INSTREAM-FLOW SCIENCE FOR SUSTAINABLE RIVER MANAGEMENT

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INTRODUCTION

After fifty years of international concern about the ecological impacts of flow alteration and 30 years of research to advance the science of instream flows (hereinafter referred to as *e-flows*) there is evidence to suggest that a pivotal point has been reached in (i) acknowledging the importance of conserving riverine ecosystems and (ii) the need to allocate water for environmental needs. The history has been reviewed by many authors in research monographs (e.g. Petts,1984), academic handbooks for practitioners (e.g. Petts and Maddock (1994), Stalnaker (1994); in-depth academic reviews (e.g. Petts, 2007), critical case studies (e.g. on the Klamath River Basin, USA, NRC, 2008) and major works aimed at promoting the *e-flows* agenda to a wider audience (Postel and Richter,2003; Annear et al., 2004). This history highlights the separate developments in physical and biological sciences and the progressive acceleration of research effort and innovation in advancing tools for setting *e-flows* to regulate rivers and manage water abstractions (withdrawals).

It is now widely accepted that human water demands must be balanced with the needs of rivers themselves but tensions in water-resource allocation are intensifying. This is not only because of growing human demands, especially for food and energy security, but also because of uncertainties in the face of climate change and in our knowledge of the water needs of riverine ecosystems. In this context, the conservation of biodiversity, improvement in ecosystem health, and restoration of ecosystem integrity are rarely prioritized by governments even though they may be embedded in strategy documents (Petts et al., 2000). Estimates suggest that by 2050 many countries will face water scarcity, placing increasing pressures on the water-dependent ecosystems of rivers and estuaries.

The fear of flood and drought, concern for food and energy security, and the priority to

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advance ‘limitless economies’ that drove water-resource development 50 years ago (Thomas 1956, p 408) continue to relegate the conservation of riverine ecosystems to ‘luxury’ status in setting political agendas. Technological solutions to water shortage involving ‘control by construction’, with large dams, major abstractions and inter-basin transfers, remain at the heart of water-resources planning. In such cases, determination of the water volume or ‘reserve’ to provide a flow regime that will conserve water-dependent ecosystems is central to sustainable water resources management. These determinations are also critical in high-level decisions about national and regional investments such as in desalination to supply the growing maritime urban conurbations and in the ‘virtual water’ of international and regional food trade to reduce unsustainable irrigation agriculture in dry regions (Rogers, 2008). Such investments could reduce demands on the ‘fluvial resource’ and increase the potential water allocations to protect riverine ecosystems. A 21st century ‘*e-flows* imperative’ has evolved as confidence has grown in our scientific knowledge, from experience of applying scientifically-informed tools, and from increasingly detailed and quantitative analyses of the ecological effects of flow regulation and abstraction. This paper offers a critical and international state-of-the-science perspective to place this ‘*e-flows* imperative’ in context.

THE BIRTH OF INSTREAM-FLOW SCIENCE

The principle of managing river flows to sustain river ecology, particularly populations of migratory fish, has been embedded in legislation within many developed nations for more than 100 years. In the UK, Private Acts towards the end of the 19th century made provision for flows below dams, taking account of navigation, public health, the rights of downstream users, and the protection of fisheries (Sheail, 1984, 1988). The Water Resources Act 1963 required the River Authorities to set ‘minimum acceptable flows’ (MAFS) and since then all new abstraction licenses have contained conditions to protect the water environment where necessary (Petts, 1996). These conditions include ‘hands-off’ flows that require abstractions to cease when flows fall below a specified level, and ‘maintained flows’ that under certain low flow conditions require river support by groundwater pumping or reservoir releases. Despite early ecological studies that demonstrated the importance of flow, through to the 1970s instream-flow recommendations were based on the ‘professional judgement’ of a biologist or engineer rather than on a quantified evaluation of the relationships between discharge and the ecology of a stream (Fraser, 1972). Thus, protection for fish was provided by a defined ‘minimum flow’, often a fixed percentage of average flows (typically 20% of the daily average flow (Baxter 1961; Tennant, 1976) or, as in the UK for example, a low-flow duration statistic, the 95th percentile flow. This latter is significant because the ratio of Q_{95} to the mean flow varies in relation to the flow regime of natural rivers (typically in the range 10% to 40%).

The roots of instream-flow science are found in (i) the quantification of the spatial and temporal variations of fundamental hydraulic parameters (flow velocity, depth, width) with changing discharge pioneered by Leopold and Maddock (1953) and (ii) the conceptualisation of ecological responses to these variations advanced by Hynes (1970). These, driven by the widespread adoption of general systems theory, advances of measurement techniques and quantitative methods throughout the natural sciences during the 1960s, paved the way for the introduction of new concepts that focused on the multivariate and dynamic character of environmental systems. Gill’s (1971) theoretical assessment of the long-term influence of river impoundment on the ecology of the Mackenzie River Delta and the detailed analysis of the influence of the Vir Valley reservoir on the ecology of the Svratka river, Czechoslovakia (Penaz et al, 1968) clearly established the need for an interdisciplinary and integrated approach to understanding key relationships between hydrology and ecology.

