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A Review of the Effects of Hydrologic Alteration on Fisheries and Biodiversity and the Management and Conservation of Natural Resources in Regulated River Systems

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http://dx.doi.org/10.5772/55963

1. Introduction

Hydrologic alterations resulting from dam construction and other human activities have negatively impacted the biodiversity and ecological integrity of rivers worldwide (Dudgeon 2000, Pringle et al. 2000). These alterations have included habitat fragmentation, conversion of lotic to lentic habitat, variable flow and thermal regimes, degraded water quality, altered sediment transport processes, and changes in timing and duration of floodplain inundation (Cushman 1985, Pringle 2000). The negative impacts of altered hydrologic regimes on aquatic organisms are well documented. For example, dam construction has blocked the migratory routes of diadromous and potamodromous species (e.g., salmonids and white sturgeon, Acipenser transmontanus), which has severely reduced their spawning and overall reproductive success (Wunderlich et al. 1994, Beamesderfer et al. 1995). In the Alabama River system (USA), flow-modification in regulated reaches has resulted in losses of river-dependent ("fluvial") fish species, and distributions of federally listed species have been restricted by main stem impoundment (Freeman et al. 2004). Several researchers have documented major changes in fish assemblage structure following dam construction (Paragamian 2002, Quinn and Kwak 2003; Gillete et al. 2005). For example, Quinn and Kwak (2003) reported that long-term changes in the fish assemblage after dam construction on the White River (Arkansas, USA) included a shift from warmwater to coldwater species, a substantial decrease in fluvial specialists, and dramatic reductions in species richness. The negative effects of dam construction are not only limited to fishes. Freshwater mussel diversity has declined substantially, particularly in the southeast USA, as a consequence of hydrologic alteration (Watters 2000).



This chapter begins with an examination of the hydrologic alterations that may be caused by dam construction. Several examples are presented for different continents, emphasizing that hydrologic alteration is an issue of global concern. Next, the effects of altered hydrologic regimes on the growth, recruitment, and survival of organisms and on the overall biodiversity and community structure in regulated river systems are reviewed. Subsequently, tools and strategies to manage and conserve aquatic fauna in regulated river systems are discussed. In the past several decades, a wealth of information has been published on these topics. This chapter provides a general overview of the impacts of hydrologic alteration and presents several management approaches, which have been developed to address it. More detailed information may be found in the review papers referenced in this chapter.

2. Alteration of the flow regime

In their highly impactful paper, Poff et al. (1997) outlined five important characteristics of a flow regime: magnitude, frequency, duration, timing (or predictability), and the rate of change (or flashiness). These major components of the flow regime are ecologically relevant to the system. For example, the magnitude of flow (e.g., mean monthly discharge) may define habitat characteristics such as wetted area or habitat volume in a stream or river (Richter et al. 1996). The frequency of episodic flows (e.g., high or low pulse frequencies) may lend insight on how often drought or flood conditions occur within a system (Richter et al. 1996). Each of these flow attributes may be altered by dam construction and hydropeaking operations. For example, flows have rapidly fluctuated between extremely low and high discharges as a result of hydropeaking operations downstream of Harris Dam on the Tallapoosa River, USA (Irwin and Freeman 2002). Extreme discharge fluctuations during a period of only four to six hours have generated a highly variable flow regime that has potentially threatened the persistence of several native fishes (i.e., fluvial specialists) below the dam (Irwin and Freeman 2002). Irwin and Freeman (2002) reported significant changes in hydrology after construction of Harris Dam in 1982, which included increases in high-pulse frequency, low-pulse frequency, fall rate, and the number of flow reversals. Irwin and Freeman (2002) documented release-driven, diel temperature fluctuations as high as 10°C, producing highly stressful conditions for resident organisms.

Hydrologic alterations that occur as a result of dam construction have been well documented (Galat and Lipkin 2000, Maingi and Marsh 2002, Yang et al. 2008). For example, Yang et al. (2008) applied the Range of Variability Approach (RVA discussed later; Richter et al. 1997) to evaluate the effects of dam construction on the hydrologic regimes of middle and lower river networks in Yellow River, China. The authors stressed that assessments of hydrologic alteration are extremely complex, particularly in systems that are impounded by more than one dam (Yang et al. 2008). In addition, both pre- and post-impact discharge data must be sufficient to effectively assess the effects of dams on hydrologic processes. The Yellow River in China was impounded by the Sanmenxia and Xiaolangdi dams to meet several objectives: flood control and electricity generation, to reduce downstream sediment deposition, and to provide water for irrigation. Unfortunately, the natural flow regime has become significantly

altered in the system, with the lower Yellow River recently experiencing zero flow conditions as a result of increased water consumption (Yang et al. 2008). Significantly reduced flows will have negative effects on biodiversity and the persistence of viable wetlands and fisheries in the Yellow River Delta (Yang et al. 2008). The analysis of Yang et al. (2008) indicated that Xiaolangdi dam significantly altered the natural flow regime of the lower Yellow River in the following ways: decreased median of monthly flow, decreased medians of annual 1-, 3-, 7-, 30-, and 90-day minimum and maximum flows, higher low pulse and high pulse counts, and decreased medians of fall rate, rise rate, and number of reversals in the post-impact period.

Maingi and Marsh (2002) studied the effects of dam construction on hydrologic conditions in the Tana River, Kenya. Kenya has a growing population, and water needs have increased as populations are forced to expand into semi-arid regions (Maingi and Marsh 2002). Five dams were constructed from 1968 to 1988 along the upper Tana, the largest river in Kenya (Maingi and Marsh 2002). The largest dam (Masinga Dam) was built to provide hydropower, to increase irrigation potential in the lower basin, and to increase use of dry season flows in the upper Tana (Maingi and Marsh 2002). Of special concern is a tract of riverine tropical forest along the mid- to lower Tana River. This forest extends 0.5 to 3 km from the bank of the river, and the forest largely depends on regular flooding and sufficient groundwater. With decreased peak flows and a declining water table due to river regulation, preservation and regeneration of this riverine forest has become a challenge (Maingi and Marsh 2002). Analyses revealed that major changes in the flow regime occurred after Masinga Dam was constructed, including a significant reduction in May flows, reduced variability in monthly discharges, reduced 7-d, 30-d, and 90-d maximum annual discharges, decreased mean low pulse duration from 14.6 to 7.9 days, increased annual rises and annual falls of the river, and increased mean fall rates from 15.1 m/s to 21.6 m/s (Maingi and Marsh 2002). Experiments with vegetation sample plots indicated that vegetation located above 1.80 m of dry season river level has experienced an average 67.7% reduction in days flooded after construction of Masinga Dam. Experiments also revealed that flood pulse duration declined significantly for all vegetation plots by an average of 87.6% (Maingi and Marsh 2002). These reductions in flood frequency and duration have negative implications for the preservation of riverine forest in the Tana River Basin.

