The ecological limits of hydrologic alteration (ELOHA): a new framework for developing regional environmental flow standards

N. LEROY POFF*, BRIAN D. RICHTER[†], ANGELA H. ARTHINGTON[‡], STUART E. BUNN[‡], ROBERT J. NAIMAN[§], ELOISE KENDY[¶], MIKE ACREMAN**, COLIN APSE^{††}, BRIAN P. BLEDSOE^{‡‡}, MARY C. FREEMAN^{§§}, JAMES HENRIKSEN^{¶¶}, ROBERT B. JACOBSON***, JONATHAN G. KENNEN^{†††}, DAVID M. MERRITT^{‡‡‡}, JAY H. O'KEEFFE^{§§§}, JULIAN D. OLDEN^{¶¶}, KEVIN ROGERS****, REBECCA E. THARME^{††††} AND ANDREW WARNER^{‡‡‡‡}

SUMMARY

- 1. The flow regime is a primary determinant of the structure and function of aquatic and riparian ecosystems for streams and rivers. Hydrologic alteration has impaired riverine ecosystems on a global scale, and the pace and intensity of human development greatly exceeds the ability of scientists to assess the effects on a river-by-river basis. Current scientific understanding of hydrologic controls on riverine ecosystems and experience gained from individual river studies support development of environmental flow standards at the regional scale.
- 2. This paper presents a consensus view from a group of international scientists on a new framework for assessing environmental flow needs for many streams and rivers simultaneously to foster development and implementation of environmental flow standards at the regional scale. This framework, the ecological limits of hydrologic alteration (ELOHA), is a synthesis of a number of existing hydrologic techniques and environmental flow methods that are currently being used to various degrees and that can support comprehensive regional flow management. The flexible approach allows

Correspondence: N. LeRoy Poff, Department of Biology, Colorado State University, Fort Collins, 80523 CO, U.S.A.

E-mail: poff@lamar.colostate.edu

Present address: James Henriksen, Environmental Flow Specialists, Inc. Fort Collins, CO 80526, U.S.A.

^{*}Department of Biology & Graduate Degree Program in Ecology, Colorado State University, Fort Collins, CO, U.S.A. [†]The Nature Conservancy, Charlottesville, VA, U.S.A.

[‡]Australian Rivers Institute and eWater Cooperative Research Centre, Griffith University, Brisbane, Qld, Australia

[§]School of Aquatic & Fishery Sciences, University of Washington, Seattle, WA, U.S.A.

[¶]The Nature Conservancy, Helena, MT, U.S.A.

^{**}Centre for Ecology and Hydrology, Wallingford, U.K.

⁺⁺The Nature Conservancy, Brunswick, ME, U.S.A.

^{‡‡}Department of Civil and Environmental Engineering, Colorado State University, Fort Collins, CO, U.S.A.

^{§§}Patuxent Wildlife Research Center, U.S. Geological Survey, Athens, GA, U.S.A.

[¶]U.S. Geological Survey, Fort Collins, CO, U.S.A.

^{***}Columbia Environmental Research Center, U.S. Geological Survey, Columbia, MO, U.S.A.

^{****}U.S. Geological Survey, West Trenton, NJ, U.S.A.

^{****}USDA Forest Service, Watershed, Fish, and Wildlife, Fort Collins, CO, U.S.A.

^{§\$\$}Department of Environmental Resources, UNESCO-IHE Institute for Water Education, Delft, The Netherlands

^{¶¶}School of Aquatic & Fishery Sciences, University of Washington, Seattle, WA, U.S.A.

^{****}University of the Witwatersrand, Johannesburg, South Africa

^{****}International Water Management Institute, Colombo, Sri Lanka

^{*****}The Nature Conservancy, University Park, Pennsylvania, PA, U.S.A.

scientists, water-resource managers and stakeholders to analyse and synthesise available scientific information into ecologically based and socially acceptable goals and standards for management of environmental flows.

3. The ELOHA framework includes the synthesis of existing hydrologic and ecological databases from many rivers within a user-defined region to develop scientifically defensible and empirically testable relationships between flow alteration and ecological responses. These relationships serve as the basis for the societally driven process of developing regional flow standards. This is to be achieved by first using hydrologic modelling to build a 'hydrologic foundation' of baseline and current hydrographs for stream and river segments throughout the region. Second, using a set of ecologically relevant flow variables, river segments within the region are classified into a few distinctive flow regime types that are expected to have different ecological characteristics. These river types can be further subclassified according to important geomorphic features that define hydraulic habitat features. Third, the deviation of current-condition flows from baseline-condition flow is determined. Fourth, flow alteration—ecological response relationships are developed for each river type, based on a combination of existing hydroecological literature, expert knowledge and field studies across gradients of hydrologic alteration.

4. Scientific uncertainty will exist in the flow alteration–ecological response relationships, in part because of the confounding of hydrologic alteration with other important environmental determinants of river ecosystem condition (e.g. temperature). Application of the ELOHA framework should therefore occur in a consensus context where stakeholders and decision-makers explicitly evaluate acceptable risk as a balance between the perceived value of the ecological goals, the economic costs involved and the scientific uncertainties in functional relationships between ecological responses and flow alteration.

5. The ELOHA framework also should proceed in an adaptive management context, where collection of monitoring data or targeted field sampling data allows for testing of the proposed flow alteration–ecological response relationships. This empirical validation process allows for a fine-tuning of environmental flow management targets. The ELOHA framework can be used both to guide basic research in hydroecology and to further implementation of more comprehensive environmental flow management of freshwater sustainability on a global scale.

Keywords: environmental flows, hydroecology, hydrologic modelling, river management, streamflow classification

Introduction

Water managers the world over are increasingly challenged to provide reliable and affordable water supplies to growing human populations. At the same time, local communities are expressing concern that water development should not degrade freshwater ecosystems or disrupt valued ecosystem services, such as the provision of fish and other sources of food and fibre as well as places for recreation, tourism and other cultural activities (Postel & Carpenter, 1997; Naiman *et al.*, 2002; Dyson, Bergkamp & Scanlon, 2003; Postel & Richter, 2003). Aquatic ecosystems

support our livelihoods, life styles and ethical values (Acreman, 2001). While people need water directly for drinking, growing food and supporting industry, water for ecosystems often indirectly equates to water for people (Acreman, 1998). There is a fundamental need to address ecological requirements and optimise social well-being across a broad array of water needs to attain sustainability in the management and allocation of water (Gleick, 2003; *Millennium Ecosystem Assessment*, 2003, 2005). Deliberate and strategic design of resilient ecosystems, including freshwaters, is now recognised as a major social-scientific challenge of the 21st century (Palmer *et al.*, 2004).

Environmental flows are defined in the Brisbane Declaration (http://www.riverfoundation.org.au/images/ stories.pdfs/bnedeclaration.pdf) as the 'quantity, timing and quality of water flows required to sustain freshwater and estuarine ecosystems and the human livelihood and well-being that depend on these ecosystems'. It is now widely accepted that a naturally variable regime of flow, rather than just a minimum low flow, is required to sustain freshwater ecosystems (Poff et al., 1997; Bunn & Arthington, 2002; Postel & Richter, 2003; Annear et al., 2004; Biggs, Nikora & Snelder, 2005; Poff, 2009), and this understanding has contributed to the implementation of environmental flow management on thousands of river kilometres worldwide (Postel & Richter, 2003). Despite this tangible progress, millions of kilometres of river and thousands of hectares of wetlands (and the human livelihoods dependent upon them) remain unprotected from the threat of over-allocation of water to offstream uses or to other alterations of the natural flow regime. These threats will only continue to increase with projected growth in the human population and its associated demand for energy, irrigated food production and industrial use (CAWMA 2007), and with uncertainties associated with climate change (Vörösmarty et al., 2000; Dudgeon et al., 2006; Palmer et al., 2008). As water development plans are being formulated to provide greater water security and other social benefits, it will be critically important to ensure that the considerable socioeconomic benefits already provided by healthy freshwater ecosystems are not lost and that degraded ecosystems be restored.

A sense of urgency has arisen for the need to develop ecological goals and management standards that can be applied globally to streams and rivers across a spectrum of ecological, social, political and governance contexts, regardless of the current stage of water-resource development. The imperative to incorporate ecosystem needs for fresh water into basin-wide and regional water-resources planning is increasingly recognised at national and international scales (Petts, 1996; Dyson et al., 2003; GWSP, 2005; NSTC, 2004; CAWMA, 2007; Brisbane Declaration, http://www.riverfoundation.org.au/images/ stories.pdfs/bnedeclaration.pdf). Unfortunately, the pace and intensity of flow alteration in the world's rivers greatly exceeds the ability of scientists to assess the effects on a river-by-river basis - this despite

notable scientific progress in the last decade in developing environmental flow methods for riverspecific applications (Brown & Joubert, 2003; Tharme, 2003; Annear et al., 2004; Arthington et al., 2004; King & Brown, 2006). Thus, a key challenge in securing freshwater ecosystem sustainability is synthesising the knowledge and experience gained from individual case studies into a scientific framework that supports and guides the development of environmental flow standards at the regional scale (Poff et al., 2003; Arthington et al., 2006), i.e. for states, provinces, large river basins or even entire countries. Defining environmental flow standards for many rivers simultaneously, including those for which little hydrologic or ecological information exists, is necessary for water managers to effectively integrate human and ecosystem water needs in a timely and comprehensive manner (Arthington et al., 2006).

In this paper, we present a consensus view from a group of international scientists on a new framework for assessing environmental flow needs that we believe can form the basis for developing and implementing environmental flow standards at the regional scale. This consensus reflects our experiences and knowledge of the science of environmental flows gained through both scientific research and practical applications. We refer to this framework as the 'ecological limits of hydrologic alteration' or ELOHA. Our goal is to present a logical approach that flexibly allows scientists, water-resource managers and other stakeholders to analyse and synthesise available scientific information into coherent, ecologically based and socially acceptable goals and standards for management of environmental flows. This presentation of the ELOHA framework focuses primarily on the scientific approaches and challenges of providing the best possible information regarding the range of ecological consequences that will result from different levels of flow modification at a regional scale. We deliberately provide only cursory treatment of the social and policy challenges inherent in gaining adoption of water management goals and implementation of environmental flow standards consistent with those goals. We expect that other authors with expertise in water policy and the social sciences will offer their perspectives on the need for, and challenges associated with, effectively implementing the ELOHA framework in a variety of social and governance contexts.

Historical scientific foundations of the ELOHA framework

The protocol for regional environmental flow assessment described in this paper is grounded in several recent and important scientific advances. First, research over the last few decades has amply demonstrated that ecological and evolutionary processes in river ecosystems are heavily influenced by many facets of a dynamic, historical flow regime (reviewed in Poff et al., 1997; Bunn & Arthington, 2002; Lytle & Poff, 2004). Indeed, streamflow has been called the 'master variable' (Power et al., 1995), or the 'maestro...that orchestrates pattern and process in rivers' (Walker, Sheldon & Puckridge, 1995). Much evidence also exists that modifications of streamflow induce ecological alterations (reviewed in Bunn & Arthington, 2002; Poff & Zimmerman, 2009). Thus, both ecological theory and abundant evidence of ecological degradation in flow-altered rivers support the need for environmental flow management. Certainly, environmental factors other than streamflow (including temperature, water quality, sediment and invasive species) also regulate riverine ecosystem structure and function, as has been well recognised (e.g. Poff et al., 1997; Baron et al., 2002; Dudgeon et al., 2006). A fuller accounting of the interactions between flow and these other environmental features remains a challenge for advancing the science of environmental flows (and this is discussed more fully below); however, we argue that our present scientific understanding of the role of flow alteration in modifying ecological processes justifies the development of regional flow standards to underpin river restoration and conservation. At a minimum, as society struggles to conserve and restore freshwater ecosystems, flow management is needed to ensure that existing ecological conditions do not decline further (Palmer et al., 2005).

