17th Australasian Fluid Mechanics Conference
Auckland, New Zealand
5-9 December 2010

Hydrodynamics of Aquatic Ecosystems: Current State, Challenges, and Prospects

V. Nikora[1]

[1]School of Engineering
University of Aberdeen, Scotland, AB24 3UE, United Kingdom

Abstract

The paper endorses a recently emerged interdisciplinary research subject *Hydrodynamics of Aquatic Ecosystems*, defined as a study of flow-organism interactions in running waters with particular focus on relevant transport processes and mutual physical impacts occurring at multiple scales from the sub-organism scale to the organism patch mosaic scale (comparable to the flow width). This new research area emerges at the interfaces between environmental fluid mechanics, biomechanics, and aquatic ecology, bridging these disciplines together and offering new promising research avenues. After a brief review of the current state, the paper focuses on the challenges that this subject area currently faces, and then outlines research directions to pursue for resolving the highlighted challenges.

Introduction

Sixteen years ago a prominent aquatic ecologist B. Statzner stressed that "a broader incorporation of aspects of fluid dynamics into studies of various ecosystems will advance general ecological theory faster than past or current research routes, which largely ignore(d) the physical principles of moving air or water" [26]. Since then, the situation has not changed much [27], reflecting a slow progress in the implementation of fluid mechanical concepts into ecological theories. There are at least three reasons for such a slow progress in the current knowledge. First, measurements at the organism scales still represent great challenges and thus data related to these scales remain very limited. Second, most studies of flow-organism interactions pay little attention to the biomechanical properties of organisms, which change significantly across species, scales, and environments and are poorly understood. Third, the subject of flow-organism interactions lies at the borders between fluid mechanics, ecology, and biomechanics, i.e., at the discipline interfaces which are typically avoided by researchers. Another problem that has also to be addressed is how to integrate fluid mechanical, biomechanical, and ecological processes together and how to upscale the effects of these processes from the sub-organism scale to the patch mosaic scale. Because of these knowledge gaps, the progress in studies of flow-biota interactions is slow and a solid unifying interdisciplinary platform is urgently required to accelerate it and to enhance current ecological concepts.

This paper and talk are an attempt to further enhance and promote such a platform as an emerging research area at the interfaces between environmental fluid mechanics, aquatic ecology, and biomechanics. This new area, *Hydrodynamics of Aquatic Ecosystems*, bridges these disciplines together and can be defined as a study of flow-organism interactions in running waters with particular focus on relevant transport processes and mutual physical impacts occurring at multiple scales from the sub-organism scale to the organism patch mosaic scale comparable to the flow width [19]. Being an important part of its mother disciplines, *Hydrodynamics of Aquatic Ecosystems* deals with two key interconnected issues: (i) physical interactions between flow and organisms (e.g., due to an interplay between flow-induced forces and reaction forces generated by organisms); and (ii) ecologically relevant mass-transfer processes (e.g., due to molecular and turbulent diffusion). The focus of *Hydrodynamics of Aquatic Ecosystems* on the interfaces between fluid mechanics, ecology and biomechanics should help with elimination of existing knowledge gaps in the least studied areas.

Hydrodynamics of Aquatic Ecosystems as a subject covers both marine and freshwater environments and therefore should include, as equal branches, *Hydrodynamics of Freshwater Ecosystems* (i.e., streams, rivers) and *Hydrodynamics of Marine Ecosystems*. The centre of attention of this paper is on freshwater systems (i.e., streams and rivers) where, compared to marine systems, development of *Hydrodynamics of Aquatic Ecosystems* is deferred and thus this talk may help in its enhancement. Key concepts of *Hydrodynamics of Aquatic Ecosystems* and current challenges will be outlined first and then future research directions will be listed.

Scale Range of *Hydrodynamics of Aquatic Ecosystems* in Relation to Streams and Rivers

Flow variability in streams and rivers covers wide ranges of temporal and spatial scales, from milliseconds to many years and from sub-millimetres to tens of kilometres (figure 1, [18]). The low frequency (large periods) range in the frequency spectrum is formed by intra-annual and inter-annual hydrological variability while the high-frequency (small periods) range is formed by flow turbulence (figure 1a). The low wave-number (large spatial scale) range in the wave-number spectrum is formed by morphological variability along the flow such as bars and/or meanders (figure. 1b). At smaller spatial scales (comparable to and less than the flow width) velocity fluctuations are due to turbulence. This 'turbulence' range of scales is most relevant to organisms as their own scales (including patchiness) typically fall within this range. In addition, turbulence is often the main mechanism controlling drag forces acting on the organisms as well as driving transport processes in biological communities. Thus, the main focus of *Hydrodynamics of Aquatic Ecosystems* in relation to streams and rivers is on the turbulent range of scales as sketched in figure 1 [18, 19].

