EDITORS

IAN MADDOCK | ATLE HARBY | PAUL KEMP | PAUL WOOD

Ecohydraulics

AN INTEGRATED APPROACH

WILEY Blackwell

Ecohydraulics

By Ian Maddock:
For Katherine, Ben, Joe and Alice.

By Atle Harby:
Dedicated to Cathrine, Sigurd and Brage.

By Paul Kemp:
Dedicated to Clare, Millie, Noah and Florence.

By Paul Wood:
For Maureen, Connor and Ryan.

Ecohydraulics

An Integrated Approach

EDITED BY

Ian Maddock
Institute of Science and the Environment, University of Worcester, UK

Atle Harby
SINTEF Energy Research, Trondheim, Norway

Paul Kemp
International Centre for Ecohydraulics Research, University of Southampton, UK

Paul Wood
Department of Geography, Loughborough University, Leicestershire, UK

WILEY Blackwell

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List of Contributors

Michael C. Acreman
Centre for Ecology and Hydrology
Maclean Building
Benson Lane
Wallingford
Oxfordshire
OX10 8BB
UK

Donald J. Baird
Environment Canada
Canadian Rivers Institute
Department of Biology
10 Bailey Drive
P.O. Box 4400
University of New Brunswick
Fredericton
New Brunswick
E3B 5A3
Canada

Rohan Benjankar
Center for Ecohydraulics Research
University of Idaho
322 E. Front Street
Boise
ID 83702
USA

Melanie Bickerton
Geography, Earth and Environmental Sciences
University of Birmingham
Edgbaston
Birmingham
B15 2TT
UK

Bernadette Blamauer
Christian Doppler Laboratory for Advanced Methods in River Monitoring, Modelling and Engineering
Institute of Water Management, Hydrology and Hydraulic Engineering
University of Natural Resources and Life Sciences Vienna
Muthgasse 107
1190 Vienna
Austria

Gudrun Bornette
Université Lyon 1
UMR 5023 Ecologie des hydrosystèmes naturels et anthropisés (Université Lyon 1; CNRS; ENTPE)
43 boulevard du 11 novembre 1918
69622 Villeurbanne Cedex
France

Rocko A. Brown
Department of Land, Air, and Water Resources
University of California
One Shields Avenue
Davis
CA 95616
USA

Anthonie D. Buijse
Deltares
P.O. Box 177
2600 MH Delft
The Netherlands

Olle Calles
Department of Biology
Karlstad University
S-651 88 Karlstad
Sweden

Sung-Uk Choi
Department of Civil and Environmental Engineering
Yonsei University
134 Shinchon-dong
Seodaemun-gu
Seoul
Korea

Claudio Comoglio
Turin Polytechnic
Corso Duca degli Abruzzi 24
c/o DITAG
10129 Torino
Italy

Bernard De Baets
Department of Mathematical Modelling
Statistics and Bioinformatics
Ghent University
Coupure links 653
9000 Gent
Belgium

Harm Duel
Deltares
P.O. Box 177
2600 MH Delft
The Netherlands

Lynda R. Eakins
International Centre for Ecohydraulics Research
University of Southampton
Highfield
Southampton
SO17 1BJ
UK

Gregory Egger
Environmental Consulting Ltd
Bahnhofstrasse 39
9020 Klagenfurt
Austria

Teresa Ferreira
Forest Research Centre
Instituto Superior de Agronomia
Technical University of Lisbon
Tapada da Ajuda 1349-017
Lisbon
Portugal

Virginia Garófano-Gómez
Institut d'Investigació per a la Gestió Integrada de Zones Costaneres (IGIC)
Universitat Politècnica de València
C/ Paranimf, 1
46730 Grau de Gandia (València)
Spain

Gertjan W. Geerling
Deltares
P.O. Box 177
2600 MH Delft
The Netherlands

Peter Goethals
Aquatic Ecology Research Unit
Department of Applied Ecology and Environmental Biology
Ghent University
J. Plateaustraat 22
B-9000 Gent
Belgium

Javier Gortázar
Ecohidráulica S.L.
Calle Rodríguez San Pedro 13
4°7
28015 Madrid
Spain

Larry Greenberg
Department of Biology
Karlstad University
S-651 88 Karlstad
Sweden

Helmut Habersack
Christian Doppler Laboratory for Advanced Methods in River Monitoring, Modelling and Engineering
Institute of Water Management, Hydrology and Hydraulic Engineering
University of Natural Resources and Life Sciences Vienna
Muthgasse 107
1190 Vienna
Austria

Atle Harby
SINTEF Energy Research
P.O. Box 4761 Sluppen
7465 Trondheim
Norway

Thomas B. Hardy
The Meadows Center for Water and Environment
Texas State University
601 University Drive
San Marcos
Texas 78666
USA

Jan Heggenes
Telemark University College
Department of Environmental Sciences
Hallvard Eikas Plass
N-3800 Bø i Telemark
Norway

Graham Hill
Institute of Science and the Environment
University of Worcester
Henwick Grove
Worcester
WR2 6AJ
UK

Alice Howe
School of Engineering
The University of Newcastle
Callaghan
NSW 2308
Australia

Ari Huusko
Finnish Game and Fisheries Research Institute
Manamansalontie 90
88300 Paltamo
Finland

Georg A. Janauer
Department of Limnology
University of Vienna
Althanstrasse 14
A-1090 Vienna
Austria

