RIVER RESEARCH AND APPLICATIONS
River. Res. Applic. **26**: 367–384 (2010)

(www.interscience.wiley.com) DOI: 10.1002/rra.1291

HYDRODYNAMICS OF AQUATIC ECOSYSTEMS: AN INTERFACE BETWEEN ECOLOGY, BIOMECHANICS AND ENVIRONMENTAL FLUID MECHANICS

V. NIKORA*
School of Engineering, University of Aberdeen, UK

ABSTRACT

The paper promotes an emerging research area at the interfaces between aquatic ecology, biomechanics and environmental fluid mechanics. This new area, *Hydrodynamics of Aquatic Ecosystems*, bridges these disciplines together and is defined as a study of flow-organism interactions at multiple scales with particular focus on relevant transport processes and mutual physical impacts. 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-uptake processes (e.g. due to molecular and turbulent diffusion). Key concepts and tools of *Hydrodynamics of Aquatic Ecosystems* are outlined first and then a promising approach that may provide a unifying platform for coupling and integrating ecological, hydrodynamic and biomechanical processes, known as the double-averaging methodology (DAM), is discussed. Copyright © 2009 John Wiley & Sons, Ltd.

KEY WORDS: aquatic ecosystems; hydrodynamics; biomechanics; flow-biota interactions; aquatic plants

Received 15 January 2009; Revised 10 April 2009; Accepted 3 June 2009

INTRODUCTION

It is now widely recognized that the structure and function of biological communities in streams, estuaries, lakes and seas are largely controlled by an interplay of biological, physical and chemical processes which shape aquatic ecosystems at multiple scales (e.g. Statzner *et al*., 1988; Hart and Finelli, 1999; Boudreau and Jorgensen, 2001; Biggs *et al*., 2005; Statzner, 2008). If earlier studies have been heavily dominated by biological methodologies the recent tendencies in aquatic ecology reflect a growing involvement of physical and chemical approaches and concepts (e.g. Denny, 1988; Vogel, 1994; Okubo and Levin, 2001). On the other hand, a number of disciplines that have traditionally dealt with largely abiotic environmental processes have recently bifurcated to create, formally or informally, ecologically-oriented branches. The number of these branches is mounting, extending the remits of traditionally-bounded disciplines towards the borders with aquatic ecology. This tendency is exciting, as step changes in our understanding of environmental processes are most likely to occur at the discipline interfaces which are least studied and understood.

Examples of recently emerged ecologically-oriented research areas include eco-geomorphology, biogeomorphology, eco-hydrology, eco-hydraulics, environmental hydraulics, biofluidmechanics and ecobiomechanics (but there are more). These new discipline branches cover a wide range of scales, organisms and aquatic environments and represent a good example of a multidisciplinary approach in modern science. However, an analysis of available definitions for these newly-emerged areas shows that, even for the same area, there is considerable variation and vagueness in terms of traditional requirements for an academic discipline. These requirements include distinct research goals, methods, terminology and styles of communication, which remain to be better defined and developed for these areas. Some of these newly-emerged branches of traditional and well-established disciplines may eventually disappear or merge with other areas.

Although it may look strange to advocate the addition of one more ‘eco’ branch to the already extensive list, this paper argues that we currently observe a natural appearance of a cohesive set of research issues with associated

---

*Correspondence to: V. Nikora, School of Engineering, University of Aberdeen, UK. E-mail: v.nikora@abdn.ac.uk tools and concepts that probably better satisfies requirements for a branch of an academic discipline compared to other 'eco' branches. This trend relates to modern developments in aquatic ecology, environmental fluid mechanics and biomechanics that create a coherent research area at their interfaces bridging these disciplines together. The goal of the paper is then to formalize and promote this emerging research area by providing an explicit definition and outlining its goals, methodologies and concepts. The suggested name for this interfacial branch of aquatic ecology, environmental fluid mechanics and biomechanics is '*Hydrodynamics of Aquatic Ecosystems*'. This subject area covers both marine and freshwater environments and therefore should include, as equal branches, *Hydrodynamics of Freshwater (lotic and lentic) Ecosystems* and *Hydrodynamics of Marine Ecosystems*. The discussion in this paper, however, is more related to freshwater systems where, compared to marine systems, development of *Hydrodynamics of Aquatic Ecosystems* is slightly delayed and thus this paper may serve for its enhancement. Furthermore, to be specific and relevant to the remit of *River Research and Applications*, the background and applications of this subject area are illustrated using lotic systems (i.e. streams and rivers), with aquatic plants as an example.

HYDRODYNAMICS OF AQUATIC ECOSYSTEMS: DEFINITION

Hydrodynamics of Aquatic Ecosystems can be formally defined as a study of flow-organism interactions with particular focus on relevant transport processes and mutual physical impacts occurring in a range of scales from the sub-organism scale to the organism patch mosaic scale (comparable to flow width). The appearance of word '*Hydrodynamics*' in the discipline title is due to the fact that flowing water is the environment where ecological, hydrodynamic and biomechanical processes occur and are interlinked. Thus, *Hydrodynamics of Aquatic Ecosystems*, being an important part of its mother disciplines, 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-uptake processes (e.g. due to molecular and turbulent diffusion).

Hydrodynamics of Aquatic Ecosystems has emerged in response to growing demands for advanced knowledge in a number of 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 mussel farms) and bio-security (e.g. control of invasive species or transport of pathogens). Figure 1 shows an example of how *Hydrodynamics of Aquatic Ecosystems* can provide a process-based basis for defining a range of environmental (i.e. ecologically-favourable) flows for a regulated river. In this particular application, physical interactions and transport processes act in opposite directions. At high flow rates, large drag forces acting on organisms have a negative effect (e.g. by destroying the organisms or their assemblages) while high mixing rates securing delivery of nutrients to organisms and efflux of wastes are favourable. At low flow rates the situation reverses: drag forces are reduced and turn to favourable while low mixing rates may become a limiting factor. Thus, the upper boundary of the environmental flow range for a particular species can be deduced from analysis of physical interactions (i.e. action of drag forces) while the lower boundary is fixed by a critical value of

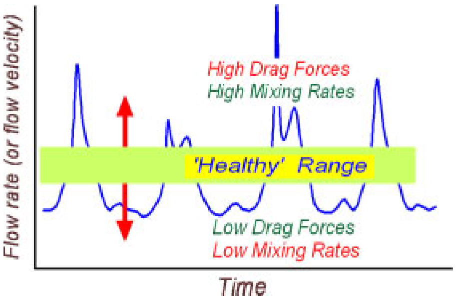

Figure 1. An example of how a range of environmental flows for a regulated river can be defined using knowledge of physical interactions and mass-transfer processes. This figure is available in colour online at www.interscience.wiley.com/journal/rra

DOI: 10.1002/rra

the mixing rate. The upper and lower boundaries of the flow range described above are species-specific. A range of environmental flow rates for the whole ecosystem can be determined by a minimum upper flow rate and a maximum lower flow rate among all species involved in the ecosystem. Although this analysis is rather conceptual, it opens a fresh perspective for determining environmental flow rates, as an alternative to largely empirical multi-regression approaches which are currently widely used in applications. Similar considerations can also be functional in designing optimal aqua-farms or in controlling invasive species, among other applications.

The next section outlines key concepts and tools of *Hydrodynamics of Aquatic Ecosystems* which will be followed by a brief discussion of a promising approach that may provide a unifying platform for coupling and integrating ecological, hydrodynamic and biomechanical processes known as the double-averaging methodology (DAM).

KEY CONCEPTS AND TOOLS

Although research methods, tools and concepts of *Hydrodynamics of Aquatic Ecosystems* are naturally derived from its mother disciplines and are still emerging, they steadily become interconnected and adjusted to address common goals. In a brief review below they are discipline-grouped (i.e. flow hydrodynamics, organism biomechanics and ecological implications), for convenience, while their interconnections are highlighted with specific examples.

Flow hydrodynamics

Traditionally, hydraulic habitat in ecological studies has been characterized by a minimum number of simple variables such as depth-averaged (or surface) water velocity and flow depth, while more detailed habitat characterizations have been reported only occasionally (e.g. Statzner *et al*., 1988 and references herein). Recently, however, a wider range of flow and bed parameters has become routinely involved, although often intuitively, providing a more complete characterization of hydraulic habitats (e.g. Hart and Finelli, 1999 and references herein). It is useful therefore to review, at least briefly, some tools and concepts offered by environmental fluid mechanics that should help in setting up a more rigorous framework for ecological considerations coupled with flow dynamics and biomechanics.

Boundary layer (BL). A canonical BL is defined as a flow region where velocity increases from zero at the surface to the mainstream velocity away from the surface. If the Reynolds number and flow submergence (i.e. BL thickness-to-roughness height ratio) are high, then the near-bed velocity distribution is expected to be logarithmic. The BL concept is probably most familiar to aquatic ecologists, being widely promoted in ecological literature (e.g. Nowell and Jumars, 1984; Statzner *et al*., 1988; Hart and Finelli, 1999; Statzner, 2008).