During the second half of the 1970s, papers on two themes developed the core of the emerging science of instream flows: (1) the ecological effects of dams (Armitage 1976; Ward, 1976) and (2) the role of the flood regime in sustaining the fisheries of large rivers (Welcomme, 1979). But it was *‘The Ecology of Regulated Streams’* (Ward and Stanford, 1979) that provided the catalyst for international, inter-disciplinary advances. Thirty years later, the basic knowledge needed to formulate policy decisions and management approaches on water allocations to meet environmental needs along rivers have been elaborated.

The ecological integrity of riverine ecosystems depends on their natural dynamic character (Poff et al., 1997). The fundamental ecological principle for the sustainable management of riverine ecosystems is the need to sustain *flow variability* that mimics the natural, climatically-driven variability of flows at least from year to year and from season to season, if not from day to day (Naiman et al. (2002). Thus, the two fundamental general principles are:

1. the natural flow regime shapes the evolution of aquatic biota and ecological processes;

2. every river has a characteristic flow regime and an associated biotic community.

However, the linkages between flow regime and ecological health are complex in both time and space. The 'natural dynamic character' relates to flow variability; water quality, especially temperature variations; sediment dynamics and channel dynamics (that are also influenced by patterns of woody vegetation growth); changes in food/energy supply; and interactions between biological populations. This level of complexity over decadal timescales has frustrated scientific developments. Nevertheless, Bunn and Arthington (2002) summarized this complexity as four specific principles for advancing the provision of environmental flows:

i) Flow is a major determinant of physical habitat in rivers, which in turn is a major determinant of biotic composition.
ii) Maintenance of the natural pattern of habitat connectivity (a) along a river and (b) between a river and its riparian zone and floodplain is essential to the viability of populations of many riverine species.
iii) Aquatic species have evolved life history strategies primarily in response to the habitats that are available at different times of the year and in both wet and dry years.
iv) The invasion and success of exotic and introduced species along river corridors is facilitated by flow regulation, especially with the loss of natural wet-dry cycles.

IN SEARCH OF TOOLS FOR WATER RESOURCES MANAGEMENT

Ward and Stanford's 1979 volume not only demonstrated the magnitude of world-wide stream regulation but also proposed directions for future scientific investigations on stream ecosystems altered by upstream impoundments. In that volume, Stalnaker's (1979) review of the emerging work of the Cooperative Instream Flow Service Group (CIFSG) had a major impact on the development of instream-flow research internationally. Their Instream Flow Incremental Methodology (IFIM) evolved as a flexible process for identifying, evaluating and comparing potential solutions to water allocation conflicts. It integrated planning concepts of water supply, hydrological time series, and analytical hydraulic and water quality models with empirically-derived habitat versus flow functions designed to assist in formulating and evaluating alternatives. For the first time, the approach explicitly linked physical habitat (hydraulic) simulation with habitat evaluation criteria for species and life stages to display changing habitat usability with flow. This was based in part on the developing predictions of instream flow needs for biota in rivers regulated by dams (Bovee, 1978; Gore 1978). These introduced ‘habitat suitability criteria’ based on the assumption that individuals of a species tend to select the most favorable conditions in a stream but will also use less favourable conditions, with the preference for use decreasing where conditions are less favourable. This concept has been aggressively challenged over the past 30 years but these challenges proved an important stimulus to advancing new science. The step-change in scientific endeavour was driven by a practical need: the threat to fisheries posed by application of a single minimum flow as the basis for issuing water permits in many of the states in USA (Stalnaker, 1994) and other countries throughout the developed world. The motivation was formally established in the USA at a multi-disciplinary symposium significantly co-sponsored by the American Fisheries Society and American Society of Civil Engineers (Osborn and Allman, 1976).

The Global Impact of PHABSIM

At the core of IFIM is the principle that physical habitat attributes provide an index of suitability for biota. Physical HABitat SIMulation (PHABSIM) integrates the changing hydraulic conditions with discharge and the habitat preferences of one or more selected species. The method relies on three principles: the chosen species exhibits preferences within a range of habitat conditions that it can tolerate; these ranges can be defined for each species; and the area of stream providing these conditions can be quantified as a function of discharge and channel structure. In the majority of PHABSIM applications, instream-flow guidelines have focused on the needs of a single species, usually a salmon or trout, although more advanced approaches considered the needs of different life stages.

