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Experimental manipulations of streamflow have been used globally in recent decades to mitigate the impacts of dam operations on river systems. Rivers are challenging subjects for experimentation, because they are open systems that cannot be isolated from their social context. We identify principles to address the challenges of conducting effective large-scale flow experiments. Flow experiments have both scientific and social value when they help to resolve specific questions about the ecological action of flow with a clear nexus to water policies and decisions. Water managers must integrate new information into operating policies for large-scale experiments to be effective. Modeling and monitoring can be integrated with experiments to analyze long-term ecological responses. Experimental design should include spatially extensive observations and well-defined, repeated treatments. Large-scale flow manipulations are only a part of dam operations that affect river systems. Scientists can ensure that experimental manipulations continue to be a valuable approach for the scientifically based management of river systems.

Keywords: rivers, flow experiments, dams, ecosystem management

Management of water resources substantially alters hydrologic regimes in freshwater and estuarine ecosystems (Poff et al. 1997, Nilsson et al. 2005). Around the world, changing societal values have compelled the modification of dam operations and water diversions to mitigate physical and biological impacts on aquatic systems (Williams RD and Winget 1979, Travnichek et al. 1995, King JM et al. 1998, Toth et al. 1998, Polet 2000, Rood et al. 2003, Hamerlynck et al. 2005, Hall et al. 2011). Scientists have advocated for an experimental framework to evaluate and develop operations that provide ecological benefits, to create a more rational basis for water-management decisions, and to advance broader scientific knowledge (Walters et al. 1992, Poff et al. 2003, Souchon et al. 2008). Indeed, flow experiments (figure 1) have been used globally to evaluate the effects of alternative dam operations on rivers, floodplains, and estuaries (Cambray et al. 1997, Bate and Adams 2000, Siebentritt et al. 2004, Decker et al. 2008, Robinson and Uehlinger 2008, Shafroth et al. 2010, King AJ et al. 2010, Schmidt and Grams 2011).

Rivers, floodplains, and estuaries are particularly challenging subjects for large-scale flow experiments, because they are open systems with strong network connectivity, spatial heterogeneity, and temporal variability arising in large part from the action of streamflow. The influence of streamflow on aquatic and riparian systems is not limited to an experimental period but extends before and after any experiment. Furthermore, the observed physical and biological conditions in these systems may not be attributed solely to the level of streamflow during the experiment. Unlike experiments on land, lakes, and small streams in experimental watersheds, flow manipulations involving whole rivers or estuaries can rarely, if ever, be isolated from their social context. Stakeholders have diverse interests in how water is used, and water managers operate facilities and systems to achieve multiple objectives. The overarching issue for scientists involved in large-scale flow experiments, then, is to design scientifically credible and tractable investigations that simultaneously inform water management about policies to achieve long-term objectives.

We review the global practice of flow manipulations in rivers as large-scale experiments to guide future efforts in this burgeoning area of interest using examples from over 40 systems (see the supplementary material, available online at *http://dx.doi.org/10.1525/bio.2011.61.12.5*). We focus on flow manipulations intended to achieve ecological objectives because of their direct relevance for informing dam operations but recognize that investigations of natural flow events and manipulations not intended for ecological outcomes provide useful information for managing rivers and advancing river ecology. We identify how flow experiments have elucidated and addressed facets of the complexity in river, floodplain, and estuary ecosystems. These examples lead us to a core set of challenges and principles for conducting effective large-scale flow experiments that have both scientific and social value.

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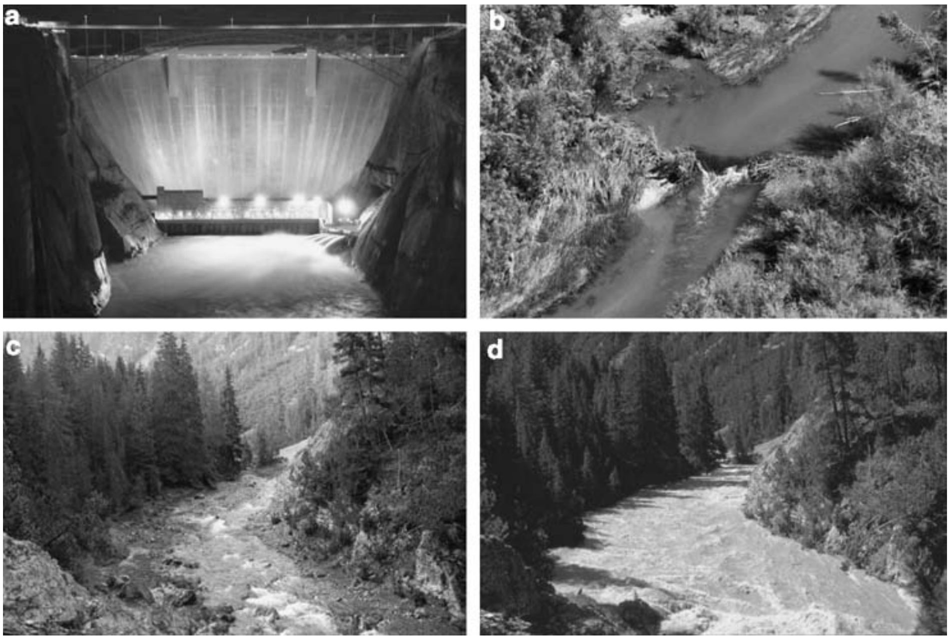

Figure 1. (a) High-flow experiment at Glen Canyon Dam, Colorado River, in 2008. (b) Flood pulse in the Bill Williams River, in Arizona, showing a major breach (more than 3 meters wide) in a beaver dam after an experimental release from Alamo Dam in 2007. The River Spöl below the dam at Punt dal Gall (Swiss National Park) (c) prior to and (d) during an experimental flood release in 2000. Photographs: Thomas Ross Reeve, Bureau of Reclamation (a); Patrick Shafroth (b); and Urs Uehlinger (c, d).