Tools and Concepts of *Hydrodynamics of Aquatic Ecosystems*

Research methods, tools and concepts of *Hydrodynamics of Aquatic Ecosystems* come from its mother disciplines and are still emerging. On one hand, they gradually become interconnected and adjusted to address common goals and research questions. On the other hand, they feed back to the original disciplines providing new challenges and making these disciplines conceptually richer. Hence, the methodological suit of *Hydrodynamics of Aquatic Ecosystems* is likely to be always strongly linked to the original mother disciplines. Fluid

Mechanics contributes to *Hydrodynamics of Aquatic Ecosystems* with concepts of boundary layers (BL), mixing layers (ML), wakes, and jets. Depending on the specific conditions these flow types may exhibit properties of two turbulence phenomena: coherent structures (CS) and/or eddy cascades (EC). These canonical flow types and concepts can be both actively utilised and significantly altered by biological communities. Furthermore, these communities, in principle, may also create unconventional flow configurations which are still unidentified in Fluid Mechanics.

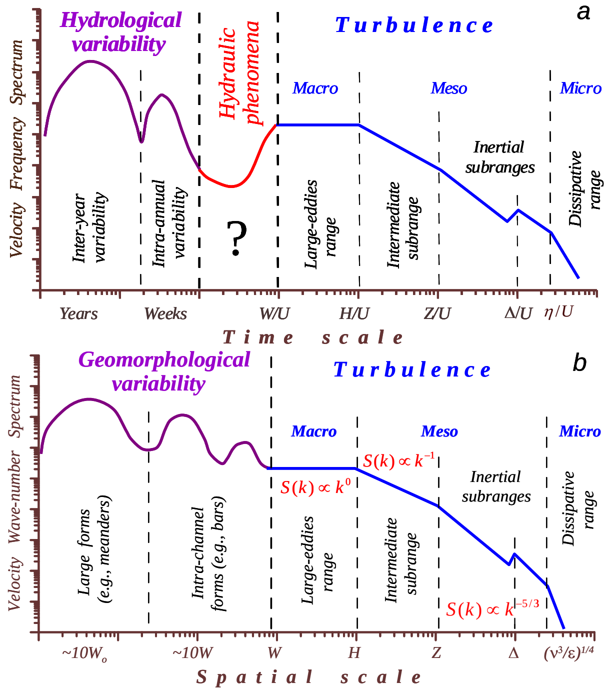

Figure 1. Schematised velocity spectra in rivers: (a) frequency spectrum; and (b) wave-number spectrum (W_o and W = river valley and river channel widths, H = depth, Z = distance from the bed, Δ = roughness height, U = flow velocity, η = turbulence micro-scale [18].

In a similar way, biomechanics, which stems from mechanics of materials and structural mechanics, provides a range of methods and concepts that help in describing biological communities at multiple scales and linking them to their fluid environments. Indeed, reactions of organisms to physical forces imposed by flow patterns described above largely depend on their biomechanical properties. This dependence has been recognised long ago and some progress has been made for terrestrial ecosystems (e.g., trees, vertebrates, and insects) and partially for marine ecosystems [2, 3, 14, 20, 22, 30, 31] while biomechanics of freshwater organisms is still largely unknown and is represented by very few studies (e.g., [10, 32]). Combined consideration of flow-induced, organism-induced, and organism-reaction forces leads to a set of similarity numbers that describe interplay between gravity, buoyancy, drag, and elastic forces. The flow-organism similarity numbers may be helpful in data interpretation and in identifying specific regimes of flow-biota interactions. They can also be introduced in a more formal way considering coupled flow-organism equations of motion, where the flow equations provide drag terms that are used in organism motion equations as external forcing. A wide expansion of this approach, however, is slowed down by very limited information on organism material parameters and their variability across species, scales, and environments. Combined together, fluid mechanical and biomechanical concepts should explain a number of ecological issues related to design, spatial and temporal patterns, and performance of aquatic organisms and their communities. Recent ecological studies suggest that organism functioning, morphology, and the role in aquatic ecosystems are largely driven by transport processes and mutual physical impacts and their interactions, i.e., remits of *Hydrodynamics of Aquatic Ecosystems*) [7, 9, 11, 15, 16, 25, 28, 30].