Klaus Jorde
KJ Consulting/SJE Schneider & Jorde Ecological Engineering
Gnesau 11
A-9563 Gnesau
Austria

Paul Kemp
International Centre for Ecohydraulics Research
University of Southampton
Highfield
Southampton
SO17 1BJ
UK

James R. Kerr
International Centre for Ecohydraulics Research
University of Southampton
Highfield
Southampton
SO17 1BJ
UK

Aleksandra Krivograd Klemenčič
University of Ljubljana
Faculty of Health Sciences
Department of Sanitary Engineering
SI-1000 Ljubljana
Slovenia

Ian Maddock
Institute of Science and the Environment
University of Worcester
Henwick Grove
Worcester
WR2 6AJ
UK

Wendy A. Monk
Environment Canada
Canadian Rivers Institute
Department of Biology
10 Bailey Drive
P.O. Box 4400
University of New Brunswick
Fredericton
New Brunswick
E3B 5A3
Canada

Ans Mouton
Research Institute for Nature and Forest
Department of Management and Sustainable Use
Ghent University
Kliniekstraat 25
B-1070 Brussels
Belgium

Markus Noack
Federal Institute of Hydrology
Department M3 – Groundwater, Geology, River Morphology
Mainzer Tor 1
D-56068 Koblenz
Germany

Jessica M. Orlofske
Canadian Rivers Institute
Department of Biology
10 Bailey Drive
P.O. Box 4400
University of New Brunswick
Fredericton
New Brunswick
E3B 5A3
Canada

Piotr Parasiewicz
Rushing Rivers Institute
592 Main Street
Amherst
MA 01002
USA;
The Stanisław Sakowicz Inland Fisheries Institute
ul. Oczapowskiego 10
10-719 Olsztyn 4
Poland

Gregory B. Pasternack
Department of Land, Air, and Water Resources
University of California
One Shields Avenue
Davis
CA 95616
USA

Mark Pegg
University of Nebraska
402 Hardin Hall
Lincoln
NE 68583-0974
USA

Adam T. Piper
International Centre for Ecohydraulics Research
University of Southampton
Highfield
Southampton
SO17 1BJ
UK

Emilio Politti
Environmental Consulting Ltd
Bahnhofstrasse 39
9020 Klagenfurt
Austria

Sara Puijalon
Université Lyon 1
UMR 5023 Ecologie des hydrosystèmes naturels et anthropisés (Université Lyon 1; CNRS; ENTPE)
43 boulevard du 11 novembre 1918
69622 Villeurbanne Cedex
France

Walter Reckendorfer
WasserCluster Lunz – Biologische Station GmbH
Dr Carl Kupelwieser Promenade 5
A-3293 Lunz am See
Austria

Rui Rivaes
Forest Research Centre
Instituto Superior de Agronomia
Technical University of Lisbon
Tapada da Ajuda 1349-017
Lisbon
Portugal

Peter Rivinoja
Department of Wildlife, Fish and Environmental Studies
SLU (Swedish University of Agricultural Sciences)
Umeå 901 83
Sweden

José F. Rodríguez
School of Engineering
The University of Newcastle
Callaghan
NSW 2308
Australia

Joseph N. Rogers
Rushing Rivers Institute
592 Main Street
Amherst
MA 01002
USA

Udo Schmidt-Mumm
Department of Limnology
University of Vienna
Althanstrasse 14
A-1090 Vienna
Austria

Matthias Schneider
Schneider & Jorde Ecological Engineering GmbH
Viereichenweg 12
D-70569 Stuttgart
Germany

Thomas Seager
Rushing Rivers Institute
592 Main Street
Amherst
MA 01002
USA

Thomas A. Shaw
U.S. Fish and Wildlife Service
Arcata Fish and Wildlife Office
1655 Heindon Road
Arcata
California 95521
USA

Antonius J.M. Smits
DSMR
Radboud University
P.O. Box 9010
6500 GL Nijmegen
The Netherlands

Nataša Smolar-Žvanut
Institute for Water of the Republic of Slovenia
Hajdrihova 28c
SI-1000 Ljubljana
Slovenia

Michael Stewardson
Department of Infrastructure Engineering
Melbourne School of Engineering
The University of Melbourne
Melbourne 3010
Australia

Morten Stickler
Statkraft AS
Lilleakerveien 6
0216 Oslo
Norway

Daniele Tonina
Center for Ecohydraulics Research
University of Idaho
322 E Front Street
Suite 340
Boise
ID 83702
USA

Teppo Vehanen
Finnish Game and Fisheries Research Institute
Paavo Havaksen tie 3
90014 Oulun yliopisto
Finland

Paolo Vezza
Turin Polytechnic
Corso Duca degli Abruzzi 24
c/o DITAG
10129 Torino
Italy

Fleur Visser
Institute of Science and the Environment
University of Worcester
Henwick Grove
Worcester
WR2 6AJ
UK

Andrew S. Vowles
International Centre for Ecohydraulics Research
University of Southampton
Highfield
Southampton
SO17 1BJ
UK

Silke Wieprecht
Institute for Modelling Hydraulic and Environmental Systems
Department of Hydraulic Engineering and Water Resources Management
University of Stuttgart
Pfaffenwaldring 61
D-70569 Stuttgart
Germany

