Ecohydraulics
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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

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Contents

List of Contributors, xi

1 Ecohydraulics: An Introduction, 1
Ian Maddock, Atle Harby, Paul Kemp and Paul Wood

1.1 Introduction, 1
1.2 The emergence of ecohydraulics, 2
1.3 Scope and organisation of this book, 4
References, 4

Part I Methods and Approaches

2 Incorporating Hydrodynamics into Ecohydraulics: The Role of Turbulence in the Swimming Performance and Habitat Selection of Stream-Dwelling Fish, 9
Martin A. Wilkes, Ian Maddock, Fleur Visser and Michael C. Acreman

2.1 Introduction, 9
2.2 Turbulence: theory, structure and measurement, 11
2.3 The role of turbulence in the swimming performance and habitat selection of river-dwelling fish, 20
2.4 Conclusions, 24
Acknowledgements, 25
References, 25

3 Hydraulic Modelling Approaches for Ecohydraulic Studies: 3D, 2D, 1D and Non-Numerical Models, 31
Daniele Tonina and Klaus Jorde

3.1 Introduction, 31
3.2 Types of hydraulic modelling, 32
3.3 Elements of numerical hydrodynamic modelling, 33
3.4 3D modelling, 49
3.5 2D models, 55
3.6 1D models, 57
3.7 River floodplain interaction, 59
3.8 Non-numerical hydraulic modelling, 60
3.9 Case studies, 60
3.10 Conclusions, 64
Acknowledgements, 66
References, 66
4 The Habitat Modelling System CASiMiR: A Multivariate Fuzzy Approach and its Applications, 75
Markus Noack, Matthias Schneider and Silke Wieprecht
4.1 Introduction, 75
4.2 Theoretical basics of the habitat simulation tool CASiMiR, 76
4.3 Comparison of habitat modelling using the multivariate fuzzy approach and univariate preference functions, 80
4.4 Simulation of spawning habitats considering morphodynamic processes, 82
4.5 Habitat modelling on meso- to basin-scale, 85
4.6 Discussion and conclusions, 87
References, 89

5 Data-Driven Fuzzy Habitat Models: Impact of Performance Criteria and Opportunities for Ecohydraulics, 93
Ans Mouton, Bernard De Baets and Peter Goethals
5.1 Challenges for species distribution models, 93
5.2 Fuzzy modelling, 95
5.3 Case study, 100
References, 105

6 Applications of the MesoHABSIM Simulation Model, 109
Piotr Parasiewicz, Joseph N. Rogers, Paolo Vezza, Javier Gortázar, Thomas Seager, Mark Pegg, Wiesław Wiśniewolski and Claudio Comoglio
6.1 Introduction, 109
6.2 Model summary, 109
Acknowledgements, 123
References, 123

7 The Role of Geomorphology and Hydrology in Determining Spatial-Scale Units for Ecohydraulics, 125
Elisa Zavadil and Michael Stewardson
7.1 Introduction, 125
7.2 Continuum and dis-continuum views of stream networks, 126
7.3 Evolution of the geomorphic scale hierarchy, 127
7.4 Defining scale units, 131
7.5 Advancing the scale hierarchy: future research priorities, 139
References, 139

8 Developing Realistic Fish Passage Criteria: An Ecohydraulics Approach, 143
Andrew S. Vowles, Lynda R. Eakins, Adam T. Piper, James R. Kerr and Paul Kemp
8.1 Introduction, 143
8.2 Developing fish passage criteria, 144
8.3 Conclusions, 151
8.4 Future challenges, 152
References, 152

Part II Species–Habitat Interactions

9 Habitat Use and Selection by Brown Trout in Streams, 159
Jan Heggenes and Jens Wollebæk
9.1 Introduction, 159
9.2 Observation methods and bias, 160
9.3 Habitat, 161
9.4 Abiotic and biotic factors, 161
9.5 Key hydraulic factors, 163
9.6 Habitat selection, 163
9.7 Temporal variability: light and flows, 166
9.8 Energetic and biomass models, 168
9.9 The hyporheic zone, 169
9.10 Spatial and temporal complexity of redd microhabitat, 169
9.11 Summary and ways forward, 170
References, 170

10 Salmonid Habitats in Riverine Winter Conditions with Ice, 177
Ari Huusko, Teppo Vehanen and Morten Stickler
10.1 Introduction, 177
10.2 Ice processes in running waters, 178
10.3 Salmonids in winter ice conditions, 182
10.4 Summary and ways forward, 186
References, 188