The current studies of flow-biota interactions in streams and rivers encounter a number of challenges related to fluid mechanical, biological, and ecological aspects which slows down the knowledge advancement in this area. These challenges, discipline-grouped for convenience, are highlighted below.

Research Challenges

Fluid mechanical challenges

In aquatic ecosystems, the canonical flow types (BL, ML, wakes, jets) are fundamental for characterisation of both (1) hydraulic habitats, as most aquatic communities live within BLs, MLs, etc; and (2) flow patterns around individual organisms that are often surrounded by BLs, MLs, or wakes generated at organism surfaces or within/around organism communities. The occurrence of these flow types in aquatic ecosystems, however, often deviates from their canonical forms, thus leading to *Challenge #1*: *What are the manifestations of the canonical flow types in aquatic ecosystems?* Figure 2 may illustrate this challenge for the case of aquatic plants which typically span a wide range of scales from a leaf scale to individual plant to the plant patch mosaic (i.e., an assemblage of plant patches of different shapes and sizes). As an example, biological communities quite often are embedded in a superposition of interacting multi-scale BLs generated by a variety of boundaries including those introduced by the organisms themselves (e.g., flow-depth BL and leaf/stem BLs in figure 2a). As a rule, these BLs have limited thicknesses and small relative submergence of roughness elements, being often organised as a cascade of internal boundary layers (e.g., [11, 15]). As a result, the conventional concepts and descriptions may not be always applicable and may require refinements (e.g., applicability of the log velocity profile in low-submergence BLs is questionable). The flow patterns, schematically summarised in figure 2 for the case of aquatic plants, include: (1) ‘conventional’ depth-scale shear-generated turbulence which may be significantly altered by the vegetation; (2) canopy-height-scale turbulence resulting from the Kelvin-Helmholtz instability (KHI) at the upper boundary of the vegetation canopy (known as the mixing-layer analogy [23]); (3) generation of small-scale turbulence associated with flow separation from stems (i.e., von Karman vortices); (4) generation of small-scale turbulence within local boundary layers attached to leaf/stem surfaces; (5) generation of small-scale turbulence behind plant leaves serving as small ‘splitter plates’ that generate local leeward mixing layers, with subsequent turbulence production through the Kelvin-Helmholtz instability (most likely occurring when the leaf surface roughness differs between sides); (6) turbulence generation due to plant waviness at a range of scales (if biomechanical properties allow this); (7) generation of large-scale 3D and 2D turbulence associated with wakes and flow separation at a patch scale; (8) generation of 3D and 2D boundary layer and mixing layer turbulence at patch sides aligned with the flow; and (9) generation of interacting vertical and horizontal internal boundary layers at the patch mosaic scale (figure 2). Among these patterns, only studies of patterns 1, 2, and 3 have been carried out [6, 12, 13, 21] while other patterns are hypothesised in figure 2 based on conceptual consideration and our preliminary results from laboratory and field studies ([1, 15, 16, 19], figure 3). The identification and quantification of interrelationships between these patterns, as well as detection of their individual and combined roles in transport processes and drag generation for a range of biomechanical parameters represent *Challenge #2: What are the combined effects of canonical flow types in aquatic ecosystems?*

Figure 2 also highlights a possibility that biological communities may create unique flow types with specific properties making them distinctly different from the canonical flow types or their combinations, leading to *Challenge 3: Do flow-biota interactions create new unconventional flow types or patterns which are still waiting for identification?*