A second scientific foundation supporting ELOHA is the extensive development and application of environmental flow methods globally (see Tharme, 2003; Acreman & Dunbar, 2004). These methods, along with the development of hundreds of ecologically relevant flow metrics and techniques for quantifying human-caused flow and ecological alteration (Richter *et al.*, 1996; Puckridge *et al.*, 1998; Olden & Poff, 2003; Arthington *et al.*, 2004, 2007; Kennen, Henriksen & Nieswand, 2007; Mathews & Richter,

2007), provide a rich toolbox for environmental flow science. Many of these methods and tools can be directly applied or readily adapted for use in regional environmental flow assessment.

Third, the conceptual foundation now exists to facilitate regional environmental flow assessments. By classifying rivers according to ecologically meaningful streamflow characteristics (e.g. Poff & Ward, 1989; Harris et al., 2000; Henriksen et al., 2006), groups of similar rivers can be identified, such that within a grouping or type of river there is a range of hydrologic and ecological variation that can be considered the natural variability for that type. Arthington et al. (2006) argued that empirical relationships describing ecological responses to flow regime alteration within river flow types should form the basis of flow management for both river ecosystem protection (proactive flow management) and sustainable restoration (reactive flow management). This perspective represents a major advance by bridging the gap between the simplistic and often arbitrary hydrologic 'rules of thumb' presently being used for regionalscale estimation of environmental flow needs and, at the other extreme, the detailed and often expensive environmental flow assessments being applied on a river-by-river basis.

Fourth, developing and implementing environmental flow standards at regional scales ultimately requires employing hydrologic models that can provide reasonably accurate estimates of ecologically meaningful streamflows in rivers or river segments distributed throughout a region, including those lacking streamflow gauging records (e.g. Snelder, Biggs and Wood, 2005; Kennen et al., 2008). Hydrologic models can be used to evaluate the nature and degree of hydrologic alteration resulting from human activities and to anticipate the degree to which proposed human activities may further alter the hydrologic regime. With modelled hydrographs, all river segments can be classified hydrologically and ecological information collected from ungauged locations can be used to support the development of relationships between flow alteration and ecological degradation.

Finally, contemporary scientific understanding acknowledges that river management involves complex, coupled social-ecological systems (Rogers, 2006) and if science is to contribute to sustainable water and ecosystem management, it must become engaged in collaborative processes with managers and other

stakeholders to illustrate alternative river visions and to help define pathways to achieve socially desirable goals (Poff et al., 2003). The complexity of river systems generates uncertainty in their response to many types of management actions (including flow manipulation); therefore, scientists must be willing to articulate an adaptive learning cycle that uses the best-available science to set ecosystem management goals and then uses monitoring to improve understanding of ecological responses to management actions. Ultimately, this approach will allow future management actions to be fine-tuned (Arthington & Pusey, 2003; King, Brown & Sabet, 2003; Richter et al., 2006; Rogers, 2006) and hopefully sustained.

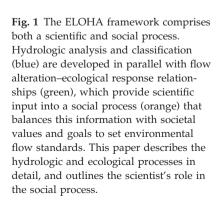
We present the ELOHA framework as a synthesis of a number of existing hydrologic techniques and environmental flow methods that are currently being used to various degrees and that can support comprehensive regional flow management. Many of the basic elements of the framework presented here are now being implemented in a variety of geographical settings and political jurisdictions around the world. As products and summaries of these early ELOHA applications become available, and pertinent tools and techniques useful in ELOHA are described in greater detail, they will be posted at: http://conserveonline.org/workspaces/ eloha.

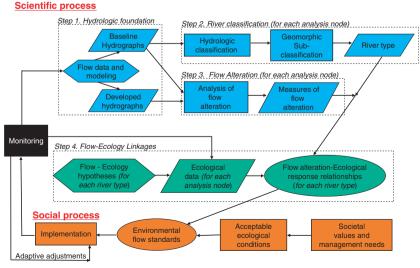
The scientific process in the ELOHA framework

The ELOHA framework involves a number of interconnected steps, feedback loops and iterations

(Fig. 1). Relationships between flow alteration and ecological characteristics for different river types constitute the key element that links the hydrologic, ecological and social aspects of environmental flow assessment. These relationships are based on paired streamflow and ecological data from throughout the region of interest. Our description of the ELOHA framework is presented in stepwise fashion, recognising that various scientific and social processes will likely proceed simultaneously and many need to be repeated iteratively.

The scientific process consists of four major steps, each with a number of technical components, building upon the approach recommended in Arthington et al. (2006). It is our express intent to provide considerable flexibility in the selection of particular input data, tools or analytical methods for accomplishing each step. A risk-based approach is encouraged, which involves choosing the most appropriate model through a trade-off between avoiding the unnecessary expense and effort of developing highly detailed and data-hungry models (often applicable at site-specific scales), while generating information and products containing sufficient certainty to support decisions at broad regional scales (Acreman & Dunbar, 2004; Booker & Acreman, 2007). Such a risk-based approach may be initiated in many regions by investing in simple tools and using readily available data, then moving to more complex and expensive approaches, including additional data collection as the need for prediction resolution increases.





Building a hydrologic foundation

A key feature of the ELOHA framework is a hydrologic database that describes flow regimes not just in 'traditional' anthropocentric terms, such as average yield or reliability, but also in terms known to be linked to ecological outcomes (described below). Hydrologic modelling is used to create the hydrographs that form the 'hydrologic foundation', which consists of two comprehensive databases of daily (or possibly longer time steps such as weekly or monthly) flow time-series representing simulated baseline and developed conditions throughout the region during a common time period. Baseline conditions refer to minimally altered or best-available conditions (the 'reference-site approach', sensu Stoddard et al., 2006), whereas developed conditions refer to altered flow regimes associated with both the direct (e.g. waterresource development) and indirect (e.g. land use change) effects of human activities.

The hydrologic foundation serves several important purposes. First, it facilitates the use of ecological information collected throughout the region, thereby expanding the number of sites that can be used in developing flow alteration-ecological response relationships beyond only those sites having streamflow gauges. Second, it provides a basis for comparing present-day flow regimes to baseline conditions, i.e. those that served as the template for recent evolution of native species and for shaping ecosystem processes, as well as sociocultural dependencies upon those ecological conditions and processes. Third, it enhances the ability of water managers and planners to understand the cumulative impacts of hydrologic alteration that have already taken place across the region, so that those alterations can be linked to observed changes in ecological conditions and ecosystem services as a basis for forecasting future ecological change in the context of regional water management planning. In a similar vein, the foundation can be combined with other regional environmental information (e.g. non-point pollution sources on agricultural lands) to generate landscape characterisations of management interest.

The coupled baseline and developed hydrologic time-series constituting the hydrologic foundation should be developed for all locations in the region where water management decisions, including environmental flow protection, are needed or anticipated. These 'analysis nodes' should be identified in close collaboration with water managers who will use the hydrologic foundation to understand and manage water allocation and environmental flows. The baseline and developed-condition hydrographs serve as independent variables in developing flow alterationecological response relationships (described Formulating flow alteration-ecological response relationships for environmental flows below). Therefore, analysis nodes should also be established for all sites at which ecological data to be used in flow alterationecological response relationships have been collected or are likely to be collected and they should include the range of geomorphic features at the river segment scale that mediate how habitat availability and diversity are expressed for a given flow regime. All of this information should be stored in a relational database and imported into a geographic information system (GIS) to enable users to easily access hydrographs and associated flow statistics.

Figure 2 illustrates the general approach for building the regional hydrologic foundation. Briefly, the approach relies on region-specific combinations of streamflow gauge analysis and hydrologic modelling. Existing streamflow gauge records for a selected time period are segregated into those that represent baseline conditions and those that represent developed conditions. Differences between baseline and developed conditions are characterised in terms of

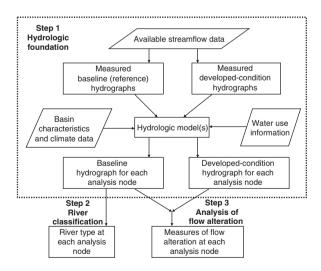


Fig. 2 Steps for developing the hydrologic foundation (ELOHA step 1 inside dashed box), showing how the resulting hydrographs are used to classify river types (ELOHA step 2) and calculate flow alteration (ELOHA step 3) at each analysis node.

statistical departures in the ecologically relevant components of the two flow regimes. At ungauged analysis nodes and for time periods not represented in the period of record, statistical techniques (Sanborn & Bledsoe, 2006; Stuckey, 2006; Zhang et al., 2008; Carlisle et al., 2009) can be used to estimate flow metrics, or hydrologic simulation models of rainfallrunoff and other catchment processes (Singh & Woolhiser, 2002; Wagener, Wheater & Gupta, 2004; Blöschl, 2005; Kennen et al., 2008) can be developed to generate flow time-series from which metrics can be extracted. In heavily modified catchments, simulation models can be especially useful in estimating baseline flow regimes through removal of flow extractions and reservoirs (e.g. Yates et al., 2009), as well as adjusting various model parameters (e.g. infiltration, interception, routing) to represent past land cover conditions (Beighley, Melack & Dunne, 2003). For rapidly changing land uses (e.g. urbanisation), developed-condition hydrographs could be modelled for both existing and alternative future scenarios, including projected climatic regimes. Ideally, daily streamflows will be generated for the hydrologic foundation, as daily data provide appropriate temporal resolution for understanding most ecological responses to flow alteration. However, in cases where daily data cannot be satisfactorily modelled, a coarser grain of resolution such as weekly or monthly hydrographs can provide some ecologically relevant information (see Poff, 1996) and may serve as a starting point for classification.

Given limited availability of streamflow gauging records with which to calibrate estimates of baseline or developed conditions, and given that climate and river runoff vary naturally over annual to decadal time scales (Lins & Slack, 1999; McCabe & Wolock, 2002), it is desirable to adopt a single time period (e.g. 10–20 years) as a climatic reference period for which baseline and developed-condition streamflows are synthesised and modelled. By using a common climatic reference period for each of these two scenarios, human influences on flow regimes can be separated from climatic influences.

The basic data required to develop the hydrologic foundation are now available for most parts of the globe (Kite, 2000), enabling hydrologists to generate a first-cut approximation of the hydrologic foundation in most, if not all, regions. Prediction accuracy is a significant concern, especially in sparsely gauged

regions, but improvements in a priori estimation of model parameters based on remotely sensed landsurface characteristics and the development of Bayesian Monte Carlo techniques have significantly improved the accuracy of hydrologic models (Duan et al., 2006; Schaake et al., 2006). An alternative to regionalisation of model parameters to simulate streamflow time series at ungauged locations is regionalisation of streamflow characteristics to generate flow statistics, which allows for explicit estimation of uncertainty (see Zhang et al., 2008). Since the objective of ELOHA is to identify ecologically significant differences in flow regimes between baseline and developed conditions, it is important to quantify apparent differences that arise due to poor model performance and true differences due to water or catchment management. For example, Acreman et al. (2009) distinguished model error from true differences between natural flows and impacted flows downstream of dams in the process of defining ecologically significant thresholds of flow alteration for the European Water Framework Directive in the United Kingdom.