Martin A. Wilkes
Institute of Science and the Environment
University of Worcester
Henwick Grove
Worcester
WR2 6AJ
UK

Wiesław Wiśniewolski
The Stanisław Sakowicz Inland Fisheries Institute
ul. Oczapowskiego 10
10-719 Olsztyn 4
Poland

Jens Wollebæk
The Norwegian School of Veterinary Science
Department of Basic Sciences and Aquatic Medicine
Box 8146
Dep. 0033 Oslo
Norway

Hyoseop Woo
Korea Institute of Construction Technology
2311 Daehwa-dong
Illsanseo-gu
Goyang-si
Gyeonggi-do
Korea

Paul Wood
Department of Geography
Loughborough University
Leicestershire
LE11 3TU
UK

Sarah Yarnell
Center for Watershed Sciences
University of California, Davis
One Shields Avenue
Davis
CA 95616
USA

Elisa Zavadil
Alluvium Consulting Australia
21–23 Stewart Street
Richmond
Victoria 3121
Australia

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Ecohydraulics: An Introduction

Ian Maddock[1], Atle Harby[2], Paul Kemp[3] and Paul Wood[4]

[1]Institute of Science and the Environment, University of Worcester, Henwick Grove, Worcester, WR2 6AJ, UK
[2]SINTEF Energy Research, P.O. Box 4761 Sluppen, 7465 Trondheim, Norway
[3]International Centre for Ecohydraulics Research, University of Southampton, Highfield, Southampton, SO17 1BJ, UK
[4]Department of Geography, Loughborough University, Leicestershire, LE11 3TU, UK

1.1 Introduction

It is well established that aquatic ecosystems (streams, rivers, estuaries, lakes, wetlands and marine environments) are structured by the interaction of physical, biological and chemical processes at multiple spatial and temporal scales (Frothingham *et al.*, 2002; Thoms and Parsons, 2002; Dauwalter *et al.*, 2007). The need for interdisciplinary research and collaborative teams to address research questions that span traditional subject boundaries to address these issues has been increasingly recognised (Dollar *et al.*, 2007) and has resulted in the emergence of new 'sub-disciplines' to tackle these questions (Hannah *et al.*, 2007). Ecohydraulics is one of these emerging fields of research that has drawn together biologists, ecologists, fluvial geomorphologists, sedimentologists, hydrologists, hydraulic and river engineers and water resource managers to address fundamental research questions that will advance science and key management issues to sustain both natural ecosystems and the demands placed on them by contemporary society.

Lotic environments are naturally dynamic, characterised by variable discharge, hydraulic patterns, sediment and nutrient loads and thermal regimes that may change temporally (from seconds to yearly variations) and spatially (from sub-cm within habitat patches to hundreds of km^2 at the drainage basin scale). This complexity produces a variety of geomorphological features and habitats that sustain the diverse ecological communities recorded in fresh, saline and marine waters. Aquatic organisms, ranging from micro-algae and macrophytes to macroinvertebrates, fish, amphibians, reptiles, birds and mammals, have evolved adaptations to persist and thrive in hydraulically dynamic environments (Lytle and Poff, 2004; Townsend, 2006; Folkard and Gascoigne, 2009; Nikora, 2010). However, anthropogenic impacts on aquatic systems have been widespread and probably most marked on riverine systems. A report by the World Commission on Dams (2000) and a recent review by Kingsford (2011) suggested that modification of the river flow regime as a result of regulation by creating barriers, impoundment and overabstraction, the spread of invasive species, overharvesting and the effects of water pollution were the main threats to the world's rivers and wetlands and these effects could be compounded by future climate change.

The impacts of dam construction, river regulation and channelisation have significantly reduced the natural variability of the flow regime and channel morphology. This results in degradation, fragmentation and loss of habitat structure and availability, with subsequent reductions in aquatic biodiversity (Vörösmarty *et al.*, 2010). Recognition of the long history, widespread and varied extent of human impacts on river systems, coupled with an increase in environmental awareness has led to the development of a range of approaches to minimise and mitigate their impacts. These include river restoration and rehabilitation techniques to restore a more natural channel morphology (e.g. Brookes and Shields Jr, 1996; de Waal *et al.*, 1998; Darby and Sear, 2008), methods to define ways to reduce or mitigate the impact of abstractions and river regulation through the definition and application of instream

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or environmental flows (Dyson *et al.*, 2003; Acreman and Dunbar, 2004; Annear *et al.*, 2004; Acreman *et al.*, 2008), and the design of screens and fish passes to divert aquatic biota from hazardous areas (e.g. abstraction points) and to enable them to migrate past physical barriers, especially, but not solely associated with dams (Kemp, 2012).

