

Salmonids and flows: a perspective on the state of the science and its application

N. J. MILNER

APEM Ltd, School of Biological Sciences Bangor, Bangor University, Bangor, UK

I. G. COWX

Hull International Fisheries Institute, University of Hull, Hull, UK

K. F. WHELAN

Atlantic Salmon Trust, Perth, UK

Abstract Water flow, volume discharge per unit time, is a master variable influencing much of the river environment and having profound effects on most of the biota, either directly or indirectly. Nevertheless, after decades of research and much accumulated knowledge, there remains much uncertainty about how to set environmental standards for flows that protect ecosystem components, including salmonids. This paper provides an overview of the findings of a conference on *Flows and Salmonids*. The aim of the conference and the papers that form this special issue is to update this information for salmonids, from which four key points are distilled that might influence future direction. (1) Fish responses to flow are very variable and flow effects are highly confounded with other related variables, which are often the proximate factors and need to be taken into account. (2) Meta-analysis of previous studies has yet to be achieved because a hydromorphological template against which to gather and display such data has not yet been satisfactorily defined. (3) Some deviation from natural conditions may not necessarily be as detrimental for salmonids as sometimes stated. (4) Local investigations of flow impacts and solutions based on local conditions, and bringing in diverse disciplines and stakeholders, appear to offer the most pragmatic and effective approach to defining and implementing protective flows. Adaptive management offers a route for such collaborative studies, and its use is strongly encouraged.

KEY WORDS: adaptive management, ecosystems, fisheries, river flows, standards.

Introduction

The flow of water down rivers is a master variable influencing the structure of channels, aquatic ecosystem function and the ecological adaptations of riverine biota (Arthington *et al.* 2006, 2010). The removal of water and the modification of flow patterns are two of man's oldest and potentially most damaging impacts on the aquatic environment and are rapidly increasing because of the growing demands on water resources for supply, energy production and agricultural and industrial expansion as well as flood alleviation (Postel *et al.* 1996). Therefore, of all environmental impacts, river flow and

its modifications should be a focus for freshwater ecology and subject to well-understood, scientifically based management. However, the contemporary debate over how best to protect rivers, through flow standards or other approaches (e.g. Acreman & Dunbar 2004; Souchon *et al.* 2008; Poff *et al.* 2010), is testament that this is only an emerging science. There are some fundamental differences in approach to establishing the flow requirements of fish, exemplified by the debate over the merits of the instream flow incremental methodology (IFIM) family of hydraulic, habitat-based, empirical methods (e.g. Dunbar *et al.* 2012) vs those promoting the maximisation of fitness through foraging and ener-

Correspondence: Nigel Milner, APEM Ltd, School of Biological Sciences, Bangor University, Brambell Building, Deiniol Rd, Bangor LL57 2UW, UK (e-mail: n.milner@apemltd.co.uk)

getics processes governing habitat patch quality (e.g. Armstrong & Nislow 2012), but both camps note the opportunities for combined approaches. Uncertainties over the science and considerable knowledge gaps have affected capacity to implement flow management at least in the United Kingdom, but the problems may go deeper. Raven (2006) drew attention to the apparent demise of freshwater ecological sciences in the British Isles, representing a systemic change in science direction and funding. On the other hand, the (almost) synonymous topics of hydroecology, ecohydrology and ecohydromorphology are now acquiring status as a single discipline (here we call it hydroecology, following Wood *et al.* 2007) in its own right (Zalewski 2002; Wood *et al.* 2007; Vaughan *et al.* 2009; Newson *et al.* 2012), and this bodes well. The imperative for good understanding and management of river flows has never been stronger, so now is a good opportunity to review the position and to push for the collaboration and resources that are widely recognised as necessary to improve knowledge and practice.

The debate over flow management in the United Kingdom has accelerated in the last 20 years because of changing legislation (principally the EU Water Framework Directive (WFD, 2000/60/EC), the increasing demand for water and renewable energy sources and the impact of climate change (Bowles & Henderson 2012; Mainstone *et al.* 2012). Consequently, tensions over allocation of water supply amongst consumptive, renewable energy and conservation purposes are high and increasing. The symposium and workshop organised by the Atlantic Salmon Trust in York, UK in 2010 (<http://www.atlanticsalmontrust.org/assets/flows-workshop-report.pdf>), the source of the papers in this edition, provided an opportunity to review the state of the science behind flow management for salmonids in the British Isles. This paper summarises the key findings and conclusions of this symposium.