Classifying rivers according to flow regimes and geomorphic features

River classification is a statistical process of stratifying natural variation in measured characteristics among a population of streams and rivers to delineate river types that are similar in terms of hydrologic and other environmental features. The classification can be developed within any 'region' of interest, from those defined by political boundaries to those representing natural biophysical domains, such as physiographic provinces or ecoregions.

River classification serves two important purposes in the ELOHA framework. First, by assigning rivers or river segments to a particular type, relationships between ecological metrics and flow alteration can be developed for an entire river type based on data obtained from a limited set of rivers of that type within the region (Arthington et al., 2006; Poff et al., 2006b). For each river type there is a range of natural hydrologic variation that regulates characteristic ecological processes and habitat characteristics (Lytle & Poff, 2004; Arthington et al., 2006), and that represents the baseline or reference condition against which ecological responses to alteration are measured across

multiple river segments falling along a gradient of hydrologic alteration.

Second, combining the regional hydrologic modelling with a river typology facilitates efficient biological monitoring and research design. Specifically, it is possible to strategically place monitoring sites throughout a region to capture the range of ecological responses across a gradient of hydrologic alteration for different river types. This is particularly valuable in regions with sparse pre-existing biological data or where monitoring and research resources are limited.

Hydrologic classification. In the ELOHA framework, river classification focuses primarily on the hydrologic regime as the main ecological driver. Examples of river types in the United States include stable groundwater-fed rivers; seasonally predictable snowmelt rivers; intermittent, rain-fed prairie and desert rivers and highly dynamic, unpredictable rain-fed perennial rivers (e.g. see Poff, 1996). We recommend classifying rivers according to similarity in hydrologic regime, using flow statistics computed from the baseline hydrographs developed in building a hydrologic foundation. A large suite of flow statistics can be calculated using software packages such as the Indicators of Hydrologic Alteration (Richter et al., 1996), the Hydrologic Assessment Tool (HAT) within the Hydroecological Integrity Process (Henriksen et al., 2006), the River Analysis Package (http://www. toolkit.net.au/rap) or GeoTools (http://www.engr. colostate.edu/~bbledsoe/GeoTool/). The number of river types in a region should generally reflect the region's heterogeneity in climate and surficial geology, with diverse regions having more river types. Deciding how many river types are appropriate requires a tradeoff between detail (i.e. small withintype variability) and interpretability (i.e. differences among types). In order to be practical to management, a relatively small number of river types should be defined that capture the major dimensions of streamflow variability. Most previous regional to continental hydrologic classifications have used four to 12 classes, depending on geographic extent, climatic and geologic variation or inclusion of other environmental factors (e.g. Poff & Ward, 1989; Poff, 1996; Snelder & Biggs, 2002; Kennen et al., 2007, 2009; Acreman et al., 2008; Kennard et al., 2009).

Three primary criteria should be considered in selecting a suite of flow statistics for building a river

classification. First, if possible, flow metrics should collectively describe the full range of natural hydrologic variability, including the magnitude, frequency, duration, timing and rate of change of flow events (Richter et al., 1996; Poff et al., 1997; Olden & Poff, 2003; Kennen et al., 2007; Mathews & Richter, 2007). Second, metrics must be 'ecologically relevant', i.e. they are known to have, or can reliably be extrapolated from ecological principles to have, some demonstrated or measurable ecological influence (Arthington et al., 2006; Monk et al., 2007) and hence will be important in assessing ecological responses to hydrologic alteration. Third, the metrics should be amenable to management, so that water managers can develop environmental flow standards using these same hydrologic metrics and evaluate the effect of other water uses in the catchment on these metrics. Hundreds of flow metrics have been published (Richter et al., 1996; Olden & Poff, 2003; Mathews & Richter, 2007) and are potential candidates for inclusion in a regional river classification. In selecting the appropriate variables, we recommend using the method developed by Olden & Poff (2003) contained in the HAT software of the Hydroecological Integrity Assessment process (Henriksen et al., 2006; Kennen et al., 2007). The software performs a redundancy analysis to determine which variables are the most informative components of the flow regime. Users have flexibility in selecting metrics from suites of inter-correlated variables to choose those that best satisfy the three primary criteria above. In addition, the 'environmental flow components' recently added to the Indicators of Hydrologic Alteration software (Mathews & Richter, 2007) are well suited for ELOHA applications due to their strong link between environmental flow assessment and implementation, their ecological relevance, and their intuitive appeal; however, their information overlap with other metrics has yet to be assessed.

Geomorphic sub-classification. At the broad, regional scale of ELOHA, it will be useful to account for some of the dominant environmental factors that can provide a context for interpreting ecological responses to flow alteration and thus for guiding development of flow management rules. Geomorphology is of prime interest in this regard, although other factors might be as well (see discussion in next section).

Geomorphic sub-classification of stream or river segments can provide a useful integration of catchment and local geomorphic characteristics such as geology, channel confinement and channel slope (Seelbach et al., 1997; Higgins et al., 2005). The physical setting of a river segment will strongly influence how the flow regime gets translated into the hydraulic habitats experienced by, and available to, the riverine biota. For example, whether a given level of flow will create a bed-moving disturbance or an overbank flow is determined by local characteristics such as channel geometry, floodplain height and streambed composition. In other words, the same level of flow in one geomorphic setting may not translate into an important ecological event, whereas in a second setting it may (Poff et al., 2006a). Therefore, differentiating rivers on the basis of physical characteristics, such as constrained versus alluvial channels or sandbedded versus cobble-bedded reaches) will contribute to development of flow alteration-ecological response relationships that reflect the direct and indirect influences of hydrologic alteration on both ecological processes and ecosystem structure and function (Snelder & Biggs, 2002; Jacobson & Galat, 2006; Vaughan et al., 2009).

Computing flow alteration

ELOHA is grounded in the premise that increasing degrees of flow alteration from baseline condition are associated with increasing ecological change. The degree by which each hydrologic variable differs between the baseline and developed condition is calculated for each analysis node using available software (e.g. Henriksen et al., 2006; Mathews & Richter, 2007). This analysis produces a set of hydrologic alteration values expressed as percent deviation from baseline condition for each analysis node, for each of the hydrologic metrics used to define that river type. These values are then used, along with any additional hydrologic variables of management interest, to develop the flow alteration-ecological response relationships that form a basis for developing environmental flow standards.

The ELOHA process calls for modelling hydrographs at ungauged locations, for both baseline and current conditions. Promising approaches (i.e. that are technically feasible and cost-effective) include catchment rainfall-runoff models that use climate and

landscape data and account for human alterations. For example, the water evaluation and planning system (WEAP; http://weap21.org) is a GIS-based software platform that uses a rainfall-runoff model to generate unimpaired hydrographs. By incorporating operational rules for water infrastructure, it can also generate current condition hydrographs throughout a stream network, allowing questions of environmental flows to be addressed (Vogel et al., 2007; Yates et al., 2009). Another approach, by Kennen et al. (2008), couples runoff modelling for pervious and impervious areas with estimates of annual water extraction, discharges and reservoir storage. This model was used to generate daily hydrographs (current conditions) at ungauged locations throughout New Jersey. It is useful for estimating unimpaired conditions at ungauged locations, degree of hydrologic alteration, and can be adapted to include hydrologic forecasting. Other catchment hydrology models are used to generate and compare unimpaired and human-altered streamflow (e.g. PRMS, HSPF, HEC-HMS, SHE and so on); but many such models are parameter-intensive and can be relatively costly to apply. For a comprehensive description and review of these and other hydrologic models that are applicable to catchment management, refer to Singh & Woolhiser (2002).

Formulating flow alteration-ecological response relationships for environmental flows

A key element in the ELOHA framework is defining relationships between altered flow and ecological characteristics that can be empirically tested with existing and newly collected field data (see Arthington et al., 2006). These relationships are hypothesised to vary among the major river types, as ecological responses to the same kind of flow alteration are expected to depend on the natural (historic) flow regime in a given geomorphic context.

Ideally, the relationships between ecological variables and degrees of flow alteration would be expressed in a fully quantitative manner (i.e. % ecological change in terms of % flow alteration as measured at multiple sites along a flow alteration gradient - e.g. Arthington et al., 2006). However, ecological changes can also be formalised, and empirically tested, when they are expressed as categorical responses (e.g. low, medium, high) or even trajectory of change (+/-). Such categorical or trajectory

relationships can often be robustly defended and provide valuable information in guiding management decisions in many cases (e.g. Arthington *et al.*, 2003; King *et al.*, 2003; King & Brown, 2006; Shafroth *et al.*, 2009).

Developing flow alteration—ecological response hypotheses. In this section, we articulate the principles behind developing testable relationships between ecological variables and flow regime alteration that can serve as a starting point for empirically based flow management at a regional scale. We also point out some key uncertainties in developing such relationships, and we pose these as challenges for near-future environmental flows research.

Riverine scientists possess a very solid, general knowledge of how ecological processes and ecosystem structure and function depend on hydrologic variation. The large literature in hydroecology is comprised of both comparative and experimental studies that relate ecological processes or aspects of ecosystem structure and function to one or more hydrologic variables (see examples below). However, very few studies have been published where ecological metrics have been quantified in response to various degrees of flow alteration per se, because this requires that hydrologic variables be expressed in terms of deviation from some baseline condition for each sampled location, and this has rarely been done (but see Freeman & Marcinek, 2006; Poff & Zimmerman, 2009). Therefore, empirical models that directly predict ecological responses to various types and degrees of flow alteration (the goal of environmental flows science) are not readily available. The development of such models is an important component of the ELOHA framework, and this can be accomplished by posing testable hypotheses based on the many published studies that document the response of ecological processes and patterns to a range of flow conditions, both natural and altered (e.g. Bunn & Arthington, 2002).

A guiding principle for such model development from the existing hydroecological literature is that ecological responses to particular components of the flow regime can be interpreted most robustly when there is some *mechanistic* or *process-based* relationship between the ecological response and the particular flow regime component. Numerous examples exist for many combinations of ecological responses and flow

components (see Poff et al., 1997; Bunn & Arthington, 2002; Nilsson & Svedmark, 2002; Poff & Zimmerman, 2009). For instance, with increasing frequency of high flow disturbances, macroinvertebrate communities shift toward species adapted to high mortality rates, such as those having short life cycles and high mobility (Richards et al., 1997; Townsend, Scarsbrook & Dolédec, 1997). More frequent flow fluctuations or increased stream flashiness (such as induced by operations of hydropower dams or urbanisation) favour fish species with more generalised versus specialised foraging strategies (Poff & Allan, 1995) or that are habitat generalists (Bain, Finn & Booke, 1988; Pusey, Kennard & Arthington, 2000) or that are more tolerant of stressful inter-flood low flow periods (Roy et al., 2005). Prolonged (and unnaturally timed) low flows can dewater floodplain vegetation and cause more drought-tolerant species to replace riparian species (Leenhouts, Stromberg & Scott, 2006) or reduce fast-flow specialist fish species and encourage habitat generalists (Freeman & Marcinek, 2006). Truncation of natural flood peaks can prevent recruitment of indigenous riparian vegetation and allow nonnative trees to become established and proliferate (Stromberg et al., 2007) and can facilitate the proliferation of non-native, flood-intolerant fish species (Meffe, 1984). The natural timing of flood peaks can prevent the establishment of non-native fish (Fausch et al., 2001), whereas the loss of such seasonal flooding can promote success of non-native fish species (Marchetti & Moyle, 2001) and even modify river food webs (Wootton, Parker & Power, 1996). The magnitude of flood peaks can determine the degree of scouring mortality of fish eggs in streambed gravel (Montgomery et al., 1999), and altering the duration of flooding can modify geomorphic processes such as lateral channel migration (Richter & Richter, 2000). In terms of ecosystem processes, magnitudes of transport of nutrients and suspended organic matter are dictated by frequency and duration components of the hydrograph (Doyle et al., 2005). In summary, these clear relationships (and many others) reflect strong linkages between flow and ecological processes in both unmodified and regulated rivers of different types. This information provides a scientifically sound and empirically robust foundation for flow-based management of streams and rivers at regional scales.