11 Stream Habitat Associations of the Foothill Yellow-Legged Frog (Rana boylii): The Importance of Habitat Heterogeneity, 193
Sarah Yarnell
11.1 Introduction, 193
11.2 Methods for quantifying stream habitat, 194
11.3 Observed relationships between R. boylii and stream habitat, 198
11.4 Discussion, 204
References, 209

12 Testing the Relationship Between Surface Flow Types and Benthic Macroinvertebrates, 213
Graham Hill, Ian Maddock and Melanie Bickerton
12.1 Background, 213
12.2 Ecohydraulic relationships between habitat and biota, 213
12.3 Case study, 216
12.4 Discussion, 223
12.5 Wider implications, 226
12.6 Conclusion, 227
References, 227

13 The Impact of Altered Flow Regime on Periphyton, 229
Nataša Smolar-Žvanut and Aleksandra Krivograd Klemenčič
13.1 Introduction, 229
13.2 Modified flow regimes, 230
13.3 The impact of altered flow regime on periphyton, 231
13.4 Case studies from Slovenia, 236
13.5 Conclusions, 240
References, 240

14 Ecohydraulics and Aquatic Macrophytes: Assessing the Relationship in River Floodplains, 245
Georg A. Janauer, Udo Schmidt-Mumm and Walter Reckendorfer
14.1 Introduction, 245
14.2 Macrophytes, 246
14.3 Life forms of macrophytes in running waters, 248
14.4 Application of ecohydraulics for management: a case study on the Danube River and its floodplain, 249
14.5 Conclusion, 255
Acknowledgements, 255
Appendix 14.A: Abbreviations used in Figure 14.5, including full plant names and authorities, 255
References, 256

15 Multi-Scale Macrophyte Responses to Hydrodynamic Stress and Disturbances: Adaptive Strategies and Biodiversity Patterns, 261
Sara Puijalon and Gudrun Bornette
15.1 Introduction, 261
15.2 Individual and patch-scale response to hydrodynamic stress and disturbances, 262
15.3 Community responses to temporary peaks of flow and current velocity, 266
15.4 Macrophyte abundance, biodiversity and succession, 268
15.5 Conclusion, 269
References, 270

Part III Management Application Case Studies
16 Application of Real-Time Management for Environmental Flow Regimes, 277
Thomas B. Hardy and Thomas A. Shaw
16.1 Introduction, 277
16.2 Real-time management, 278
16.3 The setting, 278
16.4 The context and challenges with present water allocation strategies, 281
16.5 The issues concerning the implementation of environmental flow regimes, 282
16.6 Underlying science for environmental flows in the Klamath River, 283
16.8 The solution – real-time management, 285
16.9 Example RTM implementation, 287
16.10 RTM performance, 287
16.11 Discussion, 290
16.12 Conclusions, 290
Acknowledgements, 291
References, 291

17 Hydraulic Modelling of Floodplain Vegetation in Korea: Development and Applications, 293
Hyoseop Woo and Sung-Uk Choi
17.1 Introduction, 293
17.2 Modelling of vegetated flows, 294
17.3 Floodplain vegetation modelling: From white rivers to green rivers, 300
17.4 Conclusions, 306
References, 306
18 A Historical Perspective on Downstream Passage at Hydroelectric Plants in Swedish Rivers, 309
Olle Calles, Peter Rivinoja and Larry Greenberg

18.1 Introduction, 309
18.2 Historical review of downstream bypass problems in Sweden, 310
18.3 Rehabilitating downstream passage in Swedish Rivers today, 312
18.4 Concluding remarks, 319
References, 320

19 Rapid Flow Fluctuations and Impacts on Fish and the Aquatic Ecosystem, 323
Atle Harby and Markus Noack

19.1 Introduction, 323
19.2 Rapid flow fluctuations, 325
19.3 Methods to study rapid flow fluctuations and their impact, 325
19.4 Results, 326
19.5 Mitigation, 329
19.6 Discussion and future work, 331
Acknowledgements, 333
References, 334

20 Ecohydraulic Design of Riffle-Pool Relief and Morphological Unit Geometry in Support of Regulated Gravel-Bed River Rehabilitation, 337
Gregory B. Pasternack and Rocko A. Brown

20.1 Introduction, 337
20.2 Experimental design, 338
20.3 Results, 347
20.4 Discussion and conclusions, 351
Acknowledgements, 353
References, 353