In relation to aquatic ecosystems, the BL concept is fundamental for characterization of both (i) hydraulic habitats, as most aquatic communities live within BLs and (ii) flow patterns around individual organisms that are always surrounded by BLs generated at organism surfaces. In principle, the BL concept can be used for interpretation of instantaneous, time-averaged and double-averaged (in time and in a plane parallel to the bed) flow fields. The double-averaging is required to smooth flow heterogeneities due to complex boundaries introduced by biological communities as well as to couple flow and organisms within a single framework. This issue will be discussed in more detail in the next section.

The biological communities are typically embedded in a superposition of multi-scale BLs generated by a variety of boundaries including those introduced by the organisms themselves. Figure 2 illustrates this complexity using aquatic plants as an example where one may identify BLs from the flow-depth scale (pattern #1) to a leaf/stem scale (pattern #3). Note in Figure 2 how the multi-scale BLs are combined with other flow patterns such as multi-scale mixing layers MLs and wakes. Among these patterns, only studies of patterns 1, 2 and 5 are being carried out (e.g. Nepf, 1999; Nikora *et al*. 2003a; Poggi *et al*., 2004a, b; Nepf and Ghisalberti, 2008) while other patterns are hypothesized in Figure 2 to highlight potential research directions.

There is a number of other features of BLs in natural aquatic systems that make them different from the canonical BLs and that should be taken into consideration. Some of them are illustrated in Figure 3, in particular: (i) BLs in streams and estuaries are often depth-limited; (ii) they often have a double-structure involving two superimposed

DOI: 10.1002/rra

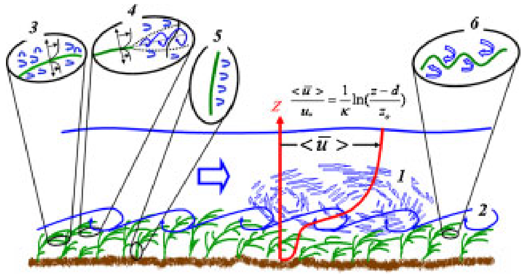

Figure 2. Patterns in a flow with aquatic plants. 1: depth-scale shear-generated turbulence within a BL formed at a vegetated bed (with a layer above the canopy where the log velocity distribution may occur as shown on the sketch; overbar defines time averaging while angular brackets define spatial averaging; u_* is shear velocity, d is displacement height, and z_o is roughness length). 2: canopy-scale turbulence generated as a result of Kelvin–Helmholtz instability at an inflection point in a velocity profile at the top of a canopy ('mixing layer' analogy). 3: leaf-scale boundary layer turbulence. 4: leaf-scale mixing layer turbulence (when a leaf can work as a splitter plate generating a mixing layer behind the leaf due to different surface roughness of opposite leaf sides). 5: stem-scale wake turbulence associated with flow separation from plant parts that may form von Karman vortices. 6: turbulence generation due to plant waviness/fluttering. This figure is available in colour online at www.interscience.wiley.com/journal/rra

BLs, generated at the bed and at the water surface; and (iii) there are internal BLs formed by organism patches themselves and embedded into larger-scale BLs as shown in Figure 3b for the case of mussel beds (Nikora *et al*., 2002a). Another important feature that needs to be highlighted is that natural BLs often have a low ratio of flow depth to roughness height (i.e. low-submergence BLs) and therefore conventional approaches for their description, such as the log velocity profile, should be used with great caution. Indeed, the logarithmic formula for velocity profile is frequently misused for estimating bed shear stresses in low-submergence flows, where it may not be applicable.

To clarify this issue, Nikora *et al*. (2001, 2007b) suggested four types of rough-bed flows depending on flow submergence H_m/Δ ($H_m = Z_{ws} - Z_t$ is the maximum flow depth, i.e. the distance between mean water surface Z_{ws} and roughness troughs Z_t; $\Delta = Z_c - Z_t$ is the roughness height, Z_{ws}, Z_c, Z_t are defined in Figure 4). This classification is illustrated in Figure 4 for the case of gravel-bed flows, although it is equally applicable for sand-wave beds, mussel beds or vegetated beds. The flow type (I) is the flow with high relative submergence, which contains several layers and sublayers (neglecting viscous sublayers (VSL) associated with gravel particles): (i) near-water-surface layer where flow structure is influenced by free-surface effects such as turbulence damping and various types of water surface instabilities; (ii) outer or intermediate layer, where viscous effects and form-induced momentum fluxes due to water surface disturbances and bed- and organism-introduced roughness are negligible; (iii) the logarithmic layer (as the relative submergence is large enough) that differs from the outer layer by characteristic velocity and length scales; (iv) the form-induced (or dispersive) sublayer, below the logarithmic layer and just above the roughness crests, where the time-averaged flow may be influenced by individual roughness elements generating form-induced stresses (see next section for more details); (v) the interfacial sublayer, which

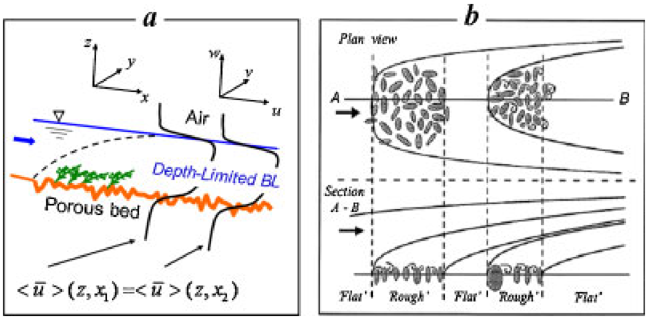

Figure 3. Double-structure of boundary layers in streams (a), and internal boundary layers formed by organisms themselves as in the case of mussel beds (modified from Nikora *et al*. 2002a). This figure is available in colour online at www.interscience.wiley.com/journal/rra

DOI: 10.1002/rra

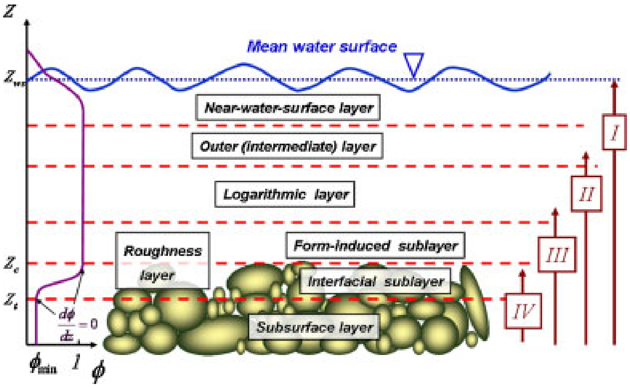

Figure 4. Flow types and flow subdivision into specific layers (modified from Nikora *et al*., 2007b). This figure is available in colour online at www.interscience.wiley.com/journal/rra

occupies the flow region between roughness crests and troughs and where momentum sink due to skin friction and form drag occurs; and (vi) subsurface layer below the interfacial sublayer. The interfacial and form-induced sublayers, combined together, can be defined as the roughness layer.

The other three flow types are: (II) flow with intermediate relative submergence consisting of the subsurface layer, a roughness layer, an upper flow region which does not manifest a genuine universal logarithmic velocity profile as the ratio H_m/Δ is not large enough, and the near-water-surface layer; (III) flow with small relative submergence with a roughness layer overlapping with the near-water-surface layer; and (IV) flow over a partially-inundated rough bed consisting of the interfacial sublayer overlapped with the near-water-surface layer (Figure 4). The above flow subdivision and flow types represent a useful schematization that may help in interpretations of flow-biota relationships.

Although the canonical BL concept is simple, its application for describing flows over biologically-modified beds or surfaces may require some adjustments such as, for instance, use of the double-averaged velocities and other flow parameters instead of the time-averaged variables (e.g. Finnigan, 2000; Nikora, 2007; de Langre, 2008).

Mixing layer (ML). A canonical ML is defined as a free shear layer that forms at the interface between two streams of different velocities as a result of Kelvin–Hemholtz instability (KHI), which may occur if an inflection point in the velocity profile is present. Such a flow pattern is formed by a shear between two streams with different velocities and therefore is known as 'free shear layer', i.e. no shear at a solid boundary, as in BLs, is involved. A classical example of MLs is spatial (plane) ML which is a free shear layer formed behind a splitter plate. In principle, MLs may be classified into spatially-growing (but stationary in time) MLs, temporally-growing (but spatially homogeneous) MLs, stationary and homogeneous MLs, stratified MLs, three-dimensional (deep-water) MLs, two-dimensional (shallow) MLs and other types. In aquatic ecosystems, MLs may be generated, similar to BLs, by external (to organisms) physical factors and by the organisms themselves. Examples of the latter are shown in Figure 2 for the case of submerged aquatic plants where at least two MLs at different scales can be identified: (i) a ML behind leaves which may serve as splitter plates with velocity difference due to different leaf surface roughness on opposite leaf sides (pattern #4 in Figure 2; this ML is hypothesized here and needs to be proven in future studies); and (ii) a ML formed at the top of the vegetation canopy where an inflection point in the velocity profile is observed (pattern #2 in Figure 2).