The exploration of relationships between flow alteration and ecological responses begins by posing

a series of plausible hypotheses that are based on expert knowledge and understanding of the hydroecological literature. In our experience scientists can readily formulate hypotheses that express testable relationships between flow alteration and ecological changes once they are asked to focus on a limited set of hydrologic variables. Initial hypotheses describing flow alteration-ecological response relationships can usually be generated fairly readily by scientists working together in a well-facilitated, collaborative setting (see Arthington et al., 2004 and Cottingham, Thoms & Quinn, 2002 for comments on expert panel approaches). Indeed, in a workshop among many of

the authors of this paper, we quickly generated a number of process-based hypotheses describing expected trajectories of ecological change associated with specific types of flow alteration based on our collective understanding of the literature (Table 1). Similar and more specific hypotheses can reasonably be developed for particular regions by scientists familiar with the ecology and hydrology of a particular region. Assembling experts to develop flow alterationecological response relationships will also assist scientists in identifying available ecological data sets and in designing monitoring programs or research projects for validating and refining the relationships.

Table 1 Examples of hypotheses to describe expected ecological responses to flow alteration, which were formulated by the authors of this paper during a 2006 workshop

Extreme low flow

Hyp: Depletion of extreme low flows in perennial streams and subsequent drying will lead to rapid loss of diversity and biomass in invertebrates and fish due to declines in wetted riffle habitat, lowered residual pool area/depth when riffles stop flowing, loss of connectivity between viable habitat patches and poor water quality

Hyp: Increased dry-spell duration in dryland or intermittent rivers will lead to reduced diversity and biomass of invertebrates and fish due to reduction in permanent, suitable aquatic habitat

Hyp: Increased duration of extreme low flows will result in riparian canopy die-back in arid to semi-arid landscapes Low flow

Hyp: Depletion of low flows will lead to progressive reduction in total secondary production as habitat area becomes marginal in quality or is lost

Hyp: Augmentation of low flows may lead to an initial increase in total primary and secondary production but this would decline with drowning of productive riffles and/or increased turbidity and decreased light penetration

Hyp: Augmentation of low flows will cause a decline in richness and abundance of species with preferences for slow-flowing, shallow-water habitats, whereas fluvial specialists or obligate rheophilic species would shift in distribution or decline in richness and abundance if low flows were depleted

Hyp: Augmentation of low flows will result in increased establishment and persistence of aquatic and riparian vegetation with concomitant shifts in species distributions towards increased dominance by fewer species

Small floods/high flow pulses

Hyp: Lessened frequency of substrate-disturbing flow events leads to shift to long-lived, large-bodied invertebrate species in non-flashy streams

Hyp: Lessened frequency of substrate-disturbing flow events leads to reduced benthic invertebrate species richness as fine sediments accumulate, blocking substratum interstitial spaces

Hyp: Increased frequency of substrate-disturbing events leads to a shift toward 'weedy' invertebrate species and loss of species with poor re-colonisation ability

Hyp: Increased flood frequency (in channels) will reduce abundance of young-of-the-year fish, but decline in flood frequency would favour flood-intolerant species

Hyp: A decrease in inter-annual variation in flood frequency (i.e. stabilised flows) will lead to a decline in overall fish species richness and riparian vegetation species richness, as habitat diversity is reduced

Hyp: Changes in small flood frequency will lead to changes in channel geometry (dependent upon stream channel materials) Large floods

Hyp: Lessened frequency or extent of floodplain inundation will lead to reduced invertebrate and fish production or biomass due to loss of flooded habitat and food resources supporting growth and recruitment

Hyp: Increases in floodplain inundation frequency will enhance productivity in riparian vegetation species through increased microbial activity and nutrient availability, up to a point of water-logging, after which productivity would decline due to anaerobic soil conditions

Scientists applying ELOHA should formulate similar hypotheses for their region of interest as a first step in developing flow alteration-ecological response relationships. Flow categories based on 'environmental flow components' from Mathews & Richter (2007).

12 *N. L. Poff* et al.

Compiling ecological data to test flow–ecology hypotheses. A great diversity of approaches exists for describing and measuring ecological responses to flow alteration. Ecological indicators (Table 2) may be categorised in a variety of ways: taxonomic identity, level of biological organisation (e.g. population or community), structural contribution (e.g. abundance of individuals or number of species), functional contribution in the system (e.g. trophic level) or traits that reflect adaptation to a dynamic environment (e.g. life-history characteristics or morphological features) and rate of response to temporal change (e.g. how quickly species and communities

respond to environmental change or whether they reflect transient or 'equilibrial' conditions). Additionally, ecological processes and biota may respond to flow alteration either directly (e.g. as a reproductive cue) or indirectly through a water quality or habitat-mediated response (see Bunn & Arthington, 2002 for guiding principles). Indicators of social value may also be used to assess flow alteration. The response times of these multiple possible response variables to flow alteration can vary significantly. For example, mature riparian forests may require decades to respond to a flow alteration (Nilsson & Svedmark, 2002), whereas riparian seedlings and macroinvertebrate

Table 2 Considerations in selecting ecological indicators useful in developing flow alteration-ecological response relationships

Mode of response

Direct response to flow, e.g. spawning or migration

Indirect response to flow, e.g. habitat-mediated

Habitat responses linked to biological changes

Changes in physical (hydraulic) habitat (width-depth ratio, wetted perimeter, pool volume, bed substrate)

Changes in flow-mediated water quality (sediment transport, dissolved oxygen, temperature)

Changes in in-stream cover (e.g. bank undercuts, root masses, woody debris, fallen timber, overhanging vegetation)

Rate of response

Fast versus slow

Fast: appropriate for small, rapidly reproducing, or highly mobile organisms

Slow: long-life span

Transient versus equilibrial

Transient: establishment of tree seedlings, return of long-lived adult fish to potential spawning habitat

Equilibrial: reflect and end-point of 'recovery' to some 'equilibrium' state

Taxonomic groupings

Aquatic vegetation

Riparian vegetation

Macroinvertebrates

Amphibians

Fishes

Terrestrial species (arthropods, birds, water-dependent mammals, etc.)

Composite measures, such as species diversity, Index of Biotic Integrity

Functional attributes

Production

Trophic guilds

Morphological, behavioural, life-history adaptations (e.g. short-lived versus long-lived, reproductive guilds)

Habitat requirements and guilds

Functional diversity and complementarity

Biological level of response (process)

Genetic

Individual (energy budget, growth rates, behaviour, traits)

Population (biomass, recruitment success, mortality rate, abundance, age-class distribution)

Community (composition; dominance; indicator species; species richness, assemblage structure)

Ecosystem function (production, respiration, trophic complexity)

Social value

Fisheries production, clean water and other ecosystem services or economic values

Endangered species

Availability of culturally valued plants and animals or habitats

Recreational opportunities (e.g. rafting, swimming, scenic amenity)

Indigenous cultural values

communities may do so on an annual cycle. Thus, selecting an appropriate suite of ecological indicators should be guided by consideration of the different timeframes within which specific ecological responses occur relative to particular kinds of flow alteration, as well as by the ability to monitor these various responses over time.

Ideal ecological (including habitat) response variables are (i) sensitive to existing or proposed flow alterations; (ii) amenable to validation with monitoring data and (iii) valued by society (e.g. a decrease in fish abundance could substantially affect important protein sources for local communities). While we advocate the use of process-based ecological response variables, some composite ecological indices may be useful as well, since they correlate with human-induced changes in streamflow. Examples include the indices of biotic integrity for fish (e.g. Fausch, Karr & Yant, 1984; Kennard et al., 2006a,b) or benthic invertebrates (e.g. DeGasperi et al., 2009), and the lotic-invertebrate index for flow evaluation scores (e.g. Monk et al., 2007). However, it may be more useful to disaggregate these indices into their component metrics, some of which may represent a mechanistic relationship to flow or habitat. As indicated above, many studies have demonstrated that ecological responses to flow variation and alteration can be inferred when viewed through the prism of the biological attributes of species (e.g. resource and habitat utilisation traits or life-history traits), and species trait databases are now being compiled regionally to globally for macroinvertebrates (e.g. Usseglio-Polatera et al., 2000; Poff et al., 2006b) and fish (Winemiller & Rose, 1992; Welcomme, Winemiller & Cowx, 2006).

In many cases, developing relationships that link flow alteration to habitat response can provide valuable information in developing regional environmental flow criteria. In particular, where biological data and scientific resources are scarce (e.g. in many developing countries), habitat assessments may provide a critical scientific basis for environmental flows. Approaches to linking flow regime alteration to habitat change are relatively well developed (Bovee et al., 1998; Bowen, Bovee & Waddle, 2003; Pasternack, Wang & Merz, 2004; Crowder & Diplas, 2006; Jacobson & Galat, 2006), and they allow some inference about many ecological responses, albeit with some uncertainty (Tharme, 2003; Gippel, 2005). Flowhabitat linkages and their ecological consequences

provide a core component of several existing environmental flow method (e.g. downstream response to imposed flow transformation: Arthington *et al.*, 2003; King *et al.*, 2003).

In general, developing characterisations of hydraulic habitat conditions that can be applied at the regional scale depends substantially on a segmentscale geomorphic sub-classification that resolves river reaches with similar channel morphology. Such geomorphic subtypes would be expected to have similar hydraulic responses to altered flow regimes. Lowintensity hydraulic habitat assessment methods may be applicable to generalise hydraulic habitat relations for specific geomorphic subclasses. For example, Lamouroux (1998), Lamouroux, Souchon & Herouin (1995) and Booker & Acreman (2007) have developed generalised models for depth and velocity at the stream reach scale, and Saraevan & Hardy (2009) present a method for extrapolating reach-specific habitat data to unmeasured reaches throughout a catchment using a process based on hydrologic and geomorphic stratification. Additionally, applications of habitat-based methods like the wetted perimeter approach (Gippel & Stewardson, 1998), PHABSIM (Bovee et al., 1998) or MesoHABSIM (Parasiewicz, 2007) could provide habitat information useful in the ELOHA framework.

Flow alteration-ecological response relationships. The functional relationship between an ecological response and a particular flow alteration can take many forms, as noted by Arthington et al. (2006). Based on current hydroecological understanding, we expect the form of the relationship to vary depending on the selected ecological response variable(s), the specific flow metric(s) and the degree of alteration for a given river type. These relationships could follow a number of functional forms, from monotonic to unimodal to polynomial. Different ecological response variables may increase or decrease with flow alteration, and the functional form of the response may depend on whether flow alteration of a particular flow variable increases or decreases. We illustrate how various ecological responses may vary with specific components of flow alteration in Fig. 3, which presents plausible relationships for three river types (Fig. 4). For each river type the reference condition is represented by the range of natural variation for both the flow variable and the ecological variable of interest, and the ecological response is depicted in terms of deviation from the reference flow condition.