Along the Missouri River (USA), a series dams were constructed for improved navigation, irrigation, and flood control, as well as hydropower generation (Galat and Lipkin 2000). Galat and Lipkin (2000) attributed the listing of the Missouri River as North America's most endangered river in 1997 (American Rivers, 1997) to the numerous alterations that have significantly impacted the ecosystem. In their study, Galat and Lipkin (2000) divided the Missouri River into three sections and classified them as 1) an upper, least-altered section with four dams, 2) a middle highly impacted section with six large mainstem dams, and 3) a regulated and channelized lower section. The authors also used Richter's RVA approach (Richter et al. 1997) to compare pre- and post-impoundment hydrologic conditions at the upper (least-altered), middle, and lower (channelized) sections (Galat and Lipkin 2000). Their analyses indicated that numerous hydrologic changes occurred after mainstem impoundment of the Missouri River including: 1) increased mean annual discharges (i.e., 30 to 38% higher at channelized locations), 2) a stabilization of mean monthly discharges with higher flows from August through February and a reduction in June and July high flows, 3) loss of a natural

bimodal flood pulse, 4) lower flow variability at most stations, 5) higher 1-, 7-, 30-day annual minimum flows at all stations, 6) altered timing of annual peak and minimum flows (particularly at middle, inter-reservoir sites), 7) increased frequency of high pulses at two middle, inter-reservoir locations and three of four lower-basin channelized stations, 8) decreased frequency of high pulses at one middle, inter-reservoir and two channelized stations, 9) changes in mean duration of high-flow pulses, 10) decrease in the number of low-flow pulses, and 11) reduction in mean rise and fall rates. Some changes, such as stabilization of mean monthly discharges and variation in the number of high pulses, were absent or mild at least-altered locations and more pronounced at middle and channelized locations (Galat and Lipkin 2000). Pegg et al. (2003) used an alternative, time-series approach for assessing the impacts of hydrologic alteration on the Missouri River, and their findings generally corroborated those of Galat and Lipkin (2000).

Modification of the landscape, or watershed, through land-use activities has also influenced hydrologic processes and has complicated our understanding of how hydrologic alteration affects the ecological integrity of freshwater ecosystems. The ability to return to some semblance of a natural flow regime will require knowledge of how land-use (e.g., residential, industrial, agriculture, etc.) also impacts hydrologic conditions in a regulated river system (Poff et al. 1997, Poff et al. 2006). Streams and rivers are four-dimensional systems (i.e., including their temporal dimension) that are intimately linked with the groundwater and landscape, and their lateral interactions with the landscape are vital to maintaining the integrity and function of these ecosystems (Fausch et al. 2002). Stream and riverine ecosystems exchange sediments, nutrients, and energy with the landscape, and, therefore, are part of a larger "riverscape" (Fausch et al. 2002), open to and affected by external processes.

Poff et al. (2006) sought to understand how geomorphological alterations due to land-use changes interact with hydrologic alterations from dam construction to influence the hydrogeomorphic integrity of streams in the USA. The interaction between the natural flow regime and geomorphology of a stream is important in defining the habitat that is available to organisms in a system (Poff et al. 2006). Therefore, alterations of the flow and/or geomorphic properties of a system will likely induce changes in resident fauna. Poff et al. (2006) also emphasized the importance of understanding how the underlying natural variation in physiography across major regions can influence the impact of land-use changes on hydrogeomorphic processes in a stream. The authors explained that the natural topographical, geological, and climatic features of a region will influence how deforestation and agricultural activities, for example, might affect the rates of sediment and nutrient input and water flow in local streams (Poff et al. 2006). In their study, four U.S. regions, distinct in their natural vegetation, climate, geology, and physiography, were identified and examined: 1) Pacific Northwest, with Pacific Lowland Mixed Forest and Cascade Mixed Forest-Coniferous Forest-Alpine Meadow provinces, 2) Southwest, with the Colorado Semi-Arid, American Semi-desert and Desert provinces, 3) Central, consisting of the Prairie Parkland Temperate Forest, and 4) Southwest Region, consisting of South Eastern Mixed Forest (Poff et al. 2006). Within each region, areas were classified as Least Disturbed, Agriculture, or Urban, and the percent of each class was calculated (Poff et al. 2006). Poff et al. (2006) discovered numerous regional differences in hydrologic responses to flow alteration along gradients of increasing urban and

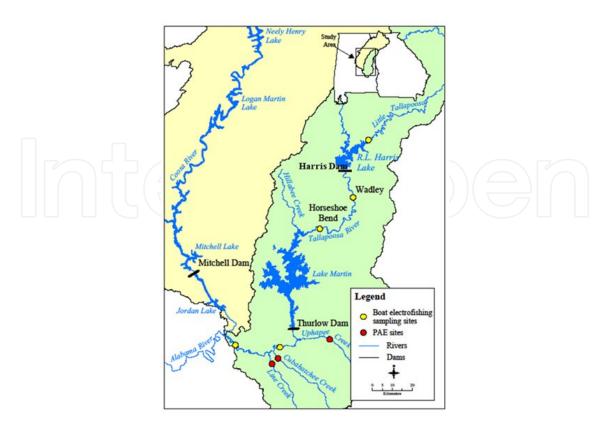


Figure 1. Hydrologic data were retrieved from USGS stream gauge stations at two regulated sites downstream of Harris Dam, Wadley and Horseshoe Bend, and at one unregulated site, Hillabee Creek (from Sakaris 2006).

agricultural land cover. For example, with increased urban cover, peak flows increased in the Southeast and Northwest regions, minimum flows increased in the Central Region and decreased in the Northwest, duration of near-bankfull flows declined in the Southeast and the Northwest, and flow variability increased in three regions (Southeast, Central, and Northwest; Poff et al. 2006). Poff et al.'s (2006) study highlighted the importance of accounting for regionally specific, landscape-level effects in the assessment of local hydrologic conditions in stream ecosystems.

3. Case study

In the Alabama River system (USA), four hydropower dams were constructed on the main stem of the Tallapoosa River (Boschung and Mayden 2004). In the Northern Piedmont, flows have rapidly fluctuated between extremely low and high flows as a result of hydropeaking operations downstream of Harris Dam on the Tallapoosa River (Irwin and Freeman 2002). Hydrologic data were retrieved from United States Geological Survey (USGS) stream gauge stations at three locations downstream of Harris Dam: 1) Wadley (USGS 02414500), a regulated site downstream of Harris Dam, 2) Horseshoe Bend (USGS 02414715), a regulated site downstream of the Wadley location, and 3) Hillabee Creek (USGS 02415000), an unregulated tributary of the Tallapoosa River (Figure 1, website: waterdata.usgs.gov/al/nwis).