Key legislative drivers have been introduced to compel regulatory authorities and agencies to manage and mitigate historic and contemporary anthropogenic impacts and, where appropriate, undertake restoration measures. The EU Water Framework Directive (Council of the European Communities, 2000) requires the achievement of 'good ecological status' in all water bodies across EU member states by 2015 (European Commission, 2012). This, in turn, has required the development of methods and techniques to assess the current status of chemical and biological water quality (Achleitner *et al.*, 2005), hydromorphology and flow regime variability, and identify ways of mitigating impacts and restoring river channels and flow regimes where they are an impediment to the improvement of river health (Acreman and Ferguson, 2010). Similar developments have occurred in North America with the release of the United States Environmental Protection Agency guidelines (US EPA, 2006). In Australia, provision of water for environmental flows has been driven by a combination of national policy agreements including the National Water Initiative in 2004, national and state level legislation and government-funded initiatives to buy back water entitlements from water users including the 'Water for the Future' programme (Le Quesne *et al.*, 2010). Important lessons can be learned from South Africa, where implementation of the National Water Act of 1998 is recognised as one of the most ambitious pieces of water legislation to protect domestic human needs and environmental flows on an equal footing ahead of economic uses. However, Pollard and du Toit (2008) suggest that overly complicated environmental flow recommendations have inhibited their implementation. This provides a key message for ecohydraulic studies aimed at providing environmental flow or indeed other types of river management recommendations (e.g., river restoration) worldwide.

1.2 The emergence of ecohydraulics

During the 1970s and 1980s it was common for multidisciplinary teams of researchers and consultants to undertake pure and/or applied river science projects and to present results collected as part of the same study independently to stakeholders and regulatory/management authorities, each from the perspective of their own disciplinary background. More recently, there has been a shift towards greater interdisciplinarity, with teams of scientists, engineers, water resource and river managers and social scientists working together in collaborative teams towards clearly defined common goals (Porter and Rafols, 2009). Developments in river science reflect this overall pattern, with the emergence of ecohydrology at the interface of hydrology and ecology (Dunbar and Acreman, 2001; Hannah *et al.*, 2004; Wood *et al.*, 2007) and hydromorphology, which reflects the interaction of the channel morphology and flow regime (hydrology and hydraulics) in creating 'physical habitat' (Maddock, 1999; Orr *et al.*, 2008; Vaughan *et al.*, 2009).

Like 'ecohydrology', 'ecohydraulics' has also developed at the permeable interface of traditional disciplines, combining the study of the hydraulic properties and processes associated with moving water typical of hydraulic engineering and geomorphology and their influence on aquatic ecology and biology (Vogel, 1996; Nestler *et al.*, 2007). Ecohydraulics has been described as a subdiscipline of ecohydrology (Wood *et al.*, 2007) although it has become increasingly distinct in recent years (Rice *et al.*, 2010). Hydraulic engineers have been engaged with design criteria for fish passage and screening facilities at dams for many years. Recognition of the need to solve river management problems like these by adopting an interdisciplinary approach has been the driver for the development of ecohydraulics. Interdisciplinary research that incorporates the expertise of hydrologists, fluvial geomorphologists, engineers, biologists and ecologists has begun to facilitate the integration of the collective expertise to provide holistic management solutions. Ecohydraulics has played a critical role in the development of methods to assess and define environmental flows (Statzner *et al.*, 1988). Although pre-dating the use of the term 'ecohydraulics', early approaches, such as the Physical Habitat Simulation System (PHABSIM) in the 1980s and 1990s, were widely applied (Gore *et al.*, 2001) but often criticised due to an over-reliance on simple hydraulic models and a lack of ecological relevance because of the way that habitat suitability was defined and calculated (Lancaster and Downes, 2010; Shenton *et al.*, 2012). State-of-the-art developments associated with ecohydraulics are attempting to address these specific gaps between physical scientists (hydraulic engineers, hydrologists and fluvial geomorphologists) and biological scientists (e.g. aquatic biologists and ecologists) by integrating hydraulic and biological tools to analyse and predict ecological responses to hydrological and hydraulic variability and change (Lamouroux *et al.* in press). These developments intend to support water resource management and the decision-making process by providing ecologically relevant and environmentally sustainable solutions to issues associated with hydropower operations, river restoration and the delineation of environmental flows (Acreman and Ferguson, 2010).

The growing worldwide interest in ecohydraulics can be demonstrated by increasing participation in the international symposia on the subject. The first symposium (then titled the 1st International Symposium on Habitat Hydraulics) was organised in 1994 in Trondheim, Norway by the Foundation for Scientific and Industrial Research (SINTEF), the Norwegian University of Science and Technology (NTNU) and the Norwegian Institute of Nature Research (NINA) with about 50 speakers and 70 delegates. Subsequent symposia in Quebec City (Canada, 1996), Salt Lake City (USA, 1999), Cape Town (South Africa, 2002), Madrid (Spain, 2004), Christchurch (New Zealand, 2007), Concepción (Chile, 2009), Seoul (South Korea, 2010) and most recently in Vienna (Austria, 2012) have taken the scientific community across the globe, typically leading to more than 200 speakers and approximately 300 delegates at each meeting.

A recent bibliographic survey by Rice *et al.* (2010) indicated that between 1997 and the end of 2009 a total of 146 publications had used the term 'ecohydraulic' or a close variant (eco hydraulic, ecohydraulics or eco-hydraulics) in the title, abstract or keywords (ISI Web of Knowledge, http://wok.mimas.ac.uk/). This meta-analysis indicated greater use of the term 'ecohydraulics' amongst water resources and engineering journals (48%) and geoscience journals (31%) compared to a more limited use in (21%) biological or ecological journals. By the end of 2011 this figure had risen to 211 publications, with 65 papers being published between 2010 and the end of 2011 (Figure 1.1). This suggests a significant increase in the use of the terms more recently, and strongly mirrors the rapid rise in the use of the term 'ecohydrology', which has been used in the title, abstract or as a keyword 635 times since 1997 (186 between 2010 and 2011). However, bibliographic analysis of this nature only identifies those publications that have specifically used one of the terms and there is an extensive unquantified literature centred on ecohydraulics and ecohydrology that has not specifically used these terms.