The latter pattern was originally identified for terrestrial canopies by Raupach *et al*. (1991, 1996) who coined a term 'mixing layer analogy'. For the case of submerged aquatic vegetation, this analogy was first implemented by Ghisalberti and Nepf (2002) and then used in a number of follow-up studies of flow-vegetation interactions (Ghisalberti and Nepf, 2004, 2006; Poggi *et al*., 2004a, b; Nepf and Ghisalberti, 2008; Nezu and Sanjou, 2008; Righetti, 2008; Sukhodolov and Sukhodolova, 2006). 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. Based on theoretical considerations and laboratory experiments with artificial vegetation, these studies demonstrated that the depth of penetration of a ML into a canopy depends on vegetation

DOI: 10.1002/rra

density, drag coefficients of vegetation elements and plant geometry. As an example, Nepf and Ghisalberti (2008 and references herein) showed that ML eddies penetrate canopies up to the bed substrate if parameter $C_D a h_c \approx< 0.2$ where C_D is the drag coefficient of a plant stem, $a h_c$ is the areal vegetation density (i.e. ratio of the total plant frontal area to the associated bed area) and h_c is the canopy height. With increase in $C_D a h_c$ (>0.2), the penetration depth steadily reduces thus decreasing the level of canopy 'ventilation'. Although this result has been obtained using submerged rigid cylinders as simplified plant models, it highlights a possible mechanism of how vegetation density and geometry may control mass and momentum exchange in real plant canopies.

Although the ML analogy for aquatic vegetation is appealing from both physical and ecological perspectives and it has already been extensively studied and promoted (e.g. Raupach *et al.*, 1991, 1996; Finnigan, 2000; Ghisalberti and Nepf, 2002, 2004, 2006; Poggi *et al.*, 2004a, b; Sukhodolov and Sukhodolova, 2006; Nepf and Ghisalberti, 2008; Nezu and Sanjou, 2008), there is still a number of issues that require clarification. First, an interrelationship between a ML at the canopy top and the overlying BL remains unclear. Indeed, many authors have noted that a velocity profile above a well-submerged canopy is logarithmic that assumes the existence of 'attached' eddies that grow from the bed (e.g. Townsend, 1976). However, if there is a ML acting between the bed and the BL above the ML, then the physical mechanism of BL above ML needs to be better understood (e.g. ML may block access of BL eddies to the canopy layer thus 'detaching' BL eddies from the surface and destroying the conventional mechanism of BL formation). A physical picture suggested by Finnigan (2000) for terrestrial canopies assumes a BL directly growing from a canopy (i.e. consistent with convention), which is intermittently interrupted near the canopy top with packets of 3–4 ML eddies formed by (and only during) strong wind gusts. Thus, this concept suggests that BL eddies and ML eddies co-exist, although they are not superimposed being separated in time and space, with ML eddies serving as a mechanism for momentum transfer from larger-scale BL eddies to the canopy. Poggi *et al.* (2004a) also noted that the production mechanisms for BL and ML eddies may impede each other and therefore ML and BL eddies cannot 'overlap' in space. However, although this picture is clear and logical for terrestrial canopies, it is not transferable to most aquatic canopies (e.g. in streams or estuaries) where separation of scales between BL eddies and ML eddies is not as wide as in the case of terrestrial canopies. Indeed, in aquatic systems the expected BL and ML scale ranges are often overlapped, making it difficult to clearly identify and separate ML effects from BL effects. On the other hand, it was reported (e.g. Nepf and Ghisalberti, 2008; Nezu and Sanjou, 2008) that the ML at the canopy top in aquatic systems is not intermittent, occupies a significant flow region, and has an overlying (apparently) logarithmic BL, which seems to be 'detached' from the bed by a permanently present ML. These features require explanation and, thus, the interrelationship between BL and ML in aquatic systems remains an open issue.

The second point deserving a highlight relates to a fact that the convection velocity of ML eddies at the canopy top well exceeds a local mean velocity. This effect has been reported for both terrestrial and aquatic canopies (Raupach *et al.*, 1996; Finnigan, 2000; Ghisalberti and Nepf, 2002; Nepf and Ghisalberti, 2008; Nezu and Sanjou, 2008). However, for conventional MLs these two velocities should be equal or very close (e.g. Ho and Huerre, 1984). For terrestrial canopies, this discrepancy could be partly explained using Finnigan's (2000) picture of short-time MLs 'living' during strong wind gusts that move appreciably faster than the time-averaged flow. For aquatic canopies, Ghisalberti and Nepf (2002) and Nepf and Ghisalberti (2008) suggest that the large ML eddies are elevated above the canopy top and therefore their propagation speed measured at the canopy top is higher than a local mean velocity at that level. On the other hand, however, it is also well known that the convection velocity of near-bed eddies in the conventional BLs and open-channel flows is much higher than the local mean velocity (e.g. Romano, 1995; Nikora and Goring, 2000), exactly as measured for eddies at the canopy top. Thus, although the measurements of convection velocities at canopy tops disagree with a conventional ML picture, they are consistent with the data for BLs and open-channel flows. This again brings to light a question of the interrelation between BL and ML eddies in canopy flows.

Another point worth mentioning is a relation of ML eddies to a monami effect (wavy motions of a canopy top often observed in natural aquatic canopies and known as 'honami' for terrestrial canopies). In a number of studies it was argued that the monami/honami on the canopy top are generated by large coherent eddies inherent for the canopy mixing layer, with the monami/honami as a 'footprint' of passing large ML eddies. Although this concept is plausible and appealing there are other possibilities that should also be checked as they may challenge a currently accepted concept. One of them has been recently discussed in Py *et al.* (2006) and de Langre (2008), who accentuated the importance of plant biomechanical properties in flow-canopy interactions. They showed that there may be a strong feedback mechanism that plants may utilize to modify the KHI and flow structure at the canopy top, and thus control parameters of large eddies associated with the monami/honami (e.g. their wavelength, frequency and other parameters).

The ML analogy briefly discussed above is not limited to vegetated channels and may have much wider representation in aquatic ecosystems. Mussel beds and fur of some aquatic animals represent other examples where it may appear to be as fruitful as for vegetated beds.

Wakes and Jets. In addition to the concepts of BL and ML, which are probably most relevant to the functioning and the structure of aquatic systems, there are other important flow patterns or types that often occur in nature and in some cases may be as important at particular scales as BLs or MLs. Among these patterns, wakes and jets deserve at least a brief mentioning. A conventional wake can be defined as a region of disturbed fluid downstream of a body (e.g. behind a cobble or an organism) where momentum transport is reduced (i.e. wake is a region of momentum deficit). Wakes may occur with or without flow separation behind a body depending on its shape and Reynolds number. Similar to BLs and MLs, wakes can be generated by external factors (e.g. behind cobbles in a gravel-bed river) or created by organisms themselves (e.g. behind mussels on the bed as sketched in Figure 3b or behind plants as sketched with pattern #5 in Figure 2). Poggi *et al*. (2004a,b) combined the wake concept with the BL and ML concepts to develop a mathematical model of flow-vegetation interactions and transport processes within canopies. Although their studies consider a simplified case of submerged rigid cylinders, the reported results are instructive for future studies of more realistic canopies. The jet is another flow pattern that *Hydrodynamics of Aquatic Ecosystems* includes in its set of tools. It is defined as a flow pattern formed by intruding one fluid into another, with associated injection into ambient fluid of either momentum, buoyancy or both. In principle, jets can be inertia-, friction- or buoyancy- dominated, and can be subdivided into laminar and turbulent jets, round and plane jets, co-flow, cross-flow jets, etc. This flow pattern is also widespread as a habitat property (e.g. at a confluence of a smaller stream with a larger stream) or as a mechanism that some organisms use to move or to exchange with the surrounding habitat (e.g. Vogel, 1994).

Coherent structures and eddy cascade. The concepts considered above represent flow types which differ from each other due to differences in forcing and background conditions. However, at large Reynolds numbers they all have a common feature which is multi-scale velocity fluctuations in time and space known as turbulence. Although there is no widely accepted formal definition of turbulence yet, there is a number of features that are currently recognized as the key qualities of turbulence, differentiating it from other hydrodynamic phenomena. They include, among others, seemingly random behaviour, wide range of length and time scales, enhanced mixing, three-dimensionality and rotationality, intermittency in both space and time, etc. All these features characterize hydraulic habitats for biota and therefore studies of turbulence effects on structure and function of aquatic ecosystems are growing (e.g. Nikora *et al*., 1998, 2002a,b, 2003a,b; Hart and Finelli, 1999; Hondzo and Wang, 2002; Green, 2005; Lancaster *et al*., 2006; Kubrak *et al*., 2008; Rice *et al*., 2008).

At present, turbulence research of aquatic systems is based on two fundamental physical concepts: eddy/energy cascade (EC) and coherent structures (CS). Originally these concepts have been developed independently, and it is only recently that researchers started viewing CSs and EC as interlinked phenomena. These concepts, together with fundamental conservation equations for momentum, energy and substances, represent statistical and deterministic facets of flow dynamics that underpin two key approaches in turbulence studies: deterministic and statistical. The deterministic approach stems from some ‘coherency’ in turbulent motions and from hydrodynamic equations based on fundamental conservation principles, while the statistical approach recognizes ‘irregular’ components in hydrodynamic fields and therefore focuses on their statistical properties. Both concepts may be equally applicable to BLs, MLs, wakes and jets, although their implementation may differ among these flow types. Knowledge of both CSs and EC can be crucial for understanding aquatic ecosystems which sometimes may even modify and control CSs and EC (as e.g. with flexible aquatic canopies that may control large ML eddies through the monami effect, Py *et al*. 2006).