PHABSIM requires quality input data and this is often time consuming and expensive to obtain. The output is location specific. Nevertheless, PHABSIM has been supported in a legal context, has had widespread application as a management tool, and has provided ecologists with a voice in water-resource decision making in more than 20 countries (Tharme, 2003). The primary approach uses a simple 1-D hydraulic model but this fails to predict spatial patterns of velocity in natural rivers, although they are useful for determining average velocity variations with changing discharge. However, this weakness has been overcome by the increasing use of 2-D hydraulic models that can describe the spatial and temporal heterogeneity of hydraulic conditions and provide a link to meso-habitat patterns (Bovee 1996, Hardy 1998, Stewart et al., 2005, Crowder and Diplas, 2006).

The scientific weaknesses of PHABSIM have attracted considerable attention but the popularity of the tool world-wide has given impetus to new research directed at establishing and understanding flow-biota relationships. Considerable efforts have been spent on attempts to assess the ecological credibility of PHABSIM by demonstrating the biological significance of 'carrying capacity' as a limiting factor of population size (Lamouroux et al., 1999; Kondolf et al., 2000). However, validation of the approach in biological terms has proved difficult not least in establishing discrete relationships between biological populations and the Weighted Usable Area (WUA) from empirically-derived habitat suitability curves. The biomass of a species or life stage within a community can vary because of biological processes such as reproduction, energetics and mortality that may be influenced by one or more unspecified environmental factors. Indeed, the quality of the habitat suitability criteria may have the strongest influence on output quality. Simple indices based on frequency of occurrence of actual habitat conditions used by a target organism in a particular reach have been criticized as too simplistic; composite indices that combine habitat use or preference indices also involve many assumptions (Bovee, 1986; Vadas and Orth, 2001; Ahmadi-Nedushan et al., 2006). Such challenges continue to stimulate new research on biological responses, not least on the behavior of biota to flow variations. From a practical perspective, there is no doubt that the accumulated experience of using PHABSIM means its strengths and weaknesses are well understood.

DEVELOPMENTS IN INSTREAM-FLOW TOOLS

Most instream-flow tools are built on a more or less complex physical element that uses hydrological or hydraulic data that have, or are assumed to have, biological significance. Some methods benchmark regulated rivers against natural ones using paired rivers or reaches, or historical (pre-impact) or naturalised data series. Many of these are also dependent upon empirical data on the range of preferred to unsuitable habitat conditions for a target species, or life stage, and assume that spatially-derived habitat suitability criteria are transferable to predict biotic responses to flow changes over time.

Societal demands for river ecosystem protection have accelerated the development of innovative, locally-applicable methods and tools especially within regions having limited databases. However, there are also many examples where sophisticated, science-based models are being applied to specific problems. For example, Grand et al (2006) used a cell-based model of backwater geometry, a pond-based temperature model and a model of invertebrate production to investigate the effects of within-day flow fluctuations caused by hydro-power operations on nursery habitats for larval and juvenile Cororado pikeminnow (*Ptychocheilus lucius*) along the Green River below Flaming Gorge dam, USA. At the other extreme, Liu et al. (in press) addressed the urgent need to set seasonal instream ecological flows along the intensively regulated Huai River, China, in the face of limited hydrological and ecological data, by developing a novel and pragmatic solution to determining monthly instream ecological water-levels for four morphologically different reaches using the Manning equation and hydraulic rating based on generalised cross-sections, and available data on fish spawning habitat.

Tharme (2003) identified over 200 approaches that have been described for advising on environmental flows in 44 countries. On the one hand, the 21st century *e-flows* imperative has led to particularly innovative approaches for setting environmental flows in ungauged catchments and along rivers having limited data, and for tools and methods that can be applied at low cost. On the other hand, increasing concerns about limits to available water resources have required greater certainty in determinations of water allocations to protect riverine ecosystems. By the early 1990s, approaches had expanded from the determination of instream flows to environmental flows. Although today the terms are confounded. Many schemes now addressed wider issues than instream-flow needs – the hydraulic habitats - of one or a few species. These new approaches increasingly addressed the sustainability of communities and ecosystems within the whole river corridor. They incorporated the access of aquatic biota to seasonal floodplain and riparian habitats as well as the need for high flows for riparian species and floods to sustain the geomorphological dynamics of the river corridor (RRA, 2003). They also focused on the determination of ecologically acceptable flow regimes (e.g. Petts, 1994; Petts et al., 1996). From a scientific perspective, this challenged scientists not only to determine the magnitude of ecologically significant flows for different times of the year (the benchmark flows) that are then integrated to establish ecologically-acceptable annual hydrographs. It also required consideration of flow frequency and the ecological significance of different time-series of hydrological events over a period of years. The combination of ecologically-acceptable hydrographs for 'normal', 'wet' and 'dry' year scenarios, of particular frequency, is needed to establish ecologically-acceptable flow duration curves. The benchmark flows inform short-term and local operational rules; the hydrographs inform seasonal and short series of annual flow management; and the duration curves inform long-term water resource planning.