A taxonomy of flow experiments

A *large-scale flow experiment* can be defined broadly as field observations and analysis used to test a hypothesis about physical and biological responses to streamflow in a river, floodplain, or estuary. Flow experiments are performed over a defined period, with distinct streamflow characteristics (the treatment) and observations or measurements of physical or biological responses. Generally, the experimental period encompasses a discrete event, such as a high-flow pulse (Wilcock et al. 1996, Polet 2000, Henson et al. 2007), reservoir drawdown (Moore et al. 2010), or other specified flow (Bureau of Reclamation 2002), although experiments can span longer-term step changes in dam operations that increase minimum flow (Travnichek et al. 1995, Bednarek and Hart 2005), reduce diurnal flow fluctuations (Connor and Pflug 2004, Patterson and Smokorowski 2010), or restore flow to bypassed reaches (Decker et al. 2008). Hypothesis testing in large-scale experiments can be composed of either a formal test of a predicted response based on observation or the estimation of model parameters that relate responses to treatments. Treatments in large-scale flow experiments are not isolated to portions of a river, floodplain, or an estuary and, in this way, differ from plot-scale field experiments or mesocosms.

These scientific criteria for an experiment contrast with both of the following common perceptions: that any management action with an uncertain outcome is an experiment and that an action with predictable outcomes is not an experiment. In our view, the certainty of responses is not central to whether a flow manipulation is an experiment, although it does bear on whether an experiment is valuable and worth conducting.

Mensurative versus manipulative experiments. Following Hurlburt's (1984) dichotomy of field experiments, flow experiments can be considered either mensurative or manipulative, depending on how the treatment is applied. In a *mensurative* flow experiment, investigators do not specify streamflow but, instead, collect information about ecosystem responses to streamflow observed over a defined time period. In a *manipulative* flow experiment, dam operation, diversions, or groundwater pumping are changed during a defined time period in order to modify streamflow in a river, floodplain, or estuary while physical and biological responses are observed.

Although Hairston (1989) argued against applying the term *experiment* to observations of ecological responses to natural events, mensurative investigations of flow can be conducted in an experimental framework designed to complement manipulative experiments (Kinsolving and Bain 1993, Rood et al. 2003). Mensurative investigations can incorporate events such as extended low flows or large floods occurring outside the range of possible flow manipulations and offer an opportunity for observing responses to flow under different conditions (e.g., water temperature, turbidity) than would occur under an experimental manipulation. Mensurative experiments may be most useful in the initial stages of hypothesis testing (e.g., Do high flows reduce macrophyte biomass?) and the development of conceptual models, but they generally cannot resolve questions with the level of precision and certainty needed by water managers (e.g., Is there a threshold flow to scour macrophytes? Will a longer duration flow result in lower macrophyte cover?).

Manipulative flow experiments allow for more explicit design than do mensurative investigations (Hairston 1989), with stronger causal links between specific flow characteristics and ecological responses. In manipulative flow experiments, water can be released repeatedly with a specified rate, duration, and timing (figure 2a, 2b), which thereby allows

