 to 96 hour) toxicity of pre- and post-treatment effluents to *Hydra attenuata* to effluent toxicity to fathead minnow (*Pimephales promelas*). These studies indicated that *H. attenuata* holds promise for use as a simple tool to assess effluent toxicity. A simple bioassay, based on the reproductive behavior of the amphipod *Gammarus pulex,* was found by Pascal *et al.* (1994) to be useful in detecting a wide range of pollutants at concentrations significantly below those causing acute lethal toxicity.

Biochemical, physiological, and pathological endpoints were evaluated for mountain whitefish and longnose sucker exposed to biologically treated bleached-kraft effluent (Kloepper-Sams *et al.,* 1994). Bodyburdens of metals and organics were evaluated for correlations with observed responses. Of the numerous biochemical endpoints evaluated, the detoxification enzyme cytochrome P4501A consistently indicated exposure to the effluent. Klopper-Sams and Benton (1994) also used P4501A as an indicator in field monitoring studies and found no correlations between induction of P4501A and other endpoints. P4501A could not be related to adverse effects in these field-related studies. Swanson *et al.* (1994) found no correlations between fish population level effects and exposure to bleached-kraft mill effluent. Robinson *et al.* (1994) used *Ceriodaphnia* and fathead minnow toxicity tests to assess the effects of pulp mill effluents. These tests indicated toxicity to fathead minnows for some ambient waters, while some ambient waters containing pulp mill effluents increased *Ceriodaphnia* reproduction. Neither type of test predicted physiological changes observed for fish collected from receiving waters. Munkittrick *et al.* (1994) surveyed receiving water environmental impacts associated with pulp mills as evaluate by fish organ weights, hepatic mixed function oxidase (MFO) activity, and plasma steroid levels. Results indicated that hepatic MFO induction occurred at some locations downstream of pulp mill discharges with and without chlorine bleaching. A laboratory assessment was made of a fish monitor used to measure significant changes in fish ventilation frequency as an indicator of the occurrence of a toxic pollutant (Baldwin *et al.,* 1994a). The monitor was found to show responses at between 10% and 250% of the LC_{50} for rainbow trout (*Salmo gairdneri*) with a response within 40 minutes. The concentration of response may be considerably higher than the suggested no response adverse levels (SNARL) when toxic symptoms are of a chronic nature. Baldwin *et al.* (1994b) performed field trials on the same monitor over a one year period to determine whether the established performance from lab testing could be sustained in operation and to identify factors which may cause false responses. The main factors causing false responses were physical disturbances: entry into fish monitor rooms, interruptions in water flow, and sudden changes in water conditions resulting from influences of extreme high tides. The false response rate was estimated to be at or below that estimated from laboratory trials. The potential of 31 secondary-treated pulp and paper mill effluents from eight different mills to induce mixed function oxidase (MFO) activity in the livers of rainbow trout (*Oncorhynchus mykiss*) was investigated by short-term (4-day) laboratory exposures to 10% effluent concentration (Martel *et al.*, 1994). The greatest increase in ethoxy-resortin-O-deethylase (EROD) activity came from thermochemical pulp (TMP) mill effluents and, specifically, from the kraft cooking process used to convert wood into pulp.

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QUESTION 1: **Chapter 4 gives a brief overview of Rosgen's Channel Classification. Get the original document and elaborate a little on the stream types. Also find a journal article that cites Rosgen (1994).**

Stream classification systems have been proposed by many scientists (Davis 1899; Culbertson et al. 1967; Kahn 1971) in an attempt to enable the understanding of fluvial processes and to predict behavior of a stream based on its appearance. Classifying objects allows for the creation of groups based on common characteristics. In the case of streams, classification may be the initial step in restoration, sediment, and flood control. Rosgen (1994) based stream classification on broad categorizations of channel slope, shape and patterns. The interplay of these geomorphic characteristics results in nine stream types ranging from steep, straight, mountain streams to wide, estuarian channels. Classes of streams include Aa+, A, B, C, D, DA, E, F, and G. These categories are based on reaches of the stream channel with similar characteristics. Rosgen's classification does not stop at this broad classification but continues to examine stream "state" factors such as substrate, riparian vegetation, stream order, and bed stability to further differentiate streams. McMahon (1996) illustrated how stream types can be divided by using size of the substrate. Delineation of streams into the nine categories serves four functions: 1) to provide for the initial integration of basin characteristics, valley types, and landforms with stream system morphology, 2) to provide a consistent framework for organizing stream information and communicating the aspects of stream morphology, 3) to assist in the setting of priorities for conducting more detailed assessments, and 4) to correlate similar general level inventories such as fish habitat, stream boating categories, and riparian habitat with companion stream inventories (Rosgen 1996). The categorization of the first nine stream types can be determined via observations and use of topographical maps versus difficult field measurements. I will discuss the nine different classes of stream channels followed by an examination of how the differences in channel slope, shape and pattern make up those classes.

Rosgen's classification groups start with steep gradient streams and progress to lower gradient areas. Rosgen's Aa+ streams are those with a slope greater than 10%. Such streams usually have deep channels with little to no meander and also no floodplain. They are distinguished by the similarity of the shape of the channel and the shape of the valley. They also tend to have waterfalls with deep scour pools. One example of such a stream is the Grand Canyon of the Yellowstone. Rosgen's A streams are very similar to the Aa+ streams although they have a lower gradient (4-10% slope). Class A streams are still narrow and deep with large substrate components, although they exhibit more lateral movement than Aa+ streams and have slightly more floodplain.

Class B streams have slopes of 2-4% and are moderately entrenched and exhibit occasional pools separating rapid dominated runs with a moderate floodplain. Class B streams do not have the expansive plains of D streams or the narrow plains of A streams. An example of a B stream is the Cache la Poudre River through the upper reaches.

Rosgen's C streams are low gradient, riffle/pool streams with well-defined floodplains. These streams are slightly entrenched with a well defined, meandering channel. An example of a C stream can be seen at the confluence of the Green and Colorado Rivers, Utah.

Streams of D and DA classification are similar due to their wide channels and broad floodplains. Streams labeled D are braided channels with slopes less than 4% and eroding banks. Streams of the DA classification have multiple channels with highly-developed wetland habitats and vegetated floodplains. Sinuosity varies between channels and the vegetation on the banks results in stable shorelines. These streams also exhibit the lowest slope category of less than 0.5%.

Slopes in the stream types E-G rise slightly from DA streams 0.5% to the 2-4% of G streams. Class E streams generally have low gradients with highly meandering channels and broad floodplains. These streams also tend to be deeply incised in relation to their channel width. Often, class E streams have abundant vegetation on banks.

Class F streams are deeply entrenched channels with wide channel width, resulting in shallow water levels. Due to the deep entrenchment, there is no established floodplain. These streams have slopes of less than 2% through a substrate that has been highly affected by weathering. Moderate meanders cut into highly erodible banks.

Streams of type G are deeply incised with very little floodplain and moderate sinuosity. A class G stream is likely to be an entrenched gully, with slopes between 2-4%, exhibiting step/pool morphology and narrow valleys.

There are three main diagnostic characteristics which create the broad classification presented above. These characteristics are slope, cross-section, and plan view or sinuosity. The most important determiner of the broad geomorphic classifications that Rosgen calls stream types, is the slope of the land through the reach of stream being studied. This criterion can be determined via topographical maps without taking measurements at the stream locale. Rosgen identified six slopes ranging from greater than 10 percent (>10%) to less than half a percent (<0.5%). Streams Aa+ and A are steep streams with gradients greater than 4%. Stream types C, DA, E, and F are streams with low gradient (< 2%) with riffle/pool patterns. Slope plays a great role in the classification of stream type because it influences channel shape and channel patterns as it shifts from steep to lower gradient regions. The impact of the slope can be seen on the composition of bed materials. Steeper slopes often have rock or boulder substrates while streams with flatter slopes have smaller substrate composites. The slope may also affect channel shape and channel patterns. Generally, the steeper the slope, the more entrenched and less meander will be found in the stream. Such a pattern can be seen in almost any stream. For example, as the Colorado River enters Glen Canyon National Resource Area through Cataract Canyon, it is a steep, straight reach with little meander and large bed material. Conversely, the Colorado River between Cisco and Moab, Utah is a wide and relatively deep and meandering channel. Simply looking at these two reaches one can see the effect slope can have on a stream, alone or in its interaction with other variables.

Another important component of Rosgen's classification system is channel shape. Channel shape (cross section) is determined by slope of the stream as well as the composition of the confining area. For example a stream bounded on either side by solid rock walls is more likely to have a deeply entrenched and straight channel than a stream which flows through lowland plains areas bordered by fields and meadows. Streams in broad valleys need not always be shallow throughout their width, but may be significantly entrenched due to regions of movable sediment and hydrology which concentrates flow into a specific region. The Michigan River flowing through North Park offers an example of an E stream type that has one narrow, deeply incised, meandering channel, that generally runs full, and has a wide floodplain. The incision of the channel is due to the combination of the slope and bed material present in a reach of a stream. Since water tends to flow in the path of least resistance, if a stream can spread out, it will. Consequently, the less momentum the water has, the smaller the bed material it can displace, which can result in braided channels with islands of rooted plants which add to the braiding. Channel shape may be more a result of the slope than a useful classification tool.

The third component of Rosgen's broad classification system for river channels is the channel pattern. The channel pattern or sinuousness of a stream plays an important role in the delineation of stream type. If a stream's contours are very similar to the valley, for example, deep, narrow canyons, it is likely that such a reach will be straight and steep, classified as an A stream. In these streams, the lack of lateral movement of the water is extremely limited and the water incises its substrate to the point of contacting solid rock. Alternatively, if the stream is found in a broad valley with room to move laterally, it will naturally spread out rather than cutting into its floor. Streams on valley floors with wide floodplains and lots of meanders or braided channels are classified as C-E streams. The channel pattern offers indications of channel entrenchment, as solid walls or vegetated banks preclude the meandering ability of the stream, causing it to cut deeper into itself. Wide flood-prone valleys are indicators of streams of either C, D, DA, and E types. Streams with smaller, flood prone areas include Aa+, A, B, F, and G. The most noticeable lack of flood-prone areas is found in Aa+, A, F, and G streams.

Determination of stream classification can be rather difficult based on many different variables which make up streams, including gradient, channel pattern, bed type, and channel shape. Rosgen, I believe has consolidated these factors into an more understandable matrix which can be used to describe streams accurately. However, I believe that the idea of a common language for describing streams may be lacking within Rosgen's classification. Without a solid understanding of how Rosgen separates streams and knowledge of the "codes" (stream types A, B, and further 1, 2, 3) individuals will not be able to discuss such a paring of this complex subject matter. It may be more realistic to have terms which describe the different types of streams (for example mountain stream versus A) to facilitate discussion of streams when parties are unaware of Rosgen's classification system. Kondolf (1995) cites that while scientists such as Rosgen are creating stream classification schemes, the use of these schemes are in the hands of non-geomorphologists who may not recognize the limitations of the classification guilds. This concern must be taken into account in restoration and other activities if quality determinations are to be achieved.

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<u>QUESTION TWO</u>: Condense what was written about sampling with rotenone down to a one page handout of what is most pertinent to a graduate wanting to sample using rotenone.

Rotenone is a chemical isolated from the roots of trees of the genus' *Derris* and *Lonchocarpus*. Rotenone kills fish by inhibiting cellular respiration. Rotenone is known under various brand names including Nuysn Nox-Fish, Cube, Derris, and Fish-Tox, and is available as either a powder or a liquid that has a 2.5 or 5% active ingredient. Rotenone is insoluable in water, so the use of EtOH acetone, CCl_4, or other organic solvents are required for use in fishery management (Haley 1978).

Rotenone has two applications in fisheries' management, to sample a selected area of a lake for population density or species composition and to reclaim lakes or streams from undesirable species. Application in lakes is more common due to the ability to contain the rotenone versus stream use. Sampling in lakes and areas which can be cordoned off (locks, coves, and specific open water habitats using nets or Wegener rings) requires the calculation of volume of water to be treated. Bettoli and Maceina (1996) present an example of volume calculation for a cove using a bathymetric map. Reclamation of lakes requires calculation of volume to hold down costs of operation, but lakes can be partially drained to reduce the necessary chemicals for total removal of fish. As with any procedure involving fishes, variation in the susceptibility to rotenone exists between species. Shad, walleye, pike, and rainbow trout are more sensitive to the effects of rotenone than species such as channel catfish, bullheads, and carp (Brunson 1997).

Sensitivity of fish to the effects of rotenone influences the amount used during a study. Effective concentrations of rotenone range from 0.5 mg/L to 3 mg/L with less rotenone being used on more sensitive species. Bettoli and Maceina (1996) stated that 3 L of rotenone/ $1000 m^3$ was a close conversion ($1 L = 10^6$ mg; $1,000 m^3 = 10^6 L$). Rotenone effectiveness of is increased when even distribution in the water is achieved. Dilution of rotenone to water at a ratio of 1:10 combined with both a surface and below surface application via outboard motor turbulence and venturi pumps assist in achieving even distributions.

The effects of rotenone can be influenced by various factors including temperature, turbidity, and aquatic plants. Temperature has the greatest impact on the toxicity and persistence. Warmer water increases the toxicity while shortening the persistence of rotenone. Gilderhus et al. (1988) stated that rotenone persisted in water at 0-5°C for 57 days and for seven days at 23-27°C. Aquatic plants absorb rotenone, limiting its abundance and its effectiveness on fish. Gilderhus (1982) noted the reduction in potency of rotenone when bentonite clay was added to the water.