21 Ecohydraulics for River Management: Can Mesoscale Lotic Macroinvertebrate Data Inform Macroscale Ecosystem Assessment?, 357
Jessica M. Orlofske, Wendy A. Monk and Donald J. Baird

21.1 Introduction, 357
21.2 Lotic macroinvertebrates in a management context, 358
21.3 Patterns in lotic macroinvertebrate response to hydraulic variables, 359
21.4 Linking ecohydraulics and lotic macroinvertebrate traits, 365
21.5 Trait variation among lotic macroinvertebrates in LIFE flow groups, 366
21.6 Upscaling from ecohydraulics to management, 370
21.7 Conclusions, 371
References, 371

22 Estuarine Wetland Ecohydraulics and Migratory Shorebird Habitat Restoration, 375
José F. Rodríguez and Alice Howe

22.1 Introduction, 375
22.2 Area E of Kooragang Island, 377
22.3 Ecohydraulic and ecogeomorphic characterisation, 378
22.4 Modifying vegetation distribution by hydraulic manipulation, 382
22.5 Discussion, 388
22.6 Conclusions and recommendations, 390
References, 392
23 Ecohydraulics at the Landscape Scale: Applying the Concept of Temporal Landscape Continuity in River Restoration Using Cyclic Floodplain Rejuvenation, 395
Gertjan W. Geerling, Harm Duel, Anthonie D. Buijse and Antonius J.M. Smits
23.1 Introduction, 395
23.2 The inspiration: landscape dynamics of meandering rivers, 397
23.3 The concept: temporal continuity and discontinuity of landscapes along regulated rivers, 399
23.4 Application: floodplain restoration in a heavily regulated river, 401
23.5 The strategy in regulated rivers: cyclic floodplain rejuvenation (CFR), 403
23.6 General conclusions, 405
References, 405

24 Embodying Interactions Between Riparian Vegetation and Fluvial Hydraulic Processes Within a Dynamic Floodplain Model: Concepts and Applications, 407
Gregory Egger, Emilio Politti, Virginia Garófano-Gómez, Bernadette Blamauer, Teresa Ferreira, Rui Rivaes, Rohan Benjankar and Helmut Habersack
24.1 Introduction, 407
24.2 Physical habitat and its effects on floodplain vegetation, 408
24.3 Succession phases and their environmental context, 410
24.4 Response of floodplain vegetation to fluvial processes, 414
24.5 Linking fluvial processes and vegetation: the disturbance regime approach as the backbone for the dynamic model, 415
24.6 Model applications, 417
24.7 Conclusion, 423
Acknowledgements, 424
References, 424

Part IV Conclusion
25 Research Needs, Challenges and the Future of Ecohydraulics Research, 431
Ian Maddock, Atle Harby, Paul Kemp and Paul Wood
25.1 Introduction, 431
25.2 Research needs and future challenges, 432
References, 435

Index, 437
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1

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 km² 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
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 Quene 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’, ‘eco hydraulics’ 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 sub-discipline 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 eco hydraulics. 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 ‘eco hydraulics’, early approaches, such as the Physical Habitat Simulation System (PHABSIM) in the 1980s and 1990s, were widely applied (Gore et al., 2001) but often criti- cised 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 eco hydraulics 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 ‘eco-hydraulic’ 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 ‘eco-hydraulics’ 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 ‘eco-hydrology’, 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.

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 ‘eco-hydraulics’ 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 ecohydrologists in 2010 (Rice et al., 2010) and two out of nine papers within a special issue devoted to ‘Fish passage: an ecohydrology approach’ in 2012 (Kemp, 2012), and clearly demonstrates that many authors do not routinely use the term ‘eco-hydraulics’. 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 ‘eco-hydraulics’ 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. 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.

References


Methods and Approaches
2

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

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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).
Table 2.1  Common terms used to describe the flow environment.

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

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, $Fr$; Reynolds number, $Re$), 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](image-url)
a different set of variables. They include bed shear stress \( (\tau) \), shear velocity \( (U_s) \), roughness Reynolds number \( (Re^*) \) and the thickness of the laminar sublayer \( (\delta) \). \( U_s \) is related to \( \tau \) (Table 2.1) which, in turn, is responsible for the appearance of a mean gradient in the vertical velocity profile. \( U_s \) 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, \( \delta \) 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, \( \delta \) 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 \( V_{\text{max}} \), 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 \( \delta \), \( Fr \), \( \tau \) 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 ecohydraulics 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.

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