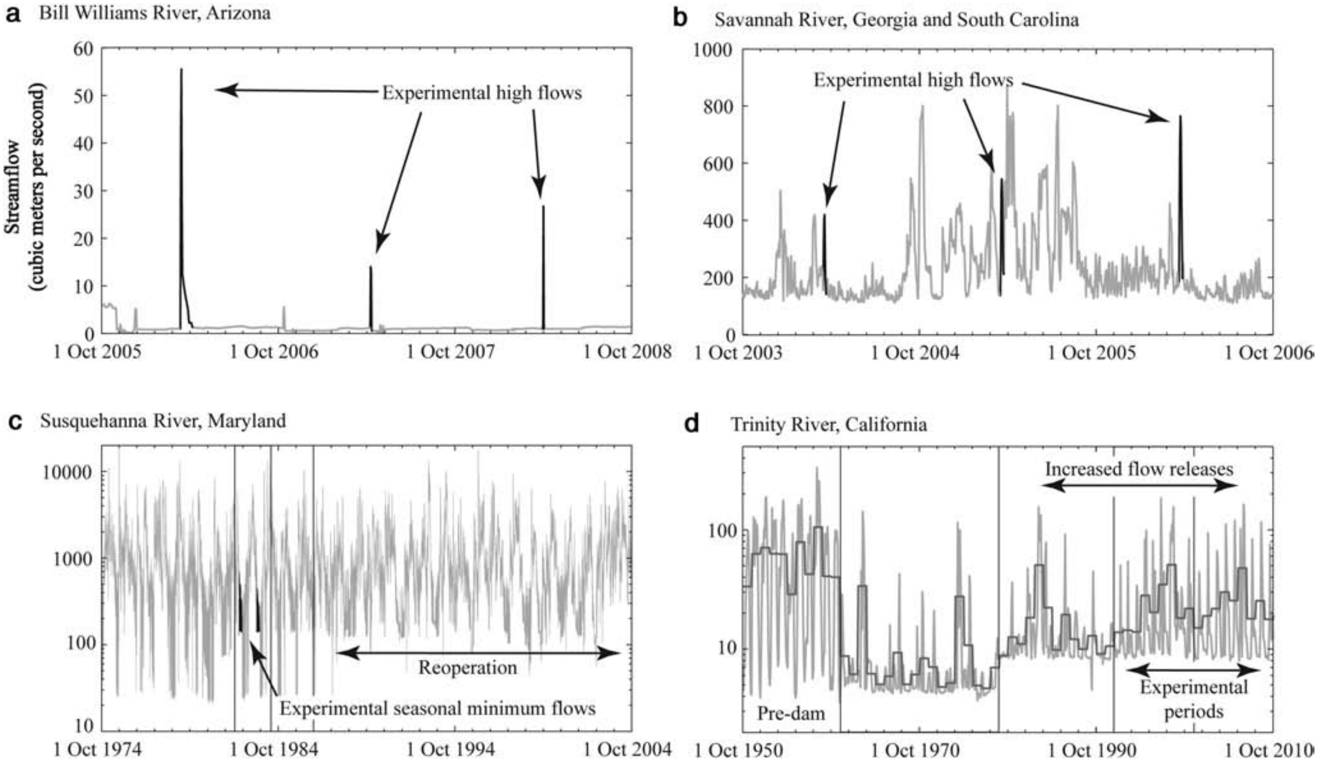

Figure 2. Hydrographs of (a) the daily mean streamflow for the Bill Williams River, in Arizona; (b) the daily mean streamflow for the Savannah River, in Georgia and South Carolina; (c) the daily mean streamflow for the Susquehanna River, in Maryland; and (d) the monthly (light line) and annual (dark line) mean streamflow for the Trinity River, in California.

the analysis of fixed treatments in a factorial design to disentangle the effects of streamflow from other factors if those factors can be controlled. Releases can be varied deliberately and precisely in order to resolve the range and sensitivity of responses to streamflow characteristics (e.g., Andersen and Shafroth 2010, Schmidt and Grams 2011) and are repeated in order to assess the influence of initial conditions (e.g., Robinson and Uehlinger 2008). The scheduling of manipulations permits logistically complex data collection and the coordination of interdisciplinary investigations (Wilcock et al. 1996, Shafroth et al. 2010). The advantages of manipulative experiments cannot be realized, however, without recognizing and addressing common challenges.

Many large-scale experiments are hybrids. In practice, large-scale flow experiments often have both mensurative and manipulative elements. Water availability for experiments in arid regions depends on recent precipitation where manipulations may coincide with or supplement natural events such as for the Kromme Estuary, South Africa (Strydom and Whitfield 2000); Lake Ichkeul, Tunisia (Smart 2004); and the Murray-Darling, Australia (Siebentritt et al. 2004, King AJ et al. 2010). For longer-term experiments, prescribed dam releases vary among wet, normal, and dry years, such as in the Trinity River, in California (figure 2d), and Klamath River, in Oregon, which leads to flow treatments that are highly correlated with natural tributary inflows (USFWS and Hoopa Valley Tribe 1999).

Most geophysical and phenological conditions are largely uncontrolled even in manipulative experiments, including the streamflow before and after the manipulations (figure 2b). The scheduling of experiments can be used to control some factors. For example, high-flow experiments on the Colorado River in the Grand Canyon in 2004 and 2008 were conducted after sediment inputs from the unregulated Paria River (Schmidt and Grams 2011). Likewise, an unregulated tributary downstream of a dam influences responses and can effectively turn a manipulative experiment into one that involves a hybrid of regulated and unregulated flows, as in the Green River below its confluence with the Yampa River in Utah (Vinson 2001). Removal of dikes from estuaries and levee setbacks, such as along the Nueces Delta, Texas, represent another type of hybrid experiment, in which flow is manipulated through structural modifications but in which the subsequent characteristics of flow to the system are not under experimental control (Montagna et al. 2002).

Challenges in large-scale flow experiments

Classical experimentation requires the testing of alternative hypotheses; documentation of initial conditions; sufficient observations to characterize responses; and the randomized assignment of replicated treatments and untreated controls, including the blocking of influential factors (Hairston 1989). Flow manipulations face challenges in meeting these and other experimental-design requirements common to large-scale ecological experiments (Hurlbert 1984, Carpenter 1989). River systems have structure in space and time, which compels extensive data collection at multiple time scales to characterize the response. The structures are unique to each system, which limits the value of using other systems as replicates and controls. Flow can act along multiple pathways, influencing hydraulic conditions, sediment transport, thermal regime, and other physical properties of water in ecosystems that complicate the analysis of discrete, testable hypotheses (e.g., Vinson 2001, Bednarek and Hart 2005, Olden and Naiman 2010). Water-management issues present another layer of challenges in terms of goals for large-scale experiments and also introduce confounding factors that must be addressed in analyses (Poff et al. 1997).

We identify five challenges in particular that must be addressed for large-scale flow experiments to become an effective part of river management (also see box 1). Aspects of these challenges are common issues for river ecology in general, so experiments that are successful in meeting these challenges advance science, in addition to fulfilling management needs.

Challenge 1. Large-scale flow manipulations are management actions inseparable from their social context. Manipulative flow experiments are inseparable from their social context, which includes competing uses for a public resources, concerns about at-risk species, and impacts on human activities in river ecosystems (Bureau of Reclamation 2002, Hamerlynck and Duvail 2003, Jacobson and Galat 2008). Scientists alone do not decide how much water to release from a reservoir for an experiment (Hamerlynck et al. 2005, Lind et al. 2007), even though they may influence those who do make these decisions (Travnichek et al. 1995, Bate and Adams 2000, Watts et al. 2010, Schmidt and Grams 2011). In practice, the decisions of how much water to release and when to release it reflect many constraints, including the availability of water, the capacity of the hydraulic structures used to release flow, and risks to water users and downstream residents. Stakeholder interests range from maintaining the status quo to reshaping water resources management, either of which may be supported or undermined by new information gained through experiments. As a result of stakeholders' interests and the resources required for planning, implementing, and monitoring flow manipulations, these types of experiments are perceived as high-risk management actions.