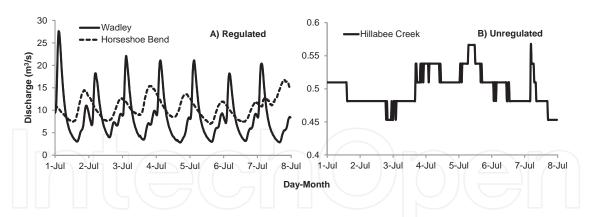


Figure 2. Daily variation in river discharge at two regulated locations (A) and at an unregulated site (B) in the Tallapoosa River Watershed.

Hourly variation in stream discharge (m^3/s) was compared among the three sites during the first week of July 2012. Ecologically relevant hydrologic variables were also calculated in the Indicators of Hydrologic Alteration Program (IHA, Sustainable Waters Program, The Nature Conservancy, Boulder, CO) for each location from water years 1987 to 2012. Water years were started on October 1 of each year and ended on September 30 of the following year (e.g., water year 1987 = 10/01/86 - 9/30/87). Analyses focused on annual high and low pulse frequencies, number of reversals, and rise rates. Annual hydrologic conditions were compared between the two regulated sites and the unregulated site, which was treated as a "reference site."

Hydrologic regimes were markedly different between the regulated locations and the unregulated site (Figure 2). In early July, daily hydropeaking operations produced unnatural flow variation below Harris Dam, while a more natural flow regime persisted in the local unregulated tributary (Figure 2). Daily variation in discharge was substantially dampened at the Horseshoe Bend site (Figure 2), which is located farther downstream of Harris Dam (Figure 1). This reduced variation in flow indicated that the effects of hydropeaking operations may not be as severe at more downstream locations. However, unnatural and rapidly fluctuating flows, such as those observed below Harris Dam, generally produce a stressful environment for the river fauna that reside there.

As expected, high pulse and low pulse frequencies, the number of reversals, and rise rates were similar between the two regulated sites, as well as the overall annual variation in these hydrologic parameters (Figure 3). All four hydrologic parameters were substantially lower at the unregulated site (Figure 3). Fewer high pulses, low pulses, and reversals at Hillabee Creek indicated that the flow regime was much less variable and may be more representative of natural flow conditions in this region. Higher rise rates at the regulated sites are likely due, in part, to the rapidly increasing flows during hydropeaking events.

4. Hydrologic effects on recruitment, growth, survival

Altered flow regimes below dams have typically produced unfavorable conditions for the recruitment of fishes (Fraley et al. 1986; Brouder 2001, Freeman et al. 2001, Wildhaber et al.

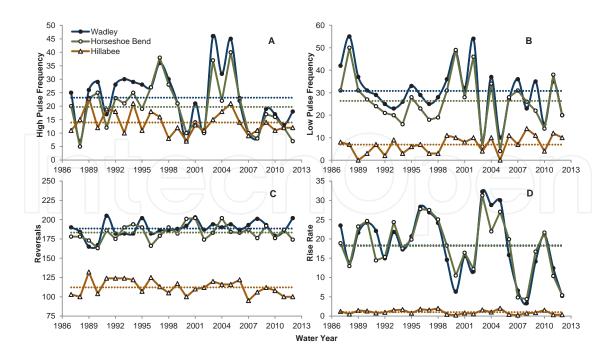


Figure 3. Annual variation in high pulse frequencies (A), low pulse frequencies (B), number of reversals (C), and rise rates (D) at two regulated locations and at an unregulated site in the Tallapoosa River Watershed. Dotted lines represent the statistical mean for each location. Mean rise rate was nearly equal at the two regulated sites.

2000, Propst and Gido 2004). Freeman et al. (2001) reported that juvenile fish abundances were strongly related to the persistence of shallow habitats in a regulated reach of the Tallapoosa River, Alabama. However, the persistence of these habitats was severely reduced by rapid flow fluctuations resulting from hydropeaking operations (Freeman et al. 2001). In a regulated section of the Neosho River (Kansas), the reduction of minimum flows below John Redmond Dam reduced the availability of riffle habitats that were suitable for Neosho madtoms (*Noturus placidus*, Wildhaber et al. 2000). Moreover, hypolimnial-release of coldwater from dams will generally slow growth and development and alter physiology of fish during early life stages; whereas, the release of warm water from small, surface release dams may result in reduced densities of coldwater fish species (Clarkson and Childs 2000, Lessard and Hayes 2003).

Recruitment of fishes has been related to hydrology in freshwater ecosystems; however, most studies have been conducted in reservoirs (see, for example: Maceina and Stimpert 1998, Buynak et al. 1999, Sammons and Bettoli 2000, Schultz et al. 2002). Few studies have directly examined relations between hydrology and recruitment of fishes in regulated river sections. In a regulated section of the Roanoke River (North Carolina), Rulifson and Manooch (1990) reported that striped bass *Morone saxatilis* recruitment was highest when river flows were low to moderate (142 – 283 m³/s) during the spawning season. During the years when recruitment was highest, *flows typically resembled pre-impoundment flow conditions* (Rulifson and Manooch 1990). Striped bass require a specific flow regime for successful transport of eggs and larvae to nursery habitats (Rulifson and Manooch 1990). Irwin et al. (1999) reported that riffle habitats (i.e., shallow-fast and shallow coarse) were utilized by juvenile channel catfish *Ictalurus punctatus* and flathead catfish *Pylodictis olivaris*. However, persistence of these habitats may

decrease in highly regulated systems (Bowen at al. 1998), thereby negatively influencing the recruitment of catfishes. Furthermore, Holland-Bartels and Duval (1988) suggested that variation in channel catfish productivity was related to river discharges. A decrease in age-0 channel catfish abundance was attributed to a sharp increase in river discharge that likely disrupted spawning activity and flushed young from nests (Holland-Bartels and Duval 1988). Therefore, one would suspect that highly variable flows (i.e., high rise and fall rates) during hydropeaking operations would negatively affect the spawning success and recruitment of channel catfish. In middle reaches of the regulated Missouri River, Pegg et al. (2003) identified a significant reduction in spring spawning flows as a major impairment of fish spawning and recruitment.