The scientific imperative to set environmental flows has progressed by advancing two types of tools: hydrological approaches and habitat approaches. But the imperative to set flow regulation rules has also led to the rise in popularity of scientifically-informed expert panel assessments.

Hydrological approaches involve analysis of historical daily flow records. Flow is considered as a simple proxy for a number of related parameters which may have a key influence on habitat. The rationale is that hydrological approaches support the fundamental ecological principle for sustainable water resources management: namely, the need to sustain flows that mimic the natural, climatically driven variability. Such approaches also move attention away from fish to consider the range of aquatic, wetland and riparian habitats along the river corridor. Two issues often hinder the apparently simple and reasonable application of hydrological approaches. First, standards need to be set to apply an appropriate record length with at least 12 years being required for statistical integrity but longer records may be needed to incorporate variable weather patterns over decadal timescales (e.g. Kelly and Gore, 2007). Second is the issue of 'naturalizing' the gauged flow regime. In many areas the pristine catchment has no relevance to the modern day. The hydrology of catchments characterized by long-term human interference – such as urban conurbations and intensive agriculture – bears little resemblance to the hydrologic character of unmodified catchments in a given ecoregion. The concept for such catchments may be to produce functionally diverse, self-regulating ecological systems that provide medium-term enhancements and allow longer-term catchment-scale planning (Petts et al., 2000). In reality this requires determination of the flow regime that would be sustained under current or future catchment conditions in the absence of existing dams, reservoirs, diversions and abstractions.

Richter et al (1996) introduced the 'Indicators of Hydrologic Alteration' (IHA) method which uses a range of hydrologic parameters for each year of flow record to characterize inter-annual variation before (reference period) and after flow regulation/abstraction. The IHA method has been shown to successfully characterize all of the major components of the flow regime (Olden and Poff, 2003) and the selection of key hydrologic parameters may be adapted to local circumstances. Richter et al (1997) proposed that the statistical characterization of ecologically-relevant hydrograph parameters could define the variability of the dimensions of the flow regime within which artificial influences should be contained. Thus, for example, Galat and Lipkin (2000) for the Missouri River, recommended changes in reservoir management to return the regulated flows to within the pattern of natural variability, thereby simulating a natural riverine ecosystem. They argued that naturalization of the flow regime would not only benefit the ecological system but also the economic value of the river, once the products of agriculture, electric-power generation and transportation are integrated with the socio-ecological benefits of a naturalized flow regime.

A focus on flow regimes has also spawned new research tools and new efforts to illuminate the significance of specific flows for biota. One example of the former is the use of wavelet analysis to assess dam operations in reconstructing desired flow characteristics (White et al. 2005) and analyzing temperature changes (Steel and Lange, 2007). The wavelet analysis provides an easy-to-interpret approach for investigating hydrological change when the management history is uncertain and time scales of important cycles are unknown. It allows examination of a range of temporal scales simultaneously and independently. An example of the second is research by Wood et al (2001) that isolated the significance of late-winter/spring high flows – especially the lack of these high flows in drought years – for the summer macroinvertebrate community in a temperate groundwater-dominated stream in England. Extending this work, Monk et al (2006) advanced a flow variability approach that used a 20-year paired flow and macroinvertebrate survey record for 83 rivers in England and Wales to highlight the ecological importance of (i) monthly flows, and (ii) the magnitude and duration of annual extreme flow conditions. In England and Wales, a LIFE (Lotic Invertebrate Index for Flow Evaluation; Extence et al., 1999) has been developed, utilizing an extensive database from two decades of ecological surveys, to assess biotic responses to flow based on species- and family-level preferences for flow velocity conditions, recognizing that some families include taxa with variable flow requirements. LIFE is used to identify sites subject to stress, such as from abstraction. Using the PCA-based method of Olden and Poff (1983), Monk et al., (2007) showed LIFE scores to be particularly sensitive to changes in runoff (mean annual discharge per unit catchment area) within two of the three flow regime types identified for England and Wales.

Habitat approaches assume that biological communities have evolved to exploit the full range of meso-habitats; the variability of flows determining when and for how long meso-habitats are available to different species at different locations throughout the stream network. Each meso-habitat (termed biotope or functional unit in some studies) is a definable area such as a pool, riffle or run that can be inferred by visual observation of surface flow character and verified by hydraulic measurements and qualitiative or quantitative substratum types (Armitage et al., 1995; Newson and

Newson 2000). Habitat duration curves provide summary statistics on average habitat availability and these could be developed to consider periods of habitat persistence related to key biological time-windows. As noted by Parasiewicz (2001) if community structure reflects habitat structure then securing habitat for the most common species might preserve the most profound characteristics of the ecosystem and provide survival conditions for the majority of the aquatic community.