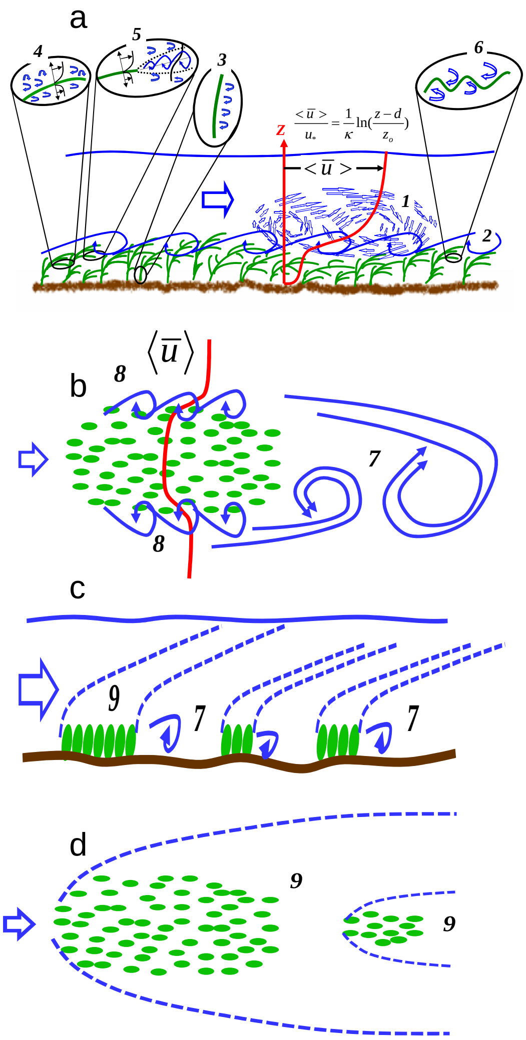

Figure 2. Hypothesised flow patterns in vegetated channels: side view at a patch scale (a); plan view at a patch scale (b); side view at a patch mosaic scale (c); and plan view at a patch mosaic scale (d).

To illustrate this point, one may look into a “mixing layer analogy” originally proposed for terrestrial canopies by Raupach *et al.* [23] and further advanced in Finnigan [4] and Finnigan et al. [5]. For the case of submerged aquatic vegetation, this analogy was first implemented by H. Nepf’s Group (e.g., [6, 12]) and then used in a number of follow-up studies of flow-vegetation interactions (e.g., [13, 21]). These studies showed that large-scale ML eddies formed as a result of KHI at the canopy top may play a crucial role in mass and momentum exchange between canopy region and flow region above the canopy. Although the mixing layer analogy for aquatic vegetation has already been explored (see citations above), there is still a number of issues that require clarification. Some of them suggest that the mixing layer analogy may be a manifestation of a new flow type that exhibits unique properties absent in canonical flows. Examples include (1) the existence of a ‘detached’ logarithmic BL above a ML at the canopy top (i.e., ML may block access of BL eddies to the canopy layer thus ‘detaching’ BL eddies from the bed and destroying the conventional conditions for BL formation); (2) big difference between the convection velocity of large eddies at the canopy top and a local mean velocity, reported for both terrestrial and aquatic canopies [4, 12, 13, 23], although for conventional mixing layers these two velocities should be equal or very close (e.g., [8]); and (3) monami effect, i.e., wavy motions of a canopy top often observed in natural aquatic canopies, known as ‘honami’ for terrestrial canopies [6, 12, 20].