Studies have indicated that reduced flooding, or a diminished flood pulse, has contributed to low fish recruitment in river systems. Bonvechio and Allen (2005) studied recruitment of sunfishes Lepomis spp. and black basses Micropterus spp. in relation to hydrology in four Florida rivers. The authors suggested that high flows in the fall would increase access to floodplain habitats, thereby increasing prey availability (i.e., invertebrates) for adult sunfishes before the spawning season (Bonvechio and Allen 2005). Sunfishes would likely consume more prey and allocate more energy towards reproduction (i.e., fecundity), producing a stronger year class. In the inter-reservoir and lower channelized sections of the Missouri River, changes in the magnitude, frequency, timing, and duration of the annual flood pulse (i.e., inundation of the floodplain) was indicated as the likely cause of reduced recruitment and production of floodplain fishes (Galat and Lipkin 2000). The elimination of a fall flood pulse in the lower Missouri River has limited fish and wildlife access to floodplain habitats (Galat and Lipkin 2000). Brouder (2001) found a strong positive relationship between maximum mean daily discharge and recruitment of the roundtail chub, Gila robusta, in the upper Verde River, Arizona. Brouder (2001) explained that a reduction or elimination of flooding through hydrologic alteration would be deleterious to the recruitment of native roundtail chub. Flooding helps to prepare spawning substrate by clearing interstitial spaces for eggs, potentially reduces population sizes of nonnative species (thereby reducing competition), and possibly dilutes contaminants that would negatively affect reproductive success (Brouder 2001).

Alteration of the thermal regime as a consequence of dam construction can also have negative effects on fish recruitment (Clarkson and Childs 2000, Horne et al. 2004). Hydroelectric dams on the Manistee River, a tributary of Lake Michigan, negatively impact steelhead (anadromous rainbow trout, *Oncoryhnchus mykiss*) recruitment, by preventing steelhead access to potential upstream spawning habitats (Horne et al. 2004). Furthermore, the release of warm surface water from the reservoir results in increased summer temperatures that reduce the survival of age-0 steelhead in the river (Horne et al. 2004). Clarkson and Childs (2000) proposed that declines of native big-river fishes of the Colorado River Basin were partly due to the release of cold, hypolimnial water from dams. In laboratory experiments, growth rates of four species (razorback sucker, flannelmouth sucker, humpback chub, and Colorado squawfish) were slower and their development was delayed at colder temperatures (Clarkson and Childs 2000). Larval fish also lost equilibrium when transferred from 20°C to 10°C (Clarkson and Childs 2000). Slow growth, delayed development, and loss of equilibrium at early life history stages all likely contribute to reduced recruitment in a system.

Growth of fishes may also be related to hydrology in river systems. Quist and Guy (1998) suggested that increased growth of channel catfish in the Kansas River (USA) resulted from floodplain inundation. Inundation of the floodplain typically provides shallower, prey-rich habitats for fishes (Welcomme 1979). Mayo and Schramm (1999) hypothesized that growth of flathead catfish was also influenced by water temperature during the growing season, in addition to the number of flood days in the lower Mississippi River system. Unfortunately, hydrologic alterations may include changes to the timing and duration of floodplain inundation as well as thermal regimes (Cushman 1985, Pringle 2000). Rutherford et al. (1995) determined that growth of age-0 channel catfish in the Mississippi River was also related to the length of the growing season, which could theoretically be shortened with the release of cold, hypolimnetic water from a dam. Coldwater from hypolimnial-release dams may dramatically lower spring and summer tailwater temperatures, which may slow the growth and development of fishes (Clarkson and Childs 2000).

Hydrologic alteration has also strongly impacted the growth and recruitment of riparian and wetland vegetation (Young et al. 1995, Burke et al. 2008). For example, the recruitment of cottonwoods (*Populus* spp.) is closely linked to hydrologic and geomorphic processes (Scott et al. 1997, Burke et al. 2008). Burke et al. (2008) applied a hierarchical approach to studying the impacts of dam operations on the Kootenai River Ecosystem, focusing on cottonwood recruitment as their ecological response to river regulation. This hierarchical approach assessed *first order* impacts (changes in hydrologic conditions) that led to *second order* impacts, such as altered sediment transport and channel morphology (Burke et al. 2008). Burke et al. (2008) then described *third-level* impacts as biological functions that are influenced by first and second-level impacts. *Fourth-level* impacts are those involving feedbacks between biological and physical conditions (Burke et al. 2008). Overall, this hierarchical approach studied the effects of hydrologic alteration at the ecosystem level, assessing the physical, chemical, and biological changes that occur in a system.

The Kootenai River system, located in parts of Idaho, Montana, and British Columbia, has been modified in various ways. Levees were constructed in lower floodplain sections of the river to convert floodplain for agriculture, and Corral Linn Dam was constructed in the 1930s for hydropower and flood control (Burke et al. 2008). In 1974, Libby Dam was constructed upstream of Corral Linn Dam to provide additional hydropower and flood control, impounding 145 km of the river upstream of Libby Dam (Burke et al. 2008). As a result, natural flow conditions were altered and inundation of the floodplain was limited in the system (Burke et al. 2008). Specifically, higher flows are now maintained during naturally low-flow periods (fall-winter), while much lower flows are maintained during naturally high-flow periods (spring-summer; Burke et al. 2008). Burke et al. (2008) analyzed three time periods in their study: 1) historic, before Corral Linn Dam was operational, 2) pre-Libby Dam, and 3) post-Libby Dam. First, second, and third-order impacts as a result of dam construction and other activities were examined in a 233-km study reach between Libby Dam and the downstream Corral Linn Dam. To examine first-order impacts, Burke et al. (2008) utilized Indicators of Hydrologic Alteration (IHA) software (Richter et al. 1996) to compare hydrologic regimes across the time periods. The authors used a one-dimensional hydrodynamic flow model to evaluate secondorder changes in hydraulics and bed mobility. Third-order impacts were assessed by changes in the recruitment potential of black cottonwoods. Due to the significant reduction of naturally high flows during the spring snowmelt, cottonwood seed germination sites are no longer prepared through the mobilization and redistribution of sediments. In addition, germination sites no longer experience the slow and gradual recession of these natural spring flows that would help maintain adequate soil moisture for the establishment of seedling roots (Burke et al. 2008). Burke et al.'s (2008) analyses revealed major changes in the hydrologic regime below Libby Dam, which included significantly greater median monthly flows during winter and the near elimination of a spring snowmelt peak (i.e., an "inverted annual hydrograph"). Notable second order, temporal and spatial alterations were also detected in stage fluctuation, stream power, shear stress, and bed mobility. The authors determined that the activities of both dams have contributed to lower cottonwood recruitment, by increasing stage recession rates during the seedling establishment period in the lower study reach and changing the timing, magnitude, and duration of flow in the upper and middle sections of the study reach (Burke et al. 2008).

Young et al. (1995) conducted a study examining how the growth of the Baldcypress, a tree common to wetlands in the southeastern United States, may respond to an altered flow regime. This tree is often found in wetlands or swamps that are subject to frequent or permanent flooding (Young et al. 1995). Before their study site was impounded by road construction in 1973, it existed as a floodplain swamp with permanent shallow flooding. The impoundment resulted in increased water levels on the upstream side of the road and apparently no effects on water levels on the downstream side (Young et al. 1995). Young et al. (1995) discovered that trees at the impacted, upstream site initially exhibited a significant growth surge due to increased flooding, but an overall decline in growth followed for 16 years. The initial surge in growth was possibly due to a pulse of sediment nutrient deposition with flooding, while the later decline in growth may have been a result of increased anoxic conditions in the rooting zone (Young et al. 1995).