Outcomes measured in terms of socially valued resources are the principal motivation for water managers to manipulate flows and may be the only acceptable justification of the costs and risks of such actions. Water managers may seek to limit manipulations if they compromise other system objectives (e.g., water delivery downstream for municipal and agricultural use, management of tail-water fisheries, providing recreational opportunities), even if the treatment's strength is reduced to a point that the results are inconclusive. Failure to develop sufficient contrast between the pretreatment period (or control system) and the treatment period can lead to uninformative results, as well as to the failure to achieve management objectives (box 2; Toth et al. 1998, Strydom and Whitfield 2000, Webb et al. 2010). Walters (1997) aptly noted the false economies for long-term resource management of scaling back experiments to reduce costs: A scaled-back or post hoc test may be inconclusive

Box 1. Challenges for large-scale flow experiments.

Flow manipulations are management actions intended to achieve outcomes rather than to provide learning opportunities. Because large-scale flow experiments are not physically isolated from society, they cannot be designed with consideration only of scientific issues. Flow manipulations are intended primarily to achieve ecological outcomes. Broad investigations driven by resource objectives may not be conclusive or may not readily inform water-management decisions.

Experimental treatments and responses span multiple time scales. Treatments and other factors contributing to ecological responses are difficult to control over long time periods and are difficult to repeat. Ecological responses exhibit varying time lags, including legacy effects from past events, human impacts, and cumulative effects under serial treatments, which influence outcomes. Responses integrate streamflow over time and may include the influence of nonexperimental operations.

Large-scale flow experiments are embedded in river networks. Treatments attenuate downstream and can also be modified through interactions with in-channel responses. Tributaries contribute flow and sediment, change the physical properties of flow, and are a source of colonists' seeding for biological recovery.

Regulated systems are impacted by temperature and sediment regime shifts. The colonization, migration, and transport of propagules or gametes may continue to be limited, despite flow manipulations. The influences of flow and other factors are difficult to isolate with interacting and interdependent management interventions.

Flow affects different taxa through distinct mechanisms. The responses of some taxa may be mediated by competition and predation rather than directly through disturbance and habitat effects. Variable life histories (flow-dependent life stages, long-lived species, reproduction, migration) result in taxa-specific responses. Invasive (nonnative, nuisance, upland) species may respond in a manner different from that of native taxa or may modulate native taxa responses.

Box 2. Reconciling management objectives in large-scale flow experiments.

Ecological outcomes depend on strong manipulations and dam operations that continue after experiments. In Kromme Estuary, South Africa, freshwater releases were not sufficient (low magnitude and duration) to increase larval fish abundance (Strydom and Whitfield 2000). In the Colorado River, in the United States, sandbars created by high flows were eroded by fluctuating flows for hydropower peaking (Schmidt and Grams 2011). In the Mitta Mitta River, in Australia, under steady flows, nuisance algae recovered weeks after scouring by high flows (Watts et al. 2010).

Repeated, frequent manipulations may be required to re-establish and maintain a community or system. In the Bill Williams River, in Arizona, high flows flushed out beaver dams and restored lotic habitats, but beavers rebuild dams and re-establish lentic habitats until the next high-flow event (Andersen and Shafroth 2010). In the River Spöl, in Switzerland, the abundances of blackflies, chironomids, stoneflies, and caddisflies increased in response to a series of high flows, which represents a shift in the invertebrate assemblage and an increase in its resiliency to flood disturbance (Robinson and Uehlinger 2008).

Achieving resource objectives depends on flow management over the life cycle of targeted taxa. In the Skagit River, in the state of Washington, successful salmon reproduction depended on flows to cue spawning that were maintained throughout the incubation period (Connor and Pflug 2006). In the Truckee River, in California and Nevada, cottonwood regeneration depended on high flows for dispersal and germination followed by sufficient base flows to allow seedling establishment without high flows that would scour young vegetation (Rood et al. 2003).

(Bednarek and Hart 2005) or even misleading when it lacks statistical power (Carpenter 1989).

Challenge 2. Experimental treatments and responses span multiple time scales. Treatments in large-scale flow experiments range from discrete events (figure 2a, 2b) that may last for a few days or months (King JM et al. 1998, Bate and Adam 2000, Smart 2004) to a series of events (Montagna et al. 2002, Robinson and Uehlinger 2008) to revisions in operating policies that modify releases for years (figure 2c, 2d; Weisberg and Burton 1993, Travnichek et al. 1995, Connor and Pflug 2004, Decker et al. 2008). Discrete manipulations generally fit within an experimental framework comprising clearly defined treatments and responses that can be attributed to the treatment with a high level of certainty (Cambray et al. 1997, Siebentritt et al. 2004, Rolls and Wilson 2010, Shafroth et al. 2010).

By contrast, changes in operating policies that affect reservoir releases over years often do not present well-defined treatments, because those policies may not be prescriptive, which results in different release patterns depending, for example, on whether the year is wet or dry (USFWS and Hoopa Valley Tribe 1999, Konrad et al. 2011). Actual releases under revised operating policies depend on natural inflows and other uses of water. In cases in which flow is reintroduced to a dewatered reach or in which minimum flows are increased substantially, changes in operating policies can be investigated in an experimental framework but only in highly regulated systems (Travnichek et al. 1995, Connor and Pflug 2004, Hall et al. 2011).

Evaluating responses over long time scales is challenging for all types of flow experiments. Some responses to a discrete manipulation extend over a long period and, as a result, are influenced by subsequent operations or experimental releases (figure 2b, 2d), which confound the attribution of observed responses to any specific flow characteristic (Korman et al. 2011). For example, sandbars and backwater habitats in the Grand Canyon that formed during high-flow pulses on the Colorado River were eroded to a significant extent in subsequent months under elevated discharges from Glen Canyon Dam (Schmidt and Grams 2011). In other cases, an experimental design may require years before any effects can be demonstrated (Souchon et al. 2008).

Because organisms depend on various flows over their life cycle and because the effects of flow are integrated with other factors over time, longer-term responses in populations cannot commonly be attributed to a single isolated manipulation of flow. Robinson and Uehlinger (2008) demonstrated a shift in invertebrate community structure in the River Spöl, in Switzerland, that only manifested after years of repeated high-flow pulses. Rood and colleagues (2003) described the sequence of flows over a period of years needed to establish cottonwoods on the Truckee River, in Nevada. Similarly, fish reproduction depends not only on flows to induce spawning but also on flows during embryo incubation and larval development (Strydom and Whitfield 2000, Connor and Pflug 2004).