The flooding regime leads to a particular configuration of aquatic and riparian habitats but the process of habitat creation and destruction results from the balance between rejuvenating flooding events and habitat stabilization and decay. Habitat turnover may be high along natural river corridors but at the sector scale (a geomorphologically distinctive river segment often of ca. 10 km in length) the composition and configuration of habitats remains relative stable (Arscott *et al*., 2002), providing a continuity of habitat associations that are available to sustain biotic populations. Thus, at this spatial scale, the dynamics of habitat turnover may be ignored for the purpose of exploring habitat-biota relationships over short timescales (say < 5 years). Within such timescales, instream hydraulics and, for marginal and riparian species, the frequency and duration of inundation/dessication are the dominant factors determining the physical environment in which organisms live.

Many species have evolved or developed physiological or behavioral characteristics and strategies for utilizing particular habitats differently in rivers having different flow regimes (e.g. Adis and Junk, 2002). However, there are few studies that attempt to model hydrological variability and river hydrodynamics in relation to species populations or the fluxes which determine dispersal triggers, lifecycle patterns and drift densities of the instream fauna (Bunn and Arthington, 2002; Poff et al., 1997).

Attempts to argue the biological significance of meso-scale hydraulic habitat surveys appear premature although mesohabitat approaches can consider multiple species and community structure. A rational framework for modelling fish community response to changing habitat conditions developed by Bain and Meixler (2008) is appropriate for integrating with physical habitat modelling (Parasiewicz, 2008b). In any case, the attractiveness of the meso-habitat approach for managers is its practicality (Newson et al., 1998) and arguments to optimize habitat diversity across a range of flows have been promoted (e.g. Dyer and Thoms 2006).

Parasiewicz (2003) advanced a PHABSIM derivative, Meso-HABSIM, to map mesohabitats at different flows along extensive sections of a river, to establish the suitability of each mesohabitat for the dominant members of the fish community, and to derive rating curves to describe changes in relative areas of suitable habitat in response to flow. MesoHABSIM focuses on mesoscale approaches to build on strengths of PHABSIM protocols while providing options for addressing large spatial scales appropriate for water resource planning (Jacobson, 2008). The fish collection survey is the most effort-intensive component of MesoHABSIM but literature-based evidence and expert opinion can be used and a 'regional' approach allows transfer of habitat use models among rivers of similar 'type' (Parasiewicz, 2007).

Science-informed Panel Assessments. During the 1980s in the US incremental methods provided the evidence for negotiation among interest groups and to decision-makers for resolving conflicts (Stalnaker, 1994). A multi-use ethic had evolved shifting focus from minimum flows to a 'conservation' water budget and involving interdisciplinary teams managing flows in real time for people, habitats, fish and wildlife. IFIM became a multi-objective planning exercise for the benefit of the range of stakeholders; it is heavily reliant on professional judgement to identify the 'best' alternative and involved group planning to enable a negotiated resolution process. It also gained a perception of being too data- and time-intensive and too expensive. In many countries the pace of reform of water policy (e.g. Australia), and/or the lack of scientific data, and political pressure to deliver environmental flow recommendations in short time frames (often less than one year) and at low cost, has seen authorities rely heavily on multi-disciplinary expert panels to assess environmental flow needs (Cottingham et al., 2002; Young et al., 2004) and to define regional *e-flow* standards (Acreman et al., in press; Poff et al., in press).

King et al., (2003) have attempted to link the productivity of large floodplain rivers to their flow characteristics using a value-based system, DRIFT (Downstream Response to Imposed Flow Transformation). This provides a data-management tool for many types and sources of information, predictive models, theoretical principles and 'expert knowledge' of a panel of scientists. Arthington et al., (2003) applied DRIFT to establish environmental flow requirements of fish in Lesotho rivers and contend that the methodology can provide a Best Practice Framework for conducting scientific panel studies, although they acknowledge that a number of risks with the approach remain.