A CS (or eddy) can be broadly defined as a three-dimensional flow region over which at least one fundamental flow variable exhibits significant correlation with itself or with another variable over a range of space and/or time (e.g. Robinson, 1991; Roy *et al*. 2004; Adrian, 2007). Many kinds of CS have been identified depending on flow type and Reynolds number, and it has been shown that they play a significant role in mass and moment transfer in

DOI: 10.1002/rra

aquatic systems (e.g. Poggi *et al*., 2004a, b; Roy *et al*., 2004; Nepf and Ghisalberti, 2008). In Figure 2, CSs are presented by patterns #1 (BL coherent structure) and #2 (ML coherent structures). Although mechanisms and quantification of CSs and their full ecological significance remain to be better understood, it is already clear that they play an important role in setting up fluctuating fluid forces and transport processes within biological communities and therefore represent an important concept of *Hydrodynamics of Aquatic Ecosystems*.

Another influential concept in turbulence research, known as eddy/energy cascade, was introduced at a conceptual level by Richardson (1922) and later has been developed by Kolmogorov (1941) at a quantitative level. The details can be found in Monin and Yaglom (1975) or in other turbulence texts and here only the key idea is briefly summarized. According to Kolmogorov (1941), turbulence is initiated at an external scale of the flow (e.g. flow depth in a stream) as a result of hydrodynamic instability that transfers the energy from an external forcing to the largest eddies comparable to the external flow scale. Then, these large eddies, being unstable themselves, transfer their energy to smaller eddies and so on until the eddy size reaches the so-called dissipative scale. At this scale, viscous forces overcome inertial forces and turbulence become suppressed by viscosity (Figure 5). The size of dissipative eddies can be measured with Kolmogorov's micro-scale $\eta = (\nu^3/\varepsilon)^{1/4}$ where ν is fluid kinematic viscosity, and ε is the rate of turbulent energy dissipation (i.e. energy transfer from a mechanical form into heat). The real size of dissipative eddies is approximately ten times bigger than Kolmogorov's micro-scale η and it varies in natural aquatic systems from 0.1–0.3 to 1–3 mm (it could even be argued that it can reach 10 mm or more in a BL formed at a deep ocean bed). Kolmogorov (1941) subdivided the whole set of eddies within this cascade into three ranges of scales: (i) the production range where energy comes from the mean flow; (ii) the inertial subrange where energy is transferred from large scales to smaller scales without production or dissipation (and where Kolmogorov's '-5/3' law acts); and (iii) the viscous range where eddy energy decays much faster than in the inertial subrange and eventually dissipates into heat. Although several plausible mechanisms of EC have been proposed (i.e. repeated instability at decreasing scale; vortex stretching; vortex compression), the debate on the cascade physical picture continues. Interrelationships between EC and CSs also remain unclear although a promising mechanism linking these two has been recently proposed by Goto (2008): the energy cascade is caused by the successive creation of smaller-scale tubular vortices (or CSs) in the larger-scale straining regions existing between pairs of larger-scale CSs. In some aquatic systems such as rivers the EC and CSs can be significantly modified by secondary currents (e.g. Nezu and Nakagawa, 1993; Knight *et al*., 2007; Albayrak, 2007) and interactions with subsurface flows (e.g. Packman *et al*., 2004; Marion *et al*., 2008), which themselves may be as important in physical and ecological considerations as already mentioned flow patterns and types.

Figure 6 illustrates, in a sketch, how the EC and CSs in a stream BL can be linked to organisms. In this sketch, the smallest flow scales are presented by the thickness δ of the VSL (that separates bed surface from a turbulent region

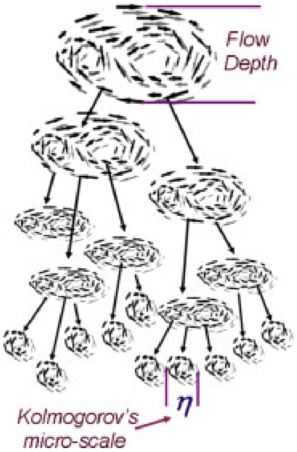

Figure 5. A sketch illustrating an eddy cascade from the largest eddies that are fed by the large-scale instabilities to the smallest eddies, which size are controlled by fluid viscosity ν and energy flux ε from the largest eddies (at equilibrium conditions ε is equivalent to energy dissipation). This figure is available in colour online at www.interscience.wiley.com/journal/rra

DOI: 10.1002/rra

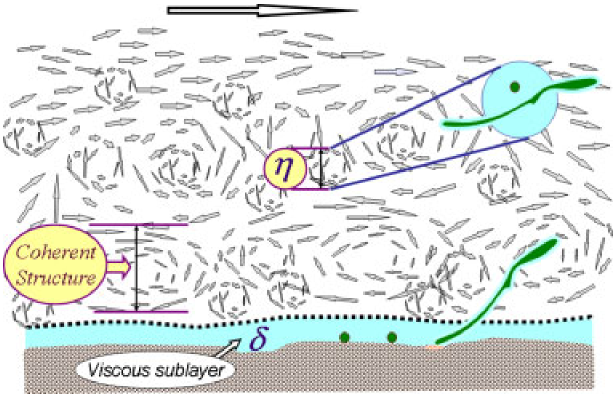

Figure 6. A sketch showing a stream boundary layer where turbulence exhibits both the eddy cascade and coherent structures embedded into a stream boundary layer. Small circles within the viscous sublayer and within a dissipative eddy present small organisms ($L << \delta, \eta$). Elongated bodies that penetrate into turbulent range of scales from the viscous sublayer and from a dissipative eddy present large organisms ($L >> \delta, \eta$). This figure is available in colour online at www.interscience.wiley.com/journal/rra

above) and by the dissipative eddies η in the flow. The largest scales are defined by the external size of the flow (i.e. flow depth) and by the scales of CSs that in general may be smaller than the external flow size. The physical interactions and transport processes between the organisms and turbulent eddies depend on their relative scales. In respect to mass-transfer processes, if an organism is much smaller than the viscous scales (δ or η) then its metabolic rate will be largely controlled by molecular diffusion and therefore will be low (small circles within the VSL and within a dissipative eddy in Figure 6 present such small organisms). When an organism size well exceeds the scales δ and η then the effects of viscosity are significantly reduced and organism's exchange with the surrounding environment is greatly enhanced due to turbulence allowing much higher metabolic rates (elongated bodies that penetrate into turbulent range of scales from the VSL and from a dissipative eddy in Figure 6 present such large organisms). In other words, when organism size L is small (i.e. $L << \delta, \eta$) we can predict a primitive form of life as the metabolic rate is limited by molecular diffusivity (e.g. single-cell organisms). At another extreme, at $L >> \delta, \eta$, the transport rate is orders of magnitude higher encouraging development of advanced forms of life (e.g. multi-cellular organisms). Similar considerations were used in Nikora *et al.* (2003a) and Larned *et al.* (2004) in studying transport processes in periphyton communities.

The ratio of scales can also control physical interactions as highlighted, for example, in Nikora *et al.* (2003a) for periphyton, and in Nikora *et al.* (2003b) and Pavlov *et al.* (2008) for fish. Within the same turbulent flow, fish with different dimensions will experience different impacts from turbulent eddies. A fish of length L will probably not feel turbulent eddies smaller than L, but will react to eddies comparable to or larger than L. Although considerations above are obviously oversimplified they are still instructive in terms of potential effects of flow on ecosystem functioning and structure.

Organism biomechanics

Reactions of organisms to physical forces imposed by flow patterns described above largely depend on their biomechanical properties. This dependence has been recognized long ago and significant progress has been made for terrestrial ecosystems (e.g. trees, vertebrates and insects) and partially for marine ecosystems (Wainwright *et al.*, 1976; Denny, 1988; Niklas, 1992; Koehl, 1999, 2003; Alexander, 2003; Niklas *et al.*, 2006). However, biomechanics of freshwater organisms is still largely unknown and is represented by very few studies (e.g. Usherwood *et al.*, 1997).