Challenge 3. Large-scale flow experiments are embedded in river networks exhibiting strong longitudinal and lateral connectivity. Rivers are open systems in which sites are embedded in networks, often with strong longitudinal and lateral connectivity. Network structure and the lack of synchronous responses in networks (figure 3) cannot be easily characterized by localized investigations or with randomized spatial sampling. Sites along a river with similar local attributes (e.g., gradient, valley confinement, bank vegetation) may not be comparable as untreated sites for controls or may display heterogeneous responses to flow manipulations because of differences in their network positions. Therefore, the responses to flow manipulations should be expected to vary, depending on tributary inflow, valley characteristics

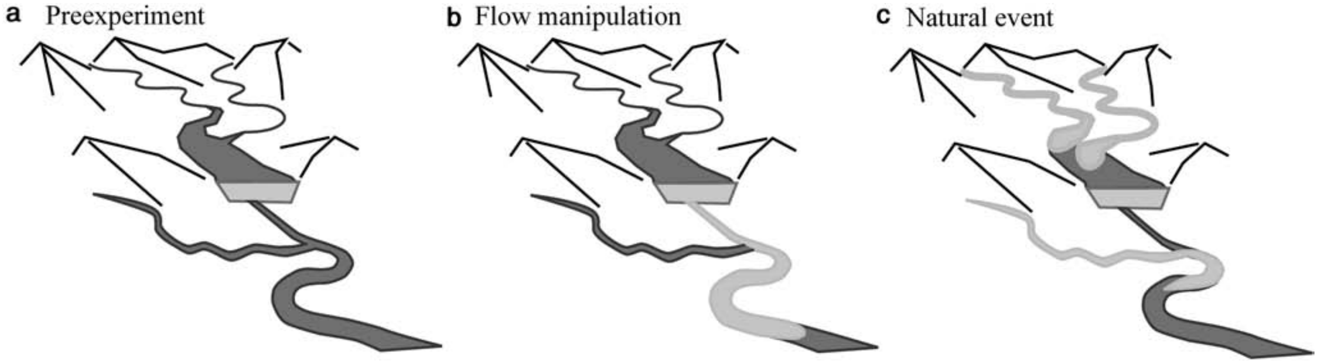

Figure 3. River network with distinct system states in different locations (a) preexperiment, (b) during flow manipulation, and (c) during a natural event.

Box 3. Influences of connectivity on ecological responses to flow manipulations.

Flow treatments attenuate downstream of dams. In the Tallapoosa River, in Georgia, recovery of the warm-water fish assemblage was limited 37 kilometers (km) downstream of the Thurlow Dam (Travnichek et al. 1995). In the Colorado River, during a high flow in 2008, sandbars were built about 160 km downstream of the Glen Canyon Dam but eroded further downstream (Schmidt and Grams 2011).

Responses to flow manipulations are influenced by the interaction of treatments with in-channel responses and by tributaries. In the Mokelumne River, in California, the river channel was a source of particulate materials, dissolved nutrients, and bacteria that modified downstream water quality of a high-flow pulse (Henson et al. 2007). In the Green River, in Utah, Red Creek is a source of warmer water, turbidity, and aquatic insects (Vinson 2001). In Kromme Estuary, South Africa, an unregulated tributary provided a refuge for some estuary fish species (Strydom and Whitfield 2000).

such as gradient and channel confinement, and in-channel processes (box 3).

After flow is released from a dam as an experimental manipulation, its influence will attenuate downstream (figure 3; Travnichek et al. 1995, Connor and Pflug 2004). En route, however, there may be a variety of changes that occur. Releases from Camanche Dam on the Mokelumne River, in California, in 2003 mobilized particulates, dissolved nutrients, and bacteria, leading to variable water-quality responses as the pulse translated downstream from the dam (Henson et al. 2007).

Tributaries can have a strong influence on the results of flow experiments, contributing biota, water with distinct physical properties (e.g., temperature), and sediment. The unregulated Geelhoutboom Tributary served as a source of larval fish to the Kromme estuary during a high-flow pulse (Strydom and Whitfield 2000). Invertebrate richness in the Green River, in Utah, increased in a reach 18 kilometers (km) downstream from Flaming Gorge Dam in response to warmer-water releases (1978–1999) but not in a reach immediately downstream of the dam (Vinson 2001). Vinson (2001) suggested that the dominance of amphipods in the upstream benthic community and the lack of colonists provided by downstream tributaries suppressed the response of native invertebrates immediately below the dam.

Challenge 4: Serial discontinuity and multiple limiting factors compromise large-scale flow experiments. Flow manipulations alone may not provide an adequate treatment when other aspects of serial discontinuity, including fragmentation of lotic habitat, changes in thermal regime, reduction in sediment supply and transport, and disruption in the migration and transport of biota, are involved (box 4). As a result, aquatic and riparian communities in regulated systems may not respond to flow manipulation in ways analogous to responses of unregulated systems to flow. Reduced *hydrochory* (the water-borne supply of seeds, gametes, or propagules) is a pervasive legacy of dams and diking that has limited the efficacy of flow manipulations in restoring marsh vegetation and populations of fishes and mussels (Toth et al. 1998, Siebentritt et al. 2004, Moles and Layzer 2008). Water temperature affects mortality, growth, survival, migration timing, and other behaviors in aquatic organisms and has been a significant factor in large-scale flow experiments around the world (Olden and Naiman 2010). Flow manipulations in the Olifants River, in South Africa, and the Savannah River, in Georgia, failed to promote fish migration and spawning, because cold, hypolimentic water was released (King JM et al. 1998, Konrad et al. 2011). Vinson (2001) noted that despite modifications of Flaming Gorge Dam to increase the temperature of releases to the Green River, the water was not warm enough (i.e., the treatment was not

Box 4. Serial discontinuity and multiple covariates.