The 21st Century *e-flows* imperative is built on confidence in scientific understanding together with evidence from experience gained in practice and includes the setting of environmental flow standards at regional scales. In the UK, driven by the EU Water Framework Directive that requires all Member States to begin the process to maintain or restore all surface water bodies to Good

Ecological Status by 2015, an 'expert panels' approach has been used to determine levels of 'acceptable abstraction' in relation to the 'ecological sensitivity' of river reaches. This has been built on two elements: consistent river classification, this being already embedded within the abstraction licensing scheme for England and Wales, and regional standards based upon a river typology (Acreman et al., in press). In the US, Poff et al., (in press) achieved a consensus view from a panel of international scientists on a framework for assessing environmental flow needs that combines a regional hydrological approach and ecological response relationships for each river type based initially on the literature, existing data, and expert knowledge. Stakeholders and decision-makers then explicitly evaluate acceptable risk as a balance between perceived value of the ecological goals, the economic costs involved, and the scientific uncertainties. New approaches to numerical processing of qualitative knowledge of experts, using a fuzzy rule-based approach for developing composite Habitat Suitability Indices that incorporates multivariate effects of variables without needing to assume independence of the input parameters, offers potential for demonstrating objective and rigorous basis of HSIs from expert judgement (Ahmadi-Nedushan et al., 2008).

A FUTURE FOR INSTREAM-FLOW SCIENCE

Despite considerable efforts to develop the science of *e-flows*, a deterministic model of ecosystem health remains elusive (Petts et al., 2006). A survey of the most recent 200 articles published in *River Research and Applications* (volume 22, 2006) shows that 39% of the papers offered new scientific insights of habitat or biological dynamics. Another 9% advanced new research tools and 12% elaborated case studies of human impacts (dams, diversions, abstractions (withdrawals), channel engineering schemes etc.). Papers specifically on instream flows comprised 28% of the total with 10% being experimental studies. A further 12% focused on new tools for instream flow studies. Perhaps the most notable feature has been the emergence of detailed monitoring studies of 'controlled' restoration projects, representing 40% of the instream-flow papers. The lessons learned from these will have significance for adaptive approaches although the transferability of these lessons remains to be tested.

The premise that healthy river ecosystems depend on maintaining the flow variability characteristic of each particular ecoregion is widely accepted (Naiman et al., 2002). But a fundamental understanding of the ways in which physical and biological processes interact to sustain the ecological integrity of rivers and streams remains to be elucidated. There is an urgent need to determine the variability of key abiotic parameters over a range of spatial scales, to measure and model the effects of these variations upon biota, habitats and ecosystems, to understand the timescales and mechanisms of ecosystem response to hydrological change, and to advance models for healthy rivers in 'developed' catchment contexts. The European Aquatic Modelling Network has reviewed the state of the art in data sampling, modelling analysis and applications of river habitat modelling (RRA, 2007). They discuss research needed to improve and develop new methods and models of assessing interactions between aquatic biota and riverine habitats, such as winter conditions for fish (Huuska et al., 2007); demonstration of the possible gains for both fish condition and hydropower production of managing flow and water temperature in a dynamic way (Halleraker et al., 2007); mesohabitat methods to assess flow change (Harby et al., 2007b); and the use of 3-D, Weighted Usable Volumes to replace WUA (Mouton et al., 2007).

Three broad areas of scientific advancement are necessary to improve confidence in *e-flow* science: understanding climatic cycles, cycles of channel change and population dynamics and then the integration of this new knowledge into river ecosystem models. A fourth need is to develop a common framework that integrates physical (hydrological and hydraulic) and biological processes (Petts et al., 2006).

Climate cycles. Improved understanding of the relationships between atmospheric circulation, climate, and streamflow is vital given the great importance of fluvial processes to natural systems and water resources, especially in the light of recent and predicted climate change (Kingston et al., 2000). The El Nino-Southern Oscillation (ENSO) is known to significantly influence climate variability around the globe, not least in semi-arid regions (Molles, Dahm and Crocker, 1992; Molles and Dahm, 1990) and the processes linking southern low and high latitudes are increasingly understood (e.g. Housego et al., 2000). Around the North Atlantic, particular attention has been paid to the climatic and hydrologic implications of the North Atlantic Oscillation (NAO) and Arctic Oscillation (AO) (Kelly and Gore, 2007). The need to develop analyses of more hydrologically meaningful climate variables beyond conventional time-averaged statistics is deemed particularly important. In one approach, the classification of flow regime shape (form) and magnitude considers the whole annual cycle rather than isolating a single month or season for analysis, which has been the common approach of previous studies (Harris et al., 2000). This classification method is particularly useful for identifying large-scale patterns in flow regimes and their between-year stability, thus providing an important context for short-term, small-scale process-based research. Bower et al. (2004) developed and tested this approach to identify spatial and temporal patterns in intra-annual hydroclimatological response. Further, they introduced a novel sensitivity index (*SI*) to assess river flow regimes' climatic sensitivity. These techniques were evaluated by application to a 25-year (1974-1999) time-series of river flow, air temperature and rainfall for a sample of 35 UK river basins.