Biomechanics as a discipline area stems from two engineering disciplines known as mechanics of materials and structural mechanics, and deals with organisms and their communities—the most complex structures created by nature. Although biomechanical considerations are species-specific, there are some common features that can be illustrated using aquatic plants in streams as an example. The first feature to be highlighted is that morphology of

DOI: 10.1002/rra

aquatic plants involves 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. Using engineering terminology, the plants can be defined as composite, anisotropic, viscoelastic, highly heterogeneous materials or structures. Living in flowing waters, aquatic plants experience complex loads which are often presented by a mixture of tension, compression, bending, torsion and shear. These complexities explain why, until now, we still do not have a set of widely accepted quantitative characteristics of plant geometry and mechanical properties. Overall, the plant characteristics can be subdivided into three groups: (i) plant morphology characteristics; (ii) plant material characteristics; and (iii) plant-flow interaction characteristics. All these characteristics are scale dependent. Examples of morphologic characteristics, which are currently in use, include linear characteristics (e.g. length, width, deflected canopy height), areal characteristics (e.g. wetted area, front-area, side-area, plane-area, and cross-sectional area), volumetric characteristics (e.g. plant volume), density characteristics (e.g. number of plants/stems per unit bed area, volume of plants per unit bed area, wetted plant area per unit bed area, and frontal plant area per unit canopy volume). Plant material characteristics include plant material density ρ_p, Young's (elasticity) modulus E, second moment of cross-sectional area I_2, flexural stiffness EI_2, and a number of others. There are also characteristics that quantify the interplay between plants and flow, including drag C_D and lift C_L coefficients, strain, tension and bending moments (third group). If these characteristics are well familiar to researchers of terrestrial systems and, to a certain degree, to marine researchers, their implementation in studies of freshwater ecosystems is still in its infancy. 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. As a matter of fact, even in studies of hydraulic resistance due to vegetation in engineering applications, the mechanical characteristics of plants are often omitted. However, for the proper coupling of hydrodynamic environments with plants one needs to consider appropriate forces and then deal with their ratios that control regimes of flow-plants interactions. As a first approximation, we can consider the following set of forces:

Flow-induced forces

$$F_D = 0.5\rho C_D U^2 A \quad \text{– Drag force}$$

$$F_L = 0.5\rho C_L U^2 A \quad \text{– Lift force}$$

Plant-induced forces

$$F_B = \rho g V_p \quad \text{– Buoyancy force}$$

$$F_G = \rho_p g V_p \quad \text{– Gravity force}$$

Plant-reaction forces

$$F_T = E\varepsilon\omega \quad \text{– Tensile(reaction) force}$$

$$F_b = EI_2/R\lambda \quad \text{– Bending(reaction) force}$$

where ρ and ρ_p are fluid and plant densities, respectively; g is the gravity acceleration; U is the reference velocity; A is the reference plant area; V_p is the plant volume; ω is the plant cross-sectional area; ε is the strain (i.e. relative elongation) imposed by fluid forces; R is the radius of curvature at a point where bending force is defined and λ is the distance from the bed to the point where the resultant fluid force acts. Several useful similarity numbers can be

DOI: 10.1002/rra

deduced considering ratios of appropriate forces from the list above, e.g.:

$$\frac{F_B}{F_G} = \frac{\rho g V_p}{\rho_p g V_p} \quad \Rightarrow \quad \mu_{B-G} = \frac{\rho}{\rho_p}$$

$$\frac{F_D}{F_G - F_B} = \frac{0.5\rho C_D U^2 A}{(\rho_p - \rho) g V_p} = \frac{\rho}{(\rho_p - \rho)} \frac{0.5 C_D U^2 L d}{g L d^2} \quad \Rightarrow \quad \mu_{D-B} = C_D \frac{\rho}{(\rho_p - \rho)} \frac{U^2}{g d}$$

$$\frac{F_D}{F_b} = \frac{0.5\rho C_D U^2 A R \lambda}{E I_2} \quad \Rightarrow \quad \mu_{D-b} = C_D \frac{\rho U^2}{E} \left(\frac{L}{d}\right)^3$$

where L is the large plant scale (e.g. shoot length), d is the small plant scale (e.g. stem diameter), $A \propto dL$, $R \propto L$ and $\lambda \propto L$. The similarity numbers $\mu_{B-G} = \rho/\rho_p$ and $\mu_{D-B} = C_D\left[\rho/(\rho_p - \rho)\right](U^2/gd)$ have been successfully used in studying and modelling organism-flow interactions and mass-transfer processes in benthic periphyton communities (Nikora *et al*., 1998, 2003a; Larned *et al*., 2004) where μ_{D-B} was defined as a 'periphyton' number. The number μ_{D-b} was not used as the periphyton flexural rigidity is typically very low and therefore we should expect complete self-similarity on this number (i.e. drag force>>elasticity load). However, for vascular plants the number $\mu_{D-b} = C_D(\rho U^2/E)(L/d)^3$ should be important. Considering the extreme values of the flow-plant similarity numbers, we may explore ways of how plants adjust to specific flow conditions. For instance, using $\mu_{D-b} = C_D(\rho U^2/E)(L/d)^3$ we can distinguish two types of plants: 'tensile' (e.g. periphyton; μ_{D-b} is large) and 'bending' (e.g. stream bank plants; μ_{D-b} is small) as illustrated in Figure 7. The ratio *L/d* in μ_{D-b} represents plant shape and thus may be viewed as a geometrical similarity number. In addition to 'static' flow-plant similarity numbers outlined above, there are characteristic numbers describing dynamic interactions such as plant fluttering that may occur at a wide range of scales, from the leaf scale to the patch mosaic scale. A ratio of a natural frequency of a plant (or its elements) to the forcing frequency is an example of such a number (known as Strouhal number). The similarity numbers similar to $\mu_{B-G} = \rho/\rho_p$, $\mu_{D-B} = C_D\left[\rho/(\rho_p - \rho)\right](U^2/gd)$, and $\mu_{D-b} = C_D(\rho U^2/E)(L/d)^3$ are frequently used in aeroelasticity and flow-structure interaction studies for physical and numerical modelling.

Although in aquatic studies the use of plant mechanical properties and flow-plant similarity numbers is still rare, useful examples include Kouwen and Unny (1973), Usherwood *et al*. (1997), and Ghisalberti and Nepf (2002). In the last of these, the authors simulated eelgrass meadow in a lab using two similarity numbers: ratio of the buoyancy force to the restoring (elastic) force and ratio of the restoring (elastic) force to the drag force imposed by flow. A wide expansion of the biomechanical approaches in aquatic studies, however, is slowed down by very limited information on plant material parameters and their variability across species, scales and environments. The collection of such information should be among the top priorities of *Hydrodynamics of Aquatic Ecosystems*.

The flow-plant similarity numbers can also be introduced in a more formal way considering coupled flow-plant equations of motion, where the flow equations provide drag terms that are used in plant motion equations as external forcing. Such equations open a new avenue in flow-biota interaction studies. Recent progress in formulation of the coupled models in flow-structure interactions (e.g. Connell and Yue, 2007) may provide a solid background for flow-biota applications.

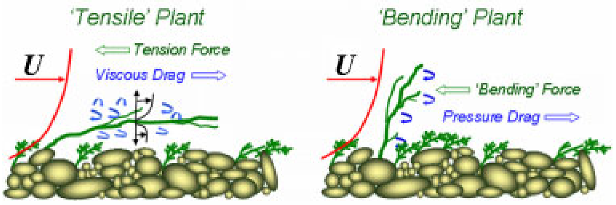

Figure 7. Two extreme plant types: (1) 'tensile' plant—plant's flexural rigidity is very low and plant passively follows the flow mainly experiencing viscous drag (left); and (2) 'bending' plant—plant's flexural rigidity is high and plant resist to flow generating downstream vortices and pressure drag. This figure is available in colour online at www.interscience.wiley.com/journal/rra

DOI: 10.1002/rra

Ecological implications

Design, spatial and temporal patterns and performance of aquatic organisms, and their communities reflect the interplay of multiple biotic and abiotic factors. Among these factors, transport processes and mutual physical impacts (i.e. remit of *Hydrodynamics of Aquatic Ecosystems*) may be of great importance, as illustrated below focusing on aquatic plants in streams as an example. Indeed, recent studies suggest that plant functioning, morphology and the role in aquatic ecosystems are largely driven by these processes and their interactions (e.g. Usherwood *et al*., 1977; Denny, 1988; Statzner *et al*., 1988; Biggs, 1996; Stevens and Hurd, 1997; Hart and Finelli, 1999; Hurd, 2000; Madsen *et al*., 2001; Okubo and Levin, 2001; Denny and Gaylord, 2002; Nikora *et al*., 2003a; Riis and Biggs, 2003; Sand-Jensen, 2003, 2008; Stevens *et al*., 2004; Biggs *et al*. 2005; Folkard, 2005; Boller and Carrington, 2006; Nishihara and Ackerman, 2006; Statzner *et al*., 2006; O'Hare *et al*., 2007; Sand-Jensen and Pedersen, 2008 and many others). In light of these studies, it is reasonable to hypothesize that submersed aquatic plants have evolutionarily adjusted to flow in such a way that these processes have become closely interrelated and optimized at multiple scales to enhance the overall plant performance. Figure 2 outlines some of the flow-induced mechanisms that determine overall physical interactions and transport processes in plant communities. Although considerations below are still hypothetical and serve as illustrations of ecological implications, they are already supported by a number of studies and may serve as potential research targets.