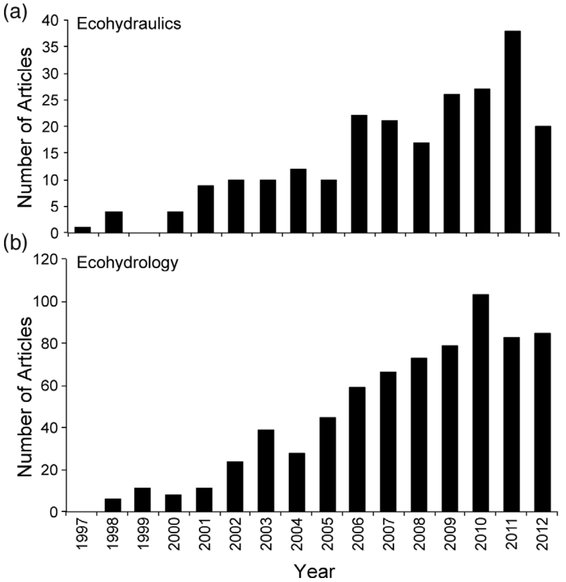

Figure 1.1 Number of peer-reviewed articles using the terms (a) ecohydraulic(s), eco-hydraulic(s) or eco hydraulic(s) and (b) ecohydrology, eco-hydrology or eco hydrology 1997–2012 as listed on Thomson Reuters ISI Web of Knowledge (http://wok.mimas.ac.uk/). Note: WoK data for 2012 compiled on 22/11/2012.

Porter and Rafols (2009) suggested that interdisciplinary developments in science have been greatest between closely allied disciplines and less well developed and slower for fields with a greater distance between them. This appears to be the case when comparing developments in ecohydrology and ecohydraulics. Ecohydrology has increasingly been embraced by an interdisciplinary audience and even witnessed the launch of a dedicated journal, *Ecohydrology*, in 2008 (Smettem, 2008), drawing contributions from across physical, biological and social sciences as well as engineering and water resources management. In contrast, publications explicitly referring to 'ecohydraulics' predominately appeared in water resources, geosciences and engineering journals and the affiliation of the primary authors remains firmly within engineering and geosciences departments and research institutes. However, the greatest number of papers has appeared in the interdisciplinary journal *River Research and Applications* (17 papers since 2003). This figure includes five out of ten papers within a special issue devoted to ecohydraulics in 2010 (Rice *et al.*, 2010) and two out of nine papers within a special issue devoted to 'Fish passage: an ecohydraulics approach' in 2012 (Kemp, 2012), and clearly demonstrates that many authors do not routinely use the term 'ecohydraulics'. Biologists have been investigating organism responses to their abiotic environments, including the role of fluid dynamics on aquatic communities, for decades and well before the term 'ecohydraulics' was coined. For example, from an environmental flow perspective, biological scientists have been involved with determining the relationship between fish (and other biota) and hydraulics since at least the 1970s (e.g. Bovee and Cochnauer, 1978). What this bibliographic analysis highlights is that geoscientists and engineers have more readily adopted the terms than colleagues in biology and ecology.

The dominance of physical scientists and engineers within some studies, many of them using modelling approaches, has been highlighted as a potential weakness of some research. It is argued they rely on faulty assumptions and lack any ecological or biological reality due to inadequate consideration of biological interactions between organisms (inter- or intra-specific), or natural population dynamics (Lancaster and Downes, 2010; Shenton *et al.*, 2012). However, these criticisms have been contested and there is growing evidence that interdisciplinarity is being embraced more widely (Lamouroux *et al.*, 2010; Lamouroux *et al.*, Lamouroux *et al.*, in press). This issue is discussed further in the concluding chapter of this volume.

1.3 Scope and organisation of this book

The aim of this research-level edited volume is to provide the first major text to focus on ecohydraulics. It is comprised of chapters reflecting the range and scope of research being undertaken in this arena (spanning engineering, geosciences, water resources, biology, ecology and interdisciplinary collaborations). Individual chapter authors have provided overviews of cutting-edge research and reviews of the current state of the art in ecohydraulics. In particular, authors have been encouraged to demonstrate how their work has been informed by and is influencing the on-going development of ecohydraulics research. The contributions use case study examples from across the globe, highlighting key methodological developments and demonstrating the real-world application of ecohydraulic theory and practice in relation to a variety of organisms ranging from riparian vegetation and instream algae, macrophytes, macroinvertebrates and fish to birds and amphibians. The chapters reflect a spectrum of research being undertaken within this rapidly developing field and examine the interactions between hydraulics, hydrology, fluvial geomorphology and aquatic ecology on a range of spatial (individual organism in a habitat patch to catchment) and temporal scales.

The book is structured into four parts: Part One considers the range and type of methods and approaches used in ecohydraulics research, with a particular focus on aquatic habitat modelling; Part Two considers a range of species–habitat relationships in riverine and riparian habitats; Part Three consists of detailed ecohydraulics case studies that have a clear management application, mostly, but not exclusively, relating to environmental flow determination, fish passage design, river channel and habitat restoration and ecosystem assessment. The final chapter (Part Four) aims to draw together the work contained in the book to outline key research themes and challenges in ecohydraulics and discuss future goals and directions. A number of chapters involve methods, species–habitat relationships and case studies and therefore could have been located in more than one part of the book. The final decision regarding which part to place them in was in some cases clear-cut and in others fairly arbitrary.