For snowmelt river types (Fig. 3a), the successful recruitment of native riparian trees often depends on seed release being coincident with the timing of flows of sufficient magnitude to raft seeds onto suitable riverbank habitat (e.g. cottonwood in the western North America; Mahoney & Rood, 1998). Some alteration of high flow timing can occur and still coincide with seed release; however, if high flows come earlier than seed release (negative change) or if they are delayed until after seed release (positive change) then recruitment is expected to drop off precipitously in a threshold-type response (Fig. 3a).

In stable groundwater-fed streams, low flows generally have relatively short duration (Poff, 1996). Reducing the duration of low flows in these systems would not be expected to have a large effect on native fish (solid line with no slope in Fig. 3b) because low flow stress is generally transient under natural conditions. By contrast, increasing the duration of low flows could dewater habitat and damage native species (see Moyle et al., 2003), perhaps via a threshold-type reduction (solid step-function line in Fig. 3a). However, the effect could depend on geomorphic context. For example, a river with deep pools would offer refuges for fish during extended low flow periods and thus a more gradual and continuous (linear) ecological response would be expected (dashed line in Fig. 3a).

Third, naturally flashy streams and rivers are typified by high frequency or rapid onset of high flows. Non-native species of fish may fail to establish in such streams if they lack behavioural adaptations to rapid onset of erosive flows (Meffe, 1984) or if the vulnerable juvenile life stage is present during periods of peak flows (Fausch et al., 2001). Figure 3c shows how a reduction in high flow frequency could benefit non-native fish species, possibly as a threshold response by allowing a sufficient number of juveniles to escape mortality and establish large populations. By contrast, increasing high flow frequency would be expected to depress the success of poorly adapted fishes (solid line with negative slope); however, high structural habitat heterogeneity or the presence of withinchannel refuges (pools, backwaters) could provide hydraulic refuges and ameliorate this response (dashed line).

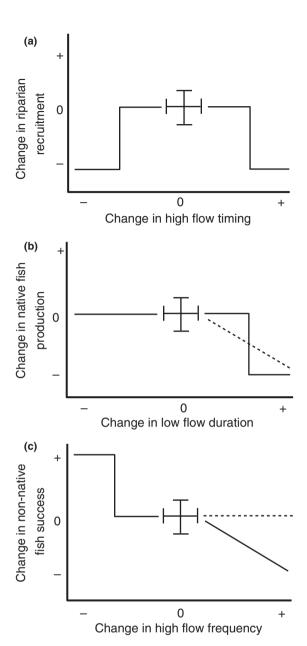


Fig. 3 Illustrative flow alteration–ecological response relationships for each of three river types: (a) snowmelt, (b) groundwater-fed and (c) flashy. For each relationship the change in the flow metric (*X*-axis) ranges from negative to positive with no change representing the reference condition. The response of the ecological variable (*Y*-axis) to the flow alteration across a number of altered sites ranges from low to high. The bracketed space in the centre of the graph represents the natural range of variation in the flow variable and ecological variable in the reference sites. Ecological responses depicted can range in functional form from no change to linear to threshold, depending on the underlying hydroecological mechanisms and, in some cases, on the specific geomorphic context (indicated by dashed line). See text for further explanation and discussion.

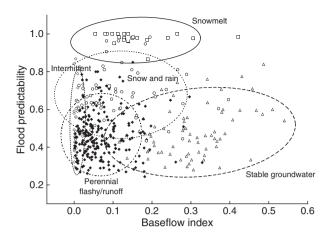


Fig. 4 Plot of five river types in U.S. (modified Olden & Poff, 2003). River types (based on 420 stream gauges) are defined in terms of 11 flow metrics but plotted here in two-dimensional space defined by two of the classification flow metrics (flood predictability and baseflow index). Ellipses reflect 90% confidence intervals and show natural range of variability for the two flow metrics for each of five river types: snowmelt (open squares), snow and rain (open circles), stable groundwater (open triangles), perennial flashy/runoff (closed diamonds) and intermittent (open diamonds – combined harsh intermittent, intermittent flashy and intermittent runoff classes from Poff 1996).

These examples illustrate the process of linking particular ecological responses to specific types of flow alterations in the context of natural flow variability for different river types. The illustrative responses shown in Fig. 3 are expressed as continuous functions; however, they could also be more generally represented as categorical or trajectory responses, which would also represent testable hypotheses of response to hydrologic alteration. Certainly a large possible number of flow alteration-ecological response relationships can be postulated and supported from the scientific literature. For any particular application of ELOHA these will reflect the diversity of river types and ecological response variables of interest in a given region.

One important reason for developing a flow regime classification is that the form and direction of an ecological response to flow alteration is hypothesised to be similar within river types and vary among river types. For example, Fig. 4 shows five river types developed for 420 streams with unmodified flow regimes in the United States (Poff, 1996). The ellipses represent the 90% confidence limits for each river type expressed in terms of two of the flow classification variables (baseflow stability and flood predictability) that are ecologically relevant and amenable to

management action. The size of each ellipse represents the natural range of variation for the river type in this two-dimensional space, and based on these natural differences, we would predict different ecological responses to similar types of flow alteration. For example, the stable groundwater type has a higher degree of baseflow constancy (x-axis) than the perennial flashy/runoff type or the intermittent type. Ecological differences exist between these types of streams (see Poff & Allan, 1995). A flow alteration that introduced fluctuations in baseflow (e.g. below a hydropower dam) would be expected to have a much greater ecological effect in the stable groundwater type than in either of the other two types, because they are already highly variable. Conversely, a stabilisation of baseflow conditions would likely induce a large ecological response in the intermittent and perennial types, but not in the stable groundwater type where baseflows are already relatively constant. On the y-axis of Fig. 4, the snowmelt type is distinguished by having a very predictable timing of peak flow. A loss of this seasonality would be ecologically important for the snowmelt type, and possibly for the snow/rain type, but less so for the perennial or stable groundwater systems where high pulse predictability is naturally low.

Compiling existing data will enable, in many cases, a statistical analysis of the form of the functional responses illustrated in Fig. 3 and a test of the degree to which such responses differ between river types. Exploring these statistical associations will allow identification of critical information gaps and research needs. For example, the ability to detect a threshold versus linear response for some ecological response variable along a flow alteration gradient may be difficult because ecological data are missing within some critical range of flow alteration or because a small sample size has insufficient statistical power to detect a threshold response (see Poff & Zimmerman, 2009). Such initial outcomes can guide strategies for targeting future field data collection at specific points along the flow alteration gradient to resolve key uncertainties (Arthington et al., 2006).

Toward setting environmental flow standards

Functional relationships between flow alteration and ecological responses provide critical input for the broader societally driven process of developing river type specific, regional flow standards (see Fig. 1). We

expect that establishing standards for limiting the degree of each type of flow alteration for different river types will ultimately depend on the ecological goals set for a region's river types, as well as on the 'risk' stakeholders and decision-makers are willing to accept to attain those goals. The degree of acceptable risk is likely to reflect the balance between the perceived value of the ecological goals (e.g. maintenance of fisheries may be of particular interest) and the scientific uncertainties in functional relationships between ecological responses and flow alteration. The benchmarking approach of Arthington et al. (2006) can be adopted to help establish an ecologically and societally acceptable level of risk. For example, where there are clear threshold responses (e.g. overbank flows needed to support riparian vegetation or provide fish access to backwater and floodplain habitat), a benchmark of low ecological risk might allow for hydrologic alteration that does not cross the threshold. For a linear response where there is no clear threshold for demarcating low from high risk, a consensus stakeholder process may be needed to determine acceptable risk. One possible process for setting such risk levels is to use expert panels to identify 'thresholds of potential concern' (Biggs & Rogers, 2003; Acreman et al., 2008), which establish where along the flow alteration gradient there is agreement among stakeholders (including scientists and managers) that further hydrologic change carries with it unacceptably high ecological risk. This approach incorporates scientifically credible professional judgement and includes multiple ecological indicators, as is commonly employed in performing river-specific environmental flow assessments based on expert judgement in South Africa (Brown & Joubert, 2003; Tharme, 2003), Australia (Cottingham et al., 2002; Arthington et al., 2004) and in the Americas (Richter et al., 2006).

We note here that the flow alteration–ecological response relationships developed for various river types can be used by water managers to guide development of flow standards for individual rivers or river segments, or for sub-catchments of individual rivers, not just for entire classes of rivers. Indeed, society may have different ecological goals for different sub-catchments or rivers within a class, and the flow–ecology relationships can support river-specific standard setting by associating different flow targets with different ecological targets.

Challenges of interpreting flow–ecology relationships for water management purposes

In interpreting flow alteration-ecological response relationships, there are some challenges that must be addressed. First, because ecological responses may be expressed in relation to multiple hydrologic drivers, decisions will have to be made about which relationships are the most important or achievable in a particular management context. One possible way to overcome this challenge would be to consider ecological response(s) in terms of some multivariate hydrologic metric(s) that describes overall flow alteration (e.g. using principal components analysis as in Black et al., 2005). Often, however, it will be most desirable to consider ecological responses in terms of independent flow variables that can be directly manipulated in a management context.

Where multiple ecological response-flow alteration relationships are generated, some process will be required to prioritise for management. In the face of multiple possible management targets, 'paralysis' can be avoided by keeping in mind the motivating objectives of the selection process for hydrologic variables. Flow metrics ideally have been selected to capture a range of natural hydrologic variability, to be ecologically relevant and to be amenable to management manipulation. Depending on what the societally acceptable ecological goals are (Fig. 1), we would imagine selecting those relationships that can be mechanistically interpreted, that are known with reasonable confidence, that best define the hydrologic and ecological character of the river type and that are especially sensitive to human alteration. For example, stable groundwater streams (Fig. 4) are likely to be sensitive to increases in baseflow fluctuations and seasonally pulsed systems (e.g. snowmelt) are likely to be very sensitive to altered timing of pulses. Such class-specific metrics could represent priority management targets, all else being equal. However, we also stress that many metrics would ideally be considered if the management goal is to promote broad ecosystem function. Ideally, a parsimonious suite of flow metrics will emerge that collectively depicts the major facets of the flow regime and explains much of the observed variation in ecological response to particular kinds of flow alteration in each river flow type.

Second, development of robust flow alterationecological response relationships will need to take into account the role that other environmental factors play in shaping ecological patterns in streams and rivers. The ecological integrity of rivers is certainly known to reflect factors other than flow regime, such as water quality and habitat structure (Poff et al., 1997; Baron et al., 2002; Kennen et al., 2008; Konrad, Brasher & May, 2008); however, a quantitative understanding of how flow interacts with these other factors is not yet well developed (e.g. Kennard et al., 2007; Stewart-Koster et al., 2007). We view this as an important research frontier in environmental flows. We have attempted to minimise this consideration by calling for a geomorphic sub-stratification within hydrologic classes to assist the translation of streamflows into appropriate hydraulic habitat contexts. However, some accounting of other environmental factors will be necessary in many cases. This could be done either by further stratification (e.g. based on water temperature or water quality; see Olden & Naiman, 2009) or by including additional environmental variables in the flow-ecology models as statistical covariates, which would allow some determination of the independent and interactive effects of flow alteration on ecological processes and metrics.