Detoxification is an important factor to be considered when using rotenone. Rotenone can be dispersed to unwanted areas via wind or water currents. Dispersal and detoxification must be prepared for by gathering information relating to physical characteristics of waters, attention to weather patterns, and having potassium permanganate available. Introduced at ratios of 1:1 or 2:1 with rotenone, Bettoli and Maceina (1996) recommended not using more than 4 mg/L or detoxification of the introduced permanganate will be necessary. Effects of unconstrained or improperly detoxified treatment in the Green River, Utah, were illustrated by Holden (1991).

Retrieval of affected fishes is a concern in rotenone sampling methodology. Although most fish killed by rotenone will come to the surface, some will lay on the bottom. For calculations of density and composition, the impacts of these fishes on calculations need to be considered. Grinstead et al. (1978) suggested a determination of species specific recovery rates although Ball (1945) and Krumholz (1950) suggested rates without regard to species.

Human safety concerns associated with the use of rotenone are related to surface contact and acute exposure. Surface contact may result in dermatitis, ulcers in the nose, and irritation of mucous membranes. Acute exposure such as inhalation or ingestion will result in nausea, vomiting, numbness, and tremors. Fish killed by rotenone are not recommended to be eaten by humans.

Other concerns which may arise prior to or during rotenone application include questions of animal rights on the necessity of killing fish when non-lethal methods such as electrofishing are available. Preparation for such situations may be advisable.

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<u>QUESTION THREE</u>: List as many reasons as you can for tagging fish.

Tagging of fish can be defined as any means in which an individual fish or groups of fishes can be differentiated from others of the same species. There are many different methods of tagging or marking. Due to the development of new techniques of tagging and marking, the applications to fisheries and aquaculture have increased. In the lists below, I view tagging as a means of identifying individuals while marking pertains to groups. Essential to the use of tags or marks is the ability to recapture and identify tagged individuals at a later date (with the exception of radio tags which transmit constantly).

Reasons for tagging individual fish

—To evaluate growth rates of fish during different life stages.

—To identify patterns of movement prior to or during reproduction.

—To be able to determine the age of a fish based on information (such as length, weight, condition) gathered at release or during an earlier capture.

—To follow individuals through a period of time to make observations on habitat, movement, feeding and reproduction.

—To develop new tags by testing prototypes on fish in either laboratory or field experiments.

—To determine exploitation of populations by recreational or commercial fishermen.

—To evaluate the effect of stress on the biological activity of fish, caused by tag implantation or other stressor.

—To evaluate the life span of individual fish.

—To determine habitat preference or use

—To monitor the diet of fish in varied habitats and relate information to growth and productivity.

—To evaluate mortality of different stocks of fish

—To determine return rates of migratory fishes to natal streams

—For monitoring to use fish as bioindicators of pollution

—To evaluate the effectiveness of fish ladders for the reestablishment of historical home ranges of migratory fishes

—To remotely measure or detect a biological function, activity or condition (biotelemetry)

—To locate spawning areas of fish populations by radiotelemetry

Reasons for marking groups of fish

—To estimate the number of fish that are present in a population

—To evaluate sex ratios of stocked fish from previous capture occasions

—To differentiate between hatchery-reared stocked fish and wild fish

—To perform mark and recapture experiments so that biologists will know approximately how many fish they are managing.

—To create survival estimates of different ages, sexes, or species of fish

—To monitor life history of fishes

—To identify different parentage of fishes reared in hatcheries

—To evaluate the contributions of hatcheries to stocks and communities of fishes

—To evaluate the contributions of hatcheries to re colonization or reestablishment of endangered fishes

—To evaluate the effects of stocking hatchery fish at different sizes

—To determine the optimum time to stock fish to provide the best results

—To determine the best temperature at which to stock fish to provide the best recruitment and survival

—To identify fish that have been released or which escaped from a fish ranching facility

—To identify densities in hatcheries which are most beneficial to optimum growth and survival

—To identify the most effective numbers and sizes of fish to release to avoid predation

—To establish timing of age dependent migrations based on otolith marking

—To evaluate the effectiveness of toxicants and the ability to retrieve fish killed

—To aid in the management of migratory species to understand timing of spawning runs

—To determine effects of various stocks of fish and use by anglers or commercial fishermen

QUESTION 4: **Chapter 15 covers PSD, along with other indices. Pretend that I asked you to present a short lecture on PSD to FW204 to allow me to get to class a little late from a meeting. Emphasis in FW204 is on techniques; it is presumed that application will be covered in other courses. Develop an outline of information that you would use in this lecture about PSD as a technique for analyzing and presenting length data.**

- Proportional Stock Density (PSD) is a technique that uses length-frequency data to manage fish populations.
- PSD predicts the balance, of a dynamic population characterized by 1) continual reproduction of predator and prey species, 2) diverse sizes of prey species so that food is available for all predators, 3) high growth rates of all fish, and 4) an annual yield of harvestable-size fish (Flickinger and Bulow 1993), of medium to large size fish in a population based on sampling a portion of the population using traditional methods such as electrofishing or seining.
- Reasons for the development of stock densities:
    - Management of fisheries was evolving from a focus on a sustained yield to an optimization of quality coupled with yields.
    - Management of populations based on early techniques (Swingle's F/C, Y/C, and A_t ratios developed in the 1940's was difficult).
        - $\text{F/C ratio} = \dfrac{\text{total weight of all forage fish}}{\text{total weight of all carnivorous fish}}$
        - $\text{Y/C ratio} = \dfrac{\text{total weight of all forage fish small enough to be eaten by average size C fish}}{\text{total weight of average size carnivorous fish}}$
        - $A_t \text{ ratio} = \dfrac{\text{weight of harvestable fish}}{\text{total weight of all fish}} \times 100$

      All of these ratios require measurement of weight, which may present a bias due to the influence of factors such as temperature, food availability, and metabolism. Balance should be determined from length information and age structure due to the fact that weight does not consistently reflect age as a result of the previously mentioned factors.

- Stock density methods proposed by Anderson (1978) allow fishery biologists to utilize simpler length information to determine the age classes present in a population and then base management decisions on that information.
- These indices reflect an interaction of reproductive rates, growth, and mortality of the age classes present (Flickinger and Bulow 1993).

- Calculation of PSD
  - Equation: $\text{PSD} = \dfrac{\text{Number of fish} \geq \text{minimum quality length}}{\text{Number of fish} \geq \text{minimum stock length}}$
  - Number of quality length fish
    - Quality length = - minimum size anglers like to catch
      species specific determination (Anderson and Neumann 1996)
  - Number of stock length fish
    - Stock length = -average length at maturity
      species specific determination (Anderson and Neumann 1996)
  - Anderson and Neumann (1996) list English and metric values for stock, quality, preferred, memorable, and trophy size fishes. These values separate fish into groups used in PSD calculations. These size categories are based on percentages of world record length and all sizes are standard.
  - Example one: 375 largemouth bass were captured during the sampling of a pond. Of the 375 fish captured 192 fish are above quality length. The remaining fish are stock size. What is the PSD of this sampled population? Quality length for largemouth bass is 30 cm and stock length is 20 cm.

    $$\text{PSD} = \frac{\text{Number of fish} \geq \text{minimum quality length}}{\text{Number of fish} \geq \text{minimum stock length}}$$

x100 .51

PSD = 192 / 375) 192.00

1575

345

PSD = 51

- Balanced populations for largemouth bass are between 40 and 70. Data is presented with no decimal places and no percent (%) sign.

- Example two: 225 largemouth bass were captured during a sampling period. 164 fish are greater than quality length. What is the PSD of this population?

- Error that may influence the outcome of the use of PSD equation includes:

  sampling error

  - Conversion of English measurements to metric.

  - PSD can be calculated using either English or metric measurements although conversion from one to the other will create error, for example stock size for white crappie is five in or 13 cm not 12.5 cm resulting from English to metric conversion.

- Variation on PSD sampling

  - Sequential sampling

    - Weithman et al (1980) established a table to allow biologists to calculate PSD by sampling a population until a specific number of quality length fish were captured in a sample of stock length fish. This technique eliminates unnecessary sampling thereby saving time and money.

- Answer to example two: PSD = 73

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North American Journal of Fisheries Management 12:182–197, 1992
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Incidence and Causes of Physical Failure of Artificial Habitat Structures in Streams of Western Oregon and Washington

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Abstract.—In recent years an increasing share of fishery management resources has been committed to alteration of fish habitat with artificial stream structures. We evaluated rates and causes of physical impairment or failure for 161 fish habitat structures in 15 streams in southwest Oregon and southwest Washington, following a flood of a magnitude that recurs every 2–10 years. The incidence of functional impairment and outright failure varied widely among streams; the median failure rate was 18.5% and the median damage rate (impairment plus failure) was 60%. Modes of failure were diverse and bore no simple relationship to structure design. Damage was frequent in low-gradient stream segments and widespread in streams with signs of recent watershed disturbance, high sediment loads, and unstable channels. Comparison of estimated 5–10-year damage rates from 46 projects throughout western Oregon and southwest Washington showed high but variable rates (median, 14%; range, 0–100%) in regions where peak discharge at 10-year recurrence intervals has exceeded $1.0\ m^3 \cdot s^{-1} \cdot km^{-2}$. Results suggest that commonly prescribed structural modifications often are inappropriate and counterproductive in streams with high or elevated sediment loads, high peak flows, or highly erodible bank materials. Restoration of fourth-order and larger alluvial valley streams, which have the greatest potential for fish production in the Pacific Northwest, will require reestablishment of natural watershed and riparian processes over the long term.

During the past decade, popular demand and financial support for restoration of fish habitats in North American streams have increased dramatically. Restoration or "enhancement" activity in the west has concentrated on direct modification of streams with artificial structures such as log weirs and gabions. Despite numerous pleas for careful scientific evaluation (e.g., Hall and Baker 1982; Reeves and Roelofs 1982; Everest and Sedell 1984; Hall 1984; Klingeman 1984; Platts and Rinne 1985), large and costly projects continue to be planned and implemented by federal and state agencies with little or no analysis of their effectiveness.

During the 1980s, habitat management programs of federal agencies became increasingly dominated by artificial-structure programs. For example, according to the U.S. Bureau of Land Management (1989), even as the number of fishery biologists in the agency dropped by more than half between 1980 and 1987, budgets increased for fish "habitat development" and "project maintenance"—a program dominated by artificial structures. The Bonneville Power Administration spends more than US$5 million annually on stream structures and related projects in Idaho, Oregon, and Washington in attempts to mitigate hydropower impacts on wild fish (Bonneville Power Administration, unpublished data). In fiscal year 1987, the U.S. Forest Service built more than 2,400 fish habitat structures in its Pacific Northwest Region, and the budget for this program far exceeded funds available to protect, monitor, and rehabilitate soil and watershed resources (U.S. Forest Service, unpublished data).

An illustration of the new reliance that resource managers are placing on artificial fish habitats appears in the Siskiyou National Forest Management Plan (USDA 1989), which prescribes structures costing more than $1.7 million over 3 years. In the computer model used to assess the economic effects of activities, Siskiyou National Forest planners assumed, without supporting evidence, a net gain of 3–4 lb (1.4–1.8 kg) of anadromous fish annually for each dollar spent on artificial structures. Logging in riparian areas and a projected influx of many tons of sediment annually caused by new roads and logging were assumed to have no significant adverse effect on fishery values (USDA 1989). The Forest Service assumed that any adverse effects on fish habitat and water quality would be more than compensated by fish habitat created with new artificial structures.

Ongoing evaluation of failures, as well as successes, is necessary to ensure that a program is achieving its objectives without costly mistakes or

unintended side effects. The few evaluations of artificial-structure projects in the Pacific Northwest have shown mixed results. Hall and Baker (1982) and Hamilton (1989) summarized published and many unpublished evaluations of the effectiveness of fish habitat modification projects in streams. Although studies of apparently successful projects (e.g., Ward and Slaney 1981; House and Boehne 1986) have been cited widely, Hamilton's review (1989) suggested that studies showing neutral or negative biological effects have been published less frequently than those with favorable results.

Several studies have indicated that structural modifications can be ineffective or damaging. For example, Hamilton (1989) observed reduced trout abundance in a northern California stream reach with artificial boulder structures, compared with an adjacent unaltered reach. A large-scale habitat modification program on Fish Creek in western Oregon produced cost-effective increases in fish production from opening of off-channel ponds, but generally negative or neutral effects from boulder berms and log structures (F. E. Everest et al., U.S. Forest Service Pacific Northwest Research Station, unpublished data). Some structures in Fish Creek were damaged by floods before they measurably affected physical or biological conditions of the stream (Everest et al., unpublished data). In Idaho, C. E. Petrosky and T. B. Holubetz (Idaho Department of Fish and Game, unpublished data) found little evidence that instream structures increased the abundance of juvenile chinook salmon *Oncorhynchus tshawytscha* and steelhead *O. mykiss*, and in one project more than 20% of the structures failed during their first winter. In Big Creek, Utah, Platts and Nelson (1985) found that outside a fenced exclosure, artificial structures were destroyed by livestock trampling and grazing-related streambank erosion. Babcock (1986) reported that nearly three-quarters of the structures in a Colorado project failed or were rendered ineffective by a flood just 2 years after construction. Several of the remaining structures apparently created migration barriers for fishes, a problem also observed in Oregon (C.A.F., personal observation).