We realise that the coverage provided in this volume is not complete and are conscious that the chapters are almost exclusively centred on freshwater, riverine ecosystems. Indeed there has been a considerable volume of research centred on marine (e.g. Volkenborn *et al.*, 2010), estuarine (e.g. Yang *et al.*, 2012) and lentic (lake) ecosystems (e.g. Righetti and Lucarelli, 2010), where equally challenging and exciting ecohydraulic research questions are being addressed. Their exclusion is driven by a desire to keep this book within a manageable size and scope rather than a view that these other parts of the natural environment are somehow less important than riverine ecosystems.

Research currently being undertaken in the arena of ecohydraulics is developing rapidly and is becoming increasingly interdisciplinary, drawing on a range of academic and practitioner traditions and addressing real-world problems. As this interdisciplinary science matures there is a growing demand from river managers and end users to be involved not just at the inception and conclusion, but throughout the studies to enhance the possibility that any management recommendations can be implemented successfully. The occurrence of this would signal a move from interdisciplinarity (between traditional disciplines) to ‘transdisciplinarity’ (that also engages with managers and end users during the research). The editors hope that the realisation of this development will be one mark of this book’s success.

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I

Methods and Approaches

2

Incorporating Hydrodynamics into Ecohydraulics: The Role of Turbulence in the Swimming Performance and Habitat Selection of Stream-Dwelling Fish

Martin A. Wilkes[1], Ian Maddock[1], Fleur Visser[1] and
Michael C. Acreman[2]

[1]Institute of Science and the Environment, University of Worcester, Henwick Grove, Worcester, WR2 6AJ, UK
[2]Centre for Ecology and Hydrology, Maclean Building, Benson Lane, Wallingford, Oxfordshire, OX10 8BB, UK

2.1 Introduction

The complexity and dynamism of river systems, the strength of their biophysical linkages and the need to respond to adverse anthropogenic impacts has led to the emergence of *hydroecology* as a key area of interdisciplinary research (Hannah *et al.*, 2007). Wood *et al.* (2007) provide an outline of the target elements of hydroecology in which they emphasise the bi-directional nature of physical–ecological interactions and the need to identify causal mechanisms rather than merely establishing statistical links between biota, ecosystems and environments. Such causal mechanisms operate in the realm of the physical habitat (Harper and Everard, 1998). A sub-discipline of hydroecology known as *ecohydraulics* has emerged from the scientific literature in recent decades (Leclerc *et al.*, 1996) and, as a contemporary science, has its roots in the hydraulic stream ecology paradigm (Statzner *et al.*, 1988). Ecohydraulics relies on the assumption that flow forces are ecologically relevant (i.e. that they influence the fitness of individual organisms and, therefore, the structure and function of aquatic communities). It lies at the interface of hydraulics and ecology where new approaches to research are required to reconcile the contrasting conceptual frameworks underpinning these sciences, which can be seen respectively as Newtonian (reductionist) and Darwinian (holistic) (Hannah *et al.*, 2007). Harte (2002) has identified elements of synthesis for integrating these disparate traditions which include the use of simple, falsifiable models and the search for patterns and laws. Newman *et al.* (2006) suggested that hierarchical scaling theory, whereby reductionist explanations are considered at different levels of organisation, could be used to integrate these two approaches. River habitat is structured at a number of scales (Frissell *et al.*, 1986) but it is at the microscale ($<10^{-1}$ m) of the hydraulic environment where reductionist explanations for ecological phenomena are most often sought (e.g. Enders *et al.*, 2003; Liao *et al.*, 2003a).

Ecohydraulics: An Integrated Approach, First Edition. Edited by Ian Maddock, Atle Harby, Paul Kemp and Paul Wood.

Table 2.1 Common terms used to describe the flow environment.

Term	Description	Notes
h	Flow depth	
y	Height above bed datum	
A	Cross-sectional area of flow	
P	Wetted perimeter	
R	Hydraulic radius	$= A/P$
S	Longitudinal bed slope	
ρ	Fluid density of water	Taken as 1000 kg m^{-3}
g	Acceleration due to gravity	9.81 m s^{-2}
k	Height of surface roughness elements	Various methods to quantify k provided by Statzner *et al.* (1988). Typically based on particle size (D) distributions for gravel-bed rivers (e.g. $3.5D_{84}$) (Clifford *et al.*, 1992)
v	Kinematic viscosity	1.004×10^{-6} $\mathrm{m}^2\ \mathrm{s}^{-1}$ at 20°C
U	Mean streamwise column velocity	Measured at $y/h = 0.4$ or depth-averaged
Fr	Froude number $= U/\sqrt{gh}$	$Fr < 1 \rightarrow$ sub-critical flow $Fr = 1 \rightarrow$ critical flow $Fr > 1 \rightarrow$ super-critical flow
Re	Bulk flow Reynolds number $= Uh/v$	$Re < 500 \rightarrow$ laminar flow $500 < Re < 10^3$–$10^4 \rightarrow$ transitional flow $Re > 10^3$–$10^4 \rightarrow$ turbulent flow
τ	Shear stress (section- or reach-averaged) $= PgRS$	Point measurements can be made using fliesswasserstammtisch (FST) hemispheres
U_*	Shear velocity or friction velocity $= \sqrt{\tau/\rho}$	Calculated from point measurements of shear stress or estimated from near-bed velocity profile
Re^*	Roughness Reynolds number $= U_* k/v$	$Re^* < 5 \rightarrow$ hydraulically smooth flow $5 < Re^* < 70 \rightarrow$ transitional flow $Re^* > 70 \rightarrow$ hydraulically rough flow
δ	Thickness of laminar sublayer $= 11.5v/U_*$	$\delta/k < 1 \rightarrow$ hydraulically smooth flow $\delta/k > 1 \rightarrow$ hydraulically rough flow