The search for simplicity in a complex environment

The need to convey environmental protection and flow regulation through legislation has understandably brought a tendency to simplify, for example, by reducing the continuous diversity of river types into river typologies (see Noble *et al.* 2007; Schmutz *et al.* 2007; Cowx *et al.* 2012) and by reducing the continua of biotic flow responses to class intervals and thresholds that are expected to transfer across the infinite variety of channel morphologies and environmental circumstances. Some classification is necessary reductionism, and the WFD ecological status classes offer structure to huge natural

complexity that is essential for regulation. However, in the case of WFD flow standards (Acreman *et al.* 2008, 2009), simplicity has not brought benefits because their effectiveness is contested, particularly in the context of heavily modified water bodies (HMWBs) where the artificial flow regimes distort the normal associations between channel morphology, hydrological regimes and ecology (Acreman *et al.* 2009; Acreman & Ferguson 2010). Therefore, a first principle is to acknowledge and work with the natural complexity, where appropriate, rather than try to tame it by over-reductionist classifications and universal standards. This brings not only biological realism, but also difficulties of specifying systematically the ecological outcome of flow management, coupled with the resource issues of having to develop multiple models in site- or region-specific contexts. Some balance is required, but this has not yet been satisfactorily met.

Salmonids in ecosystems

The focus of this symposium and workshop was on migratory salmonids, which raises the questions: can individual species be considered in isolation from other ecosystem components and how representative are salmonids of ecosystem sensitivity in their relevant river types? There are good reasons to suggest that they may be good ecological indicators. Migratory salmonids occupy dispersed habitats at widely contrasting scales during their life cycle (Armstrong & Nislow 2012; Malcolm *et al.* 2012), and are dependent upon suitable flow and morphological conditions throughout the rivers and estuaries that they inhabit (Bendall *et al.* 2012; Dunbar *et al.* 2012; Milner *et al.* 2012; Newson *et al.* 2012). There are demonstrable, if inconsistent, dependences between fish and other trophic levels (Kelly-Quinn 1990; Power 1992; Orth 1995), but if prescribed flow regimes protect salmonids will they protect other components of the ecosystems and offer indicator value? The answer is a tentative 'generally yes, but not all', although this remains to be tested. Irrespective of the general attributes of salmonids as bioindicators, pragmatically they are unquestionably important as a major interest in water use disputes where their fisheries are involved. Moreover, they have considerable conservation value, and salmon is an Annex II listed species under the EU Habitats Directive (Council Directive 92/43/EEC of 21 May 1992 on the conservation of natural habitats and of wild fauna and flora).

Modern approaches to environmental assessment through ecosystem services analysis (MEA 2005; Watson & Albon 2011) are bringing a requirement to understand how salmonids link with other ecosystem

components, and one framework for this is their role as predators and prey in riverine food webs. Although there are many emerging theories (Orth 1995; Poff & Huryn 1998), this is a poorly researched field, but one that is becoming increasingly important (Power & Dietrich 2002; Woodward & Hildrew 2002; Vaughan *et al.* 2009). A consequence of this prospect is that the metrics appropriate for defining ecological status, *sensu* WFD, may need to extend beyond conventional abundance or biomass measures to include the emergent properties of populations and communities, such as lifetime fitness, resilience and energy flow.

The natural flow paradigm

The idea that riverine ecological processes and organisms are adapted to river structure and natural flow regimes is an exemplar of basic ecological theory and is not new (e.g. Hynes 1970; Ward & Stanford 1979; Vannote *et al.* 1980), but the formal incorporation of hydroecology into flow management has been comparatively recent (Petts 2007). Poff *et al.* (1997) spelt out the natural flow paradigm, which led to the concept of environmental flows (Richter & Thomas 2007) that identifies the components of natural hydrographs important for maintaining all biota life stages. This approach is the basis of the 'Building Block Methodology' [BBM] (Tharme 2003; Arthington *et al.* 2006; King *et al.* 2008). The BBM approach has much to recommend it and has been adopted in guidance flow regimes for heavily modified water bodies (HMWBs) (Acreman *et al.* 2009) and has been applied recently to Atlantic salmon (Enders *et al.* 2009).