For artificial structures to function successfully, they must meet carefully defined objectives specific to target species, life history stage, and prevailing physical factors (Everest and Sedell 1984), and design must be closely tailored to geomorphic and hydraulic conditions (Klingeman 1984). To meet specific biological and economic objectives, most structures employed to date (e.g., wire gabions and log weirs) must remain intact at the installation site for their projected life span. Yet in the Northwest, few projects have been in place long enough for researchers to assess their durability across a range of stream flows. In this paper, we evaluate the incidence and causes of physical damage to artificial stream structures at several projects in Washington and Oregon. A flood of a magnitude that recurs at 2–10-year intervals occurred within the first few years after construction, which provided an opportunity to evaluate how well these projects could be expected to survive and function for their projected life spans. We examine the incidence of structure impairment and failure in relation to design, stream characteristics, and regional hydrologic conditions, and we discuss the implications of structure dysfunction for fish habitat management in the Pacific Northwest.

Methods

Study sites.—In the summer of 1986, we determined the incidence of physical impairment or failure of artificial structure projects on eight streams in southwest Oregon and seven streams in southwest Washington (Figure 1; Table 1). The sample comprised 161 structures built by the state of Oregon's Salmon and Trout Enhancement Program and by the U.S. Forest Service between 1981 and 1985.

South coastal Oregon has intense winter precipitation, flashy streamflow, and very high sediment yields, particularly from heavily logged watersheds. Projects in southwest Oregon were intended to increase spawning habitat for fall chinook salmon by stabilizing gravel and providing cover for adults, and to improve rearing habitat for juvenile chinook salmon, steelhead, and cutthroat trout *Oncorhynchus clarki* by increasing area, depth, and complexity of pools (Johnson 1984; USDA 1989; G. Westfall, Oregon Department of Fish and Wildlife, unpublished data). Structures consisted of lateral log deflectors, cross-stream log weirs, multiple-log structures, and cabled natural debris jams. Benefit–cost projections were based on a life span of 20–25 years for all structures (Johnson 1984; USDA 1989).

In southwest Washington, a region of moderately high sediment yield and high peak flows from winter rain-on-snow, projects were intended to increase pool area for rearing of juvenile salmonids (USDA 1987). Steelhead, brook trout *Salvelinus fontinalis*, and spring chinook salmon occurred in project streams. The structures consisted of log

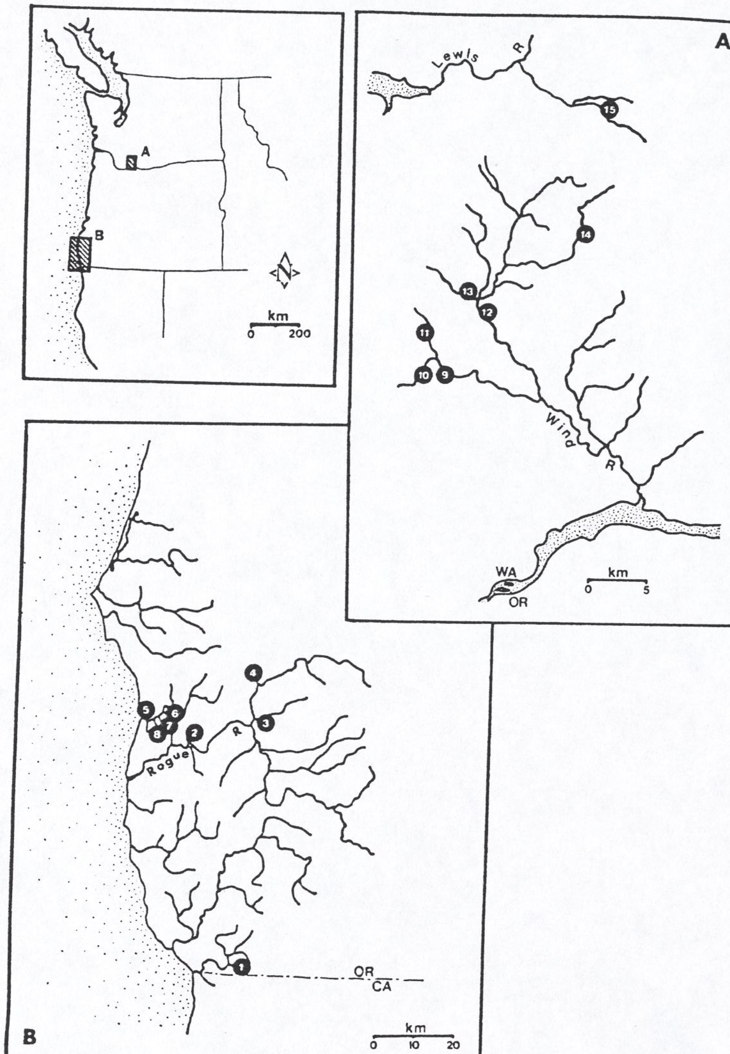

FIGURE 1.—Location of stream structure projects evaluated in (A) southwest Washington and (B) southwest Oregon during 1986. Oregon sites are 1, Bear Creek; 2, Silver Creek; 3, Shasta Costa Creek; 4, Foster Creek; 5, Euchre Creek; 6, Crooked Bridge Creek; 7, "Outcrop Creek"; and 8, Boulder Creek. Washington sites are 9, Lower Trout Creek; 10, Layout Creek; 11, Upper Trout Creek; 12, Wind River; 13, Trapper Creek; 14, Falls Creek; and 15, Rush Creek.

TABLE 1.—Physical characteristics of study sites. Valley segment types are large-scale geomorphic units, slightly modified from Frissell and Liss (unpublished) and Cupp (1989). Valley segment codes are: AV = alluvial valley; AFV = alluvial fan-influenced valley; TBV = terrace-bound valley; AC = alluviated canyon; IUH = incised U-shaped valley, high gradient. A slash between two codes means both valley types occurred within the project area.

Stream	Elevation (m)	Drainage area (km²)	Mean channel slope (%)	Mean active channel width (m)	Mean active channel depth (m)	Valley segment type
Southwest Oregon						
Bear Creek	50	22.9	2.0	10.9	0.7	AC
Foster Creek	60	30.6	1.5	9.6	0.8	TBV
Silver Creek	20	25.1	1.0	8.9	0.4	AFV
Shasta Costa Creek	50	46.0	1.0	18.2	0.9	TBV
Euchre Creek	25	51.4	1.0	30.0	1.0	AV/AFV
Crooked Bridge Creek	25	2.7	2.5	6.0	0.7	AV
"Outcrop Creek"	25	1.2	4.0	5.5	0.5	AFV
Boulder Creek	25	5.9	2.0	12.0	0.7	AFV/AV
Southwest Washington						
Rush Creek	945	17.8	2.0	10.4	0.7	AV
Falls Creek	830	24.8	6.0	8.1	0.6	IUH
Layout Creek	540	14.8	1.0	15.6	0.7	AV
Upper Trout Creek	565	10.8	2.0	9.3	0.6	AV
Lower Trout Creek	535	62.7	1.0	20.0	1.0	AV
Wind River	335	632.0	1.0	31.2	1.0	AV
Trapper Creek	340	28.8	1.5	25.6	0.8	AV

weirs, diagonal log deflectors, multiple-log structures, cabled natural woody debris jams, and single and clustered boulders.

Flood peak estimation.—Because none of the project streams were gauged, we used several methods to estimate recurrence interval of the February 1986 flood, the primary event affecting our study. At that time gauged streams in southwest Oregon experienced an instantaneous peak flow with about a 2-year recurrence interval (Geological Survey Water Resources Data for Washington and Oregon, Water Year 1986; Friday and Miller 1984). However, the 1986 flood was unusual in its duration, causing high flows for several consecutive days. After adjustment for duration, the estimated recurrence interval was 5–7 years based on the estimates of Friday and Miller (1984) for Chetco River near Brookings and South Fork Coquille River at Powers. McGavock et al. (1986) estimated the recurrence interval of the February 1986 flood in gauged southwest Washington streams at 3–5 years.

To assess variation in the February 1986 peak flow among the project streams in southwest Oregon, we surveyed cross sections at the project sites and reconstructed flood crests based on flotsam lines. Using the Manning equation (Richards 1982; Thorne and Zevenbergen 1985) with roughness estimated visually (Barnes 1967), we estimated peak flows for each stream. We then estimated flood recurrence intervals (for instantaneous peak flow) following three regional prediction procedures (Harris et al. 1979; Campbell et al. 1982; Andrus et al. 1989). Final estimates for each stream are the averaged results of the three procedures except for two watersheds of less than 5 km², where only the Andrus et al. (1989) method appeared to provide reasonable estimates. Because estimates of peak discharge often err by as much as 30% (Thorne and Zevenbergen 1985), and because predictions of recurrence intervals introduce additional error, these estimates—which varied from slightly less than 2 years to 10 years among the Oregon streams (Table 2)—should be viewed as rough approximations.

Definitions.—We classified structures into three categories, depending on their physical condition and function. A structure that had been washed downstream, severely fragmented, or grossly dislocated so it retained little or no contact with the low-flow channel or was otherwise incapable of achieving its intended physical objective (e.g., creating or enlarging a pool) was classified as a "failure." A structure that remained in its original location but, because of alteration to it or the stream channel, no longer functioned in the intended mode or appeared to be at least temporarily ineffective, was classified as "impaired." A structure that had been buried under bed-load deposits was considered impaired. A structure not visibly damaged or

TABLE 2.—Flood magnitude estimates, and rates of damage and failure for fish habitat structures surveyed in 1986. Flood peak is the estimated peak discharge; the estimated recurrence interval is in parentheses. A dash indicates discharge data were not available; recurrence intervals at these sites were estimated from nearby streams or from regional analyses by the U.S. Geological Survey.

Stream	1985–1986 flood peak, m³/s (recurrence interval)	Number of structures	Damage rate (%)	Failure rate (%)
Southwest Oregon				
Bear Creek	28 (2 years)	19	79	32
Foster Creek	30 (2 years)	15	27	7
Silver Creek	17 (2 years)	6	50	17
Shasta Costa Creek	45 (<2 years)	18	83	55
Euchre Creek	92 (5 years)	19	100	95
Crooked Bridge Creek	12 (10 years)	6	100	100
"Outcrop Creek"	7 (5 years)	5	40	40
Boulder Creek	— (5 years)	5	60	40
Southwest Washington				
Rush Creek	— (<2 years)	9	22	11
Falls Creek	— (<2 years)	6	0	0
Layout Creek	— (3–5 years)	9	89	11
Upper Trout Creek	— (3–5 years)	19	42	0
Lower Trout Creek	— (3–5 years)	5	40	0
Wind River	— (3–5 years)	10	70	0
Trapper Creek	— (3–5 years)	10	60	20

debilitated was categorized as functioning roughly as intended or "successful."

We defined "damage rate" as the proportion of structures of a project in the failed and impaired categories (structures not successfully meeting physical objectives). "Failure rate" was defined as the proportion of structures of a project in the failure category only (structures lost or completely dysfunctional). Based on the time since installation and the estimated recurrence interval of the February 1986 flood, we assumed these rates reflected the incidence of damage and failure to be expected over a 5–10-year time span.

Obviously, some subjectivity was involved in judgments about impairment and, to a lesser extent, about failure, particularly where the intent of the designer was not immediately clear. We based our determination of whether structures achieved design objectives primarily on the general physical objectives outlined in project plans (e.g., "create new rearing pools"), but criteria varied somewhat depending on structure type. For example, a log weir would be expected to produce a plunge pool, a single boulder was probably intended to create a small scour hole, and a cabled natural debris jam would be expected to stay in place and maintain preexisting pool and cover conditions. Within these limitations, damage rate is a useful indicator of the effective life of a project, maintenance requirements, the importance of unintended side effects, and the likelihood of future failure.

Structural evaluation.—As we surveyed a stream, we recorded the location and type of each structure. We measured reach slope with an Abney level, measured width of the active (unvegetated) channel with a meter tape, and measured the depth and surface area of the pool associated with each structure. We recorded processes and events contributing to impairment or failure of the structure, and in some cases we drew a small sketch map. Previous knowledge of structure design and placement at many of the projects helped us reconstruct failure processes, but we avoided speculation where no physical evidence of failure mode remained. Because failed structures sometimes wash away and leave no trace, we undoubtedly underestimated the number of structures originally present in some projects, making our estimates of failure rates conservative. We recorded information on streambank materials and riparian landforms in the field, and we compared these data with topographic maps to classify stream segments following C.A.F. and W. Liss (Oregon State University, unpublished data) and Cupp (1989). We calculated failure and impairment rates for each structure type and each stream, and we compared them with stream-specific data on flood flow magnitude, mean channel width, slope, drainage area, and stream segment type (Table 1).

Interregional comparisons.—To set our results in broader context, we compared our summary data with unpublished information on other projects constructed during 1981–1985 by the U.S. Forest Service (B. Higgins and H. Forsgren, Mount Hood National Forest, unpublished data; D. Hohler, Mount Hood National Forest, unpublished data) and the Bureau of Land Management (House et al. 1989). Although our impairment and failure estimates often were somewhat greater than those of agency biologists responsible for the projects, we believe these data are comparable as a rough approximation of regional patterns. Because most of the projects had experienced a flood of between 5- and 25-year recurrence intervals during the 2–8 years they had been in place, we used the data to approximate average failure and impairment rates (Appendix 1).

Because climatic and geomorphic conditions in western Oregon are diverse, we grouped the data for all projects into five regions defined by geology, topography, elevation, climate, and streamflow patterns. We examined streamflow statistics for gauged streams in each region (Friday and Miller 1984) and used these to characterize regional peaks for flood flows (Appendix 2).

Results

Damage Rates in Relation to Stream Characteristics

The incidence of structure failure and damage varied widely among streams (Table 2). Overall, failure rates were higher in southwest Oregon streams (median, 40%; mean, 48%; range, 7–100%) than in southwest Washington streams (median, 0%; mean, 6%; range, 0–20%). Rates of overall damage were less disparate but appeared to be higher in southwest Oregon (median, 70%; mean, 67%; range, 27–100%) than in southwest Washington (median, 42%; mean, 46%; range, 0–89%).