The recruitment and survival of native riparian vegetation may not only depend on the restoration of more natural flow conditions, but also the removal of invasive riparian species that have better success in altered flow conditions (Merritt and Poff 2010). In western North America, the cottonwood, *Populus deltoides*, has declined substantially, while the invasive saltcedar, *Tamarix*, has become well established (Merritt and Poff 2010). Merritt and Poff (2010) determined that recruitment potential of *Tamarix* was highest along unregulated reaches in the Southwestern United States, *but remained high across a gradient of regulated flows*. In contrast, recruitment of cottonwoods was highest under natural flow conditions and declined abruptly with even slight flow modification (Merrit and Poff 2010). In addition, *Tamarix* was most dominant along the most altered river reaches, whereas *Tamarix* and *Populus* were equally dominant at the least regulated sites. The authors concluded that altered flow regimes have further enhanced the dominance of *Tamarix* over native plant species (Merritt and Poff 2010).

River regulation can also affect the reproductive success of marine fishes and invertebrates (Drinkwater and Frank 1994). For example, the recruitment of marine fish and invertebrates

appears to be highly correlated with freshwater input (Drinkwater and Frank 1994). In most cases, increased river runoff into coastal oceans positively influences fish and invertebrate production, by increasing nutrient inputs that enhance primary production (Drinkwater and Frank 1994). The impoundment of rivers by dams, the diversion of water for agricultural purposes (irrigation), and regulated release of water from dams can modify the amount and/or timing of freshwater released to coastal estuaries. See Drinkwater and Frank (1994) for a thorough review of the effects of river regulation on marine fish and invertebrates.

5. Hydrologic effects on community structure and biodiversity

The effects of hydrologic alteration on community structure of aquatic organisms have been well documented (Dudgeon 2000, Pringle et al. 2000, Marchetti and Moyle 2001, Humphries et al. 2008). Marchetti and Moyle (2001) reported that most native fish species of the regulated Putah Creek, a tributary of the Sacramento River, were more often found in habitats that were characteristic of the natural flow regime (i.e., increased canopy, higher streamflow, decreased conductivity, cooler temperatures, and fewer pools). In contrast, most nonnative species appeared to be adapted to conditions opposite to those of the natural flow regime (Marchetti and Moyle 2001). Therefore, restoration of a native-dominated fish assemblage would require a return to natural flow conditions. In the regulated Campaspe River (Australia), only four of ten native species were consistently documented from 1995 to 2003, while historically an estimated 18 to 20 native fishes once inhabited the river (Humphries et al. 2008). The authors also documented the presence of six exotic fishes, with common carp and European perch being the most abundant fishes (i.e., 36% of the overall fish abundance, Humphries et al. 2008).

Dam construction and river regulation has threatened aquatic and terrestrial biodiversity worldwide (Dudgeon 2000, Pringle et al. 2000). Pringle et al. (2000) provided a thorough review of the effects of hydrologic alterations on riverine biota in temperate and neotropical regions. The authors explain that, although construction of new dams in the United States has declined, large dam construction has occurred more recently in tropical regions of South America (Pringle et al. 2000). In temperate regions, migratory diadromous fishes, such as salmon, sturgeon, American shad, and American eel, have been extirpated from much of their native ranges due to dams that block their spawning migrations (Drinkwater and Frank 1994, Pringle 2000). Movements of potamodromous fishes have also been impeded, restricting their reproductive success and overall distributions (Pringle et al. 2000). Habitat fragmentation and the conversion of lotic, free-flowing habitat to more lentic conditions, in the form of impoundments, reservoirs, etc., have resulted in the imperilment of small-bodied fishes, particularly fluvial-dependent species (Pringle et al. 2000). This increase in availability of lentic habitat has also allowed for the expansion of lentic fishes and the introduction of lentic fishes into systems beyond their native range (Pringle et al. 2000). As mentioned in the previous section, Pringle (2000) also identified a reduction or alteration in the timing and/or duration of floodplain inundation as a major factor contributing to the decline of flood-dependent taxa. Reduced freshwater flows into estuarine habitats have also threatened species, such as the delta smelt in San Francisco Bay, California (Pringle et al. 2000). In Pringle et al.'s (2000) case study of the Mobile River Basin in the southeast USA, the authors report from the literature that at least 16 endemic mussels and 38 gastropods are thought to be extinct.

Although the negative impacts of hydrologic alterations on biota are well documented in North America, less is known about the effects of river regulation on South American tropical systems (Pringle et al. 2000). Pringle et al. (2000) explained that biota of Neotropical rivers are highly vulnerable to hydrologic alterations for several reasons. The habitat heterogeneity of tropical ecosystems has produced highly diverse communities with high rates of endemism. Many South American fishes are highly migratory and have complex life cycles and depend on seasonal floodplain inundation that provides food, refuge, and nursery habitat for young fishes. The accumulation of organic material in reservoirs of low-gradient Amazonian streams has led to undesirable water quality conditions (e.g., hypoxia) that can result in fish kills. Reduced freshwater input to estuaries has also led to an increased presence of marine fishes in lower sections of rivers, replacing native freshwater species (Pringle et al. 2000). Agostinho et al. (2008) provided a more recent, extensive review of the effects of dams on fish fauna in the Neotropical Region. The authors focused on the highly regulated Paraná River, which flows through the most highly populated region in Brazil. Data are presented illustrating the negative impacts of dams on fish diversity and fisheries in the region. Agostinho et al. (2008) expressed the need for improved management approaches in Brazil, such as taking a more ecosystem-level rather than reductionist approach. The authors also mention that little information exists regarding the effects of hydrologic alteration (dams), fishery exploitation, and other impacts on aquatic resources in Brazil. These data needs must be addressed so that managers can formulate and inform effective management decisions (Agostinho et al. 2008).

Asia possesses a proportionately high number of dams, with the number of large dams increasing from 1,541 in 1950 to a staggering 22,701 in 1982 (Dudgeon 2000). China has constructed the greatest number of dams in tropical Asia (Dudgeon 2000). The climate of this region alternates between a wet and dry season, with many organisms depending on the wet season and the associated flood pulse for sustenance and access to floodplain habitats (Dudgeon 2000). Dam construction, however, has focused on flood control during wet periods and storing water during dry periods, resulting in significantly altered hydrologic regimes in most major rivers (Dudgeon 2000). Dudgeon (2000) also mentions that other factors, such as pollution, deforestation, overharvesting and rapidly growing human populations in the landscape, have further exacerbated conditions in these systems. Hydrologic alteration has negatively impacted a wide diversity of taxa in this region, including crocodiles, terrestrial mammals, fishes, and river dolphins (Dudgeon 2000). The Mekong River Basin supports a high diversity of over 500 fishes. Unfortunately, the construction of large dams on the Mekong River has threatened the persistence of many species (Dudgeon 2000). See Dudgeon (2000) for a thorough overview of the ecological consequences of large dam construction on the Mekong River.