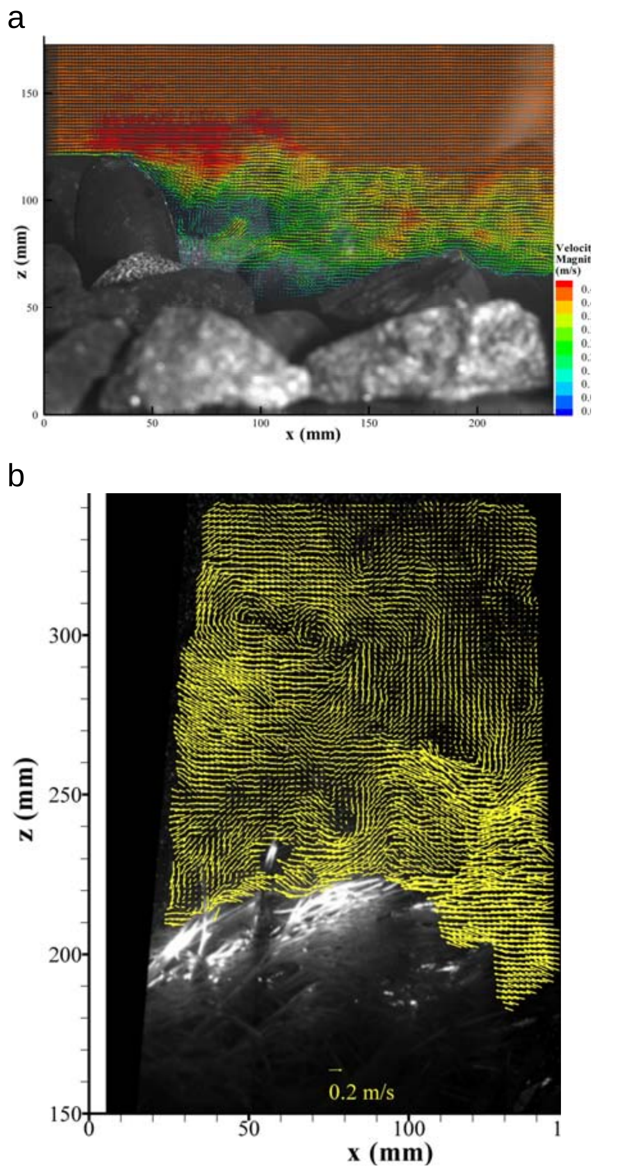

Figure 3. Examples of a laboratory PIV study of freshwater mussels *Margaritifera margaritifera* (2d/2c PIV; velocity vectors on the downstream side of a mussel are shown; the experiment was conducted in the Aberdeen Open Channel Facility, AOCF), (a); and a field PIV study of a freshwater macrophyte Myriophyllum alterniflorum in the Urie River, Scotland (stereoscopic 2d/3c PIV, velocity vectors are shown), (b). Custom-made 4-camera 100Hz multi-modular PIV system and associated software have been designed and developed by Dr Stuart Cameron at the University of Aberdeen, http://www.abdn.ac.uk/engineering/ research/ envhrg/facilities/aocf.php.

Biomechanical challenges

Biomechanics of freshwater organisms is still in its infancy and poses significant challenges for studies of flow-biota interactions. They can be illustrated using aquatic plants in streams as an example. Aquatic plants in streams and rivers exhibit a great variety of morphological forms and encounter complex loads due to a mixture of tension, compression, bending, torsion, and shear. These complexities take place at multiple scales, from sub-cell scale to cell scale, sub-leaf scale, leaf scale, shoot (leaves + stem) scale, individual plant (sum of shoots), plant patch (aggregation of plants) scale, and plant patch mosaic (aggregation of plant patches) scale. Biomechanical characteristics at larger scales represent some integration of properties at smaller scales and, thus, at each of these scales the plants should be treated as structures rather than simple materials. Preliminary studies (e.g., [10, 32]) suggest that the plants can be defined as composite, anisotropic, viscoelastic, highly heterogeneous materials or structures. Thus the primary key challenge to address on this front is *Challenge 4: What are the most appropriate structural models of biota?* Indeed, it is not even clear how accurately the Hookean model (i.e., linear stress – strain relation) and the associated elasticity modulus E represent aquatic plants at different scales.

The mentioned complexities may explain why, until now, we do not have a set of widely accepted quantitative characteristics of plant geometry and mechanical properties. There are at least three groups of parameters that may be required: (1) plant morphology characteristics; (2) plant material characteristics; and (3) plant-flow interaction characteristics. The translation of biomechanical properties from one scale to another may involve techniques of spatial-averaging and homogenisation similar to those developed for modelling composite materials and material microstructure (e.g., [29]). The definition of these parameters and recipes for their estimates represent *Challenge 5: How can morphological and biomechanical properties of biota be defined, measured and/or quantified at different scales?*

Assuming that suitable measures of biomechanical properties are found then the next significant issue to resolve is *Challenge 6: How can hydrodynamic and biomechanical properties be linked together?* In principle, coupling fluid mechanical and biomechanical processes can be done at different levels of rigour, from consideration of joint similarity numbers to spatially-averaged coupled differential equations. Examples of the first approach are given in [2, 19] while the second approach will be briefly described in the next section.

Ecological challenges

Traditional approaches in aquatic ecology are largely descriptive and are mainly based on bulk parameters such as community composition, biomass, population size, and other measures. The effects of hydraulic habitat on these parameters are typically studied using a variety of statistical techniques that link ecological parameters to bulk flow properties such as flow rate, depth-averaged velocity, surface velocity, or stream power. *Hydrodynamics of Aquatic Ecosystems* provides a process-based alternative to these approaches which are essentially empirical in nature. Indeed, preliminary considerations (e.g., [7, 9, 19, 20, 26-28] and references therein) suggest that organism functioning, morphology, and role in river ecosystems are largely driven by the interplay of two key groups of environmental processes: (i) physical interactions between flow and organisms (e.g., due to flow-induced forces and reaction forces generated by organisms); and (ii) ecologically relevant mass-transfer-uptake processes (e.g., due to molecular/turbulent diffusion), including photosynthesis aspects when relevant. This primary hypothesis leads to a number of secondary hypotheses that may further advance understanding of flow-biota interactions. Specifically, the following hypothesis can be explored:

- Secondary hypothesis #1: within a wide range of scales (from the sub-organism scale to the patch mosaic scale comparable to the lateral flow size) there are distinct scales where flow-organism interactions and transport processes are scale-specific and interconnected. There are at least four such scales: sub-organism scale, organism scale, patch scale, and patch mosaic scale.
- Secondary hypothesis #2: to enhance adaptation to river environments, the organisms effectively control and optimise hydrodynamic drag forces at multiple scales by adjusting their own shape, flexibility, and the flow itself.
- Secondary hypothesis #3: to enhance adaptation to river environments, the organisms effectively control and optimise transport processes at multiple scales by modifying existing flow patterns and creating new turbulence-generation mechanisms (as illustrated in figure 2 for the case of aquatic plants).