Rates of damage were higher in larger and wider streams (Figure 2B). Projects in streams with active channel widths wider than 15 m had a median damage rate of 79% (range, 50–100; $N = 6$), whereas those with active channels narrower than 15 m were highly variable and had a median damage rate of 50% (range = 0–100; $N = 9$). Southwest Oregon data suggested a roughly linear increase in failure rate with stream width (Figure 2A). In southwest Washington, failure rate apparently was not correlated with stream width, although impairment and therefore damage rate were correlated with stream size. There was no clear relationship between drainage basin area and failure or damage rates. Because climatic and hydrologic characteristics of individual streams vary within a region, active channel width is a better site-specific, integrated measure of streamflow and associated hydraulic stresses than is basin area. Channel width is influenced by bank material erodibility (Schumm 1960; Richards 1982), which also affects structure performance (see Mode of Failure).

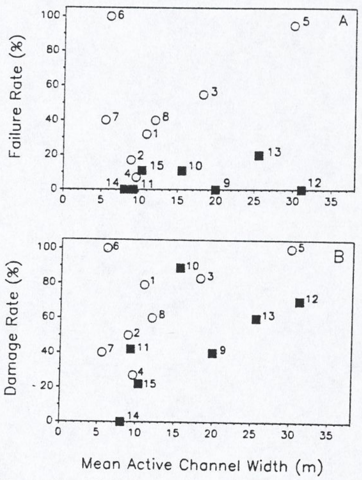

FIGURE 2.—(A) Failure and (B) damage rates of projects in southwest Oregon (open circles) and southwest Washington (solid squares) in relation to active channel width. Stream numeric codes are given in Figure 1. Damage rate includes both failed and impaired structures.

Although Hamilton (1989) concluded that projects in high-gradient streams had higher failure rates than those in gently sloping streams, we found no evidence to support this generalization in our study streams. In southwest Washington the incidence of damage actually increased as slope decreased (regression analysis, $P < 0.04$, $r = -0.79$), largely because structures became buried in low-gradient reaches. In southwest Oregon, damage rate did not vary significantly with slope, nor did failure rate in either region. However, high-gradient streams were not well represented in our sample; only three projects were in stream reaches exceeding 2% slope. Regression of failure and damage rates against an index of stream power, defined as the product of channel slope and mean active channel depth, were similar to regressions based on channel slope alone.

Neither failure nor overall damage rates appeared to be strongly related to the estimated absolute or relative magnitude of the flood peak experienced by projects during 1986. There was little difference in median or range of failure rates between one group of projects subjected to peak flows of a 2-year recurrence interval and another group subjected to 5–10-year peak flows. Falls Creek was the only project for which no damage or failure was recorded, perhaps because this high-elevation stream (830 m) did not experience a large rain-on-snow peak flow in 1986.

The correlation between active channel width and slope (regression analysis, $P < 0.01$, $r = -0.68$), and the relationships among these variables and drainage area, discharge, and bed and bank texture, make simple, univariate explanations of damage patterns difficult. There was no obvious overall relationship between failure or damage rates and valley segment type, a broad classification that accounts for covariation of numerous geomorphic variables (Frissell et al. 1986). In general, however, there appeared to be a trend of more extensive damage in wide, low-gradient reaches in alluvial valleys and alluvial fans, which are susceptible to bed-load accumulation and bank erosion when the drainage catchment has been disturbed by logging or large natural landslides. Additionally, some projects in terrace-bound valley or alluviated canyon segment types (comparatively narrow channels with restricted floodplains) in southwest Oregon had high failure rates which, based on field evidence, appeared to result from the scouring effects of high-energy, sediment-charged flood flows.

Mode of Damage

Processes that damaged structures included design- or material-related phenomena, such as failure of cables and anchoring devices, and a wide variety of processes that produce changes in the immediate environment of structures, such as bank erosion and bed-load deposition (Table 3). In some cases, such channel changes appeared to be largely a direct but unanticipated hydraulic consequence of placement of the structures themselves (e.g., bank erosion at the lateral margins of log weirs; see Cherry and Beschta 1989). In most instances, however, the channel changes that damaged structures appeared to be driven primarily by watershed-scale phenomena, such as active landslides or road failures upstream that caused massive bed-load deposition in the project area. Many structures exhibited evidence of multiple, and sometimes interacting, modes of damage.

Southwest Oregon projects suffered damage from a wide variety of processes, ranging from failure of anchoring devices and structural breakage indicative of high hydrodynamic stress, to burial and channel shifting indicative of high rates of bed-load transport and deposition. In comparison,

TABLE 3.—Percentage of structures in each project for which there was evidence that the indicated process contributed to failure or impairment. Because many structures exhibited multiple-failure modes, percentages across rows do not necessarily sum to 100. Modes of damage are arranged from high-energy, scour-related processes at left to low-energy, deposition-related processes at right.

Stream	Log breakage	Anchor bolt failure	Cable failure	Logs stranded out of channel	Bed scour undermined structure	Bank erosion	Anchor tree washout	Bar or channel shift	Burial by bed load	Unknown
Southwest Oregon										
Bear Creek	0	21	21	0	16	16	0	0	5	0
Silver Creek	0	0	17	0	0	17	0	0	33	0
Shasta Costa Creek	6	11	17	22	0	11	17	6	0	0
Foster Creek	0	0	7	0	7	7	0	0	13	0
Euchre Creek	0	0	0	0	0	16	0	16	0	89
Crooked Bridge Creek	0	0	0	0	0	0	0	0	0	100
"Outcrop Creek"	0	0	0	20	0	20	0	0	0	20
Boulder Creek	0	0	0	0	20	20	0	0	0	40
Southwest Washington										
Layout Creek	0	0	0	0	4	6	0	11	11	0
Upper Trout Creek	0	0	0	0	80	0	0	20	20	20
Lower Trout Creek	0	0	0	0	0	0	0	0	40	0
Wind River	0	0	0	0	0	0	0	30	80	0
Trapper Creek	0	0	10	0	10	0	0	20	20	10
Falls Creek	0	0	0	0	0	0	0	0	0	0
Rush Creek	0	0	11	0	0	0	0	0	0	0

fewer failure modes were observed in southwest Washington projects, and these were mostly indicative of changes in erosion and deposition in low-gradient reaches. For example, a series of boulder placements in Wind River, expected to scour pools within a long riffle, instead triggered deposition of a large midchannel gravel bar that isolated the structures from the low-flow channel.

At numerous sites, structures caused inadvertent physical effects that we judged to be adverse rather than beneficial. Adverse effects for which we found evidence included (1) accelerated bank erosion at log weirs, (2) direct damage to gravel bars and riparian vegetation by heavy equipment, (3) felling of key streamside trees to provide sources of materials, causing loss of shade and bank stability, (4) flood rip-out of riparian trees used to anchor log structures, (5) aggradation of gravel bars or silt and sand deposits (see also Platts and Nelson 1985), which caused shallowing and loss of microhabitat diversity in preexisting natural pools, and (6) torrents of bed load and debris triggered by collapse of structures during the flood. Eggs and fry of fish that spawned in the gravel above log weirs, as well as juvenile fishes wintering in and near the structures, may have been killed when the structures failed and washed out. Fragments of epoxy or resins used to anchor structures were very common in many pools, and there is evidence that these materials can be toxic to fishes (Fontaine and Merrit 1988). Frayed cables and sheets of ripped out geotextile or chain-link anchoring material at damaged structures created obvious aesthetic liabilities. Furthermore, repairs may have exacerbated initial damage. Riprap, which was used extensively to repair bank erosion associated with log weirs, may adversely affect stream habitat over the long term (Richards 1982; Sedell and Frogatt 1984; Bravard et al. 1986; Li et al. 1984; Knudsen and Dilley 1987).

Effect of Structure Type

Of the eight structure designs for which we had sufficient sample size, only two—cabled natural woody debris and individual boulder placements—were not impaired or did not fail in more than half the cases (Figure 3). All log weir designs had high rates of impairment or failure, and one type, the downstream-V weir, failed or was impaired in every instance. Boulder structures had lower failure rates than log weirs. Previous studies have shown low failure rates for boulder structures in streams of less than 2% gradient but higher failure rates in steeper streams (Hamilton 1989). Although many boulders had been almost completely buried in place by bed-load deposits, we classified these as impairments rather than failures, because they might someday be reexcavated by the stream.

To some extent, failure and impairment rates

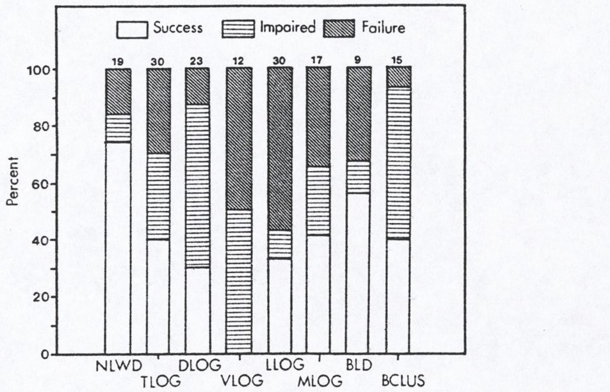

FIGURE 3.—Failure and impairment rates of structures classified by design. Number at top of each bar indicates the number of structures in the sample. NLWD = cabled natural large woody debris or jam; TLOG = transverse log weir; DLOG = diagonal log weir; VLOG = downstream-V log weir; LLOG = lateral log deflector; MLOG = multiple-log structure; BLD = individually placed boulders; BCLUS = clustered boulders.

presented in Figure 3 are biased because not all designs were represented in all streams. For example, the higher success rate of boulder projects is partly related to their concentration in relatively stable southwest Washington streams where damage to structures of all types was small.

Interregional Comparisons

When we compared our results with data from other regions in western Oregon (Appendix 1), we found that the projects we studied had higher-than-average rates of impairment and failure. However, the projects we evaluated were in regions with intense winter precipitation and substantially higher peak discharge than most other regions (Figure 4; Appendix 2). There was a positive relationship between impairment and failure rates and peak flows. Streams in regions characterized by 10-year-recurrence peak flows exceeding 1 $m^3 \cdot s^{-1} \cdot km^{-2}$ had high but variable rates of damage (range, 0–100%; median, 46%) and failure (range, 0–100%; median, 14%) (Figure 5).

The regions with highest peak flows include the north Coast Range and south Coast Range–Klamath Mountains in Oregon, which are very steep areas with intense rainfall and frequent rain-on-snow events, and the Columbia Cascades, part of the Cascade Range immediately north and south of the Columbia River subject to severe and frequent winter storms that funnel through the Columbia Gorge either from coastal or interior areas. The south Coast Range–Klamath Mountains region, which had the highest incidence of damage to structures, has mean 10-year peak flows in excess of 2.0 $m^3 \cdot s^{-1} \cdot km^{-2}$. Projects in other parts of western Oregon experienced much lower peak flows and had lower rates of damage (range, 0–67%; median, 12%) and only limited incidence of failure (range, 0–35%; median, 0.5%) (Figure 5).

We had limited data for Oregon streams in the north Coast Range. We expect that when more projects are evaluated, many will be found to suffer high failure and impairment rates because of the region's high peak flows and high frequency of long-runout debris flows (our unpublished data). However, the abundance of clays and the lower proportion of fine sands and silt in soils of this region may render streambanks more resistant to erosion than those of Oregon's south Coast Range, thereby moderating failure rates.

Our experience indicates that sediment yield might be positively correlated and channel stability negatively correlated with regional peak flow. Undoubtedly, these patterns reflect relationships among many aspects of geology, precipitation, soils, and hydrologic and geomorphic processes that are of critical importance to habitat management, from both an ecological and an engineering standpoint. The data for the south Coast Range–Klamath Mountains region of Oregon probably represent conditions in much of northwest California as well.

Discussion

Artificial stream structures suffered widespread damage in most of the streams we surveyed in

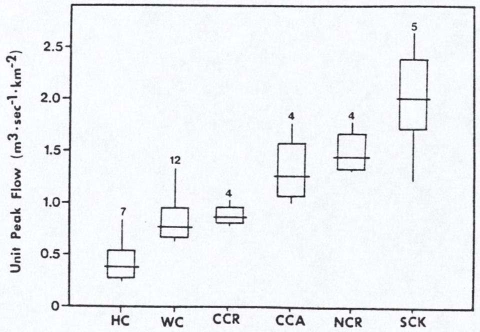

FIGURE 4.—Box plots of 10-year peak flows standardized by drainage area for streams in six regions of western Oregon. Horizontal bar is the median, box is the interquartile range, and vertical line is the data range. Number is the sample size. HC = High Cascades; WC = western Cascades; CCR = central Coast Range; CCA = Columbia Cascades; NCR = north Coast Range; and SCK = south Coast Range–Klamath Mountains.

southwest Oregon and southwest Washington. Rather unpredictable damage rates and the wide range of causes of failure indicate that complex, multiscale interactions between watershed conditions, fluvial processes, and structure design determine the physical success or failure of individual structures and projects. Because streams in these two regions have intense floods, high bed-load yields, and often unstable channels, artificial structures are highly vulnerable to damage.

The wide range of failure modes indicates that simple changes in structure design or materials are unlikely to overcome the problem of high damage rates. Overall, processes of failure and impairment were dominated by changes in channel morphology that, apparently, had not been anticipated by project designers. These changes often were related to dynamic conditions in the watershed or riparian zone, particularly as they affected sediment load, streambank stability, and hydrology. Failure of internal structure or materials—the dominant concern of most biologists and hydrologists who build these projects—appears to be a far less important cause of damage than are watershed-driven aspects of channel dynamics.