Learning by doing: the scientist's long-term involvement

An environmental flow 'standard' is a statement of flow regime characteristics needed to achieve a certain desired ecological outcome. In the ELOHA framework, environmental flow standards are determined by combining the scientific understanding of flowecology relationships with a societally defined goal of environmental health and a particular level of risk of ecosystem degradation. Flow standards may take the form of restrictive management thresholds, such as maximum limits of abstraction, or active management thresholds, such as specific flow releases from reservoirs (Acreman & Dunbar, 2004). Attempts to establish such regional standards are evolving in several political jurisdictions in the United States. For example, the State of Michigan has proposed a standard on groundwater pumping that protects fisheries resources for each of 11 classes of streams in the state (MGCAC, 2007). In developing the flowresponse lines in Fig. 5, fisheries ecologists examined

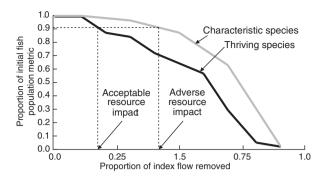


Fig. 5 Progression from flow alteration-ecological response relationships to environmental flow standards (modified from MGCAC, 2007). Using existing fish population data across a gradient of hydrologic alteration, scientists developed two flowecology relationships between populations of 'thriving' and 'characteristic' fish species versus proportion of 'index' flow (median August discharge divided by mean annual discharge) flow reduction in 11 stream types in Michigan, U.S.A. A diverse stakeholder committee then proposed a 10% decline in the thriving fish population index as an acceptable resource impact, and a 10% decline in the characteristic fish population index as an adverse impact. The corresponding flow alteration (X-axis) would trigger environmental flow management actions associated with each of these ecological conditions. The 'ten-percent rule' applies to all of the 11 stream types, but the shapes of the curves - and therefore the allowable degree of hydrologic alteration - vary with stream type.

the range of variation in the biological response across the flow alteration (depletion) gradient and effectively smoothed the statistical scatter to create a trend line with cut-points reached by consensus through a stakeholder process (MGCAC, 2007) comparable to benchmarking (see Arthington *et al.*, 2006).

We recognise that assessing the ecological effects of modified flows is only one part of a complex socioeconomic-environmental process to decide on the use and protection of a region's water resources. The decision to exploit those resources to any particular level is one that will be taken by governments and stakeholders in the context of their perceived priorities for development and sustainability. In essence, a partnership of managers, scientists and those parts of society that will experience the effects of management actions decides on a redistribution of the costs and benefits of water use within the management area (e.g. Naiman, 1992; Poff et al., 2003; King & Brown, 2006; Rogers, 2006). The scientist's role is to support that decision-making process by accurately and usefully communicating the importance of ecosystem

goods and services provided by streams, rivers and wetlands and the ecological and societal consequences that will result from different levels of flow modification represented in the flow—ecology relationships.

Scientists can also assist in implementing flow standards once they have been established. Specifically, the regional approach of ELOHA affords the opportunity to quantitatively incorporate environmental flow standards within integrated water resources and river basin management. ELOHA's hydrologic foundation synthesises all of the controls – both natural and engineered – on streamflow patterns into one usable database. Thus, it can be useful not only for establishing flow-ecology relationships, but also for integrating them into the social decisionmaking process. In principle, scientists and managers could use the hydrologic model to test various stakeholder-developed scenarios for coordinating and optimising all geographically referenced water uses in a basin, while maintaining environmental flows. The model should also be able to incorporate predicted hydrologic impacts of climate change. By accounting for the cumulative effects of all water uses, the model could be used to assess the practical limitations to, and opportunities for, implementing environmental flow targets at multiple nodes simultaneously. This would support efforts to prioritise development of restoration projects, optimise water supply or hydropower generation efficiency, or account for cumulative upstream and downstream impacts in permitting decisions. For basins in which water is already over-allocated, such a model could help target flow restoration options such as dam re-operation, conjunctive management of ground water and surface water, drought management planning, demand management (conservation) and water transactions (e.g. leasing, trading, purchasing, banking).

Finally, scientists must maintain an active role in adaptively managing environmental flows. New information may be required to refine flow alteration–ecological response relationships where few data presently exist, and to extend the relationships in places where climate change and other stressors expand the types and gradients of flow alteration and ecological response. Effective adaptive management means designing, implementing and interpreting research programs to refine flow alteration-ecological response relationships, and ensuring that this new

knowledge translates into updated, implemented flow standards (Poff *et al.*, 2003).

Conclusion

The scientific process and recommendations presented in this paper represent our consensus view for greatly enhancing sustainable management of the world's rivers for ecological and societal benefits in a timely manner and over greater spatial scales than are typically attempted. We recognise that the strength of relationships between flow alteration and ecological response is likely to be subject to various interpretations in many instances. Many relationships are likely to be supported in a trajectory or categorical mode, whereas strong statistical support for incremental or continuous relationships is more difficult to establish. We also recognise that the strength of the relationships necessary to support management or policy action may be a key issue in developing and implementing regional flow guidelines in certain socialpolitical settings.

Despite these acknowledged constraints, the consensus of this group of authors is that the body of scientific knowledge and judgement is strong enough to provide a firm foundation for moving forward. Much remains to be learned, but we know enough to start. One of the key goals of restoration ecology is to 'do no harm' and to attempt to achieve ecosystem selfsustainability through management action (Palmer et al., 2005). The ecological health of the world's riverine ecosystems is presently so threatened that we posit it is in society's best interest to promote regional environmental flow management for freshwater sustainability. Further, through future adaptive learning and research the ELOHA framework can provide a foundation for refining efforts to optimise the tradeoffs inherent between resource exploitation and resource conservation (Dudgeon et al., 2006).

We have emphasised in this paper that scientific knowledge and theory pertaining to flow alteration-ecological response principles has advanced markedly in recent decades, and the calibre of data and 'professional judgement' available to inform relationships between flow alteration and ecological response has vastly improved. Ideally, the ELOHA framework should be used to set initial flow standards that can be updated as more information is collected in an adaptive cycle that continuously engages water

managers, scientists and stakeholders to 'fine tune' regional environmental flow standards (Fig. 1). The process of setting standards during this first iteration should include recognition of knowledge gaps and the need to quantify ecological responses in key areas and in relation to known risk factors. Subsequent iterations will then be informed by more quantified information as needed to satisfy managers and stakeholders. Importantly, we expect that initial applications of the ELOHA framework will greatly help to inform decision-makers and stakeholders about the ecological consequences of flow alteration, and will generate support for the additional data collection needed to further refine the hydrologic foundation, the flow alteration-ecological response relationships and regional environmental flow standards.

Acknowledgments

We thank various members of the Instream Flow Council (of the United States and Canada) for anonymous and constructive comments on an early draft of the manuscript. We also thank J. David Allan and David Dudgeon who provided critical reviews that improved the final version of the manuscript. Thomas Wilding's assistance in collecting reference information is also appreciated.

References

- Acreman M.C. (1998) Principles of water management for people and the environment. In: *Water and Population Dynamics* (Eds A. de Shirbinin & V. Dompka), pp. 25–48. American Association for the Advancement of Science, New York.
- Acreman M.C. (2001) Ethical aspects of water and ecosystems. *Water Policy Journal*, **3**, 257–265.
- Acreman M.C. & Dunbar M.J. (2004) Defining environmental flow requirements a review. *Hydrology and Earth System Sciences*, **8**, 861–876.
- Acreman M.C., Dunbar M.J., Hannaford J. *et al.* (2008) Developing environmental standards for abstractions from UK rivers to implement the EU Water Framework Directive. *Hydrological Sciences Journal*, **53**, 1105–1120.
- Acreman M.C., Aldrick J., Binnie C., Black A.R., Cowx I., Dawson F.H., Dunbar M.J., Extence C., Hannaford J., Harby A., Holmes N.T., Jarrett N., Old G., Peirson G., Webb J. & Wood P.J. (2009) Environmental flows from dams: the water framework directive. *Engineering Sustainability*, **162**, 13–22.

- Annear T., Chisholm I., Beecher H. *et al.* (2004) *Instream Flows for Riverine Resource Stewardship* (revised edn) Instream Flow Council, Cheyenne, WY.
- Arthington A.H. & Pusey B.J. (2003) Flow restoration and protection in Australian Rivers. *River Research and Applications*, **19**, 377–395.
- Arthington A.H., Rall J.L., Kennard M.J. & Pusey B.J. (2003) Environmental flow requirements of fish in Lesotho Rivers using the DRIFT methodology. *River Research and Applications*, **19**, 641–666.
- Arthington A.H., Tharme R., Brizga S.O., Pusey B.J. & Kennard M.J. (2004) Environmental flow assessment with emphasis on holistic methodologies. In: *Proceedings of the Second International Symposium on the Management of Large Rivers for Fisheries*, Vol. II (Eds R. Welcomme & T. Petr), pp. 37–65. RAP Publication 2004/17. FAO Regional Office for Asia and the Pacific, Bangkok.
- Arthington A.H., Bunn S.E., Poff N.L. & Naiman R.J. (2006) The challenge of providing environmental flow rules to sustain river ecosystems. *Ecological Applications*, **16**, 1311–1318.
- Arthington A.H., Baran E., Brown C.A., Dugan P., Halls A.S., King J.M., Minte-Vera C.V., Tharme R.E. & Welcomme R.L. (2007) Water Requirements of Floodplain Rivers and Fisheries: Existing Decision Support Tools and Pathways for Development. Comprehensive Assessment of Water Management in Agriculture Research Report 17. International Water Management Institute, Colombo. Available at: http://www.iwmi.cgiar.org/assessment/files_new/publications/CA%20Research% 20Reports/CARR17.pdf (last accessed on 18 March 2009).
- Bain M.B., Finn J.T. & Booke H.E. (1988) Streamflow regulation and fish community structure. *Ecology*, **69**, 382–392.
- Baron J.S., Poff N.L., Angermeier P.L., Dahm C.N., Gleick P.H., Hairston N.G., Jackson R.B., Johnston C.A., Richter B.D. & Steinman A.D. (2002) Meeting ecological and societal needs for freshwater. *Ecological Applications*, 12, 1247–1260.
- Beighley R.E., Melack J.M. & Dunne T. (2003) Impacts of California's climatic regimes and coastal land use change on streamflow characteristics. *Journal of the American Water Resources Association*, **39**, 1419–1433.
- Biggs H.C. & Rogers K.H. (2003) An adaptive system to link science, monitoring, and management in practice. In: *The Kruger Experience. Ecology and Management of Savanna Heterogeneity* (Eds J.T. du Toit, K.H. Rogers & H.C. Biggs), pp. 59–80. Island Press, Washington, DC.
- Biggs B.J.F., Nikora V.I. & Snelder T.H. (2005) Linking scales of flow variability to lotic ecosystem structure and function. *River Research and Applications*, **21**, 283–298.