How to devise protective flows with restricted knowledge

If flow management to protect the environment is to have scientific credibility, it needs to be based on some form of testable relationship (a model) between the impact on the element being protected (e.g. salmon abundance, survival, movement pattern or fitness) and the state of the river flow. For flow regulatory purposes, the state is conventionally some measure of the deviation from the normal, unmodified condition of the natural flow regime (Fig. 1). This conceptual model is an inescapable tenet of scientific flow management. The forms of the relationship may be different from the one shown here and range from fully quantitative to some evidence-based expert opinion, but even in the case of expert opinion, some intuitive form of modelling is implied. There is always some conceptual relationship involved, even if it cannot be displayed unambiguously. The

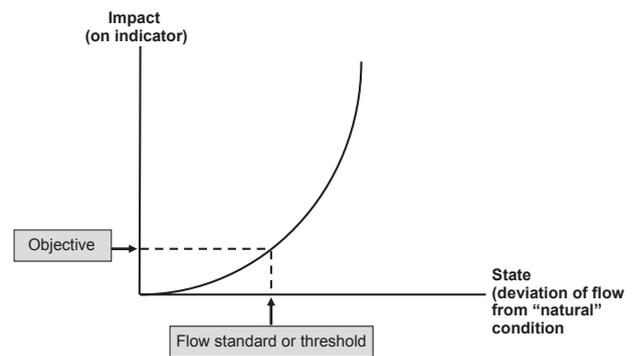


Figure 1. Conceptual model for defining a flow standard. There are three key steps: (i) the specification of the objective, being the point of acceptable impact, with risk aversion included as appropriate; (ii) some form of modelling (the line, which might take a different form to that shown here, with its error) of impact (indexed by the state of the chosen indicator) vs deviation from the natural condition and (iii) selection of the protective flow standard or threshold, being the level of deviation (from natural flow metric) associated with the objective.

papers in this volume are mostly about these relationships, and the body of scientific experience from the salmonid perspective illustrates four key points.

First, the model in Figure 1 is the ideal; in practice, the relationships are inconsistent, highly variable even within species (e.g. Thorstad *et al.* 2008; Poff & Zimmerman 2010) and influenced by confounding factors that need to be incorporated into the models (Bendall *et al.* 2012). Thus, the good intention to develop generic models that might support widely applicable standards is probably misplaced and unachievable (Poff & Zimmerman 2010), because the relationships often do not transport well to contexts other than the ones in which they were developed. The reasons for inconsistency are not hard to see. Salmonids are phenotypically highly plastic in their response to environmental factors and to flow in particular (Moore *et al.* 2012), which is a dominant influence on lotic habitat. They appear to have evolved life history strategies that thrive in highly variable flow regimes of montane, high-gradient channels, but have also the capacity to occupy many other stream types, chalk aquifer rivers for example, providing that the key habitat of useable spawning gravels (Malcolm *et al.* 2012) is available (Dunbar *et al.* 2012). Disturbance, through floods and droughts, is a natural part of their experience, to which they are adapted (Lytle & Poff 2004; Vincenzi *et al.* 2008). Different life stages have contrasting and sometimes conflicting seasonal flow requirements. Furthermore, flow is a composite variable, almost always confounded with other aquatic environmental variables that vary temporally and spatially. Thus, it is not surprising that studies in different locations have given contrasting answers to the water man-

ager's standard question: 'How much flow do salmon [and other fish species] need?'

This is not to say that there are not broad preferences of depth or velocities for each species: there clearly are (e.g. Armstrong *et al.* 2003). However, for a given discharge, these hydraulic variables can be delivered in a huge variety of ways in different mosaics of mesohabitats (e.g. riffle/pool/glide/run type habitats) or hydraulic conditions around physical obstructions. Furthermore, similar hydraulic variables, coupled with channel morphologies, can offer very different habitat patch qualities (and thus fish carrying capacity) depending upon site productivities, prevailing trophic webs and the salmonid stock demographics and dynamics.