We sampled only a subset of the projects present in southwest Oregon and southwest Washington in 1986, but we believe our results are representative of other nearby projects. For example, we observed complete failure of structures in Deep Creek, a tributary of Pistol River in southwest Oregon, caused by sediment-laden flood pulses that originated from large landslides in recent clearcuts. We did not survey Deep Creek and several other projects in detail because repairs were already well under way before we were able to inspect the sites.

Few simple rules about design of artificial structures have emerged from our study, but we can offer some general guidelines for stream restoration programs. Structure designs that failed least often were those that minimally modified the preexisting channel, such as cabling intended to stabilize natural accumulations of woody debris. Elaborate log weirs and other artificial structures, which (if they stay in place) cause immediate and more obvious changes in channel morphology and hydraulics, were subject to high rates of damage. In large, low-gradient streams, configuration of the valley and large-scale roughness elements such as major channel bends exert primary control of the location and morphology of pools and riffles (Lisle 1986), and sediment yield and peak flows strongly constrain channel stability and streambed dynamics. Smaller-scale structures such as log weirs can work effectively only within limits imposed by these larger-scale processes and patterns. Our observations suggest that, at least in southwest Washington and southwest Oregon, it is unrealistic to expect the installation of new artificial structures to stabilize channels; the opposite result may be as likely.

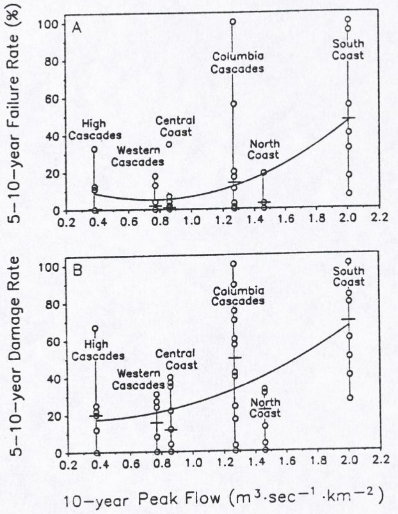

FIGURE 5.—Relation between rates of (A) failure and (B) overall damage of projects and regional median 10-year-recurrence peak flows standardized by drainage area. Each point represents one or more projects (full data are in Appendix 1). Horizontal bars indicate regional medians. Curves are second-order regressions fitted to indicate trend, and are not necessarily statistically significant. Southwest Washington projects from Table 2 are classified as Columbia Cascades region except for Rush Creek and Falls Creek in the High Cascades. Southwest Oregon projects from Table 2 constitute the sample for the south Coast Range–Klamath Mountains region.

Within the study areas, the stream habitats most important for fish, and most in need of restoration, are those least amenable to structural modification with existing technology. We observed the highest rates of failure and impairment in streams draining watersheds severely damaged by roads, logging, and landslides. Projects with the highest failure rates in southwest Washington were in alluvial deposition areas of Trapper Creek and Layout Creek, in valley segments prone to natural instability, that has been aggravated by removal of natural woody debris and logging of riparian vegetation. Deposition of bed-load sediments in wide, low-gradient alluvial valley segments and the erosion of streambanks and shifting of channels associated with this deposition were the most common causes of damage to structures in our study streams.

Low-gradient alluvial valleys are also the most critical of stream habitats for spawning and rearing of chinook salmon, coho salmon *Oncorhynchus kisutch*, and steelhead (Reimers 1971; Stein et al. 1972; Leider et al. 1986; Lichatowich 1989; our unpublished data). Sediment accumulation in alluvial valley streams can cause numerous adverse effects: loss of pools, destabilization of woody debris, frequent channel shifting and abandonment, increased fine sediments and increased scour of spawning gravel, channel widening, and increased summer stream temperature because of loss of shade (e.g., Lisle 1982; Hagans et al. 1986; Everest et al. 1987). The dominance of sand and gravel in streambanks of alluvial valleys and in alluvial fans makes them highly susceptible to erosion, particularly when riparian vegetation—the roots, stems, and foliage of which help stabilize riparian soils—has been removed by logging, grazing, floods, or builders of artificial structures.

It may take decades or centuries for low-gradient channels in alluvial valleys to recover from downstream-propagating impacts of bed-load accumulation (Lisle 1981; Madej 1984; Hagans et al. 1986). Such recovery proceeds only after sediment yield from the watershed declines to natural levels, which has not yet occurred in many southwest Oregon basins. These basins continue to suffer impacts from failing roads, high erosion rates along streams in second-growth forests, increased logging on steep, highly erodible federal lands (Frissell and Nawa 1989), and repeated short-rotation logging on private lands where there is little regulatory protection for unstable slopes and headwater stream channels (Bottom et al. 1985). Reestablishment of mature riparian forests to stabilize streambanks and floodplain surfaces is also needed for recovery of channel morphology (Lisle 1981).

Implications for Economic Analyses

Existing environmental and economic analyses assume life spans of 20–25 years for artificial structures in south coastal Oregon (Johnson 1984; USDA 1989). This means that the average life span or half-life for all structures (not the maximum life span) must approach 20 years. More than half the structures should survive much longer than 20 years. Our data indicate that a flood of less than a 10-year recurrence interval caused failure rates often exceeding 50%. Given that the probability of occurrence of a 10-year or greater flood within the first decade after installation is about 0.65, and that within the first 20 years it is about 0.88, a majority of projects in southwest Oregon probably will experience failure rates exceeding 50% before they are 20 years old.

Larger floods might have more severe effects. The probability of at least one 20-year flood occurring within any 20-year period is 0.64, and the probability of a flood of a 50-year or greater recurrence interval within 20 years is 0.33—significant enough to be factored into half-life calculations that would be necessary to accurately estimate average life span for projects. Considering these factors, we estimate that the average half-life (the time elapsed when 50% of the structures are destroyed) of projects is less than 10 years in southwest Oregon and 15 years or less in southwest Washington.

It is unlikely that most stream structure projects in southwest Oregon and southwest Washington would appear cost-effective if planners used realistic estimates of project life, maintenance costs, and adverse side effects. The high rates of impairment we observed indicate structural damage and wear that, if not repaired, greatly increase the risk of failure during subsequent years. The repair of flood damage that is necessary to reduce future failures of structures imposes a heavy maintenance burden, the costs of which are seldom factored into the economic analyses used to justify such projects. Unintended adverse effects, or "negative benefits," are also neglected in most benefit–cost analyses of artificial structures. Where projects have high impairment rates, there is a high likelihood of net damage rather than benefit to fish and water quality; such risks should be explicitly addressed in project plans and disclosed in environmental analyses.

Implications for Habitat Management

Despite the rather high incidence of physical failure and damage, and despite the lack of demonstrated biological success of surviving structures in the study areas, an inflexible cookbook approach continues to dominate the analysis, planning, and budgeting processes within agencies responsible for fish habitat management in the region.

Currently, most habitat projects in the Pacific Northwest seem to rest on the assumption that the problem is simply a lack of woody debris, and that the solution is to add standard devices such as log weirs, with each new structure creating an incremental improvement of habitat and a known poundage of new fish. However, the widespread loss of woody debris and habitat diversity in Pacific Northwest streams is symptomatic of a complex of ecological problems driven by changes in riparian forests, channelization, and basin-scale erosion and sedimentation (Bisson et al. 1987; Elmore and Beschta 1987; Hicks et al. 1991). Events such as sediment-laden floods and debris flows often reshape channel morphology and fish habitat many kilometers downstream from their origin (Benda 1990).

Restoration programs in the regions we studied should follow a hierarchical strategy that emphasizes (1) prevention of slope erosion, channelization, and inappropriate floodplain development, especially in previously unimpacted habitat refugia; (2) rehabilitation of failing roads, active landslides, and other sediment sources; and (3) reforestation of floodplains and unstable slopes (Lisle 1982; Overton 1984; Reichard 1984; Weaver et al. 1987). Unless these larger-scale concerns are dealt with first, direct structural modifications of channels are unlikely to succeed.

Our results point to the general need to consider physical (as well as biological) phenomena in regional and watershed-scale contexts when stream restoration projects are planned. In the long run, evaluation and planning of stream modification projects could greatly benefit from application of a hierarchical classification system comparable to those proposed for land systems by Warren (1979) and Lotspeich and Platts (1982) and for streams by Platts (1979) and Frissell et al. (1986). Such an approach could provide a conceptual framework for ordering, analyzing, and predicting complex aspects of system behavior across different scales of space and time; it would do so by setting local, site-specific concerns in the context of large-scale dynamics of the system (Frissell et al. 1986).

If a hierarchical and contextual approach were used to plan and implement fish habitat restoration programs, many of the costly failures we observed undoubtedly could be avoided, and resources could be directed to effectively treat the primary causes of habitat problems: sedimentation from eroding roads and logged slopes, and logging, grazing, channelization, and urbanization in riparian areas and floodplains.

Acknowledgments

This research was funded by Wallop–Breaux funds under the Sport Fish Restoration Act, contracted through the Oregon Department of Fish and Wildlife. Additional support was provided by Oregon State University. Preliminary results of this study were presented at a workshop held October 21–23, 1986, in Portland, Oregon. Bruce Sims, now of the Santa Fe National Forest, encouraged this investigation and assisted in locating projects. George Westfall of the Oregon Department of Fish and Wildlife, Don King of the Siskiyou National Forest, Dave Heller of U.S. Forest Service Region 6, and Bob House of the Bureau of Land Management–Salem District provided helpful information and constructive criticism. We thank Eric Leitzinger for assisting in data analysis and J. Dambacher, J. D. Hall, W. J. Liss, R. J. White, W. S. Platts, and R. W. Wiley for constructive reviews of the manuscript. This is report 9810 of the Oregon Agricultural Experiment Station.

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Appendixes follow

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Evaluation of the Fisheries Impact Assessment and Monitoring Program for the Terror Lake Hydroelectric Project

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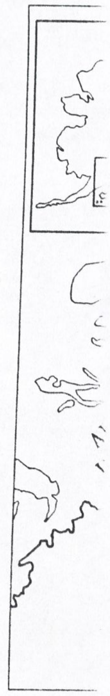
ABSTRACT: The success of the salmon fisheries impact assessment and monitoring program for the Terror Lake Hydroelectric Project (Kodiak Island, Alaska) was evaluated by considering whether (1) the project's license requirements for monitoring were appropriate, given the predicted impacts; (2) the monitoring methods were appropriate for meeting the license requirements and evaluating predicted impacts; and (3) the prelicensing assessment accurately predicted the fisheries impacts. The project's license required monitoring of streamflows, temperatures, and salmon runs for 9 years. Some, but not all, of the monitoring requirements and methods were appropriate for the types and magnitudes of predicted impacts. The preproject impact assessment was generally accurate but some inaccuracies occurred because postproject streamflows were different than expected; a successful impact assessment must be based on an accurate representation of postproject flows. This case study indicates that a monitoring program is most likely to be successful if specific monitoring objectives are based on the impacts predicted in the preproject assessment and included in hydropower project licenses. Monitoring to test and improve impact assessment methods can be beneficial to hydropower operators and resource agencies.

KEY WORDS: Environmental impact assessment, instream flow, salmon, temperature.

INTRODUCTION

Purpose and Objectives

This paper evaluates the fisheries impact assessment and monitoring program for the Terror Lake Hydroelectric Project. Hundreds of hydroelectric projects have been reviewed and licensed by the Federal Energy Regulatory Commission (FERC) since environmental considerations assumed a major role in licensing de-



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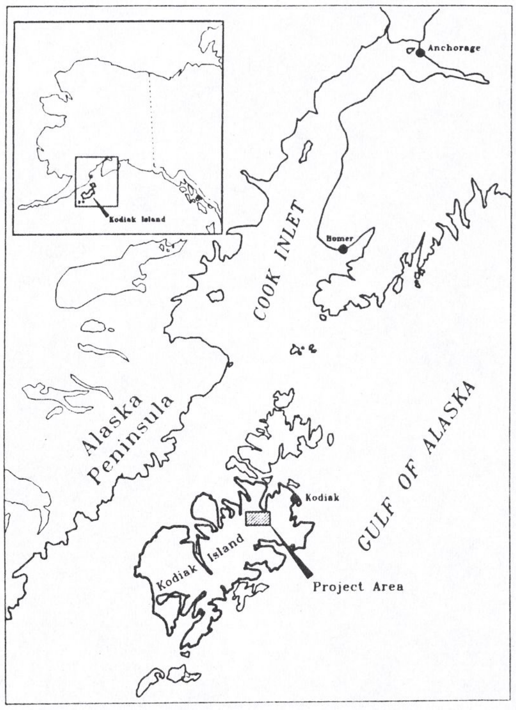

FIGURE 1. **Location of the Terror River Project.**

cisions in the early 1980's. The methods used to predict hydro project effects on fisheries have become firmly established in practice and policy, but have received relatively little critical evaluation or rigorous testing (Sale et al. 1991). In acknowledging the uncertainties in fisheries assessment methods, the FERC often requires postconstruction monitoring. Sale et al. (1991) report that monitoring the effects of instream flow requirements on fisheries was conducted for about 20% of projects licensed between 1980 and 1990.

One important purpose of monitoring programs, including the Terror Lake program, is to test whether effects are significantly different than predicted and, therefore, whether changes in mitigation requirements are needed. Although rarely required by the FERC, a second potential purpose of monitoring is to test the methods used to predict environmental impacts so that the methods can be improved and more efficient mitigation measures designed (Bernard et al. 1993). In one follow-up evaluation of predicted effects at 11 Canadian hydropower projects, a majority of the predictions for downstream fisheries were shown to be either inaccurate or uncertain, mainly because of the complexity of the effects (Marmorek et al. 1986). However, postconstruction evaluations of the predicted effects of hydro projects are relatively infrequent; few FERC-licensed projects with detailed preproject impact assessments have been in operation long enough to complete the monitoring period, and few studies have been published. Roelle and Manci (1993) identify only six published or unpublished mitigation evaluations for dams or reservoirs since 1984.