- Blöschl G. (2005) Rainfall–runoff modeling of ungauged catchments. In: *Encyclopedia of Hydrological Sciences* (Ed. M. Anderson), John Wiley and Sons; doi: 10.1002/0470848944.hsa 140. Available at http://mrw.interscience.wiley.com/emrw/9780470848944/ehs/article/hsa140/current/abstract (last accessed on 10 March 2009).
- Booker D.J. & Acreman M.C. (2007) Generalisation of physical habitat–discharge relationships. *Hydrology and Earth System Sciences*, **11**, 141–157.
- Bovee K.D., Lamb B.L., Bartholow J.M., Stalnaker C.B., Taylor J. & Henriksen J. (1998) Stream habitat analysis using the instream flow incremental methodology. U.S. Geological Survey, Information and Technology Report. USGS/BRD-1998-0004. 143 pp.
- Bowen Z.H., Bovee K.D. & Waddle T.J. (2003) Effects of flow regulation on shallow-water habitat dynamics and floodplain connectivity. *Transactions of the American Fisheries Society*, **132**, 809–823.
- Brown C.A. & Joubert A. (2003) Using multicriteria analysis to develop environmental flow scenarios for rivers targeted for water resource development. *Water SA*, **29**, 365–374.
- Bunn S.E. & Arthington A.H. (2002) Basic principles and ecological consequences of altered flow regimes for aquatic biodiversity. *Environmental Management*, **30**, 492–507.
- Carlilse D.M., Falcone J., Wolock D.M., Meador M.R. & Norris R.H. (2009) Predicting the natural flow regime: models for assessing hydrological alteration in streams. *River Research and Applications*. Published online in Wiley InterScience (www.interscience.wiley.com) DOI: 10.1002/rra.1247.
- CAWMA (Comprehensive Assessment of Water Management in Agriculture) (2007) Water for Food, Water for Life: A Comprehensive Assessment of Water Management in Agriculture. Earthscan and Colombo: International Water Management Institute, London.
- Cottingham P., Thoms M.C. & Quinn G.P. (2002) Scientific panels and their use in environmental flow assessment in Australia. *Australian Journal of Water Resources*, **5**, 103–111.
- Crowder D.W. & Diplas P. (2006) Applying spatial hydraulic principles to quantify stream habitat. *River Research and Applications*, **22**, 79–89.
- DeGasperi C.L., Berge H.B., Whiting K.R., Burkey J.L., Cassin J.L. & Fuerstenberg R. (2009) Linking hydrologic alteration to biological impairment in urbanizing

- streams of the Puget Lowland, King County, Washington. *Journal of the American Water Resources Association*, **45**, 512–533.
- Doyle M.W., Stanley E.H., Strayer D.L., Jacobson R.B. & Schmidt J.C. (2005) Effective discharge analysis of ecological processes in streams. *Water Resources Research*, **41**, W11411; doi:10.1029/2005WR004222.
- Duan Q., Schaake J., Andreassian V. *et al.* (2006) Model parameter estimation experiment (MOPEX): an overview of science strategy and major results from the second and third workshops. *Journal of Hydrology*, **320**, 3–17.
- Dudgeon D., Arthington A.H., Gessner M.O. *et al.* (2006) Freshwater biodiversity: importance, threats, status and conservation challenges. *Biological Review*, **81**, 163–182.
- Dyson M., Bergkamp M. & Scanlon J. (2003) Flow: The Essentials of Environmental Flows. IUCN, Gland, Switzerland, Cambridge.
- Fausch K.D., Karr J.R. & Yant P.R. (1984) Regional application of an index of biotic integrity based on stream fish communities. *Transactions of the American Fisheries Society*, **113**, 39–55.
- Fausch K.D., Taniguchi Y., Nakano S., Grossman G.D. & Townsend C.R. (2001) Flood disturbance regimes influence rainbow trout invasion success among five Holarctic regions. *Ecological Applications*, 11, 1438–1455.
- Freeman M.C. & Marcinek P.A. (2006) Fish assemblage responses to water withdrawals and water supply reservoirs in piedmont streams. *Environmental Management*, **38**, 435–450.
- Gippel C.J. (2005) Environmental flows: managing hydrological environments. In: *Encyclopedia of Hydrological Sciences* (Ed. M.G. Anderson), pp. 1–19. John Wiley and Sons, New York.
- Gippel C.J. & Stewardson M.J. (1998) Use of wetted perimeter in defining minimum environmental flows. *Regulated Rivers: Research and Management*, **14**, 53–67.
- Gleick P.H. (2003) Global freshwater resources: soft-path solutions for the 21st century. *Science*, **302**, 1524–1528.
- (GWSP) Global Water System Project (2005) Science Framework and Implementation Activities. ESSP Report No. 3, Earth System Science Partnership. Available at: http://www.gwsp.org/products.html (last accessed on 18 March 2009).
- Harris N.M., Gurnell A.M., Hannah D.M. & Petts G.E. (2000) Classification of river regimes: a context for hydroecology. *Hydrological Processes*, **14**, 2831–2848.
- Henriksen J.A., Heasley J., Kennen J.G. & Nieswand S. (2006) Users' Manual for the Hydroecological Integrity Assessment Process Software (Including the New Jersey Assessment Tools). Open-File Report 2006-1093. U.S. Geological Survey, Fort Collins Science Center, Fort Collins, CO.

- Higgins J.V., Bryer M.T., Khoury M.L. & Fitzhugh T.W. (2005) A freshwater classification approach for biodiversity conservation planning. *Conservation Biology*, 19, 1–14.
- Jacobson R.B. & Galat D.L. (2006) Flow and form in rehabilitation of large-river ecosystems: an example from the Lower Missouri River. *Geomorphology*, 77, 249–269.
- Kennard M.J., Harch B.D., Pusey B.J. & Arthington A.H. (2006a) Accurately defining the reference condition for summary biotic metrics: a comparison of four approaches. *Hydrobiologia*, 572, 151–170.
- Kennard M.J., Pusey B.J., Arthington A.H., Harch B.D. & Mackay S.J. (2006b) Development and application of a predictive model of freshwater fish assemblage composition to evaluate river health in eastern Australia. *Hydrobiologia*, **572**, 33–57.
- Kennard M.J., Olden J.D., Arthington A.H., Pusey B.J. & Poff N.L. (2007) Multiscale effects of flow regime and habitat and their interaction on fish assemblage structure in eastern Australia. *Canadian Journal of Fisheries and Aquatic Sciences*, **64**, 1346–1359.
- Kennard M.J., Pusey B.J., Olden J.D., Mackay S.J., Stein J.L. & Marsh N. (2009) Classification of natural flow regimes in Australia to support environmental flow management. *Freshwater Biology*, doi: 10.1111/j.1365-2427.2009.02307.x.
- Kennen J.G., Henriksen J.A. & Nieswand S.P. (2007) Development of the Hydroecological Integrity Assessment Process for Determining Environmental Flows for New Jersey Streams. Scientific Investigations Report 2007-5206. US Geological Survey, New Jersey Water Science Center. Available at: http://pubs.er.usgs.gov/usgspubs/sir/sir20075206 (last accessed on 18 March 2009).
- Kennen J.G., Kauffman L.J., Ayers M.A. & Wolock D.M. (2008) Use of an integrated flow model to estimate ecologically relevant hydrologic characteristics at stream biomonitoring sites. *Ecological Modelling*, **211**, 57–76.
- Kennen J.G., Henriksen J.A., Heasley J., Cade B.S. & Terrell J.W. (2009) *Application of the Hydroecological Integrity Assessment Process for Missouri Streams*. U.S. Geological Survey Open File Report. U.S. Geological Survey, Fort Collins Science Center, Fort Collins, CO. (in press).
- King J. & Brown C. (2006) Environmental flows: striking the balance between development and resource protection. *Ecology and Society*, **11**, 26.
- King J., Brown C. & Sabet H. (2003) A scenario-based holistic approach to environmental flow assessments for rivers. *River Research and Applications*, **19**, 619–639.
- Kite G.W. (2000) Developing a Hydrological Model for the Mekong Basin: Impacts of Basin Development on Fisheries Productivity. IWMI Working Paper 2. International Water Management Institute, Colombo.

- Konrad C.P., Brasher A.M.D. & May J.T. (2008) Assessing streamflow characteristics as limiting factors on benthic invertebrate assemblages in streams across the western United States. *Freshwater Biology*, **53**, 1983–1998.
- Lamouroux N. (1998) Depth probability distributions in stream reaches. *Journal of Hydraulic Engineering*, **124**, 224–227.
- Lamouroux N., Souchon Y. & Herouin E. (1995) Predicting velocity frequency distributions in stream reaches. *Water Resources Research*, **31**, 2367–2376.
- Leenhouts J.M., Stromberg J.C. & Scott R.L. (2006) Hydrologic Requirements of and Consumptive Ground-Water Use by Riparian Vegetation Along the San Pedro River, Arizona. Scientific Investigations Report 2005– 5163. U.S. Geological Survey, Arizona Water Science Center, Tucson.
- Lins H.F. & Slack J.R. (1999) Streamflow trends in the United States. *Geophysical Research Letters*, **26**, 227–230.
- Lytle D.A. & Poff N.L. (2004) Adaptation to natural flow regimes. *Trends in Ecology and Evolution*, **19**, 94–100.
- Mahoney J.M. & Rood S.B. (1998) Streamflow requirements for cottonwood seedling recruitment an integrative model. *Wetlands*, **18**, 634–645.
- Marchetti M.P. & Moyle P.B. (2001) Effects of flow regime on fish assemblages in a regulated California stream. *Ecological Applications*, **11**, 530–539.
- Mathews R. & Richter B. (2007) Application of the Indicators of Hydrologic Alteration software in environmental flow-setting. *Journal of the American Water Resources Association*, **43**, 1–14.
- McCabe G.J. & Wolock D.M. (2002) A step increase in streamflow in the conterminous United States. *Geophysical Research Letters*, **29**, 2185–2188.
- Meffe G.K. (1984) Effects of abiotic disturbance on coexistence of predator–prey fish species. *Ecology*, **65**, 1525–1534.
- MGCAC (Michigan Groundwater Conservation Advisory Council) (2007) Report to the Michigan Legislature in Response to Public Act 34. Groundwater Conservation Advisory Council, Department of Environmental Quality, MI. Available at: http://www.michigan.gov/documents/deq/Groundwater_report_206809_7.pdf. (last accessed on 18 March 2009).
- Millennium Ecosystem Assessment (2003) *Ecosystems and Human Well-Being: A Framework for Assessment*. Island Press, Washington, DC.
- Millennium Ecosystem Assessment (2005) Millennium Ecosystem Assessment Synthesis Report. Island Press, Washington, DC.
- Monk W.A., Wood P.J., Hannah D.M. & Wilson D.A. (2007) Selection of river flow indices for the assessment