Altogether, these hypotheses represent *Challenge 7: How are organism functioning, morphology, and role in aquatic ecosystems controlled by the interplay of drag forces and transport processes?* To address this challenge one also needs to define measurable ecological parameters and how they can be measured simultaneously with fluid mechanical and biomechanical parameters, tasks that constitute *Challenge 8*.

Unifying framework

The integration of fluid mechanical, biomechanical, and ecological processes together and upscaling the effects of these processes from the sub-organism scale to the patch mosaic scale constitute another task awaiting to be completed. This task, *Challenge #9*, should lead to the development of the unifying framework expected to be (1) quantitative by nature; (2) capable of coupling fluid mechanical, ecological, and biomechanical processes in a reasonably rigorous way; (3) a convenient and rigorous tool for upscaling small-scale flow-organism interactions to a larger scale (e.g., from the organism scale to patch or patch mosaic scale); (4) suitable as a basis for mathematical modelling and computer simulations; and (5) appropriate for guiding field and laboratory studies and data interpretation and generalisation.

The spatially averaged (but instantaneous in time domain) hydrodynamic, transport, and biomechanical equations, which couple flow and organisms together through a rigorous spatial averaging operation (over local volume or area in the plane parallel to the mean bed surface, figure 4) may serve as a potential candidate for such a framework. The coupled spatially averaged equations can be derived for both fluid (considering organisms as embedded media) and organisms (considering fluid as embedded media). The flow and 'organism' equations are linked by the interface terms describing physical interactions and/or exchange of substances (e.g., the same term describing transport of nutrients through organisms' surfaces will be included in both 'flow' and 'organism' equations, but with opposite signs). The 'instantaneous' equations can also be simultaneously spatially- and time-averaged to produce the double-averaged (in time and space) coupled equations for fluid and organisms. The double-averaged equations for the fluid phase have been originally proposed to describe flow properties within and above terrestrial canopies (e.g., [4] and references therein).

Hence, the operation of spatial averaging allows, in principle, the integration of biomechanical and fluid mechanical processes together. On the other hand, the spatial averaging essentially serves as a scaling-up procedure that changes the scale of consideration from one level in time-space-probability domain to another level. Detailed derivation and discussion of the spatially averaged equations can be found in [4, 17]. The instantaneous spatially averaged equations and double-averaged equations explicitly contain important (although still unconventional) terms such as form-induced stresses and fluxes, and for the flow region with embedded organisms, form and viscous drag terms, wake and waving production terms (e.g., energy production due to the wake effects behind mussels or due to mobile interfaces such as plants), and source/sink terms describing interface transport and heterogeneous reactions (e.g., sediment 'breathing' or nutrient uptake by aquatic organisms). In addition, the spatial averaging methodology is conceptually close to the Large-Eddy Simulation (LES) philosophy, which is currently actively used in turbulence research. In relation to organisms, the spatial averaging approach can be supplemented with the homogenisation techniques such as those developed in composite materials mechanics (e.g., [29]).

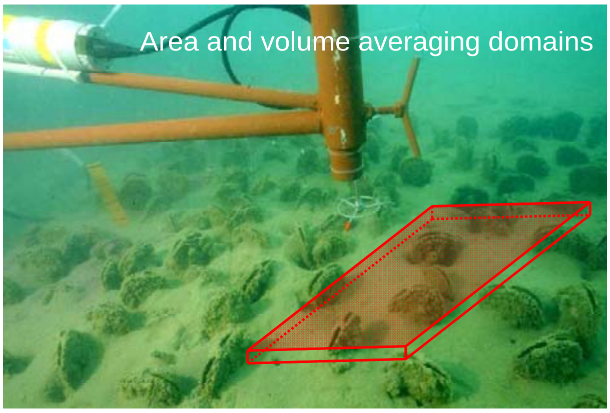

Figure 4. An example of the spatial averaging volume for the case of a mussels' bed [15].

Prospects

The key challenges of Hydrodynamics of Aquatic Ecosystems outlined above set up priorities for the forthcoming studies. Among them are:

- Integration of the canonical flow concepts into realities of natural aquatic systems.
- Identification of biota-induced flow types and patterns, which are still unknown.

- Identification of appropriate models of biota biomechanics.
- Development and implementation of biomechanical parameters.
- Coupling of biomechanical and hydrodynamic descriptions.