We evaluated a recently completed 9-year fisheries monitoring program required by the Terror Lake Hydroelectric Project's FERC license (No. 2743). We examined how useful the monitoring program was in testing the predictions made in the prelicensing environmental assessment. In addition, we compared the predicted changes in streamflow, temperature, spawning habitat, and incubation success to those observed during the monitoring program to evaluate the prediction accuracy. The following questions were used to evaluate the monitoring program:

1. Given the predicted impacts, were the FERC license requirements for monitoring appropriate?
2. Were the design and implementation of the monitoring studies appropriate to meet the license requirements and allow evaluation of impacts?
3. Did the prelicensing assessment accurately predict impacts of the project on fisheries?

The Terror Lake Project

The Terror Lake Project was designed to meet the entire electric demand of the city of Kodiak, on Kodiak Island, Alaska (Figure 1) by diverting water from the upper Terror and Kizhuyak river basins into the lower Kizhuyak River (Figure 2). Project features include (1) Terror Lake, a natural lake expanded via construction of a dam into a storage reservoir on the upper Terror River; (2) a 5-mile power tunnel and penstock that deliver water from the lake to the powerhouse; (3) diversions on Shotgun, Falls, and Rolling Rock creeks in the upper Kizhuyak Basin, which feed into the power tunnel; (4) a 20-megawatt powerhouse on the lower Kizhuyak River; and (5) a valve house at Terror Lake Dam that

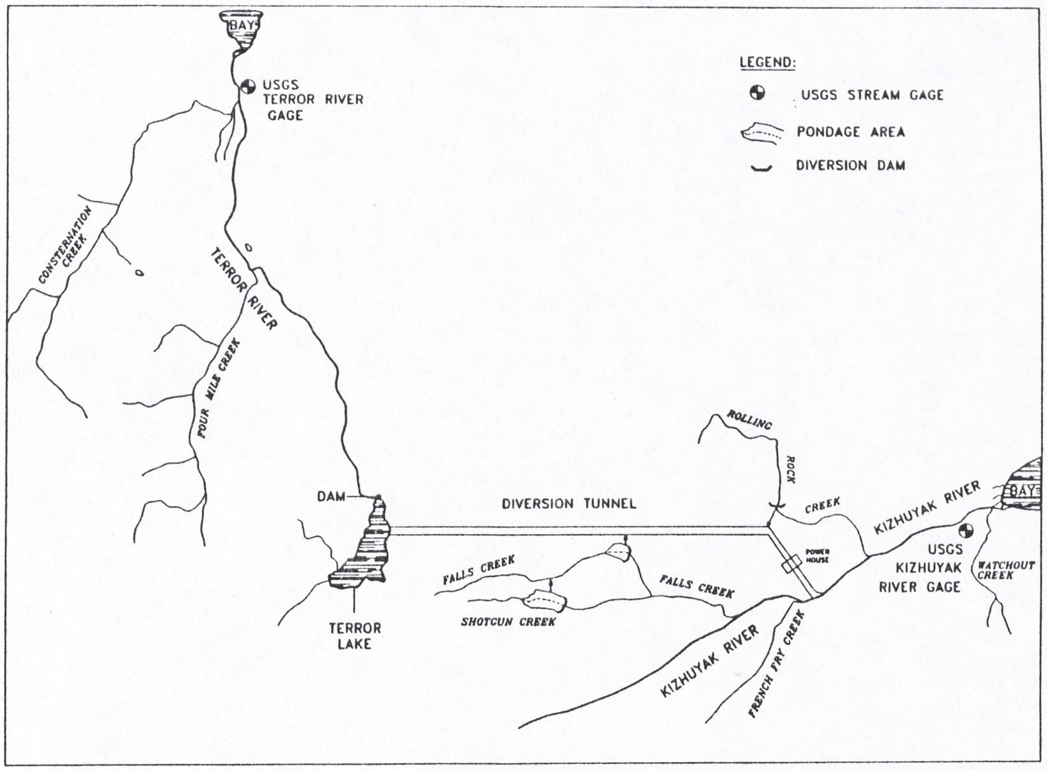

FIGURE 2. Features of the Terror River Project.

controls flow releases into the upper Terror River. Terror Lake typically fills during June or July and is drawn down during the fall and winter (Figure 3).

The Terror and Kizhuyak rivers support commercially important runs of pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon, along with smaller runs of coho salmon (*O. kisutch*). Spawning has historically been limited to the intertidal zones and lower few miles of each river. Fish arrive at the rivers in July and continue to enter them through September; spawning peaks from late August through mid-September. Incubation lasts until late March through mid-May, when most fry are believed to have emerged and migrated downstream to intertidal areas.

The Terror Lake Project was highly controversial when an application to build it was filed with FERC in 1978, mainly because of its location in a national wildlife refuge and its envisioned effects on salmon runs that are important to commercial fishers and to the brown bears for which Kodiak Island is known (Olive and Lamb 1984). The principal fisheries concerns were effects of altered streamflows and temperatures on salmon spawning and incubation. Negotiations between project proponents and opponents resulted in detailed studies of the proposed project's effects on salmon and brown bear habitat. The studies included a pioneering application of the Instream Flow Incremental Methodology (IFIM) to predict the effects of alternative instream flows on salmon habitat in the lower 4 miles of the Terror and Kizhuyak rivers (Trihey 1981; Wilson et al. 1981). The instream flow study was based on post-project flows estimated by the design engineers. Following this analysis, instream flow requirements and a mitigation agreement were negotiated and implemented in a 1981 FERC license.

The mitigation agreement and FERC license called for fisheries monitoring for 3 years during the project's construction and for 6 years after operation began. The reservoir began filling in May 1984, and power production first occurred in December 1984; therefore, the pre- and postproject

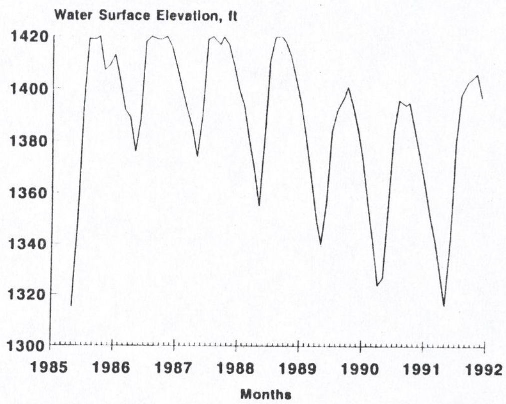

FIGURE 3. Time series of monthly mean elevations for Terror Lake.

monitoring periods were 1982–1984 and 1985–1990.

Two FERC license articles requiring monitoring were adapted from the mitigation agreement. These license articles defined the general objectives of the monitoring programs but left the choice of monitoring methods with the project licensee and the fisheries agencies. Article 41 of the project license called for monitoring of temperatures and flows and, at the completion of the monitoring program, a review of observed effects of project operations on these parameters.

> Licensee shall, in consultation with the Alaska Department of Fish and Game, the U.S. Fish and Wildlife Service, and the National Marine Fisheries Service develop a satisfactory study plan to determine the effects of the project's operation on (1) the surface and intragravel water temperatures of the Terror and Kizhuyak rivers and (2) the thermal regime of Terror Lake. This plan shall include measures to allow for the modeling of the pre- and post-operational thermal characteristics of both the Terror and Kizhuyak rivers, and Terror Lake.
>
> The plan shall further provide for the monitoring of discharge in the Terror and Kizhuyak rivers and continued monitoring of intragravel and stream water temperatures for a minimum of 6 years after the commencement of project operations. After the sixth year, the Licensee shall, in consultation with the above listed agencies and in conjunction with the results of the study conducted pursuant to Article 40, review the measured effects of project operations on discharge and water temperature, and file a report with the Commission containing recommendations for revisions of project structures or operations, if any, necessary to mitigate adverse effects of the project's operation on the aquatic biota.

Requirements for salmon monitoring are in Article 40.

> Licensee shall, in consultation with the Alaska Department of Fish and Game, the U.S. Fish and Wildlife Service, and National Marine Fisheries Service, monitor the size, species composition, and spawning distribution of anadromous salmonid runs in the Terror and Kizhuyak rivers during the construction and initial 6-year operating period of the project. During the course of these studies, Licensee shall file annual reports of its findings with the Commission, with copies to the above listed agencies. After the sixth year, the Licensee shall, in consultation with the above listed agencies, and in conjunction with the results of the study conducted pursuant to Article 41, review the effects of project operations on the fishery resources, and file a report with the Commission containing recommendations for revisions of project structures or operations, if any, necessary to mitigate any adverse effects of the project's operation on the fishery resources.

METHODS

We evaluated the appropriateness of the monitoring requirements and methods, and the accuracy of the preproject assessment of fisheries effects for each of four major mechanisms by which the Terror Lake Project was predicted to affect salmon production. The first mechanism is altered flows in the Terror and Kizhuyak rivers caused by the interbasin diversion and the use of reservoir storage to capture high spring and summer flows and augment winter flows in both rivers. The second is stream temperature changes resulting from releasing water from the reservoir's deep outlets, altered flow rates, and the increased volume of Terror Lake, which reduces the response of lake temperatures to air temperatures. The third is changes in salmon spawning habitat availability resulting from streamflow changes. The fourth mechanism is changes in incubation success of salmon eggs and fry; incubation is affected by scouring during high flows, dewatering during low flows, and temperature-induced changes in development rates.

Results and recommendations from the prelicensing fisheries studies were reported by Wilson et al. (1981). The monitoring program and its results were summarized by Blackett (1992), Railsback and Trihey (1992), and Trihey et al. (1992). Salmon spawning and incubation aspects of the monitoring program were described by Blackett (1989) and the Division of Fisheries Rehabilitation, Enhancement, and Development (1991). These reports are the primary sources of information for this paper.

We evaluated the monitoring requirements and methods by analyzing whether the monitoring objectives were appropriately based on expected impact mechanisms, and whether the data collection programs were appropriate for meeting the monitoring objectives. MacDonald et al. (1991) discuss the design of stream monitoring programs and identify appropriate monitoring objectives as one of the most important characteristics of a well-designed program. Bernard et al. (1993), in a discussion of monitoring for evaluation of hydropower impact assessments, state that "Each portion of a monitoring program should be targeted at either measuring some postulated environmental impact or at analyzing causal relations between project activities and valued ecosystem components." Monitoring objectives state what processes are to be monitored and should be based on the expected mechanisms by which effects to fisheries are expected; the processes monitored should be those predicted to most likely change and affect fisheries. Data collected in a good monitoring program allow the monitoring objective to be met (MacDonald et al. 1991); the field studies should be appropriate to answer the questions posed by the monitoring objectives. The FERC license articles 40 and 41 define the objectives of the monitoring program. We evaluated these objectives by whether they were appropriately focused on the mechanisms by which changes were expected. We evaluated the monitoring methods designed and implemented by the licensee and fisheries agencies by whether they provided the information needed to meet the monitoring objectives. We based these evaluations on the fisheries impacts and impact mechanisms that were identified in the prelicensing assessment and the monitoring methods developed by the licensee and agencies.

The accuracy of the prelicensing fisheries impact assessment was evaluated by comparing the predicted impacts (from Wilson et al. 1981) to those detected by the monitoring program. We also compared the assumed conditions on which the impact assessment was based to observed conditions to explain inaccurate predictions.

RESULTS

Streamflow

Evaluation of the Impact Assessment. Prelicensing streamflow measurements included continuous monitoring by the U.S. Geological Survey (USGS), and spot measurements made throughout the project basins as part of project design in 1980. Continuous monitoring was conducted at the outlet of Terror Lake for a total of about 7 years between 1964 and 1980, and at the mouth of the Terror River for 5 years starting in 1964. Continuous measurements near the mouth of the Kizhuyak River were made during parts of 1980. These data, along with watershed areas and 27 years of record from the nearby Uganik River, were used by the design engineers in a regression analysis to predict monthly mean, peak, and low flows (Wilson et al. 1981). A water balance simulation was also used by project designers to predict how reservoir operations would affect monthly flows in both rivers; these monthly flows were the basis of fisheries impact predictions.

The prelicensing mitigation agreement and the FERC license require releases from

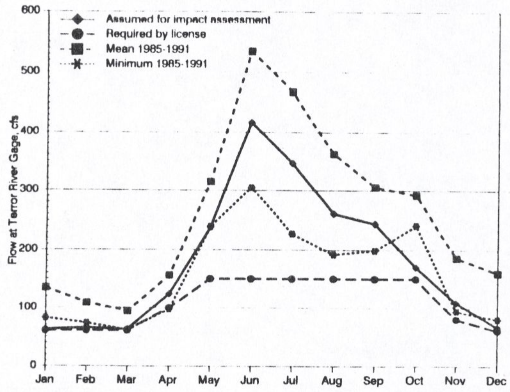

FIGURE 4. Terror River instream flows assumed in the impact assessment, minimum flows required in the project license, observed mean monthly postproject flows, and observed minimum monthly postproject flows.

TABLE 1
Pre- and postproject mean annual flows.

	Terror River	Kizhuyak River
Preproject period of record, years	8	5
Postproject period of record, years	7	7
Mean of preproject annual flows, cfs	290	212
(sample standard deviation)	(63)	(37)
Mean of postproject annual flows, cfs	260	254
(sample standard deviation)	(52)	(36)
Difference between pre- and postproject mean annual flow, cfs (P^a)	−30 (0.33)	+42 (0.08)

[a] The "P" value from a two-sample t-test for differences in the means of the pre- and postproject mean annual flow series, which can be interpreted as a level of confidence that the means are the same for the two periods.