2.1.1 'Standard' ecohydraulic variables

Much research has focused on the relationship between instream biota and the 'standard' ecohydraulic variables of flow depth (h), mean streamwise velocity (U) and combinations of these. These simple hydraulic quantities, and indices derived from them (e.g. Froude number, $U{:}h$), have traditionally been used to classify a range of mesoscale (10^{-1}–10^{1} m) units of instream habitat (e.g. channel geomorphic units, hydraulic biotopes, functional habitats) for habitat assessment and design purposes (Jowett, 1993; Padmore, 1997; Wadeson and Rowntree, 1998; Kemp *et al.*, 2000). U is typically measured at 'point six' depth ($y/h = 0.4$, where y is height above the bed) and (ensemble) averaged over 10–60 s. Other commonly used variables describing the bulk flow are the Froude number (Fr, ratio of inertial to gravitational forces) and the Reynolds number (Re, ratio of inertial to viscous forces) (Table 2.1). These are dimensionless variables representing gradients from tranquil (sub-critical) to shooting (super-critical) and laminar to fully developed (turbulent) flow respectively. Because the flow environment experienced by benthic organisms living very close to the bed differs markedly to that farther up in the water column (Statzner *et al.*, 1988), the inner region (see Figure 2.1) has often been characterised by

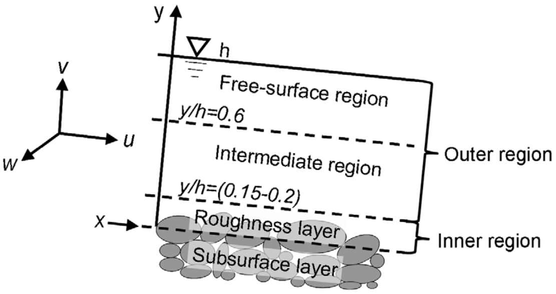

Figure 2.1 Co-ordinate system for three-dimensional flows and structure of flow over rough, permeable boundaries.

a different set of variables. They include bed shear stress (τ), shear velocity (U_*), roughness Reynolds number (Re^*) and the thickness of the laminar sublayer (δ). U_* is related to τ (Table 2.1) which, in turn, is responsible for the appearance of a mean gradient in the vertical velocity profile. U_* can be interpreted as a velocity scale for flow statistics in the inner region. Re^* describes the 'roughness' of the near-bed flow environment. Finally, δ approximates the thickness of the laminar sublayer where viscous forces predominate over inertial forces. In rivers with coarse bed material (i.e. gravel-bed rivers) which are characterised by hydraulically rough flow ($Re^* > 70$), however, δ is typically very small in comparison to roughness size (k) (Davis and Barmuta, 1989; Kirkbride and Ferguson, 1995), rendering it irrelevant to the study of all but the smallest organisms (Allan, 1995).

Flow forces are reported to be the dominant factors influencing the processes of dispersal, reproduction, habitat use, resource acquisition, competition and predation in river ecosystems (Table 2.2). The passive dispersal of benthic organisms is controlled by the same mechanisms as sediment transport (Nelson *et al.*, 1995; McNair *et al.*, 1997), although many invertebrates actively enter the water column and are able to swim back to the substrate (Waters, 1972; Mackay, 1992). Hydraulic limitations to fish migration are related to body depth and maximum sustained and burst swimming speeds $V_{\max}$, which vary considerably between species and with water temperature (Beamish, 1978). h and U are key factors in the segregation of rheophilic species (e.g. Bisson *et al.*, 1988), whilst the distribution of benthic organisms has been related to δ, Fr, τ and Re^* (e.g. Statzner, 1981a, 1981b; Scarsbrook and Townsend, 1993; Brooks *et al.*, 2005). Most instream biota exhibit a subsidy-stress response to flow as resources (e.g. food, nutrients, oxygen) may be limiting at low U, whilst at high U drag disturbance and mass transfer may be the limiting factors (Hart and Finelli, 1999; Nikora, 2010). Thus, for example, the energetic cost of swimming for juvenile Atlantic salmon (*Salmo salar*) is negatively related to U, whilst prey delivery is positively related to U (Godin and Rangeley, 1989). Some of these examples offer mechanistic explanations for flow–biota interactions on which predictive models may be built (e.g. Hughes and Dill, 1990) but ecohydraulic research more often relies on correlative techniques to describe abundance–environment relationships. Whilst correlative approaches may represent a pragmatic compromise in the absence of detailed mechanistic knowledge (Lamouroux *et al.*, 2010), ecohydraulics should strive to establish a more ecologically realistic foundation for modelling the response of populations to environmental change and management interventions (Lancaster and Downes, 2010; Frank *et al.*, 2011).