- Identification and implementation of ecological parameters which are scale-consistent with hydrodynamic and biomechanical parameters.
- Identification of physically-driven organism adaptation mechanisms.
- Quantification of organisms' responses to physical environment.

- Identification of a conceptual framework for coupling hydrodynamic, biomechanical, and ecological processes.
- Development of up-scaling and down-scaling approaches.

Conclusions

Addressing the described challenges should help in eliminating multiple knowledge gaps at the borders between fluid mechanics, ecology and biomechanics, i.e., areas where the probability of new discoveries is highest. In this respect, *Hydrodynamics of Aquatic Ecosystems* will provide a missing platform for developing process-based models, to replace current approaches such as diffusion-type approximations, often operating with coefficients disconnected to the underlying processes and actual organisms [20]. The knowledge on specific mechanisms of flow-biota interactions will also enhance capabilities of large-scale models based on complex systems approaches which are currently under active development (e.g., [24]) and may have significant practical relevance. Thus, *Hydrodynamics of Aquatic Ecosystems* promises not only step changes in the current understanding of our aquatic environments but also responds to the growing demands for advanced knowledge in numerous applications, including civil and environmental engineering (e.g., stream restoration design), resource management (e.g., definition and determination of 'environmental flows' for regulated rivers), aquaculture (e.g., optimal design for aqua-farms), and bio-security (e.g., control of invasive species or transport of pathogens). It will also provide a solid biophysical basis for eco-hydraulics which has been formed as an applied research area based on largely empirical or semi-empirical approaches.

Finally, the integration of methodologies of fluid mechanics, ecology and biomechanics and the focus on the interfaces between these disciplines creates the strong possibility of major breakthroughs not only in the understanding of aquatic ecosystems but also beyond it, with benefits for as diverse fields as design of bio-mimicking devices, fluid-structure interactions, and the adaptive evolution concept, among others.

Acknowledgments

The author is grateful to the Organizing Committee of the 17th Australasian Fluid Mechanics Conference for its kind invitation to give this paper. Stimulating discussions of this topic with I. Albayrak, J. Aberle, B. Biggs, S. Coleman, S. Cameron, J. Finnigan, D. Goring, D. Hart, C. Howard-Williams, I. Jowett, N. Lamouroux, S. Larned, S. McLean, O. Miler, N. Nikora, M. O'Hare, G. Parker, S. Rice, T. Riis, M. Righetti, P. Sagnes, B. Statzner, A. Sukhodolov, A. Suren, and S. Thrush are greatly acknowledged. The work was partly supported by the Leverhulme Trust, Grant F/00 152/Z "Biophysics of flow-plants interactions in aquatic systems".

References

[1] Albayrak, I., Nikora, V., Miler, O. & O'Hare, M., Flow-plant interaction at a leaf scale: effects of leaf shape, serration, surface roughness, and flexural rigidity, *Aquatic Sciences*, 2010 (submitted).

[2] de Langre E., Effects of wind on plants, *Annual Rev. Fluid. Mech*., **40**, 2008, 141-168.

[3] Denny, M. & Gaylord, B., The mechanics of wave-swept algae, *J. Exp. Biology*, **205**, 2002, 1355–1362.

[4] Finnigan, J.J., Turbulence in plant canopies, *Annu. Rev. Fluid. Mech*., **32**, 2000, 519-571.

[5] Finnigan, J., Shaw, R. & Patton, E., Turbulence structure above a vegetation canopy, *J. Fluid Mech*., **637**, 2009, 387-424.

[6] Ghisalberti, M. & Nepf H. The structure of the shear layer in flows over rigid and flexible canopies. *Environmental Fluid Mechanics*, **6**, 2006, 277-301.

[7] Hart, D.D. & Finelli, C.M., Physical-biological coupling in streams: The Pervasive effects of flow on benthic organisms, *Annu. Rev. Ecology System*., **30**, 1999, 363-395.

[8] Ho, C.-M. & Huerre, P., Perturbed free shear layers, *Ann. Rev. Fluid Mech*., **16**, 1984, 365–424.

[9] Hurd, C.L., Water motion, marine macroalgal physiology, and production, *J. Phycol.,* **36**, 2000, 453– 472.

[10] Miler, O., Albayrak, I., Nikora, V. & O'Hare, M., Biomechanical properties of aquatic plants and their effects on plant–flow interactions in streams and rivers, *Aquatic Sciences*, 2010 (submitted).