Terror Lake that provide instream flows at the mouth of the Terror River of 60 cubic feet per second (cfs) in winter and 150 cfs in summer (Figure 4). These required flows are less than those assumed in the fisheries impact assessment that led to the agreement (Wilson et al. 1981; Figure 4). The project was designed to release up to 180 cfs through the powerhouse into the lower Kizhuyak River. A design mean annual diversion from the Terror to Kizhuyak basins of about 120 cfs was used for the impact assessment.

Following construction of the project, daily flows were monitored by the USGS using gages near the mouths of the Terror and Kizhuyak rivers (Figure 2). Flows through the powerhouse were not measured during the monitoring period and can only be roughly estimated from monthly power production. The three diversions in the upper Kizhuyak Basin also were not gaged; it was assumed when the monitoring study was designed that such flow measurements would be made by project operators, but they were not. Therefore, neither the runoff in each basin nor the amount of flow diverted from the Terror to the Kizhuyak Basin can be directly determined from the monitoring program.

We compared pre- and postproject annual mean flows at the USGS gages to roughly estimate the project's effects on river flows (i.e., the amount diverted between basins) but such a comparison is complicated by the high interannual variability in flows. It appears that mean annual Kizhuyak River flows increased by about 40 cfs and Terror River flows decreased by 30 cfs, but there is little statistical confidence that the mean of the Terror River annual flow series changed between pre- and postproject periods (Table 1). A comparison of the percent of the combined runoff from the two basins that passed each gage between pre- and postproject periods provided somewhat less variable results and an estimated mean annual diversion of 50 cfs from the Terror to Kizhuyak basins (Trihey et al. 1992). This is much less than the 120 cfs the project was expected to divert.

The impact assessment did not accurately reflect postproject streamflows because the minimum flow requirements had not been established at the time the assessment was prepared and because the hydrologic analysis performed by project designers was apparently inaccurate. Two differences between expected and actual operation of the project also contributed to the higher-than-expected Terror River flows. The project operators had weather-related difficulty regulating winter releases and thus chose to release excess flow to avoid violating the instream flow requirements. The impact assessment assumed that the reservoir would not be filled until early October, so it could store late summer high flows; however, in most years the reservoir was filled by midsummer.

Evaluation of Monitoring Requirements. The project affects flows spatially by diverting water between basins and temporally by storing water during high-runoff seasons; these changes are important mechanisms by which the project affects spawning habitat and incubation success. Article 41 of the project license requires monitoring the discharge in both rivers, with no more specific requirements. Some flow-driven effects, such as scouring flows and winter dewatering of redds, could occur over 1-day or shorter times; therefore, a requirement for monitoring of daily flows (which occurred anyway) would have been appropriate. The flow in both rivers varies spatially, due to tributary and groundwater inflows, within reaches where spawning occurs, and there are reaches upstream of the flow gages where flows are controlled partially by project releases and partially by inflows. A requirement for monitoring flows in reaches where flows clearly vary due to accretion, although expensive, would have allowed a better understanding of how the project affects important spawning areas. The FERC requirement for flow monitoring was not explicit enough to ensure that flow-driven biological effects of the project could be explained by the monitoring program; instead, the licensee and resource agencies were given the responsibility to select monitoring objectives. Requirements to measure the flow diverted at each dam and the flow through the powerhouse may have allowed a better understanding of some of the project's biological effects, as well as more efficient operation of the project.

Evaluation of Monitoring Methods. The flow monitoring program met the general conditions of the FERC license and demonstrated compliance with the instream flow requirements. The flow monitoring program did not directly measure the diversion rate between watersheds or the runoff in each basin, but Article 41 does not clearly require such measurements. The daily flow records were appropriate to evaluate project effects on the most important spawning areas, which are near the flow gages.

Water Temperature

Evaluation of the Impact Assessment. Temperature changes were predicted in a modeling study that used regional weather data and generic channel geometry variables instead of site-specific data (Simons et al. 1980, cited by Wilson et al. 1981). Predictions for August through February, when most salmon egg and fry development occurs, were that Terror River surface water temperatures would increase by less than 1°C and Kizhuyak River surface temperatures would increase by up to 1.5°C. Changes in the intragravel temperatures to which salmon eggs are exposed were also of concern; differences between intragravel and surface water temperatures are common in Alaskan rivers in winter, due to groundwater inflow.

The monitoring program estimated project effects on water temperatures by comparing measured temperatures from the pre- and postproject periods. River temperatures were monitored continuously at the USGS stream gages (Figure 2). These gages were supplemented by several stations that provided the temperature of surface and intragravel water at locations other than at the USGS gages. These stations were operated from 1985 to 1990, although bears and other animals frequently disturbed them.

Early results of the temperature monitoring program confirmed that the project had little effect on stream temperatures. Therefore, the project's operators and the fisheries agencies agreed that extensive reservoir monitoring and modeling need not be completed. Because a comparison of surface water and intragravel temperatures measured concurrently at many sites showed no significant differences, surface water temperatures were accepted as an accurate indicator of the temperatures to which incubating salmon eggs are exposed in the project rivers (Railsback and Trihey 1992; Trihey et al. 1992).

Monitoring showed that the temperature of the instream release from Terror Lake was altered by the project, but the difference between pre- and postproject temperatures in downstream spawning areas is small. At the USGS gage on the Terror River, postproject stream temperatures averaged approximately 1°C lower during March and late summer than the preproject temperatures. Winter stream temperatures 2 miles upstream of this gage appear to be consistently 1 to 1.5°C higher during the postproject period. Winter salmon incubation temperatures in the most extensively used spawning areas, which are near and downstream of the gage, appear to be unaffected by the project. At the USGS gage on the Kizhuyak River, postproject stream temperatures are about 1°C lower than preproject temperatures between July and December, with little difference during late winter and spring. As in the Terror River, winter stream temperatures upstream of the gage are warmer because of the project. Winter stream temperatures in the most extensively used spawning areas of the lower Kizhuyak appear to have changed little.

The postproject monitoring confirmed the preproject predictions that changes in temperature would be minor and that there would be a slight increase in winter temperatures. Postproject temperatures observed in late summer were 1°C lower than preproject temperatures, not higher as predicted, so it appears that the temperature impact assessment did not accurately predict seasonal differences in project effects. In addition, flows during the monitoring period were substantially higher than those assumed for the impact assessment and required by the FERC license. Because flow can affect stream temperature, the monitoring program has not necessarily shown what temperatures would be if flows were as low as allowed by the license, although changes in temperature resulting from lower flows could probably be inferred accurately from the monitoring data.

Evaluation of Monitoring Requirements. Article 41 calls for a temperature monitoring program with only the general objectives of modeling temperatures in Terror Lake and the two rivers to support a preproject decision of whether a multilevel reservoir outlet was needed. Given the uncertainties in modeling reservoir and stream temperatures, especially where ice formation occurs, a requirement for temperature monitoring is appropriate. The license left it to the licensee and resource agencies to develop the specific objectives necessary to decide if the project's effects were adequately mitigated.

Evaluation of Monitoring Methods. The temperature monitoring program was sufficiently extensive to test the predicted temperature changes at sites including spawning areas upstream and downstream of the two permanent gages. Early verification that temperature changes were minor resulted in modification of the monitoring program to eliminate unneeded reservoir and intragravel temperature studies.

Spawning Habitat

Evaluation of the Impact Assessment. The Terror River assessment used an early application of the IFIM to predict effects of changes in flow on the amount, quality, and location of spawning habitat, as defined by velocities, depths, substrate types, and temperatures. Methods described by Bovee and Cochnauer (1977), Bovee and Milhous (1978), and Trihey (1979) were used. As noted above, the IFIM study assessed the impacts of the project assuming a postproject flow regime that turned out to be higher than the minimums required by the project license but lower than the observed flows.

The preproject assessment predicted changes in spawning habitat in the delta and intertidal waters, lower river, and upper river reaches of each stream (Table 2). In the Terror River, the project was predicted to decrease pink salmon spawning habitat availability during periods of low flow by further reducing flows and to have negligible effects during high flow periods, when the project's effects on flow are minor compared to the natural flow. The overall effect of the project on chum spawning habitat in the Terror River was predicted to be very minor. In the Kizhuyak, the project was predicted to slightly improve pink salmon spawning habitat availability during low flow periods and have little effect during high flow periods. The project was also predicted to result in minor overall decreases in chum spawning habitat in the Kizhuyak, with little effect

TABLE 2

Predicted effects on spawning habitat availability (summarized from Wilson et al. 1981).

Location	Pink salmon	Chum salmon
Terror River		
Delta, intertidal	little change	little change
Lower river	minor decrease	minor decrease
Upper river	minor increase	minor decrease
Kizhuyak River		
Delta, intertidal	minor increase	minor increase
Lower river	minor decrease	minor decrease
Upper river	major increase	(not present)

during high flows and slight decreases during low flows.

The effects of the project on salmon spawning habitat were monitored by observing spawner distribution and density in the river and measuring fry densities at known spawning areas. The geographic distribution and estimated numbers and density of spawners were determined by making visual observations from aircraft and marking spawner locations on maps. The observations were scheduled to occur twice per week from July through October, but weather and scheduling difficulties limited the actual number of annual observations from 4 to 6 for the Kizhuyak River and from 6 to 17 for the Terror River (Blackett 1992). The density of salmon fry (number per square meter of stream bed), a gross index of spawning success, was monitored at between 8 and 50 randomly selected locations at each of 11 sites in each river. These preemergence sampling methods were the same as used for monitoring commercial fisheries (Division of Fisheries Rehabilitation, Enhancement, and Development 1991). Fry density measurements were usually made in March of each year. Average fry density data from two nearby rivers, also sampled in March, and from other sites throughout Kodiak and Afognak islands were used for comparison with fry density data from the project area (Blackett 1992). Fry development rates, as a percent of yolk sac absorption, were noted at the same time fry density was observed.

The monitoring program showed that both pink and chum salmon spawned as much as 1.6 mile further upstream in the Terror River during the postproject period, and pink salmon increased their use of the upper reaches more than chum did. During the postproject period, pink salmon were observed spawning up to 1 mile further upstream in the Kizhuyak than in the preproject period; no expansion in chum salmon spawning was observed.

The fry density monitoring data were of little use in evaluating impacts of the hydro project. The data show that average fry densities were generally higher during the postproject period in both rivers, but the variability among sites and among years at a site was much higher than the differences between pre- and postproject averages. These measurements are highly variable by nature because the fry density in spawning gravel varies greatly over short distances.

The predicted effects of changes in flow on spawning distribution and density were upheld; spawning appeared to increase in spatial extent and more adults returned from postproject spawns than during the preproject monitoring period. However, the flows used to predict project effects and the actual flows during postproject monitoring were higher than the required minimums for the Terror River; therefore, spawning success under the minimum Terror River instream flows required by the project license was not evaluated by the monitoring program. The IFIM study indicates for most Terror River sites that habitat availability increases little as flows increase from the required minimums (Wilson et al. 1981), implying that slightly more spawning habitat was available during the monitoring program than would have been with the minimum required flows.

Evaluation of Monitoring Requirements. The project was expected to affect salmon spawning habitat by relatively small degrees, by altering flows; the amount by which the project changes flow was expected to vary among sites on each river due to inflows (Table 2). License Article 40 called for monitoring the size, species composition, and spawning distribution of salmon runs. These requirements are appropriate to verify the predicted minor effects of flow changes and, by requiring monitoring of the spatial distribution of spawners, they consider the differences among sites on each river in how spawning habitat could change.

Evaluation of Monitoring Methods. The fisheries monitoring methods used were designed for commercial harvest management and are not necessarily appropriate for measuring the effects of a hydropower project. The methods used to monitor spawning distribution and density appear to have been partially successful; the observations of spawning salmon from aircraft were frequent enough, compared to the duration of redd building and spawning, to document where spawning occurred. However, in several years the observations were too infrequent to produce reasonably accurate estimates of spawning run sizes (Blackett 1992). A consistent schedule of aerial and ground observations was needed to effectively monitor adult spawning run sizes, distributions, and timing.

The monitoring program for fry density was not appropriate for detecting the predicted impacts of the hydropower project. The low-resolution monitoring methods (i.e., relatively few, highly variable samples) were unlikely to detect the small predicted changes; a program with many more replicates and control sites would probably be required to do so. Fry density appears not to be a cost-effective monitoring parameter in this case.

Incubation

Evaluation of the Impact Assessment. The success of natural salmon egg and fry incubation was believed to be limited largely by low winter streamflows that dewatered redds along the channel margins and in riffles, and by high flow events that scoured out redds. The effects of the project on incubation success were therefore predicted by determining how the project would affect the frequency and intensity of scouring and dewatering events (Wilson et al. 1981). Water temperature changes were also recognized as affecting egg and fry development rates.

The project was predicted to reduce dewatering of salmon redds in the Terror River. The project's reductions in streamflows during August and September were expected to cause salmon to build their redds in deeper parts of the channel, which would be less likely to be dewatered when streamflows decreased in winter. More importantly, the project's winter releases were expected to eliminate the extreme low flows that naturally dewatered large numbers of redds. The project augments Kizhuyak River flows throughout the main channel areas used for spawning, so dewatering in the Kizhuyak was predicted to be reduced or eliminated.