This leads to the second point that studies have mostly not been conducted in ways that easily allow for comparison or meta-analysis outside their own category. It is widely accepted that fish probably do not respond to volume discharge (=flow), but to the proximate factors that they can detect such as hydraulic variables like depth, velocity, shear stress or other factors often related to flow such as temperature and chemical cues. Most experimental and field studies have dealt with morphological or hydraulic variables, individually or in combination, which can be altered or measured to explore the influence of the three-dimensional habitats of water bodies. However, water resource management deals with volume discharge, so the requirement for field studies is, at least, to express relationships in ways that permit the exchange between the two metric forms. Moreover, even when discharge is reported at a site, for example, this tells little unless it can be set in the context of the flow duration statistics for that site and in turn the site can be located within the continua of catchment flow and geomorphological characteristics. This may appear demanding, but such information is essential if hydroecology is to develop into a science that has coherence and common currency expressed through a template of river and reach types defined by hydromorphological features. That such information is not always reported, and certainly not to any common format, says something about the lack of coordination and common goals in this science area.

Third, the assumption in Figure 1 is that deviation from natural flow regimes is *per se* a 'bad thing' and counter to the natural flow paradigm. However, in HMWBs where flow regimes may be greatly altered, in some circumstances, production of some fish species can increase. Elevated, but stabilised summer flows through compensation releases, for example, may bring increased growth rates and biomass production for salmonids (Nislow & Armstrong 2012). This raises challenging questions about the nature of natural flows and

the environmental aims of flow management and regulation (Brummett *et al.* in press). Ecosystem protection must consider other components as well as fish, for example, emergent gravel bar invertebrate fauna requiring extended low flows or the maintenance of geomorphological channel forming processes and sediment transport, which require 1- to 2-year floods (King *et al.* 2008). If the benefits of modified flows are corroborated as genuine enhancements of lifetime fitness to the fish populations without detrimental effects on ecosystem function, this may be a fruitful area for exploring new ways to manage flows. It should be noted that HMWBs are not natural and what constitutes good ecological potential (*sensu* WFD) is not clear. It may be that creative flow management could bring benefits to particular flow components without unduly jeopardising other elements. Such trials would lend themselves to adaptive management and collaboration between water users, researchers and the regulators.

Fourth, the most informative flow impact relationships and successful implementations are likely to be those that are developed and applied locally, in association with all stakeholders (Bowles & Henderson 2012; Mainstone *et al.* 2012), to meet the specific circumstances of hydromorphology and hydroecology. This is perhaps the major shift in thinking in recent years, and while it appears to conflict with the reductionism implicit in European legislation, it may be the only pragmatic way to deliver protective flow management (Poff *et al.* 2010). This is particularly the case for active management, that is, the HMWB situation where flows are actively released for various purposes (HEP for example), but applies also to restrictive management where limits are put on flow reduction through abstraction.

Hydroecology, as it relates to fish, is at a crossroads in the United Kingdom. Scientific progress has been made in discrete areas over the last 20 years, so lack of understanding, whilst still an important factor, is not the major limitation. The way ahead is principally subject to constraints of limited resources and a diversity of interest groups. Progress requires better coordination, clearer definition of aims than has been the case in the past, plus the willingness and organisation to collaborate across the regulators, users and research communities. Adaptive management (Walters 1986) offers a well-established framework for collaboration and appears to be essential when the infrastructures and operational capacity that might be used for large-scale trials of flow regimes lie strictly in the domain of the water industry. Identifying and taking up more opportunities to practise adaptive flow management appears to be of great potential for the future.