Physical interactions between plants and flow in streams. Submersed aquatic plants encounter substantial drag forces, which can be considered as the superposition of two components: viscous friction at the water-plant interfaces and form (pressure) drag with associated flow separation. To enhance performance, plants need to minimize the total drag to the degree that is still appropriate in terms of conflicting requirements for mass-transfer and photosynthesis, which ideally should be maximized. The total drag can be minimized by utilizing two approaches: (i) minimizing the plant surface area (to minimize viscous drag) and/or (ii) making plants flexible and streamlined to prevent or reduce flow separation by plant reconfiguration (to minimize form drag). The ability to use the first approach is limited by the necessity to have a larger plant surface area to satisfy the requirements for nutrient uptake and photosynthesis. The second approach is much less limited in this respect and thus the total drag acting on plants can be effectively reduced by minimizing the form drag. This latter task can be achieved by the appropriate combination of plant geometry and flexibility in such a way that the form drag is suppressed, at least at a scale(s) where it is most significant. This conceptual consideration leads to a hypothesis that submersed aquatic plants mainly experience viscous drag, while form drag is significantly suppressed and in some cases can even be neglected. The relative magnitudes of the viscous drag and form drag may vary across the scales and should also depend on the relative position of the plant within a community (e.g. a plant at a patch edge may experience significantly higher drag force compared to a plant in the middle of the patch). Preliminary experimental support to this hypothesis can be found in Usherwood *et al*. (1977); Sand-Jensen (2003); Nikora and Nikora (2007); Nikora *et al*. (2008).

Mass-transfer and photosynthesis in plant communities. Submersed aquatic plants in flowing water always fluctuate due to plant flexibility and multi-scale turbulence, as has been outlined in a number of studies (Ennos, 1999; Koehl, 1999; Hurd, 2000; Sand-Jensen, 2003, 2008; Stevens *et al*., 2004; Statzner *et al*., 2006). These studies suggest that an important role of plant flapping is to secure additional mechanisms for enhancing nutrient uptake and photosynthesis, which may include: (i) reduction of the mean thickness of the VSL attached to plant surfaces, as well as the mean thickness of the imbedded within VSL diffusion boundary layers (DBL); (ii) temporal and spatial fluctuations of the VSL and DBL thicknesses leading to the enhanced renewal of the fluid (with associated substances) in close proximity to plant surfaces; and (iii) approximately uniform exposure of plant surfaces to the sunlight due to the flapping of leaves, branches and whole plants. The first two mechanisms weaken the mass-transfer control over the transport of carbon dioxide, oxygen and nutrients across plant surfaces. The third mechanism provides fluctuating light penetration/interception within plant canopies and thus may significantly improve photosynthetic efficiency. Indeed, a number of studies of terrestrial plants have showed that the growth rates under fluctuating light are higher compared to those under constant light (Ogren and Sundin, 1996). There are indications that a similar effect is also valid for aquatic plants (Greene and Gerard, 1990). The overall gain due to fluctuating light may depend on the spectrum of light fluctuation, which in turn may depend on the interplay between the turbulence spectrum, plant morphology and mechanical properties of plants (e.g. stiffness). Of course, there is a number of other important factors influencing photosynthesis and uptake rates (e.g. water temperature,

DOI: 10.1002/rra

nutrient concentration, chemical composition, etc) but hydrodynamic and biomechanical factors may often be dominant.

The intermediate patch density concept. A growing number of studies suggests that the interplay between turbulent structures (including those generated by the organisms themselves), hydrodynamic drag, organism reaction forces and mass-transfer processes (molecular/convective/turbulent) should be largely responsible for aggregation of organisms into patches which, in turn, are often 'organized' into even larger aggregations called patch mosaics (e.g. Biggs, 1996; Hart and Finelli, 1999; Nikora *et al*., 1999; Boudreau and Jorgensen, 2001; Okubo and Levin, 2001; Folkard, 2005; Lancaster *et al*., 2006; Rice *et al*. 2008; Sand-Jensen and Pedersen, 2008). Such multi-scale aggregations represent a form of organisms' 'self-organization', in addition to the traditionally considered patchiness 'imposed' by heterogeneity of habitat properties and/or nutrient supply. In general, the hydrodynamic and biomechanical factors may concurrently control and be controlled by biological interactions. The upper scale of the self-organized patchiness is typically comparable to the flow width.

Joint consideration of physical interactions and transport processes suggests that the most persistent organism patches (e.g. plant or mussel patches) should maintain intermediate (not too low—not too high) densities, which balance the effects of drag forces and mass-transfer-uptake processes (and photosynthesis when relevant). Indeed, with increase in organism patch density from low to high values, the mean total drag acting on individual organisms will reduce from undesirable large values at low density to favourable small values at high density. This positive trend, however, occurs simultaneously with a negative trend in mass-transfer (and light penetration when relevant), which changes from favourable large values at low density to adverse small values at high density. The interplay between these two contradicting trends should lead to *a self-regulation mechanism that controls organism density (number) within a patch*. Using Figure 2 as an illustration, we highlight ML eddies (pattern #2 in Figure 2) as one of such self-regulation mechanisms that may control mass-transfer and drag forces in the organism 'canopies'. This idea is based on experiments with rigid rods (e.g. Nepf and Ghisalberti, 2008) showing that the penetration depth of ML eddies into rod canopies may strongly depend on their density. One can hypothesize that, responding to changing flow conditions, submerged plant communities can regulate the depth of penetration of large ML eddies into canopies by controlling interrelationships between plant density, geometry (morphology) and canopy height. The organisms may either maximize this penetration to secure full access to nutrients and oxygen or, in some circumstances, the depth of penetration may also be reduced to decrease sediment re-suspension within canopies (e.g. to improve optical properties of in-canopy water, as discussed in Luhar *et al*., 2008). Thus, it is quite likely that the plant canopies not only create MLs at their tops but also control them through a self-regulation mechanism involving plant density, geometry and height. The described concept can be defined as *the intermediate patch density concept*. Similar concepts can be also considered for a patch mosaic scale.

The examples above could be further extended to cover many other ecologically significant processes where both physical impacts and transport processes are important (e.g. prey-predator relations or dispersal of propagules/seeds; Okubo and Levin, 2001). The common feature of these examples is that they illustrate how *Hydrodynamics of Aquatic Ecosystems* can supplement mainstream ecological concepts such as the habitat templet theory, river continuum or nutrient spiralling by providing quantitative mechanistic descriptions, explanations and predictions of the processes involved.

DOUBLE-AVERAGING METHODOLOGY (DAM): AN INTEGRATIVE UP-SCALING FRAMEWORK

As already illustrated, physical interactions and ecologically relevant mass-transfer processes occur in a wide range of scales and depend on how physical scales match biological scales such as organism dimensions, patch/community dimensions, life cycles and others. This multi-scale property together with the physical and biological complexity of boundary conditions in aquatic ecosystems highlight a need for an appropriate framework that would serve for flow-biota coupling and integration (i.e. up-scaling) of physical interactions and mass-transfer processes. A promising approach for such a framework, often defined as the 'double-averaging' methodology (DAM, Nikora *et al*., 2007a), was originally developed for the 'air flow-terrestrial canopy' problem (e.g. Finnigan, 2000).

The double-averaging procedure gives the continuity, momentum, advection-diffusion, energy and other high-order equations for the fluid phase, which are averaged in both time (ensemble) and space (in the plane parallel to the mean bed) domains. These equations explicitly contain important (although still unconventional) terms such as

DOI: 10.1002/rra

form-induced stresses and fluxes, and for the flow region below roughness tops, 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 principle, the double-averaged equations can be formulated for both fluid (considering organisms as embedded media) and organisms (considering fluid as embedded media), which are coupled through interface transport terms (e.g. the same term describing transport of nutrients through organisms' surface will be included in both 'flow' and 'organism' equations, but with opposite signs). This methodology allows scale decomposition (or separation of scales) and can be viewed as a scaling-up procedure that changes the scale of consideration from one level in time-space-probability domain to another level. In other words, this methodology provides a natural way for up-scaling, i.e. integrating small-scale biophysical processes into large-scale behaviour.

Detailed derivation and discussion of the double-averaged hydrodynamic equations have been recently presented in Nikora *et al.* (2007a). Therefore, this section will only briefly outline the double-averaged continuity equation and equations for conservation of momentum and passive (dissolved) substances, i.e. equations most relevant for aquatic ecosystems.

Continuity equation

$$\rho\frac{\partial\phi}{\partial t} + \rho\frac{\partial\phi\langle\overline{u}_i\rangle}{\partial x_i} = 0 \tag{1}$$

Momentum equation

$$\begin{aligned}\frac{\partial\langle\overline{u}_i\rangle}{\partial t} + \langle\overline{u}_j\rangle\frac{\partial\langle\overline{u}_i\rangle}{\partial x_j} = {} & g_i - \frac{1}{\rho\phi}\frac{\partial\phi\langle\overline{p}\rangle}{\partial x_i} - \frac{1}{\phi}\frac{\partial\phi\langle\tilde{u}_i\tilde{u}_j\rangle}{\partial x_j} - \frac{1}{\phi}\frac{\partial\phi\left\langle\overline{u_i'u_j'}\right\rangle}{\partial x_j} + \frac{1}{\phi}\frac{\partial}{\partial x_j}\phi\left\langle\overline{\nu\frac{\partial u_i}{\partial x_j}}\right\rangle \\ & + \frac{1}{\rho}\frac{1}{V_f}\overline{\iint\limits_{S_{\text{int}}} p n_i dS} - \frac{1}{V_f}\overline{\iint\limits_{S_{\text{int}}} \nu\frac{\partial u_i}{\partial x_j}n_j dS}\end{aligned} \tag{2}$$