High streamflows between August, when spawning begins, and November, after which flows decrease because high-elevation precipitation occurs as snow, can scour spawning areas and flush incubating eggs from the gravel. Preproject studies estimated that scouring occurred in the lower mainstem of the Terror River at streamflows near 1,000 cfs, and that the project's reservoir storage would reduce the frequency, magnitude, and duration of scouring flows. Reductions in scouring flows were predicted to primarily benefit salmon spawning in the main channels; intertidal areas, distributaries, and spring-fed side channels are much less susceptible to scouring by flood events. At peak capacity, the powerhouse can increase streamflows in the Kizhuyak River by approximately 180 cfs, which is insignificant during the 2,000–4,000 cfs peak natural flows. Therefore, the project was predicted to cause only minor increases in scouring in the Kizhuyak; preproject studies did not estimate a Kizhuyak flow rate at which scouring begins.

The minor predicted temperature increases in both rivers were considered to have the potential to reduce incubation times in the mainstems, but overall effects on salmon development were expected to be minor because most spawning occurs in spring-fed delta distributaries and in lower mainstem reaches where temperature effects were predicted to be negligible.

Considering the cumulative effects of changes in dewatering, scouring, and temperatures, the Terror Lake Project was predicted to have an overall net benefit to salmon incubation in the Terror River. The project was expected to reduce the frequency of high-flow events that scour redds and to prevent winter low flows that dewater redds, whereas seasonal stream temperature changes were expected to be insignificant. The project was predicted to have minor net benefits to incubation in the Kizhuyak River. Augmented winter flows were expected to eliminate severe dewatering events and salmon were expected to spawn further upstream using more of the main channel, whereas project effects on scouring and water temperature in the Kizhuyak were predicted to be minor.

The monitoring program evaluated project effects on scouring and dewatering by analyzing how the project altered the frequency of high and low daily flow extremes. The pre- and postproject frequencies of high flows during the late summer through early winter period were compared. The fry density and development data discussed earlier were intended to provide a direct but relative measure of incubation success. In addition, returns of adult salmon to both rivers were estimated using commercial harvest estimates and the aircraft observations of the number of fish spawning (Blackett 1992).

A reduction in the dewatering of redds occurred as predicted. In the Terror River, the project has not consistently provided the lower streamflows during August and September that were predicted to encourage salmon to spawn in deeper sites, but it has consistently provided winter flows that prevent dewatering of main channel redds. The preproject 90% exceedance flows during months when incubation occurs were as low as 26 cfs (February and March), but postproject 90% exceedance flows were all above 65 cfs. Winter streamflows below 60 cfs at the Terror River gage have not occurred since 1986. The Terror Lake Project has eliminated the severe low flows that historically dewatered salmon redds in the main channel of the Kizhuyak. During the preproject period, the monthly mean streamflow at the Kizhuyak River gage during the salmon incubation period was as low as 5 cfs (in March 1982), and the 90% exceedance flows were as low as 2 cfs in March and 4 cfs in April. The lowest postproject mean monthly flow was 87 cfs in December 1990, and the postproject 90% exceedance flows for all months were above 55 cfs.

The project has reduced the overall frequency and magnitude of scouring flow events, but these reductions occur less in months when salmon eggs are incubating than in May and June. The project has been less effective than expected in detaining storm flows in the late summer-early fall period because the reservoir has been operated to fill before August (Figure 3), although the reservoir has not filled completely in several recent years. Terror River scour events (flows above 1,000 cfs) have generally occurred less frequently during the postproject period. However, the frequency of streamflows above 1,000 cfs has changed little in the months of August, October, and December (Trihey et al. 1992). Peak flows appear to have been unexpectedly reduced in the Kizhuyak. The postproject 10% exceedance flows have been greater than the preproject values by 90 to 200 cfs in August through December, except in November when the postproject value was 200 cfs less than the preproject value. However, flows of less than 10% exceedance (even less frequent, higher flood flows) were lower during the postproject period during September through December. The fact that peak Kizhuyak River flows in months critical to salmon have been lower, instead of higher as predicted, during the postproject period may be attributed to two factors. First, the periods of pre- and postproject record are short for comparison of such infrequent flows, so the differences may result from chance. Second, the diversions on Falls, Shotgun, and Rolling Rock creeks in the Kizhuyak Basin may be diverting a substantial portion of the high-elevation snowmelt runoff from the Kizhuyak River basin into Terror Lake. No measurements have been made that would allow a determination of whether such storage of Kizhuyak water actually occurs or at what rate.

The small increases observed in Terror River winter temperatures are not expected to measurably affect fry development rates in the areas of dense spawning. The project apparently reduces temperatures by about 1°C in July through December at the Kizhuyak River gage. Salmon eggs and alevins exposed to such decreases in incubation temperature could have increased incubation periods; for example, pink salmon eggs spawned at the beginning of September would have accumulated about 120 fewer of the 530–610 degree days needed for hatching (Bailey et al. 1980; cited by Groot and Margolis 1991) by the end of December.

The degree of yolk sac absorption for salmon fry was observed along with preemergent fry densities at a number of sites, indicating that average fry development rates were higher in both rivers in the postproject periods, by less than 10%. This difference is small compared to the variability of observed development rates among years and sites, so the observations of yolk sac absorption were incapable of indicating any significant influence of the project on fry development rates.

The adult salmon return data showed that the hydropower project did not significantly reduce salmon production. For both rivers and both salmon species, average adult returns were higher for cohorts spawned after the project began operation. Although two-sample t-tests show none of the postproject increases to be significant at $P < 0.15$ and similar differences between pre- and postproject periods were observed at control sites in nearby rivers, these data show that no significant decrease in production occurred. These comparisons are not entirely rigorous because chum salmon ages at spawning vary, making it impossible to completely isolate pre- and postproject cohorts; in addition, the *Exxon Valdez* oil spill resulted in no harvest in 1989, with unknown effects on return estimates.

Our evaluation shows that the preproject assessment of effects on salmon fry incubation were generally upheld. Dewatering of redds was greatly reduced by steady winter flow releases. However, the lower August and September flows predicted to cause fish to spawn in deeper water in the Terror River did not occur. The project appears to have reduced spring scouring flows in the Kizhuyak River even though not predicted to, possibly due to diversion of upper basin water into the reservoir. However, the project did not reduce fall scouring flows in the Terror River as predicted because the reservoir was usually operated so that it filled by the middle of most summers and had no storage available as predicted, to retain flood flows. The prediction that water temperature changes would be minor was accurate, although seasonal changes in temperature effects and the direction of some changes were not predicted accurately. The counts of adult returns confirmed the prelicensing prediction that no major adverse effects would occur, but direct effects of the Terror Lake Project on incubation success cannot be evaluated with the available fish data.

Evaluation of Monitoring Requirements. Increased salmon incubation success was perhaps the most important effect of the Terror Lake Project predicted in the preproject impact assessment, but the fisheries monitoring requirements of Article 40 do not specify monitoring of incubation success or, with the exception of temperature, of the processes affecting it. To directly evaluate the mechanisms by which the project was predicted to affect incubation success, the monitoring requirements should have included site-specific monitoring of scouring and dewatering flows, especially in spawning areas where the project most affects flow rate. The important predicted effects of the project on mainchannel spawning and incubation may have been detected most directly by monitoring the number and timing of smolts migrating out of the rivers. Monitoring smolt outmigration, although possibly more expensive, is recommended as a way to eliminate the additional, high uncertainties that occur when project effects must be inferred from data on adult salmon returns (Lawson 1993).

High flows that scour redds are relatively infrequent events (postproject flows above 1,000 cfs occur in the Terror River on less than 10% of the days in even the wettest months); a monitoring period longer than 6 years may be needed for a statistically significant evaluation of scour flows.

Evaluation of Monitoring Methods. We found that the fisheries monitoring methods were generally unable to distinguish project effects from natural variability. The fry density and development rate data were of too low resolution and too variable to detect the predicted small effects of the project on incubation. The adult harvest and escapement data were also too variable and dependent on factors other than spawning and incubation success for direct evaluation of project effects; for example, the monitoring program was incapable of determining whether or not low adult returns in 1990 were due to reduced spawning or incubation success or to low ocean survival. Although these methods may be suitable for salmon harvest management, the very different objectives of monitoring a hydropower project require more direct measurement of predicted effects.

CONCLUSIONS

Since 1981, when the Terror Lake Project was licensed, the FERC's procedures for assessing environmental impacts and developing mitigation requirements have changed significantly. The FERC staff is now more active in the process, fisheries agency staff have more experience with hydroelectric projects, and impact assessments are not finalized until after mitigation negotiations have been conducted. However, we believe several conclusions drawn from the Terror Lake case are relevant to future licensing cases.

Monitoring Program Purposes

The monitoring program successfully showed that the Terror Lake project, as predicted, did not have significant adverse impacts on salmon fisheries, but the program did not test all the supporting predictions made in the impact assessment. Therefore, the program met one important purpose of a monitoring program, that of verifying the magnitude of predicted impacts and showing whether changes in mitigation are needed, but only partially met a second potential purpose, that of testing the analysis methods used to make predictions. Because many fisheries impact assessment methods are relatively uncertain, monitoring programs should include the purpose of evaluating assessment methods so that they can be improved. Although testing and improving prediction methods is rarely required by the FERC, integration of monitoring programs with industry- or agency-sponsored research could meet this purpose. Such research to improve assessment methods would benefit water project operators and fisheries managers by making impact assessment studies and mitigation requirements more cost-effective.

Monitoring Objectives

Monitoring objectives should be based on the effects predicted in an impact assessment in three ways. First, monitoring objectives should reflect the mechanisms by which effects are expected to occur; at the Terror Lake Project, effects on incubation success due to changes in scouring and dewatering of salmon redds and temperature changes were among the most important predicted effects, but monitoring of only one of these processes was specifically required. When the most important predicted effects are driven by changes in flow, flow monitoring objectives should be specific enough to allow evaluation of such impacts. Second, monitoring objectives should reflect the magnitude of predicted effects; for example, project effects on temperature were predicted to be small, so monitoring objectives were appropriately limited to verifying this prediction. However, the uncertainty in the predictions should also be considered; more rigorous monitoring may be appropriate if there is little confidence in the methods used to predict effects. Third, monitoring objectives should reflect the spatial and temporal scales over which effects are expected. Predicted effects on several processes (e.g., spawning habitat) vary among sites with the degree to which flow is affected by the project. Time scales vary among impact mechanisms; for example, minimum spawning habitat is relatively constant for long periods, but scouring is caused by infrequent, short-duration events, so the frequency and duration of monitoring measurements could also vary. Monitoring programs that are appropriate in these three ways will, by accurately quantifying the processes controlling fisheries, facilitate effective and efficient changes in mitigation if such changes are needed.

Terror Lake Project monitoring objectives were generally not detailed in the FERC license, but were identified by the licensee and consulting agencies. However, a hydro project's license appears to be an appropriate place for defining specific monitoring objectives because the license is issued at the conclusion of the environmental impact assessment process. This assessment process predicts the causes and magnitude of environmental impacts, which should be the basis for determining monitoring objectives. The license may also be an appropriate place to define the level of effects that, if observed in postproject monitoring, would require additional mitigation. Monitoring objectives in the FERC license also have the weight of law to ensure that they are met, making the FERC one of the few federal agencies to routinely monitor the results of their environmental impact assessments.

Monitoring Methods

Monitoring to determine the effects of a hydroelectric project is a very different problem than most kinds of monitoring typically conducted by fisheries biologists. One of the most important lessons from Terror Lake is that standard fisheries monitoring methods can be inappropriate, due to differences in objectives and in the scale of the potential effects being examined, for monitoring hydro effects. Monitoring methods should provide data that allow the objectives to be met in the manner of scientific hypothesis testing. The Terror Lake Project monitoring program generally met the objectives of the FERC license and in some cases provided information that was essential for determining the project's effects even though not specifically required in the license. However, experience with such methods for large-scale harvest management as harvest, escapement, fry density, and fry development rate measurements should have indicated that they are of too low resolution to detect the predicted effects of the project. Monitoring methods that measure the predicted effects in the most direct and certain way (in this case, monitoring numbers of downstream migrating smolts as well as spawners) should be used. This is demonstrated by inability of the Terror Lake program to distinguish any effects of the *Exxon Valdez* spill and resulting harvest closure from effects of the hydro project. Published environmental monitoring methods (e.g., Osenberg and Schmitt 1994) can be adapted for use at hydropower projects.

Impact Assessment

The environmental impact assessment for the Terror Lake Project appears to have been generally accurate. Inaccuracies in the impact assessment such as scouring in the Terror River not being reduced as much as expected and peak flows in the Kizhuyak River being unexpectedly reduced, and uncertainties in results such as predictions of flow-based effects not being fully tested because observed flows were higher than predicted, occurred because hydrology and river flows were not as expected. Inaccuracies in hydrology occurred in part because preproject data were limited, the reservoir was operated to fill earlier in the summer than assumed for the assessment, and difficulties in controlling flow releases and over-releases to meet instream flow requirements were not foreseen. Over-releases of instream flows to avoid violations of the FERC license requirements are difficult to avoid and occur at many hydro projects (Federal Energy Regulatory Commission 1991). Such over-releases should be considered in predicting the effects of projects. To be successful an impact assessment and monitoring program must be based on an adequate understanding of flows; thus, project effects on flows need to be fully explored and predictions must reflect actual operations as closely as possible.

Acknowledgments

The accuracy and organization of this paper benefitted immeasurably by reviews by E. Woody Trihey (Trihey & Associates), David Nease (Kodiak

Electric Associates), Glenn Čada (Oak Ridge National Laboratory), Dr. Margaret Lang (Humboldt State University), Robert Krska, Larry Ohmsted, and Gordon Russell. The figures were produced by Erika Amdur. We also acknowledge the hard work and dedication of the agency and contractor staff that conducted the Terror Lake Project fisheries studies.

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Submitted: 17 March 1994
Accepted: 15 August 1994
Discussion open until: 30 June 1995