[11] Monismith, S.G., Hydrodynamics of coral reefs, *Annu. Rev. Fluid Mech*., **39**, 2007, 37-55.

[12] Nepf, H. & Ghisalberti, M., Flow and transport in channels with submerged vegetation**,** *Acta Geophysica,* **56**(3), 2008, 753-777.

[13] Nezu, I. & Sanjou M., Turbulence structure and coherent motion in vegetated canopy open-channel flows, *J. Hydro-environment Res.,* **2**, 2008, 62-90.

[14] Niklas KJ, Spatz H-S, & Vincent, J., Plant biomechanics: an overview and prospectus, *American Journal of Botany*, **93**(10), 2006, 1369–1378.

[15] Nikora, V., Green, M., Thrush, S., Hume, T. & Goring, D., Structure of the internal boundary layer over a patch of horse mussels (*Atrina zelandica*) in an estuary, *J. Marine Res.*, **60**(1), 2002a, 121-150.

[16] Nikora, V., Goring, D. & Biggs, B.J.F., Some observations of the effects of microorganisms growing on the bed of an open channel on the turbulence properties, *J. Fluid Mech*. **450**, 2002b, 317-341.

[17] Nikora, V., McEwan, I., McLean, S., Coleman, S., Pokrajac, D. & Walters, R., Double averaging concept for rough-bed open-channel and overland flows: Theoretical background, *J. Hydraul. Eng*., ASCE, **133**(8), 2007, 873-883.

[18] Nikora, V., Hydrodynamics of gravel-bed rivers: scale issues, in *Developments in Earth Surface Processes*, v. 11, Gravel-Bed Rivers VI, editors H. Habersack, H. Piegay, M. Rinaldi, eds., Springer, 2008, 61-81.

[19] Nikora, V., Hydrodynamics of aquatic ecosystems: an interface between ecology, biomechanics and environmental fluid mechanics, *River Research and Applications*, 2010, **26**, 367-384, DOI: 10.1002/rra.1291.

[20] Okubo, A. & Levin, S.A., *Diffusion and Ecological Problems. Modern Perspectives,* Springer, New York, 2001.

[21] Poggi, D., Porporato, A., Ridolfi, L., Alberston, J.D. & Katul G.G., The effect of vegetation density on canopy sublayer turbulence, *Boundary-Layer Meteorol.*, **111**, 2004, 565-587.

[22] Py, C. & de Langre, E, Moulia, B., A frequency lock-in mechanisms in the interaction between wind and crop canopies, *J. Fluid Mech*., **568**, 2006, 425-449.

[23] Raupach, M.R., Finnigan, J.J. & Brunet, Y., Coherent eddies and turbulence in vegetation canopies: the mixing layer analogy, *Boundary-Layer Meteorol*., **78**, 1996, 351–382.

[24] Rodriguez-Iturbe, I., Muneepeerakul, R., Bertuzzo, E., Levin, S.A. & Rinaldo, A., River networks as ecological corridors: A complex systems perspective for integrating hydrologic, geomorphologic, and ecologic dynamics. *Water Resour. Res*., **45**(1), 2009, W01413.

[25] Statzner, B., Gore, J.A. & Resh, V.H., Hydraulic stream ecology: Observed patterns and potential applications. *J. North Amer. Benthological Soc*., **7**, 1988, 307-360.

[26] Statzner, B. & Borchardt, D., Longitudinal patterns and processes along streams: modelling ecological responses to physical gradients, in *Aquatic Ecology: Scale, Pattern, and Process*, editors P.S. Giller, A.G. Hildrew, D.G. Raffaelli, Blackwell Scientific Publications, Oxford, 1994, 113-140.

[27] Statzner, B., How views about flow adaptations of benthic stream invertebrates changed over the last century, *Intern. Rev. Hydrobiol*., **93**, 2008, 593-605.

[28] Stevens, C.L., Hurd, C.L. & Smith, M.J., Interaction between fronds of the large intertidal seaweed Durvillaea Antarctica, *J. Mar. Syst.*, **49**(1–2), 2004, 145–157.

[29] Torquato, S., *Random Heterogeneous Materials*, Springer, New York, 2002.

[30] Vogel, S., *Life in Moving Fluids*. Princeton University Press, Princeton, 1994.

[31] Vogel, S., *Comparative Biomechanics*, Princeton University Press, Princeton and Oxford, 2003.

[32] Usherwood J.R., Ennos, AR, Ball, D.J., Mechanical and anatomical adaptations in terrestrial and aquatic buttercups to their respective environments, *J. Experim. Botany*, **48**, 1997, 1469-1475.