Negative impacts of hydrologic alteration are not only limited to aquatic organisms. Riverine forest along the regulated Tana River in Kenya serves as habitat for two endemic primates, the rare Tana River Red Colobus and the critically endangered Tana River Mangabey (Maingi and Marsh 2002). Regulation of the Tana River threatens the persistence of riverine forest along mid and lower sections of Tana River and, therefore, further endangers these rare primates

(Maingi and Marsh 2002). Hill et al. (1998) examined the effects of dams on the shoreline vegetation of lakes and reservoirs in southern Nova Scotia, Canada. Hill et al.'s (1998) study included 37 unregulated and 13 regulated lakes, for which plant species inventories were conducted. Plant communities of regulated lakes were less diverse, contained more exotic species, and typically lacked rare shoreline herbs. The authors attributed this reduction in diversity and introduction of nonnative species to the altered hydrologic regimes of reservoirs that produce extreme fluctuations in water levels.

A significant reduction in hydrologic connectivity, as a result of dam construction and other anthropogenic activities in the landscape, has also threatened aquatic biodiversity in riverine systems (Pringle 2003). Hydrologic connectivity refers to "the water-mediated transfer of matter, energy, and/or organisms within or between elements of the hydrologic cycle (Pringle 2001, Pringle 2003)." Pringle's (2001, 2003) definition of hydrologic connectivity emphasizes its importance at a regional or global scale, whereas river connectivity refers to the continuity or linkages of a river ecosystem as it operates across its four dimensions (i.e., temporal, and longitudinal, lateral, and vertical spatial dimensions, Freeman et al. 2007). Dam construction (i.e., reduced hydrologic connectivity) has impeded the spawning migrations of anadromous fishes, preventing these fishes from returning to their natal sites. Substantial reductions in the distribution and abundance of freshwater mussel species have been attributed to reduced habitat connectivity. Fragmentation of habitats isolates local populations from others, limiting or eliminating the exchange of individuals and the potential for recolonization of habitat patches when a local extinction occurs. Reduced hydrologic connectivity also has negative impacts on broader-scale functions, such as biogeochemical cycling in ecosystems (Pringle 2003). For example, dams act as barriers to the transport of silica to coastal oceans, limiting primary production (i.e., diatom production) and the integrity of coastal food webs (Pringle 2003, Freeman et al. 2007).

6. Flow management and modeling

In 1997, Poff et al. succinctly explained that "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." Although in today's society returning riverine systems to their "natural dynamic character" is nearly impossible, the authors indicated that conservation and management strategies should attempt to restore the ecological integrity of these regulated systems by enhancing their "natural" flow variability (Poff et al 1997). Although regulated rivers can never be fully restored to natural conditions, flows below dams should be managed to best represent natural flow conditions (Poff et al. 1997). Previous management strategies focused on improving water quality and simply implementing minimum flow requirements (Poff et al. 1997, Richter et al. 1997, Arthington et al. 2006). Richter et al. (1996) also mentioned that past management strategies focused on the flow requirements of only a few selected aquatic species and neglected the flows needed to maintain aquatic-riparian systems and broader ecosystem functions. Management of freshwater resources was also conducted in a compartmentalized or "fragmented" fashion (Poff et al.

1997, Karr 1991). Management approaches today have evolved to incorporate the prescription and implementation of natural aspects of the flow regime. In addition, a more concerted effort is applied to coordinate management activities among various resource agencies. Furthermore, current strategies attempt to apply a more holistic, ecosystem-level (rather than reductionist) approach to the management of regulated rivers and conservation of freshwater resources.

Various techniques and modeling approaches have been developed to enhance our understanding of how hydrologic alteration affects aquatic ecosystems, as well as improve our management of regulated rivers (Richter et al. 1996, Richter et al. 1997, Irwin and Freeman 2002, Olden and Poff 2003, Arthington et al. 2006, Poff et al. 2009, Merrit and Poff 2010, Sakaris and Irwin 2010). Richter et al. (1996) emphasized the importance of selecting hydrologic parameters that are most "biologically relevant" when assessing hydrologic alteration in a regulated system. In other words, we should focus on the parameters that most influence the ecological integrity of a system. Richter et al. (1996) presented a well-structured approach for hydrologic assessment, Indicators of Hydrologic Alteration (IHA), which accounts for the most biologically relevant parameters. This approach defines and calculates a series of hydrologic attributes and then compares the hydrologic regime of a system before and after impact (e.g., impoundment). A total of 32 biologically relevant hydrologic parameters are calculated for each year from these five IHA statistics groups: 1) magnitude of monthly water conditions, 2) magnitude and duration of annual extreme water conditions, 3) timing of annual extreme water conditions, 4) frequency and duration of high and low pulses, and 5) rate and frequency of water condition changes (Richter et al. 1996). These parameters account for the five important and ecologically relevant characteristics of a flow regime: magnitude, frequency, duration, timing, and the rate of change (Poff et al. 1997). The four steps of Richter et al.'s (1996) approach are: 1) define the data series for pre- and post-impact periods (usually collected from USGS flow gauges), 2) calculate values of hydrologic attributes for each year in each data series (i.e., pre-impact and post-impact data series), 3) compute inter-annual statistics for the 32 parameters in each data series, specifically 32 measures of central tendency and 32 measures of dispersion, and 4) calculate values of the IHA. The fourth step involves comparing the 64 interannual statistics between pre- and post-impact periods, as a percent deviation of one time period to the other (Richter et al. 1996). The IHA approach can also be used to compare hydrologic regimes between regulated and "reference" sites.

Richter et al. (1997) further improved the approach to river management with the development of the "Range of Variability Approach (RVA)." Richter et al. (1997) mention that previous approaches did not provide specific flow targets to be met, focused on a limited number of features of the hydrologic regime, and/or focused on only a few target species and a limited number of their habitat requirements. In addition, research studies examining relationships between hydrologic conditions and ecological responses in a system are typically time-consuming (often taking several years) and are usually not completed within the timeframe during which flow management decisions are typically made (Richter et al. 1997). Richter et al.'s (1997) RVA assists river managers in the identification of flow-based management targets that should enhance the overall ecological integrity of a system. For systems with highly altered hydrologic regimes, the main idea is to restore hydrologic conditions within the historical or "natural" range of variation, particularly for streamflow characteristics that are well outside the historical range

(Richter et al. 1997). Richter et al. (1997) recommended that the RVA be applied in the preliminary stages of adaptive flow management programs (see below), providing initial flow management targets that can be modified as more ecological information is gathered for a specific ecosystem. The RVA approach has six steps, which are briefly described here. For a more in-depth overview, see Richter et al. (1997). The six steps are as follows: 1) Characterize the natural range of streamflow variation using the IHA approach (Richter et al. 1996) described above. 2) Select management targets, one for each of the 32 hydrologic parameters, with the idea that each management target should fall within the natural range of variation. Each target may have upper and lower bounds (e.g., ± 1 standard deviation). 3) The river management team formulates a management "system" or plan, using the RVA targets as design guidelines. 4) Scientists conduct routine ecological monitoring and/or river research program to evaluate ecological effects of the management system as it is implemented. 5) Characterize actual streamflow variation using the IHA method at the end of each year and compare the values of hydrologic parameters with the RVA target values. 6) Revise either the management system or RVA targets based on new information that is collected (Richter et al. 1997).