In this chapter we argue that the inclusion of higher order (turbulent) properties of the flow constitutes a more complete and ecologically relevant characterisation of the hydraulic environment that biota are exposed to than standard ecohydraulic variables alone. The use of turbulent flow properties in ecohydraulics, therefore, has the potential to contribute towards achieving river research and management goals (e.g. river habitat assessment, modelling, rehabilitation) but more information on the mechanisms by which turbulence affects biota is required before this potential can be realised. After outlining the theory, structure and measurement of turbulent flow in open channels we focus on the swimming performance and habitat selection of stream-dwelling fish as an example of how the hydrodynamics of river ecosystems may affect resident biota. The discussion is biased towards salmonids (*S. salar, S. trutta, Oncorhynchus mykiss*) as most research has focused on these species due to their ecological (Wilson and Halupka, 1995; Jonsson and Jonsson, 2003) and socio-economic (e.g. Murray and Simcox, 2003) importance and our ability to measure turbulence at the focal point of these organisms, although the turbulent flow properties discussed are likely to be relevant to a range of other aquatic biota. Our scope is generally confined to small to medium (second–fourth order) lowland gravel-bed rivers, although there may well be wider applicability both in terms of river size and type. We acknowledge that many factors (e.g. physico-chemical, biological) make up the multidimensional niche of biota (e.g. Kohler, 1992; Sweeting, 1994; Lancaster and Downes, 2010) but ecohydraulics serves to emphasise the physical environment, which many have cited as the dominant factor in the ecology of lotic communities (e.g. Statzner *et al.*, 1988; Hart and Finelli, 1999; Thompson and Lake, 2010). The discussion, therefore, is restricted to the hydraulics of river habitats.

2.2 Turbulence: theory, structure and measurement

Turbulence in fluid flows was recognised by Leonardo Da Vinci as early as 1513 and is a ubiquitous phenomenon in river ecosystems, where $Re \gg 500$ (Davidson, 2004). Despite this, however, there is still no formal definition of turbulence, although a number of key qualities have been identified. Turbulent flow exhibits seemingly random

Table 2.2 Some examples of flow-biota links identified in the ecohydraulics literature.

Reference	Variable(s)	Species/community/process influenced by variable
Dispersal and reproduction		
Silvester and Sleigh (1985); Reiter and Carlson (1986); Biggs and Thomsen (1995)	τ, U_*	Positively correlated with loss of biomass of filamentous and matt-forming algal communities
Stevenson (1983); Peterson and Stevenson (1989)	U	Negatively correlated with diatom colonisation rates on clean ceramic tiles
Deutsch (1984); Becker (1987) cited in Statzner *et al.* (1988)	Re, Fr	Oviposition sites of certain caddis fly (Trichoptera) genera correlated with Re and Fr
McNair *et al.* (1997)	U_*	Transport distance positively related to Rouse number ($= V_s/U_*$, where V_s is settling velocity)
Beamish (1978); Crisp (1993); Hinch and Rand (2000)	h, U	Fish migration inhibited when $h \ll$ body depth and/or when $U > V_{\max}$
Habitat use		
Biggs (1996)	U	Growth rate and organic matter accrual of periphyton and macrophytes enhanced at intermediate U
Scarsbrook and Townsend (1993); Lancaster and Hildrew (1993)	τ	Macroinvertebrate community structure related to spatial and temporal variation in τ
Statzner (1981a)	δ	Body length of freshwater snails (Gastropoda) and shrimps (Gammarus) positively correlated with δ
Statzner (1981b)	δ, Fr	Abundance of *Odagmia ornata* (Diptera:Simuliidae) negatively correlated with δ and positively correlated with Fr
Statzner *et al.* (1988)	$Re > U > \delta > Re_* > Fr$	Order of best explanatory variables to predict distribution of water bug *Aphelocheirus aestivalis*
Brooks *et al.* (2005)	Re_*	Strongest (negative) correlation with macroinvertebrate abundance and species richness
Bisson *et al.* (1988); Lamouroux *et al.* (2002); Moir *et al.* (1998, 2002); Sagnes and Statzner (2009)	h, U, Fr	Fish species and life stages segregated by hydraulic variables due to morphological and ecological traits
Resource acquisition, competition and predation		
Wiley and Kohler (1980); Eriksen *et al.* (1996); Stevenson (1996)	U, δ	U controls the delivery of limiting resources. Laminar sublayer (δ) limits rate of molecular diffusion.
Godin and Rangeley (1989); Hayes and Jowett (1994); Heggenes (1996)	U, h	U positively correlated with prey delivery and negatively correlated with capture rates for salmonids; velocity gradients determine energetic costs of drift-feeding by insectivorous fish; high h provides refuge from predators and competition
Peckarsky *et al.* (1990); Malmqvist and Sackman (1996); Hart and Merz (1998)	U	High U serves as a refuge from predators for blackflies (Simuliidae) and stoneflies (Plecoptera)
Poff and Ward (1992, 1995); DeNicola and McIntire (1991)	U	Negatively correlated with rates of algal consumption by snails and certain caddis flies (Trichoptera)
Matczak and Mackay (1990); Hart and Finelli (1999)	U	Higher U reduces competition and increases carrying capacity of filter-feeding macroinvertebrates