- Montgomery D.R., Beamer E.M., Pess G.R. & Quinn T.P. (1999) Channel type and salmonid spawning distribution and abundance. *Canadian Journal of Fisheries and Aquatic Sciences*, **56**, 377–387.
- Moyle P.B., Crain P.K., Whiener K. & Mount J.F. (2003) Alien fishes in natural streams: fish distribution, assemblage structure, and conservation in the Cosumnes River, California, U.S.A. *Environmental Biology of Fishes* **68**, 143–162.
- Naiman R.J. (1992) New perspectives for watershed management. In: *Watershed Management: Balancing Sustainability and Environmental Change* (Ed. R.J. Naiman), pp. 3–11. Springer-Verlag, New York.
- Naiman R.J., Bunn S.E., Nilsson C., Petts G.E., Pinay G. & Thompson L.C. (2002) Legitimizing fluvial ecosystems as users of water: an overview. *Environmental Management*, **30**, 455–467.
- Nilsson C. & Svedmark M. (2002) Basic principles and ecological consequences of changing water regimes: riparian plant communities. *Environmental Manage*ment, 30, 468–480.
- (NSTC) National Science and Technology Council (2004) Science and Technology to Support Fresh Water Availability in the United States. Committee on Environment and Natural Resources, Subcommittee on Water Availability and Quantity. Executive Office of The President Washington DC National Science And Technology Council, Washington, DC.
- Olden J.D. & Naiman R.J. (2009) Broadening the science of environmental flows: managing riverine thermal regimes for ecosystem integrity. *Freshwater Biology*, doi: 10.1111/j.1365-2427.2009.02279.x.
- Olden J.D. & Poff N.L. (2003) Redundancy and the choice of hydrologic indices for characterizing streamflow regimes. *River Research and Applications*, **19**, 101–121
- Palmer M.A., Bernhardt E., Chornesky E. et al. (2004) Ecology for a crowded planet. Science, 304, 1251–1252.
- Palmer M.A., Bernhardt E.S., Allan J.D. *et al.* (2005) Standards for ecologically successful river restoration. *Journal of Applied Ecology*, **42**, 208–217.
- Palmer M.A., Reidy Liermann C.A., Nilsson C., Flörke M., Alcamo J., Lake P.S. & Bond N. (2008) Climate change and the world's river basins: anticipating management options. *Frontiers in Ecology and the Environment*, **6**, 81–89.
- Parasiewicz P. (2007) Using MesoHABSIM to develop reference habitat template and ecological management scenarios. *River Research and Applications*, **23**, 924–932.
- Pasternack G.B., Wang C.L. & Merz J.E. (2004) Application of a 2D hydrodynamic model to design of

- reach-scale spawning gravel replenishment on the Mokelumne River, California. *River Research and Applications*, **20**, 205–225.
- Petts G.E. (1996) Water allocation to protect instream flows. *Regulated Rivers Research & Management*, **12**, 353–365.
- Poff N.L. (1996) A hydrogeography of unregulated streams in the United States and an examination of scale-dependence in some hydrological descriptors. *Freshwater Biology*, **36**, 71–91.
- Poff N.L. (2009) Managing for variation to sustain freshwater ecosystems. *Journal of Water Resources Planning and Management*, **135**, 1–4.
- Poff N.L. & Allan J.D. (1995) Functional organization of stream fish assemblages in relation to hydrologic variability. *Ecology*, **76**, 606–627.
- Poff N.L. & Ward J.V. (1989) Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences*, **46**, 1805–1818.
- Poff N.L. & Zimmerman J.K. (2009) Ecological responses to altered flow regimes: a literature review to inform environmental flows science and management. *Freshwater Biology*, doi: 10.1111/j.1365-2427.2009.02272.x.
- Poff N.L., Allan J.D., Bain M.B., Karr J.R., Prestegaard K.L., Richter B.D., Sparks R.E. & Stromberg J.C. (1997) The natural flow regime: a paradigm for river conservation and restoration. *BioScience*, 47, 769– 784
- Poff N.L., Allan J.D., Palmer M.A., Hart D.D., Richter B.D., Arthington A.H., Rogers K.H., Meyer J.L. & Stanford J.A. (2003) River flows and water wars: emerging science for environmental decision making. Frontiers in Ecology and the Environment, 1, 298–306.
- Poff N.L., Olden J.D., Pepin D.M. & Bledsloe B.D. (2006a) Placing global stream flow variability in geographic and geomorphic contexts. *River Research and Applications*, **22**, 149–166.
- Poff N.L., Olden J.D., Vieira N.K.M., Finn D.S., Simmons M.P. & Kondratieff B.C. (2006b) Functional trait niches of North American lotic insects: trait-based ecological applications in light of phylogenetic relationships. *Journal of the North American Benthological Society*, 25, 730–755.
- Postel S. & Carpenter S. (1997) Freshwater ecosystem services. In: *Nature's Services: Societal Dependence on Natural Ecosystems* (Ed. G.C. Daily), pp. 195–214. Island Press, Washington, DC.
- Postel S. & Richter B. (2003) Rivers for Life: Managing Water for People and Nature. Island Press, Washington, DC.

- Power M.E., Sun A., Parker G., Dietrich W.E. & Wootton J.T. (1995) Hydraulic food-chain models. *BioScience*, **45**, 159–167.
- Puckridge J.T., Sheldon F., Walke R.K.F. & Boulton A.J. (1998) Flow variability and the ecology of large rivers. *Marine and Freshwater Research*, **49**, 55–72.
- Pusey B.J., Kennard M.J. & Arthington A.H. (2000) Discharge variability and development of predictive models relating stream fish assemblage structure to habitat in north-eastern Australia. *Ecology of Freshwater Fish*, **9**, 30–50.
- Richards C., Haro J., Johnson L.B. & Host G.E. (1997) Catchment and reach-scale properties as indicators of macroinvertebrate species traits. *Freshwater Biology*, 37, 219–230.
- Richter B.D. & Richter H.E. (2000) Prescribing flood regimes to sustain riparian ecosystems along meandering rivers. Conservation Biology, 14, 1467–1478.
- Richter B., Baumgartner J.V., Powell J. & Braun D.P. (1996) A method for assessing hydrologic alteration within ecosystems. *Conservation Biology*, **10**, 1163–1174.
- Richter B.D., Warner A.T., Meyer J.L. & Lutz K. (2006) A collaborative and adaptive process for developing environmental flow recommendations. *River Research and Applications*, **22**, 297–318.
- Rogers K.H. (2006) The real river management challenge: integrating scientists, stakeholders and service agencies. *River Research and Applications*, **22**, 269–280.
- Roy A.H., Freeman M.C., Freeman B.J., Wenger S.J., Ensign W.E. & Meyer J.L. (2005) Investigating hydrologic alteration as a mechanism of fish assemblage shifts in urbanizing streams. *Journal of the North American Benthological Society*, **24**, 656–678.
- Sanborn S.C. & Bledsoe B.P. (2006) Predicting streamflow regime metrics for ungaged streams in Colarado, Washington, and Oregon. *Journal of Hydrology*, **325**, 241–261.
- Saraeva E. & Hardy T.B. (2009) Extrapolation of site-specific weighted usable area curves and instream flow requirements to unmeasured streams within the Nooksack watershed in support of strategic watershed planning. *International Journal of River Basin Management*, 7, 91–103.
- Schaake J., Duan Q., Andreassian V., Franks S., Hall A. & Leavesley G. (2006) The model parameter estimation experiment (MOPEX). *Journal of Hydrology*, **320**, 1–2.
- Seelbach P.W., Wiley M.J., Kotanchik J.C. & Baker M.E. (1997) A Landscape-Based Ecological Classification System for River Valley Segments in Lower Michigan (MI-VSEC Version 1.0). Fisheries Research Report 2036. Michigan Department of Natural Resources, Ann Arbor, MI.

- Shafroth P.B., Wilcox A.C., Lytle D.A., Hickey J.T., Andersen D.C., Beauchamp V.B., Hautzinger A., McMullen L.E. & Warner A. (2009) Ecosystem effects of environmental flows: modelling and experimental floods in a dryland river. *Freshwater Biology*, doi: 10.1111/j.1365-2427.2009.02271.x.
- Singh V.P. & Woolhiser D.A. (2002) Mathematical modeling of watershed hydrology. *Journal of Hydrologic Engineering*, 7, 270–292.
- Snelder T.H. & Biggs B.J.F. (2002) Multiscale river environment classification for water resources management. *Journal of the American Water Resources Association*, 38, 1225–1239.
- Snelder T.H., Biggs B.J.F. & Wood R.A. (2005) Improved eco-hydrological classification of rivers. *River Research and Applications*, **21**, 609–628.
- Stewart-Koster B., Kennard M.J., Harch B.D., Sheldon F., Arthington A.H. & Pusey B.J. (2007) Partitioning the variation in stream fish assemblages within a spatiotemporal hierarchy. *Marine and Freshwater Research*, **58**, 675–686.
- Stoddard J.L., Larsen D.P., Hawkins C.P., Johnson R.K. & Norris R.H. (2006) Setting expectations for the ecological condition of streams: the concept of reference condition. *Ecological Applications*, **16**, 1267–1276.
- Stromberg J.C., Beauchamp V.B., Dixon M.D., Lite S.J. & Paradzick C. (2007) Importance of low-flow and high-flow characteristics to restoration of riparian vegetation along rivers in arid south-western United States. *Freshwater Biology*, **52**, 651–679.
- Stuckey M.H. (2006) Low-Flow, Base-Flow, and Mean-Flow Regression Equations for Pennsylvania Streams. Survey Scientific Investigations Report 2006-5130. U.S. Geological Survey, Reston, VI.
- Tharme R.E. (2003) A global perspective on environmental flow assessment: emerging trends in the development and application of environmental flow methodologies for rivers. *River Research and Applications*, **19**, 397–441.
- Townsend C., Scarsbrook M. & Dolédec S. (1997) Quantifying disturbance in streams: alternative measures of disturbance in relation to macroinvertebrate species traits and species richness. *Journal of the North American Benthological Society*, **16**, 531–544.
- Usseglio-Polatera P., Bournaud M., Richoux P. & Tachet H. (2000) Biological and ecological traits of benthic freshwater macroinvertebrates: relationships and definition of groups with similar traits. *Freshwater Biology*, **43**, 175–205.
- Vaughan I.P., Diamond M., Gurnell A.M., Hall K.A., Jenkins A., Milner N.J., Naylor L.A., Dear D.A., Woodward G. & Ormerod S.J. (2009) Integrating ecology with hydromorphology: a priority for river

- science and management. *Aquatic Conservation-Marine* and *Freshwater Ecosystems*, **19**, 113–125.
- Vogel R., Sieber J., Archfield S., Smith M., Apse C. & Huber-Lee A. (2007) Relations among storage, yield and instream flow. *Water Resources Research*, **43**, W05403; doi: 10.1029/2006WR005226.
- Vörösmarty C.J., Green P., Salisbury J. & Lammers R. (2000) Global water resources: vulnerability from climate change and population growth. *Science*, **289**, 284–288.
- Wagener T., Wheater H.S. & Gupta H.V. (2004) Rainfall— Runoff Modeling in Gauged and Ungauged Catchments. Imperial College Press, London.
- Walker K.F., Sheldon F. & Puckridge J.T. (1995) A perspective on dryland river ecosystems. *Regulated Rivers: Research and Management*, **11**, 85–104.
- Welcomme R.L., Winemiller K.O. & Cowx I.G. (2006) Fish environmental guilds as a tool for assessment of ecological condition of rivers. *River Research and Applications*, **22**, 377–396.

- Winemiller K.O. & Rose K.A. (1992) Patterns of lifehistory diversification in North American fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences*, **49**, 2196–2218.
- Wootton J.T., Parker M.S. & Power M.E. (1996) Effects of disturbance on river food webs. Science, 273, 1558–1561.
- Yates D., Purkey D., Sieber J., Huber-Lee A., Hector Galbraith., West J. & Herrod-Julius S. (2009) A climatically driven, water resource planning model of the Sacramento Basin, California USA. *ASCE Journal of Water Resources Planning and Management* (in press).
- Zhang Z., Wagener T., Reed P. & Bhushan R. (2008) Ensemble streamflow predictions in ungauged basins combining hydrologic indices regionalization and multiobjective optimization. *Water Resources Research*, 44, W00B04; doi: 10.1029/2008WR006833.

(Manuscript accepted 11 February 2009)