An adaptive approach, termed adaptive-flow management, has been recommended for the management of regulated river systems (Irwin and Freeman 2002). In adaptive-flow management, managers attempt to restore rivers to near-natural flow regimes while accounting for societal needs (Irwin and Freeman 2002). The main goal of adaptive-flow management is to continually improve management as uncertainty about a river system is reduced. This management approach requires the cooperation and long-term commitment of natural resource personnel, private industry, landowners, and other stakeholders. Adaptive-flow management can be best described as an iterative process with a series of steps that include 1) prescription of a flow/management regime that satisfies all stakeholders, 2) monitoring and evaluation of the flow regime's effect on habitat and biota, and 3) the recommendation of a new and improved management regime. By quantifying relationships between features of the flow regime and responses in the biota and overall ecosystem, models can be developed to predict how populations, communities or the ecosystem may respond to the prescription of flow regimes, or an "environmental flow standard (Arthington et al. 2006)." These models can be continually improved as more is learned about the ecological responses to hydrologic alteration in the managed river system.

Olden and Poff (2003) addressed a major issue confronting managers in determining which of the many published approaches and hydrologic (and "ecologically relevant") parameters should be used in river management. The authors recognized that many of the hydrologic variables proposed for use in the characterization of a flow regime (e.g., 32 hydrologic parameters, Richter et al. 1996) were inter-correlated, and little guidance was provided for the selection of appropriate parameters. Olden and Poff's (2003) main goal was to provide a standardized framework for the selection of a reduced set of hydrologic indices and to minimize redundancy among the selected parameters. This reduced set of indices would still account for the majority of the statistical variation in the complete set of hydrologic indices, minimize multicollinearity among the selected hydrologic variables, and adequately represent the critical attributes of a system's flow regime. The authors also examined the effectiveness of IHA and the overall transferability of indices to facilitate comparisons across systems that

differ in their streamflow characteristics (Olden and Poff 2003). See Olden and Poff (2003) for a detailed overview of the approach and a review of the 171 hydrologic indices published in the literature.

In 2006, Arthington et al. proposed a mechanism for developing regional environmental flow "standards." Their rationale was that hydrologic and ecological data are often lacking for specific streams or rivers in a region, which makes it quite difficult to prescribe system-specific flow regimes in the management of regulated rivers. Arthington et al. (2006) recommended classifying rivers and streams that share important flow attributes into "ecologically meaningful groups." Within a region, the logical assumption is that rivers that are similar in their flow variability and geomorphic properties would exhibit similar ecological responses to management regimes. Arthington et al. (2006) described their approach as grouping the systems into "practical management units." See Arthington et al. (2006) for a complete overview of their management approach, which shares common features with the ELOHA approach described below.

Poff et al. (2010) explained that a strong need exists to develop ecological goals and management standards for streams and rivers at a regional or even global scale. Water resource and environmental flow management has become highly complex, because management must account for diverse societal needs while attempting to restore the ecological integrity of degraded ecosystems. Meanwhile, rapidly growing human populations will further increase water consumption and energy demands and require increased food production. As a result, restoring systems with highly altered flow regimes to "natural" flow conditions will become even more difficult. The authors, consisting of a group of international scientists, presented a framework for evaluating environmental flow needs that could potentially form the basis for implementing flow standards at a regional scale (Poff et al. 2009). Poff et al. (2009) refer to this framework as the Ecological limits of hydrologic alteration (ELOHA), with the goal of presenting "a logical approach that flexibly allows scientists, water resource managers and other stakeholders to analyze and synthesize available scientific information into coherent, ecologically based and socially acceptable goals and standards for management of environmental flows." Poff et al. (2010) recognize that water resource managers from different regions are often confronted with unique challenges, may operate in different social and political environments, and may be at different stages of water-resource development. The necessary scientific foundations of the ELOHA framework exist and consist of: 1) essentially years of research has been conducted examining the effects of altered hydrologic regimes on population dynamics, community structure, and ecosystemlevel functions, 2) the previous application of various methods for managing environment flows, which the authors refer to as a "rich toolbox" from which methods or tools can be applied by water resource managers, 3) a conceptual foundation that facilitates regional flow assessments, 4) the development of hydrologic models, and 5) an understanding that river management is complex and adaptive and must meet both ecological and societal goals (Poff et al. 2010).

The ELOHA framework consists of four major steps that can be flexibly applied by managers from different regions (Poff et al. 2009). 1) *Building a "hydrologic foundation" for the region* involves collecting hydrologic time-series data and constructing hydrographs that represent "baseline" (minimally altered) and "developed" (altered) hydrologic conditions throughout

the region, particularly for all locations that require environmental flow management and protection. 2) Classifying rivers according to their hydrology and geomorphology assumes that rivers with similar hydrologic regimes (e.g., snowmelt driven rivers) and geomorphic characteristics would likely respond similarly to hydrologic alteration and other disturbances, whereas rivers that are dissimilar in type (e.g., snowmelt vs. desert rivers) would likely respond differently when altered. When classifying rivers based on their hydrologic regimes, chosen hydrologic features should collectively characterize the flow regime of the system and avoid redundancy in the parameters used (Olden and Poff 2003). The selected hydrologic metrics should also be ecologically relevant and be applicable in management. River classification is important, because flow management decisions will likely vary based on river type. Furthermore, if the "hydrologic foundation" is not fully built for a region, the hydrologic models and management targets developed for one river may be extrapolated to similar systems until more systemspecific data are collected. 3) Computing flow alteration involves estimation of the degree of hydrologic alteration for each system, for which hydrologic data are available. Any deviation in the hydrologic regime from "natural" (baseline) conditions may have an ecological impact, and this ecological impact generally becomes more severe as the disparity between developed and baseline conditions widens. Programs, such as IHA (Richter et al. 1996; Mathews and Richter 2007), can be used to calculate a set of hydrologic alteration values as a percent or absolute deviation from baseline condition for each developed site. 4) Conducting research and monitoring programs to assess ecological responses to altered hydrologic regimes addresses the critical need for improved understanding of biotic and ecosystem responses to flow alteration in the ELOHA framework. Flow alteration-ecological response relationships guide river managers in establishing flow management targets, or "standards," and in developing flow management plans that will most likely enhance the ecological integrity of an altered system. It is important to note that the ELOHA approach is an adaptive process. Scientists play an important role in this process, by conducting research programs that attempt to reduce uncertainty and build our understanding of ecological responses to hydrologic alteration. With new information, management flow standards can be updated and implemented over time. See Poff et al. (2010) for a detailed overview of the application of ELOHA, the various models and tools that can be used in each step of the process, and the potential challenges that may confront river managers and scientists that adopt this approach.