Transport (advection-diffusion) equation for a passive substance

$$\frac{\partial\langle\overline{C}\rangle}{\partial t} + \langle\overline{u}_j\rangle\frac{\partial\langle\overline{C}\rangle}{\partial x_j} = \frac{1}{\phi}\frac{\partial}{\partial x_j}\phi\left\langle\overline{\chi_m\frac{\partial C}{\partial x_j}}\right\rangle - \frac{1}{\phi}\frac{\partial\phi\langle\tilde{u}_j\tilde{C}\rangle}{\partial x_j} - \frac{1}{\phi}\frac{\partial\phi\left\langle\overline{u_j'C'}\right\rangle}{\partial x_j} - \overline{\frac{1}{V_f}\iint\limits_{S_{\text{int}}}\left(\chi_m\frac{\partial C}{\partial x_j}\right)n_j dS} + \langle\overline{F}\rangle \tag{3}$$

In the equations above, we use Reynolds' decomposition $\theta = \overline{\theta} + \theta'$ for instantaneous variables and the decomposition $\overline{\theta} = \langle\overline{\theta}\rangle + \tilde{\theta}$ for time-averaged variables where θ is the flow variable (e.g. scalar, vector or tensor component) defined in the fluid but not in the space occupied by the organisms; angle brackets denote spatial (volume) averaging, overbar denotes time averaging and prime and tilde denote temporal and spatial fluctuating components, respectively. The following symbols are used in equations (1)–(3): u_i is the i-th component of the velocity vector; p is the pressure; g_i is the i-th component of the gravity acceleration; ρ is the fluid density; ν is the fluid kinematic viscosity; C is the passive substance concentration; χ_m is the molecular diffusion coefficient; and F is the source/sink of substance C. The parameter $\phi = \phi_s\langle\phi_t\rangle$ is the generalized 'porosity' where $\phi_s = V_f/V_o$ is the spatial porosity; $\phi_t = T_f/T_o$ is the 'time' porosity; V_f is the volume occupied by fluid within the total averaging volume V_o; T_0 is the total averaging time interval including periods when the spatial points are intermittently occupied by fluid and organisms (e.g. by flapping plants) and T_f is the averaging time interval equal to the sum of time periods when a spatial point under consideration is occupied by fluid only.

Compared to the conventional time-averaged equations, Equations (1)–(3) contain two groups of additional terms: (i) form-induced stresses $\langle \tilde{u}_i \tilde{u}_j \rangle$ and fluxes $\langle \tilde{u}_j \tilde{C} \rangle$ due to correlations of spatial variations in time-averaged fields; and (ii) the form drag per unit fluid volume $f_{p_i} = -(1/V_f)\overline{\iint_{S_{\text{int}}} p n_i dS}$, the viscous drag per unit fluid volume $f_{vi} = (1/V_f)\overline{\iint_{S_{\text{int}}} \left(\rho \nu \partial u_i / \partial x_j\right) n_j dS}$, and the diffusive flux at the water - organisms interface $J = (1/V_f)\overline{\iint_{S_{\text{int}}} \left(\chi_m \partial C / \partial x_j\right) n_j dS}$ (including bed surface when relevant). The roles of these unconventional terms for different hydrodynamic and bed roughness conditions and their modelling/parameterizations represent a topic of active current research in a number of groups worldwide (e.g. Special Issue on the Double-Averaging Methodology in Environmental Hydraulics, Springer's Acta Geophysica, 2008, 56, #3).

Although applications of this methodology in studying and modelling aquatic ecosystems are at an early stage, there are examples already available that demonstrate benefits and advantages of this approach (e.g. Nikora, 2007; Nikora *et al*., 2007b; Special Issue on the Double-Averaging Methodology in Environmental Hydraulics, Springer's Acta Geophysica, 2008, 56, #3).

CONCLUSIONS

Fifteen years ago a prominent lotic ecologist B. Statzner, a pioneer of hydraulics implementation in lotic ecology (Statzner *et al*., 1988), 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* (Statzner and Borchardt, 1994). Today's situation is not much different (Statzner, 2008), highlighting the urgency of the truly interdisciplinary methodology. This paper is an attempt to enhance this approach.

The establishment of a new discipline *Hydrodynamics of Aquatic Ecosystems* should eliminate multiple knowledge gaps at the borders between fluid mechanics, ecology and biomechanics, i.e. areas where probability of new discoveries is the highest. The author is confident that *Hydrodynamics of Aquatic Ecosystems* will provide a missing research platform that will 'synchronize' and enhance flow-biota studies in aquatic ecology. 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. To make it successful, this development should be carefully informed and guided by ecological considerations. *Hydrodynamics of Aquatic Ecosystems* promises not only step changes in current understanding of our aquatic environments but also responds to the growing demands for advanced knowledge in numerous applications, including civil and environmental engineering, resource management, aquaculture and bio-security. Finally, *Hydrodynamics of Aquatic Ecosystems* highlights an emerging tendency in modern science: the creation of a new type of discipline which integrates several different fields. From this perspective, the establishment of *Hydrodynamics of Aquatic Ecosystems* may have a wide scholarly impact offering a useful example of a systematic development of an integrative discipline in the environmental area.

ACKNOWLEDGEMENTS

The author is grateful for collaboration and stimulating discussions of flow-biota interactions to I. Albayrak, J. Aberle, B. Biggs, S. Coleman, A. Dittrich, J. Finnigan, D. Goring, D. Hart, C. Howard-Williams, I. Jowett, N. Lamouroux, S. Larned, A. Marion, S. McLean, O. Miler, N. Nikora, M. O'Hare, G. Parker, S. Rice, T. Riis, M. Righetti, P. Rowinski, P. Sagnes, B. Statzner, A. Sukhodolov, A. Suren and S. Thrush. The work was partly supported by the Leverhulme Trust, Grant F/00152/Z 'Biophysics of flow-plants interactions in aquatic systems'.

REFERENCES

Adrian RJ. 2007. Hairpin vortex organization in wall turbulence. *Physics of Fluids* **19**: 041301.

Albayrak I. 2007. Secondary currents and coherent structures, their distribution across a cross section and their relation to surface boils in turbulent gravel-bed open-channel flow. *Proceedings of 32nd Congress of IAHR*. Venice: Italy.

Alexander RMcN. 2003. Modelling approaches in biomechanics. *Philosophical Transactions of the Royal Society of London. Series B* **358**: 1429–1435.

Biggs BJF. 1996. Hydraulic habitat of plants in streams. *Regulated Rivers: Research and Management* **12**: 131–144.

Biggs BJF, Nikora VI, Snelder TH. 2005. Linking scales of flow variability to lotic ecosystem structure and function. *River Research and Applications* **21**: 283–298.

Boller ML, Carrington E. 2006. The hydrodynamic effects of shape and size change during reconfiguration of a flexible macroalga. *Journal of Experimental Biology* **209**: 1894–1903.

Boudreau B, Jorgensen BB. 2001. *The Benthic Boundary Layer*. Oxford University, Press: Oxford.

Connell BSH, Yue DKP. 2007. Flapping dynamics of a flag in a uniform stream. *Journal of Fluid Mechanics* **581**: 33–67.

de Langre E. 2008. Effects of wind on plants. *Annual Review of Fluid Mechanics* **40**: 141–168.

Denny MW. 1988. *Biology and the Mechanics of the Wave-Swept Environment*. Princeton, University Press: Princeton.

Denny M, Gaylord B. 2002. The mechanics of wave-swept algae. *Journal of Experimental Biology* **205**: 1355–1362.

Ennos AR. 1999. The aerodynamics and hydrodynamics of plants. *Journal of Experimental Biology* **202**: 3281–3284.

Finnigan JJ. 2000. Turbulence in plant canopies. *Annual Review of Fluid Mechanics* **32**: 519–571.

Folkard AM. 2005. Hydrodynamics of model *Posidonia oceanica* patches in shallow water. *Limnology and Oceanography* **50**(5): 1592–1600.

Ghisalberti M, Nepf H. 2002. Mixing layers and coherent structures in vegetated aquatic flows. *Journal of Geophysical Research C: Oceans* **107**(2): 1–3.

Ghisalberti M, Nepf H. 2004. The limited growth of vegetated shear layers. *Water Resources Research* **40**(7): W075021–W0750212.

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

Green JC. 2005. Velocity and turbulence distribution around lotic macrophytes. *Aquatic Ecology* **39**: 1–10.

Greene RM, Gerard VA. 1990. Effects of high-frequency light fluctuations on growth and photoacclimation of the red alga *Chondrus crispus*. *Marine Biology* **105**: 337–344.

Goto S. 2008. A physical mechanism of the energy cascade in homogeneous isotropic turbulence. *Journal of Fluid Mechanics* **605**: 355–366.

Hart DD, Finelli CM. 1999. Physical-biological coupling in streams: the pervasive effects of flow on benthic organisms. *Annual Review of Ecology and Systematics* **30**: 363–395.

Ho C-M, Huerre P. 1984. Perturbed free shear layers. *Annual Review of Fluid Mechanics* **16**: 365–424.

Hondzo M, Wang H. 2002. Effects of turbulence on growth and metabolism of periphyton in a laboratory flume. *Water Resources Research* **38**(12): 1277.

Hurd CL. 2000. Water motion, marine macroalgal physiology, and production. *Journal of Phycology* **36**: 453–4472.