Geomorphological cycles. Improved knowledge of the roles of channel dynamics over decadal timescales is required to develop realistic models of riverine ecosystems. Along large rivers in natural settings within most biogeographical regions, channel morphology is determined by the interplay of valley gradient and width, flood magnitude and frequency, sediment supply, and the growth of woody vegetation. Patterns of channel development related to climatic fluctuations, variations in sediment delivery from sub-catchments and riparian woodland development must be assessed in order to understand the dynamic baseline. 'Cycles' of channel development may be initiated by catastrophic inputs of sediments and wood, associated with natural fires or landslips, or phases of high sediment delivery from tributary basins that drive periods of aggradation along the main channel. Biological factors may also induce morphological cycles. Although flow resistance initially increase from early- to mid-successional stages, as vegetation ages and stem density decreases, vegetation may become less effective at providing flow resistance so that the geomorphological threshold for erosion could decline over time (McKenney et al., 1995). Vegetation plays an active role in developing heterogeneous channel forms through (a) biotic processes such as seed dispersal, vegetative regeneration and succession and (b) abiotic effects such as increasing flow resistance inducing sedimentation and decreasing bank erodibility. Wooded islands are characteristic of some sectors along many natural rivers and these sectors have particularly high species richness (Gurnell et al., 2005). However, the natural influences of flood disturbance, wood accumulation, vegetation growth, island development and tree die-off cause island-dominated reaches to undergo cycles of island growth and decay that are related to cycles of aquatic habitat diversification and simplification (Gurnell and Petts, 2002).

Biological dynamics. It is clear that river hydrodynamics affect aquatic organisms in various ways. The effect on each individual depends on its particular characteristics (e.g. physiology) and consequently it varies with species, and even within single species it may vary with life stage and between rivers with different flow regimes, where organisms develop in environments with different stresses. Because populations vary over differing time scales, ranging from instantaneous mortality due to intolerable environmental conditions, seasonal variations due to reproduction and migration patterns, and cycles dictated by the typical life spans of the organisms, the overall effect of a given environmental condition may not be immediately apparent. It will, however, be evident as a long-term legacy on community distribution and functioning (e.g. Strayer et al., 2004).

It is clear that major advances in understanding require long-term and coupled hydrological, hydraulic (reflecting the dynamics of channel morphology) and biological datasets from relatively undisturbed catchments. Understanding biological responses to habitat temporal variability is needed to identify the magnitude, duration and frequency of habitat-limiting periods or carrying capacity (Capra et al., 1995). Recent models of responses of trout populations to flow variability has suggested the importance of winter flows in determining recruitment (Cattaneo et al., 2002; Lobon-Cervia, 2003; Mitzo et al., 2003), summer low flows that limit adult trout biomass, and spring flows that limit the young-of-the-year numbers between emergence and their first summer (Sabaton et al., 1997; Gourand et al. 2001). For floodplain rivers, Halls and Welcomme (2004) used an age-structured population dynamics model, incorporating density-dependent growth, mortality and recruitment to show that exploitable biomass of a common floodplain fish species is maximized by minimizing the rate of flood recession and maximizing the flood duration and area inundated. Such models are useful for developing and testing concepts, but their role as management tools remains limited until they can be validated by empirical studies involving multi-site sampling.

Convergence of traditions. The different traditions and conventions used by hydrologists, hydraulic engineers and freshwater biologists exacerbates the difficulties of developing a common science framework. Physical scientists are developing suites of increasingly sophisticated tools that can be used (i) to predict river stage, velocity fields, and bedform as a function of discharge, (ii) to predict velocity and shear stress at multiple points within the river channel, and (iii) to simulate the bulk flow of water at a resolution sufficient to route stage and various conservative and non-conservative constituents. These tools simulate processes that can be approximated by the Eulerian-based approach of discretizing complex geometries with a grid (or mesh) and then applying sets of governing equations to each node, and they work well for simulating processes that are easy to aggregate into control volumes, such as water flow or water quality (e.g. Clifford et al 2006). Ecologists continue to make conceptual advances through empirical descriptions of how important riverine processes vary over time and space and these are being used to set general guidelines for conservation action on individual rivers (e.g. Richter *et al*., 1996; 1997). Such approaches are very useful from a heuristic or theoretical standpoint, but cannot be used *a priori* to address many river management issues, as they are insufficiently quantitative at the scale at which management decisions are often made (Petts et al., 2006).

There is a need, therefore, to promote the development of integrated approaches that will allow the tools of physical and biological scientists to be coupled together. A key factor is providing an appropriate representation for each ecosystem element contained in the model, and as each element may involve processes with markedly different scales of variation in time and space, the best results are often obtained by applying different simulation approaches for each element (Nestler *et al*., 2005). For example, environmental conditions, commonly defined in terms of river hydrodynamics and water quality, can be simulated appropriately with Eulerian models. The value of a given environmental condition for the population can be simulated by a habitat suitability model and the response of the population to environmental conditions can be simulated with a population dynamics model. New approaches (Mynett, 2004) include spatially explicit models, such as cellular automata, which simulate population dynamics as the large-scale effect of local interactions between neighboring cells in a lattice, and individual-based models that simulate population dynamics as the result of local interactions between individuals and between individuals and their environment.