The ELOHA framework (Poff et al. 2010) requires the assessment of "ecologically significant" differences between baseline and developed hydrologic regimes in a region. Merritt and Poff (2010) recently developed an *index of flow modification* (IFM), which is a composite metric of the most biologically relevant hydrologic variables that essentially measures how modified an altered flow regime is compared to unregulated (or baseline) conditions. Pre-dam and post-dam flow data are collected for each location (or study reach), typically from USGS (United States Geological Survey) gauges. Biologically relevant hydrologic variables are then obtained for pre-dam and post-dam periods using IHA (Indicators of Hydrologic Alteration) software (Richter et al. 1996), and then the absolute or percent change in each variable is calculated from pre-dam to post-dam periods. In their study, Merritt and Poff (2010) calculated the percentage change in spring flow (mean of April through June), summer flow (mean of July through September), low flow (mean of October through February flows), and 2-, 10-, and 25-year

recurrence interval peak flows. The change in the number of days of minimum flow and the change in maximum flow were also calculated (Merrit and Poff 2010). Principle Components Analysis (PCA) is then conducted using these calculated metrics (i.e., hydrologic metrics) of all study sites, and only significant principle component axes are used in the calculation of IFM. Merrit and Poff (2010) developed the IFM "by calculating the Euclidean distance of each observation (study reach) from the centroid of the significant PCA axis scores of relatively unregulated rivers for the hydrologic metrics." The IFM can then be used, for example, to examine relationships between the recruitment, abundance, and/or growth of organisms and the degree of flow modification (IFM) across sites ranging from relatively unregulated to regulated conditions.

Population matrix models have also been developed by scientists to evaluate and predict how riparian and aquatic populations respond to hydrologic variation in systems with altered flow regimes (Lytle and Merritt 2004, Sakaris and Irwin 2010). These models may be useful in step 4 of the ELOHA approach. Lytle and Merritt (2004) developed a stochastic, density-dependent model to predict how annual hydrologic variation affects the mortality, recruitment, and population dynamics of the riparian cottonwood and to project how altered flow regimes might affect cottonwood populations. Lytle and Merritt (2004) simulated the effects of channelization and damming in the Yampa River, Colorado, and their model suggested that the observed natural flow regime would likely produce the most abundant mature cottonwood forest. Sakaris and Irwin (2010) developed matrix models for predicting the effects of altered flow regimes on the dynamics of a flathead catfish population in a regulated section of the lower Coosa River, Alabama. Matrix construction required the collection of fertility, survival, and body growth data (for size-classified matrices) for the fish population. The authors conducted multiple regression analyses to assess the influence of hydrologic features of the altered flow regime on annual recruitment of the flathead catfish in the system. Using this information, the effects of environmental stochasticity (hydrologic variation) on the long-term growth dynamics of the catfish populations was projected. Sakaris and Irwin (2010) also used their model to predict the effects of prescribed flow regimes on fish population dynamics in the river. Sakaris and Irwin (2010) presented their model as a potential tool that could be used in the adaptive flow management of regulated rivers (e.g., below Harris Dam on the Tallapoosa River, Alabama, Irwin and Freeman 2002).

Arthington et al. (2006) mentioned that general agreement exists among scientists and most river managers that to maintain the ecological integrity and biodiversity of a system, we must attempt to restore, or "mimic," natural flow conditions. That is, all general features of the natural flow regime (magnitude, frequency, duration, timing, and the rate of change, Poff et al. 1997), to some degree, should be accounted for when prescribing a flow-management regime in a regulated system. As mentioned earlier, previous management strategies typically focused on implementing a single environmental flow standard, such as maintaining a minimum flow requirement below a dam. For example, on the Tallapoosa River in the East Gulf Coastal Plain in Alabama (USA), a minimum continuous flow (34 m³/s) was established below Thurlow Dam as part of a re-licensing agreement in 1991. Although diversity of fishes increased approximately 3 km downstream of the dam (Travnichek et al. 1995), Thurlow Dam has still exhibited high annual variability in discharge that often exceeds dam capacity, which

has typically resulted in prolonged periods of high flow (> 283 m³/s). Wildhaber et al. (2000) evaluated relations between Neosho madtom densities and flows in the Neosho River Basin below John Redmond Dam and suggested that higher minimum flows be prescribed in the river to improve densities of Neosho madtoms and other ictalurids. Studies have evolved since to prescribe or, at least, model flow regimes that are more natural in character. For example, Propst and Gido (2004) attempted to partially mimic the natural flow regime in a regulated reach of the San Juan River (Colorado), by increasing reservoir releases to mimic timing and only partially mimicking the amplitude, volume, and duration of spring snowmelt discharge. Densities of native fishes typically increased in years with high spring discharges (Propst and Gido 2004). Horne et al. (2004) modeled the effects of two management scenarios, bottom withdrawal and actual dam removal, on the recruitment of steelhead in the Manistee River. The authors' models predicted that bottom withdrawal (of hypolimnetic water) would slightly cool summer water temperatures and modestly enhance steelhead recruitment in the river (Horne et al. 2004). Horne et al. (2004) mention, however, that their model for dam removal did not account for the added benefit of increased steelhead access to upstream spawning habitat, which would likely improve recruitment in the system. In the lower Kootenai River, Burke et al. (2008) discovered that recruitment potential of the back cottonwood improved in 1997 and 1999, partly due to experimental flow releases from Libby Dam. These water releases helped to mimic pre-dam hydrologic conditions during the spring snowmelt, with a sustained peak in flow during the early growing season and a subsequent gradual recession of flow (Burke et al. 2008). These experimental flow releases have been implemented since 1993 to enhance the spawning success of white sturgeon (Burke et al. 2008).

River management and the conservation of natural resources in regulated rivers will become increasingly difficult, as the ecological needs of an ecosystem must be delicately balanced with societal needs. Furthermore, the management of altered flow regimes has become quite complex, as we must also account for and understand how the interaction of local climate, land use, and the unique geological and topographical features of a region influence hydrologic processes in a river system. Future management approaches will require the involvement and cooperation of governmental agencies, scientists, non-profit organizations, and the public to develop solutions that attempt to restore features of the natural flow regime, conserving and enhancing biodiversity, while providing for the needs of society.

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