Flow manipulations do not address all ecological impacts in regulated systems. In the Olifants River, South Africa, after high flows cued spawning by Clanwilliam yellowfish, cold, hypolimentic water prevented the successful recruitment of embryos and larvae to juvenile stages (King et al. 1998). In the Green River, in Utah, temperature control and flow manipulations were not sufficient for the recovery of aquatic insects immediately downstream of Flaming Gorge Dam (Vinson 2001). In the Tennessee River basin, the relative abundance and richness of sensitive aquatic insects increased more with a combination of flow manipulation and reaeration than with flow manipulations alone (Bednarek and Hart 2005).

Hydrochory, reproduction, and recolonization depend on proximate sources of propagules, gamete, or colonists. In the Green River, in Kentucky, mussel fertilization is limited immediately downstream of a dam in part because of the lack of an upstream supply of gametes (Moles and Layzer 2008). In the Kissimmee River, in Florida, reestablishment of a seven-to-nine-month hydroperiod on a floodplain allowed the recolonization of broadleaf marsh species because of a viable seed bank and remnant propagules (Toth et al. 1998). In the Murray River, in Australia, a flood did not result in the recruitment of new aquatic vegetation, possibly because of the lack of a seed bank, although it did promote the growth of already established vegetation (Siebentritt et al. 2004).

sufficiently strong) to elicit invertebrate responses until it mixed with warmer inflows from downstream tributaries.

Resource managers may implement multiple interventions (e.g., sequential flow manipulations, invasive species removal, sediment augmentation, or water temperature control) to increase the likelihood of achieving resource goals under multiple stressors (Vinson 2001, Korman et al. 2011). Simultaneous or sequential treatments, however, limit the potential to isolate effects and to attribute them to specific flow characteristics. Bednarak and Hart (2005) noted the difficulty in distinguishing the effects of flow and dissolved-oxygen treatments for dams operated by the Tennessee Valley Authority when those interventions were applied as sequential step changes within a few years of each other but without adequate time to document responses to flow alone.

Challenge 5. Reconciling diverse taxonomic responses to large-scale flow experiments. The responses of different taxa to streamflow reflect their habitat preferences, life histories, competitive and trophic interactions with other taxa (competition, predation), the degree to which species are evolutionarily adapted to flow characteristics, and the initial conditions of their populations prior to flow manipulations (Toth et al. 1998, Propst and Gido 2004, Shafroth et al. 2010). In the Tallapoosa River, in Alabama, Travnichek and colleagues (1995) demonstrated increased species richness and abundance of fluvial-specialist fishes relative to habitat generalists in response to increased minimum flows. A. J. King and colleagues (2010) observed benefits to native fishes from managed high flows in the Murray River, Australia. Different taxa responded through distinct mechanisms: Some fishes increased spawning, whereas others had high survivorship of larvae. Taxa-specific responses may be mediated by habitat preferences and availability (e.g., Propst and Gido 2004, Connor and Pflug 2004, King AJ et al. 2010, Shafroth et al. 2010), or they may be a result of trophic changes initiated by flow manipulations (Weisberg and Burton 1993, Korman et al. 2011). Divergent taxonomic responses lead to community shifts that, in turn, can affect community responses to subsequent flow manipulations.

Life-history differences among taxa are important for assessing responses to flow manipulations: Longer-lived species are likely to be influenced strongly by survival or mortality of individuals extant before a flow manipulation, whereas the response of shorter-lived species may be due primarily to changes in growth and reproduction immediately after the manipulation. From an evolutionary perspective, floods and droughts that are predictable over time can exert primary selective pressures that favor life histories synchronized to avoid or exploit extreme flow events. Extreme flows that are frequent and large in magnitude but unpredictable have low selection strength for life-history timing, even though they might inflict high mortality on populations (Lytle and Poff 2004). Robinson and Uehlinger (2008) observed distinct response times of moss, periphyton, and invertebrates to the high flows in the River Spöl, which led to differences in cumulative effects from a series of 15 floods on these different parts of the aquatic community. The invertebrate assemblage, for example, was increasingly dominated by species adapted to flood disturbance, which enhanced the resiliency of the assemblage to floods over time. Flow manipulations may have little effect where a community has shifted to another state because of the presence of nonnative species, such as the shrub *Ludwigia peruviana*, which Toth (2010) implicated in the failure of flow manipulations to restore broadleaf marsh along the Kissimmee River, in Florida.

Principles for enhancing the scientific and social value of large-scale flow experiments

Large-scale flow experiments can be effective tools for advancing scientific knowledge and resource-management goals when they address the challenges described above. We present five principles that have been used to address these challenges and to serve as guidance for scientists conducting effective large-scale flow experiments in the future.

Principle 1. Experiments are for learning. Scientists, water managers, and stakeholders should understand the motivations for conducting large-scale experiments and should distinguish between what is needed for learning and what is needed to achieve management objectives. Even though manipulative experiments are management actions, they are not surrogates for the operational changes needed to achieve long-term resource-management objectives. Flow manipulations that are intended principally to achieve management objectives should not be considered experiments unless there is an explicit design that permits learning (e.g., estimation of model parameters, refutation of hypotheses). Even flow manipulations that failed to achieve management objectives have been effective experiments when they informed future water-management decisions (King JM et al. 1998, Strydom and Whitfield 2000, Rolls and Wilson 2010).