References

- Acreman M. & Dunbar M.J. (2004) Defining environmental river flow requirements – a review. *Hydrology and Earth System Sciences* **8**, 861–876.
- Acreman M. & Ferguson J.D. (2010) Environmental flows and the European Water Framework Directive. *Freshwater Biology* **55**, 32–48.
- Acreman M., Dunbar M., Hannaford J., Mountford O., Wood P., Holmes N. *et al.* (2008) Developing environmental standards for abstractions from UK rivers to implement the EU Water Framework Directive. *Hydrological Sciences Journal* **56**, 1105–1120.
- Acreman M., Aldrick J., Binnie C., Black A., Cowx I.G., Dawson H. *et al.* (2009) Environmental flows from dams; the Water Framework Directive. *Proceedings of the Institution of Civil Engineers-Engineering Sustainability* **162**, 13–22.
- Armstrong J.D. & Nislow K.H. (2012) Modelling approaches for relating effects of changes in river flow to populations of Atlantic salmon and brown trout. *Fisheries Management and Ecology* **19**, 527–536.
- Armstrong J.D., Kemp P.S., Kennedy G.J.A., Ladle M. & Milner N.J. (2003) Habitat requirements of Atlantic salmon and brown trout in rivers and streams. *Fisheries Research* **62**, 143–170.
- 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., Naiman R.J., McClain M.E. & Nilsson C. (2010) Preserving the biodiversity and ecological services of rivers: new challenges and research opportunities. *Freshwater Biology* **55**, 1–16.
- Bendall B., Moore A., Maxwell D., Davison P., Edmonds N., Archer D. *et al.* (2012) Modelling the migratory behaviour of salmonids in relation to environmental and physiological parameters using telemetry data. *Fisheries Management and Ecology* **19**, 475–483.
- Bowles F.J. & Henderson P. (2012) Water resource management—the water utilities view. *Fisheries Management and Ecology* **19**, 484–489.
- Brummett R.E., Beveridge M.C.M. & Cowx I.G. (in press) Functional aquatic ecosystems, inland fisheries and the Millennium Development Goals. *Fish and Fisheries* DOI: 10.1111/j.1467-2979.2012.00470.x.
- Cowx I.G., Noble R.A., Nunn A.D., Bolland J., Walton S., Pierson G. & Harvey J.P. (2012) Flow requirements of non-salmonids. *Fisheries Management and Ecology* **19**, 548–556.
- Dunbar M.J., Alfredsen K. & Harby A. (2012) Hydraulic-habitat modelling for setting environmental river flow needs for salmonids. *Fisheries Management and Ecology* **19**, 500–517.
- Enders E.C., Scruton D.A. & Clarke K.D. (2009) The “natural flow paradigm” and Atlantic salmon – moving from concept to practice. *River Research and Management* **25**, 2–15.
- Hynes H.B.N. (1970) *The Ecology of Running Waters*. Liverpool: University of Liverpool Press, 555pp.
- Kelly-Quinn M. (1990) A seasonal analysis of the diet and feeding dynamics of brown trout *Salmo trutta* L. in a small nursery stream. *Aquaculture and Fisheries Management* **21**, 107–124.
- King J.M., Tharme R.E. & De Villiers M.S. (eds) (2008). *Environmental Flow Assessments for Rivers: Manual for the Building Block Methodology (Updated Edition)*. Pretoria, South Africa: Water Research Commission Report TT 131/100, 339pp.
- Lytle D.A. & Poff N.L. (2004) Adaptation to natural flow regimes. *Trends in Ecology and Evolution* **19**, 94–100.
- Mainstone C.P., Thomas R., Bean C.W. & Waterman T. (2012) The role of the UK conservation agencies in protecting river flows. *Fisheries Management and Ecology* **19**, 557–569.
- Malcolm I.A., Gibbins C.N., Soulsby C., Tetzlaff D. & Moir H. J. (2012) The influence of hydrology and hydraulics on salmonids between spawning and emergence: implications for the management of flows in regulated rivers. *Fisheries Management and Ecology* **19**, 464–474.
- MEA [Millennium Ecosystem Assessment] (2005) *Ecosystem and General Well-Being: General Synthesis*. Vancouver, BC: Island Press, 64pp.
- Milner N.J., Solomon D.J. & Smith G.W. (2012) The role of river flow in the migration of adult Atlantic salmon, *Salmo salar*, through estuaries and rivers. *Fisheries Management and Ecology* **19**, 537–547.
- Moore A., Bendall B., Barry J., Waring C., Crooks N. & Crooks L. (2012) River temperature and adult anadromous Atlantic salmon, *Salmo salar*, and brown trout, *Salmo trutta*. *Fisheries Management and Ecology* **19**, 518–526.
- Newson M.D., Sear D. & Soulsby C. (2012) Incorporating hydromorphology in strategic approaches to managing flows for salmonids. *Fisheries Management and Ecology* **19**, 500–517.
- Nislow K.H. & Armstrong J.D. (2012) Towards a life-history based management framework for the effects of flow juvenile salmonids in streams and rivers. *Fisheries Management and Ecology* **19**, 451–463.
- Noble R.A.A., Cowx I. & Starkie A. (2007) Development of fish-based methods for the assessment of ecological health in English and Welsh rivers. *Fisheries Management and Ecology* **14**, 495–508.
- Orth D.J. (1995) Food web influences on fish population responses to instream flow. *Bulletin Français de la Pêche et de la Pisciculture* **337/338/339**, 317–328.
- Poff N.L. & Huryn A.D. (1998) Multiscale determinants of secondary production in Atlantic salmon (*Salmo salar*) streams. *Canadian Journal of Fisheries and Aquatic Sciences* **55**(Suppl. 1), 201–217.
- Poff N.L. & Zimmerman J.K.H. (2010) Ecological response to altered flow regimes: a literature review to inform the science and management of environmental flows. *Freshwater Biology* **55**, 194–205.