An approach to integrating physical and biological models has been demonstrated by Morales et al (2006a) for the analysis of freshwater mussel communities. The approach is 3-dimensional, coupled to physical hydrodynamic models and is species specific. The model uses data on river hydrodynamics, substrate composition, water quality, and fish distribution within a river reach. It applies deterministic habitat suitability rules derived from quantitative information on population distribution and habitat use, incorporating seasonal variations, to compute the distribution of suitable habitats. Then an individual-based model simulates the population response to environmental conditions in terms of mortality, food competition, growth, reproduction, larvae and juvenile dispersion, and the movement of juvenile and adults in search of suitable habitats. These functional processes are simulated by applying traditional ecological concepts, like the basic bioenergetics equation, and novel ideas like adapting principles from sediment transport to simulate the passive dispersion of mussel larvae with the flow (Morales et al. 2006a). Thus, knowledge and information about the biology of mussels has been coupled with fundamental principles describing the dynamics of the physical system, to assess the overall evolution of the mussel population in space and time in a 10-km reach of the Upper Mississippi River (Morales *et al*., 2006b).

CONCLUSIONS

In most parts of the world, the 21st century has witnessed a recognition by governmental organizations of the *e-flows* imperative to sustain healthy riverine ecosystems. This requires maintenance of 'an appropriate', 'ecologically-acceptable' flow regime and tools to determine environmental water allocations: 'appropriate' and 'acceptable' volumes available for abstraction and 'rules' to regulate abstractions and flows along rivers. Over the past 50 years there has been steady progress in developing models of ecological dynamics in relation to flow. The introduction of PHABSIM in the late 1970s stimulated a generation of innovation and scientific advancement in response to both its perceived strengths, particularly its interdisciplinary focus, and scientific limitations. Then there was a second phase of innovation from the mid-late 1990s in response to the *e-flows* imperative, with two distinct strands to develop (i) locally-appropriate tools especially for ungauged rivers and (ii) 'holistic' approaches that seek to advance scientifically-informed decision-support systems, building on the framework established by the IFIM. This most recent phase of innovation has been driven by a need to develop environmental standards and the realization that there is a lack of data on many rivers to determine empirical or more sophisticated mathematical models of river flow and ecological status.

But increasingly a gap has been widening between the rate of progress in advancing *e-flow* science and the massive growth of international effort that is increasingly dominated by site- and often species-specific empirical studies although the quality of the coupled datasets is improving. Emphasis on field-based empirical studies leading to the development of ideas and concepts in descriptive terms is appropriate because of the number of assumptions required to produce more sophisticated models. However, such studies should be advanced as the natural precursor to experimental and theoretical investigations that seek to elaborate the natural generating mechanisms for the patterns or anomalies illuminated by empirical studies. Too often they are presented as ends in themselves. In the physical sciences, mechanistic hydrodynamic modelling is being increasingly used for predicting velocity and depth patterns in rivers from detailed surveys of channel morphology but these are often inappropriate for management purposes not least because predictive ecology is not sufficiently advanced to benefit from the detailed, spatially-explicit information provided by hydrodynamic simulations (Schweizer et al., 2007). Nevertheless, a key component of the necessarily long-term vision must be the development of models to evaluate the complex effects of changes in hydrological regime upon habitats, communities and species, and their interactions.

'How much water does a river ecosystem need?' remains a challenging question. What we now know is that it requires understanding of the direct and indirect interactions between flows and biota over a range of time and space scales. It requires consideration of the flow variability over tens of years; it involves consideration of sector-scale habitat mosaics and micro-scale hydraulics. We know that fluvial systems are highly dynamic and respond to changes in flows and water levels in complex ways, and that changes caused by human impacts can be cumulative and may be irreversible. From a scientific perspective, advances are required to integrate human and environmental water needs in river management through commitment to long-term research designed to better describe abiotic–biotic responses using coupled datasets and coupled analyses at the level of ''first principles'' level in an hypothesis-testing setting. The incorporation of climate variations, cycles of channel change, and improved population models over decadal timescales is needed to advance realistic models of riverine ecosystems. Recent scientific advances have been inspired by the *e-flo*ws imperative and the inadequacies or inappropriateness of the tools previously derived but the independence of physical scientists and biologists also remains a major constraint. From a management perspective, there is still an infatuation with maximizing economic yield and a belief that technology provides the solution to environmental risks; to educate politicians and the public about the importance of *variability* in sustaining riverine ecosystems, and the benefits of floods, droughts and moving channels, is a major challenge that remains to be addressed.

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