Scientists and water managers bear the responsibility for justifying an experimental approach in terms of its practical ability to help resolve uncertainty (e.g., What management question will be informed by an experiment?) and the likelihood of outcomes that will achieve management goals weighed against the costs and risks of proposed manipulations. Flow experiments can be effective for answering specific questions to inform decisionmaking in water management, including the following: Did the expected direct response occur as a result of a flow manipulation? Are there threshold effects that depend on precise manipulations? Were there unintended, negative outcomes from the manipulations? Resource objectives simply rephrased as hypotheses, however, require years to evaluate in many cases, and it may not even be possible to test them experimentally.

Linkages between flow manipulations and management objectives are numerous, indirect, and uncertain. Scientists need to better articulate their understanding of ecological functions involving flow, the time scales of those functions, and the likely outcomes of flow manipulations. The potential risks of the experiment to valued resources (e.g., endangered species, bank at risk of erosion, water quality, property) should be acknowledged (Kondolf and Wilcock 1996, Bureau of Reclamation 2002), but they should be compared with actual risks under the status quo.

Scientists have alternatives to large-scale experiments, including mesocosm experiments, simulation models, or mensurative investigations, that may be more efficient for learning. Conceptual, statistical, or simulation models of ecosystems can be used to identify the most uncertain linkages between management actions and resource goals that may need to be resolved experimentally. Scientists can use models to determine the treatment strength needed to produce measurable responses and to predict the differences among the outcomes of possible treatments (Alexander et al. 2006, Jacobson and Galat 2008, Schuwirth et al. 2008, Webb et al. 2010). Mensurative investigations (Rood et al. 2003, Smart 2004) can serve as benchmarks for the potential benefits from future flow manipulations. Combining mensurative and manipulative approaches (figure 3b, 3c) can increase the number of events examined, can expand the range of treatment strength, and can determine initial conditions and covariates so that their influence can be assessed (King JM et al. 1998, Rood et al. 2003, King AJ et al. 2010). These alternatives should be considered in conjunction with large-scale experimentation in developing approaches for investigation.

Experiments by themselves are not sufficient to solve resource issues without a framework for using new information in dam operations. Managers and stakeholders must be explicit about the level of evidence or certainty required to make decisions so that scientists can design relevant experiments that provide sufficiently strong evidence. Scientific interpretations of experiments must extend to evaluating the differences among management options, identifying the conditions that determine when water managers should conduct manipulations, and recommending how future manipulations could be more effective (Bate and Adam 2000, King AJ et al. 2010, Watts et al. 2010, Konrad et al. 2011, Schmidt and Grams 2011). In regulated systems, continuing flow manipulations are needed in order to achieve resource objectives (Bate and Adam 2000, Siebentritt et al. 2004, Watts et al. 2010), regardless of whether those manipulations are treated as experiments.

Principle 2. Modeling and monitoring can be integrated with experiments to evaluate long-term outcomes of flow manipulations. Experiments become more difficult to control, interpret, and repeat as they span longer time periods. Experiments that examine flow manipulations that last weeks or longer must deal with potentially numerous, interacting effects of streamflow during that period (figure 2c, 2d). The causal link between any specific characteristic of that time series (e.g., peak flow rate) and the ecological outcomes is tenuous, because the outcomes integrate the effects of the entire sequence of flows with other ecological processes. In a few cases, experiments have extended over multiple years with documentation of baseline conditions and sufficient contrast in dam operations between the baseline and the experimental periods to overcome climatic differences among those periods (e.g., Robinson and Uehlinger 2008, Hall et al. 2011). Effective long-term experiments are only possible in highly regulated systems in which the influences from confounding factors (e.g., weather patterns) can be controlled and in which trials can be repeated.

Despite the advantages of short-term, discrete experiments in which the mechanistic actions of flow are examined, short trials may be inadequate to produce the predicted responses (Strydom and Whitfield 2000). Moreover, the relevance of such experiments to long-term resource-management objectives, such as the recovery of viable fish populations, increased native biodiversity, or the reestablishment of the structure of communities with long-lived species, may not be evident.

A challenge for scientists, then, is to design experiments that can be scaled in order to understand the broader or longer-term impacts. In the Columbia River, in the state of

Washington, tests that route water over dam spillways rather than through turbines have produced statistically significant decreases in the in-reservoir travel time for juvenile salmon but only represent hours over a 3-kilometer reach of a total journey that may take weeks and cover hundreds of kilometers. The systemwide passage of fish through spillways and spillway chutes, however, has decreased travel time by as much as four days in recent years. In this case, experimental evidence of the direct, short-term responses to flow manipulations had to be integrated with broader monitoring and modeling to demonstrate the significance of flow at the level of populations (Williams JG et al. 2005).

Principle 3. Spatially explicit observations are needed to define the spatial extent and gradients in treatments and responses in large-scale flow experiments. At the most basic level, data collection in large-scale flow experiments should define the extent of treatmaents and responses in rivers and estuaries. Gradient analyses may be needed in order to address the longitudinal (downstream or seaward) variation of treatments and responses in which, for example, mixed-effect regression models were used, rather than analyses of variance, to integrate the results from different sampling locations (Kinsolving and Bain 1993, Webb et al. 2010).

Spatially extensive monitoring is needed in order to account for the influence of connectivity on experimental results, especially with regard to tributaries (box 3). If it is possible to do so, tributaries can be incorporated in the experimental design in order to determine whether the introduction of biota and sediment or the modification of physical characteristics of water, such as temperature, influences responses to flow manipulations (Strydom and Whitfield 2000, Vinson 2001, Schmidt and Grams 2011).

Principle 4. Experiments with well-defined treatments, repeated over time, can isolate the ecological influences of flow. Repeated, discrete flow manipulations will generally be more informative for the adaptive management of dams than will investigations limited to periodic monitoring. Infrequent, nonsystematic, or variable manipulations with interacting responses cannot isolate the effects of different factors or attribute responses to specific flow characteristics. Flow manipulations should be applied individually through separate trials to rule out alternative hypotheses without other simultaneous management interventions (Korman et al. 2011).