- Poff N.L., Allan J.D., Bain M.B., Karr J.R., Prestegard K.L., Richter B.D. *et al.* (1997) The natural flow regime: a paradigm for river conservation and restoration. *BioScience* **47**, 769–784.
- Poff N.L., Richter B.D., Arthington A.H., Bunn S.E., Naiman R. J., Kendy E. *et al.* (2010) The ecological limits of hydrological alteration (ELOHA): a new framework for developing regional environmental flow standards. *Freshwater Biology* **55**, 147–170.
- Postel S.L., Daily G.C. & Ehrlich P.R. (1996) Human appropriation of renewable freshwater. *Science* **271**, 785–788.
- Power M.E. (1992) Habitat heterogeneity and the functional significance of fish in river food webs. *Ecology* **73**, 1675–1688.
- Power M.E. & Dietrich W.E. (2002) Food webs in river networks. *Ecological Research* **17**, 451–471.
- Raven P. (2006) Freshwater ecological science in the UK: last rites or a new dawn? *Aquatic Conservation: Marine and Freshwater Ecosystems* **16**, 109–113.
- Richter B.D. & Thomas G.A. (2007) Restoring environmental flows by modifying dam operations. *Ecology & Society* **12**, 12. Available at: <http://www.ecologyandsociety.org/vol12/iss1/art12/>.
- Schmutz S., Cowx I.G., Haidvogel G. & Pont D. (2007) Fish-based methods for assessing European running waters: a synthesis. *Fisheries Management and Ecology* **14**, 369–380.
- Suchon Y., Sabaton C., Deibel R., Reisner D., Kershner J., Gard M. *et al.* (2008) Detecting biological responses to flow management: missed opportunities; future directions. *River Research and Management* **24**, 506–518.
- 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.
- Thorstad E.B., Økland F., Aarestrup K. & Heggberget T.G. (2008) Factors affecting the within river migration of Atlantic salmon, with emphasis on human impacts. *Reviews in Fish Biology and Fisheries* **18**, 345–371.
- Vannote R.L., Minshall G.W., Cummins K.W., Sedell J.R. & Cushing C.E. (1980) The river continuum concept. *Canadian Journal of Fisheries and Aquatic Sciences* **37**, 130–137.
- Vaughan I.P., Diamond M., Gurnell A.M., Hall K.A., Jenkins A., Milner N.J. *et al.* (2009) Integrating ecology with hydromorphology: a priority for river science and management. *Aquatic Conservation. Marine and Freshwater Ecosystems* **19**, 113–125.
- Vincenzi S., Crivelli A.J., Jesensek D. & De Leo G.A. (2008) The role of density-dependent individual growth in the persistence of freshwater salmonid populations. *Oecologia* **156**, 523–534.
- Walters C.J. (1986) *Adaptive Management of Renewable Resources*. New York, NY: Mc Graw Hill.
- Ward J.V. & Stanford J.A. (eds). 1979. *The Ecology of Regulated Streams*. New York, NY: Plenum, 398pp.
- Watson R. & Albon S. (2011) *UK National Ecosystem Assessment: Understanding Nature's Value to Society*. Cambridge, UK: UNEP-WCMC, 87pp.
- Wood P.J., Hannah D.M. & Sadler J.P. (eds) (2007) *Hydroecology and Ecohydrology: Past, Present and Future*. Chichester: Wiley, 436pp.
- Woodward G. & Hildrew A.G. (2002) Food web structure in riverine landscapes. *Freshwater Biology* **47**, 777–798.
- Zalewski M. (2002) Ecohydrology – the use of ecological and hydrological processes for sustainable management of water resources. *Hydrological Sciences Journal* **47**, 823–832.