Although concurrent management actions, such as variable-elevation intakes for temperature control or sediment augmentation, are difficult to analyze, they may be the best possible approach for improving downstream resources (King JM et al. 1998, Bednarek and Hart 2005, Olden and Naiman 2010). If resource managers have committed to the implementation of multiple approaches, there may be no need to assess the effects of flow alone, but such situations do not constitute effective experiments.

Replication and the randomized assignment of treatments and controls is not a feasible approach for flow experiments involving whole systems (figure 3) and cannot be achieved by monitoring at multiple sites within one system or by the repeated application of treatments to one system (Hurlbert 1984). Regression analysis (e.g., Propst and Gido 2004) and parameter estimation (e.g., Webb et al. 2010) offer alternatives to fixed-effect hypothesis testing (e.g., Lind et al. 2007) for analyzing repeated trials (manipulations or natural events). Maximum likelihood and Bayesian methods, in particular, are suited for comparing the performance of competing models or estimating model parameters given weak contrasts and a lack of replication (Reckhow 1990). Paired-system studies comprising a treated system and an untreated control system, which Carpenter (1989) suggested as a feasible alternative to large-scale ecological experiments with replication, have not been used widely in large-scale flow experiments (Connor and Pflug 2004, Patterson and Smokorowski 2010), so it is difficult to assess their value relative to the simple and widely used before-and-after design.

The lack of replication is not a design flaw: Large-scale flow manipulations are motivated primarily by site-specific objectives rather than by the goal of increasing general knowledge about river ecosystems. In this context, repeated manipulations over time in a single system are useful for understanding the influence of initial conditions and factors other than flow (Lind et al. 2007, Robinson and Uehlinger 2008, King AJ et al. 2010, Schmidt and Grams 2011). A series of variable manipulations can be used to assess responses as a function of treatment strength, as in the case of the flood characteristics needed to breach beaver dams in the Bill Williams River, in Arizona (Andersen and Shafroth 2010).

Principle 5. Effective flow manipulations depend on other management actions. Long-lived aquatic and riparian organisms integrate the legacy effects of past water management and historical land use, multiple flow treatments, and other (nonexperimental) managed or natural flows. Even though experiments may be most informative when they can be isolated from the confounding effects of dam operations before and after the experiment, this type of experiment would depict only a part of the broader dam operations affecting river systems (Schmidt and Grams 2011). Flow manipulations that achieve short-term ecological objectives (e.g., seedling germination, fish spawning, sediment deposition) must be followed by subsequent flows that support the next stage in the life history of biological targets (box 2; Rood et al. 2003, Connor and Pflug 2004).

Resource managers can manipulate flow to target the differential responses of taxa on the basis of their life histories in order to suppress invasive species, although these efforts have had mixed results. High-flow pulses promoted cottonwood and willow germination and recruitment and suppressed tamarisk along the Bill Williams River, in Arizona (Shafroth et al. 2010). In the San Juan River, in Colorado and Utah, native fish densities increased in response to elevated releases from Navajo Dam in the spring to mimic snowmelt runoff; however, the nonnative fish density increased in response to the lowering of summer flows, which also mimics unregulated flow patterns (Propst and Gido 2004). Increases in nonnative fish abundance were also observed after high-flow pulses in the Murray River (King AJ et al. 2010) and the Colorado River (Korman et al. 2011). Flow manipulations may be essential for achieving resource goals, but they alone will not restore river ecosystems that continue to face human impacts.

Future of large-scale flow experimentation

Rivers, floodplains, and estuaries are vital parts of landscapes that support diverse biological communities. Plant and animal species in these systems have evolved under conditions of natural flow variability and longitudinal and lateral connectivity that integrates environmental influences and allows migration and biotic interactions at basin and even continental scales. Large-scale flow experiments have contributed to the understanding of some of the ecological elements, such as streamflow patterns of the evolutionary history of riverine species, that are essential for their continued survival. Evidence from large-scale experiments supports the notion that natural flow variability is critical to sustaining the structure and function of riverine ecosystems and at time intervals ranging from days (ecological effects) to generations of populations (evolutionary effects).

Although large-scale flow experiments are motivated by and accountable to site-specific interests, greater standardization of flow treatments has general theoretical and practical value in its ability to facilitate information transfer across sites. Treatments aimed at four flow characteristics in particular would have broad relevance to river management: (1) the range of diurnal flow fluctuations associated with hydropower peaking; (2) the magnitude and duration of high flows when a given volume of water is released (e.g., either allocated for environmental purposes or as part of flood control operations); (3) the frequency of high-flow events; and (4) the magnitude of base flow, particularly for estuaries. The integration of results across sites requires consistent approaches for normalizing measures of flow, such as the percentage of unregulated flow, the area of floodplain inundated per reach length, or volume as a fraction of estuary volume. Standardized measures of ecological responses are also needed for multisite analysis but are difficult to adopt because of system uniqueness, biogeographic variation, and site-specific management. Nonetheless, community- or system-level attributes, such as the relative abundance of species with similar traits or life-history strategies, primary production, and the spatial extent of habitat types, could serve as common measures across many sites (Bednarek and Hart 2005, Konrad et al. 2011).

Large-scale flow manipulations conducted within an experimental framework will continue to play an important role in enhancing the understanding of how flow regimes function in river ecosystems. They will likely be critical for the development of ecologically sustainable water-management schemes that address shifting water supply and demand caused by climate change and an increasing human population. Although rigorous large-scale experiments require substantial commitment by scientists, managers, and stakeholders, they may offer the only practical approach to inform water policies and decisions with the level of certainty and precision needed for the management of one of our most vital and increasingly scarce resources. By recognizing the challenges and adopting the principles demonstrated in this article for large-scale flow experiments, scientists will ensure that such experiments continue to be a valuable approach for the scientifically based management of river systems.

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