Knight DW, Omran M, Tang X. 2007. Modeling depth-averaged velocity and boundary shear in trapezoidal channels with secondary flows. *Journal of Hydraulic Engineering of ASCE* **133**(1): 39–47.

Koehl MAR. 1999. Ecological biomechanics of bethic organisms: life history, mechanical design and temporal patterns of mechanical stress. *Journal of Experimental Biology* **202**: 3469–3476.

Koehl MAR. 2003. Physical modelling in biomechanics. *Philosophical Transactions of the Royal Society of London. Series B* **358**: 1589–1596.

Kolmogorov AN. 1941. The local structure of turbulence in incompressible viscous fluid for very large Reynolds numbers. *Doklady Akademii Nauk SSSR* **30**: 301–305.

Kouwen N, Unny TE. 1973. Flexible roughness in open channels. *Journal of Hydraulic Engineering of ASCE* **99**(HY5): 713–728.

Kubrak E, Kubrak J, Rowinski PM. 2008. Vertical velocity distributions through and above submerged, flexible vegetation. *Hydrological Sciences–Journal–des Sciences Hydrologiques* **53**(4): 905–919.

Lancaster J, Buffin-Bélanger T, Reid I, Rice SP. 2006. Flow- and substratum-mediated movement by a stream insect. *Freshwater Biology* **51**: 1053–1069.

Larned S, Nikora V, Biggs B. 2004. Mass-transfer-controlled nitrogen and phosphorus uptake by stream periphyton: a conceptual model and experimental evidence. *Limnology and Oceanography* **49**(6): 1992–2000.

Luhar M, Rominger J, Nepf H. 2008. Interaction between flow, transport and vegetation spatial structure. *Environmental Fluid Mechanics* **8**(5–6): 423–439.

Madsen JD, Chambers PA, James WF, Koch EW, Westlake DF. 2001. The interaction between water movement, sediment dynamics and submerged macrophytes. *Hydrobiologia* **444**: 71–84.

Marion A, Packman AI, Zaramella M, Bottacin-Busolin A. 2008. Hyporheic flows in stratified beds. *Water Resources Research* **44**(9): W09433.

Monin AS, Yaglom AM. 1975. *Statistical Fluid Mechanics: Mechanics of Turbulence*. Vol. 2, MIT Press: Boston.

Nepf HM. 1999. Drag, turbulence, and diffusion in flow through emergent vegetation. *Water Resources Research* **35**(2): 479–489.

Nepf HM, Ghisalberti M. 2008. Flow and transport in channels with submerged vegetation. *Acta Geophysica* **56**(3): 753–777.

Nezu I, Nakagawa H. 1993. Turbulence in open-channel flows. Balkema, Rotterdam: The Netherlands.

Nezu I, Sanjou M. 2008. Turbulence structure and coherent motion in vegetated canopy open-channel flows. *Journal of Hydro-Environment Research* **2**: 62–90.

Niklas KJ. 1992. *Plant Biomechanics: An Engineering Approach to Plant Form and Function*. The University of Chicago Press: Chicago.

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

Nikora N, Nikora V. 2007. A viscous drag concept for flow resistance in vegetated channels. *Proceedings of 32nd Congress of IAHR, Venice, Italy, CD ROM*.

Nikora V. 2007. Hydrodynamics of aquatic ecosystems: spatial-averaging perspective. *Acta Geophysica* **55**(1): 3–10.

Nikora V, Aberle J, Biggs B, Jowett I, Sykes J. 2003b. Effects of fish size, time-to-fatigue, and turbulence on swimming performance: a case study of *Galaxias maculatus* (inanga). *Journal of Fish Biology* **63**: 1365–1382.

Nikora V, Goring D. 2000. Eddy convection velocity and Taylor's hypothesis of'frozen' turbulence in a rough-bed open-channel flow. *Journal of HydroScience and Hydraulic Engineering of JSCE* **18**(2): 75–91.

Nikora V, Goring D, Biggs BJF. 1998. A simple model of stream periphyton-flow interactions. *Oikos* **81**: 607–611.

Nikora V, Goring D, Biggs BJF. 2002b. Some observations of the effects of microorganisms growing on the bed of an open channel on the turbulence properties. *Journal of Fluid Mechanics* **450**: 317–341.

Nikora VI, Goring DG, McEwan I, Griffiths G. 2001. Spatially-averaged open-channel flow over a rough bed. *Journal of Hydraulic Engineering of ASCE* **127**(2): 123–133.

Nikora V, Green M, Thrush S, Hume T, Goring D. 2002a. Structure of the internal boundary layer over a patch of horse mussels (*Atrina zelandica*) in an estuary. *Journal of Marine Research* **60**(1): 121–150.

Nikora V, Larned S, Biggs BJF. 2003a. Hydrodynamic effects in aquatic ecosystems with a focus on periphyton. *Recent Research Developments in Fluid Dynamics* **4**: 41–70.

Nikora V, McLean S, Coleman S, Pokrajac D, McEwan I, Campbell L, Aberle J, Clunie D, Koll K. 2007b. Double-averaging concept for rough-bed open-channel and overland flows: applications. *Journal of Hydraulic Engineering of ASCE* **133**(8): 884–895.

Nikora V, McEwan I, McLean S, Coleman S, Pokrajac D, Walters R. 2007a. Double averaging concept for rough-bed open-channel and overland flows: Theoretical background. *Journal of Hydraulic Engineering of ASCE* **133**(8): 873–883.

Nikora V, Pearson C, Ude Shankar. 1999. Scaling properties in landscape patterns: New Zealand experience. *Landscape Ecology* **14**(1): 17–33.

Nikora V, Larned S, Nikora N, Debnath K, Cooper G, Reid M. 2008. Hydraulic resistance due to aquatic vegetation in small streams: a field study. *Journal of Hydraulic Engineering of ASCE* **134**(9): 633–641.

Nishihara GN, Ackerman JD. 2006. The effect of hydrodynamics on the mass transfer of dissolved inorganic carbon to the freshwater macrophyte *Vallisnerria americana*. *Limnology and Oceanography* **51**(6): 2734–2745.

Nowell ARM, Jumars PA. 1984. Flow environments of aquatic benthos. *Annual Review of Ecology and Systematics* **15**: 303–328.

Okubo A, Levin SA. 2001. *Diffusion and Ecological Problems: Modern Perspectives*. Springer: New York.

Ogren E, Sundin U. 1996. Photosynthetic responses to variable light: a comparison of species from contrasting habitats. *Oecologia* **106**: 18–27.

O'Hare MT, Hutchinson KA, Clarke RT. 2007. The drag and reconfiguration experienced by five macrophhytes from a lowland river. *Aquaitic Botany* **86**: 253–259.

Pavlov DS, Mikheev VN, Lupandin AI, Skorobogatov MA. 2008. Ecological and behavioural influences on juvenile fish migrations in regulated rivers: a review of experimental and field studies. *Hydrobiologia* **609**: 125–138.

Packman AI, Salehin M, Zaramella M. 2004. Hyporheic exchange with gravel beds: basic hydrodynamic interactions and bedform-induced advective flows. *Journal of Hydraulic Engineering of ASCE* **130**(7): 647–656.

Poggi D, Porporato A, Ridolfi L, Alberston JD, Katul GG. 2004a. The effect of vegetation density on canopy sublayer turbulence. *Boundary-Layer Meteorology* **111**: 565–587.

Poggi D, Katul GG, Albertson,JD. 2004b. Momentum transfer and turbulent kinetic energy budgets within a dense canopy. *Boundary-Layer Meteorology* **111**: 589–614.

Py C, de Langre E, Moulia B. 2006. A frequency lock-in mechanisms in the interaction between wind and crop canopies. *Journal of Fluid Mechanics* **568**: 425–449.

Raupach MR, Antonia RA, Rajagopalan S. 1991. Rough wall turbulent boundary layers. *Applied Mechanics Review* **44**(1): 1–25.

Raupach MR, Finnigan JJ, Brunet Y. 1996. Coherent eddies and turbulence in vegetation canopies: the mixing layer analogy. *Boundary-Layer Meteorology* **78**: 351–382.

Rice SP, Buffin-Bélanger T, Lancaster J, Reid I. 2008. Movements of a macroinvertebrate (*Potamophylax latipennis*) across a gravel-bed substrate: effects of local hydraulics and micro-topography under increasing discharge. In *Gravel-bed rivers VI: From Process Understanding to River Restoration*, Habersack H, Piegay H, Rinaldi M (eds). Elsevier B. V. 637–660.

Richardson LF. 1922. *Weather Prediction by Numerical Process*. Cambridge University Press: Cambridge.

Righetti M. 2008. Flow analysis in a channel with flexible vegetation using double-averaging method. *Acta Geophysica* **56**(3): 801–823.

Riis T, Biggs BJF. 2003. Hydrologic and hydraulic control of macrophyte establishment and performance in streams. *Limnology and Oceanography* **48**(4): 1488–1497.

Robinson SK. 1991. Coherent motion in the turbulent boundary layer. *Annual Review of Fluid Mechanics* **23**: 601–639.

Romano GP. 1995. Analysis of two-point velocity measurements in near-wall flows. *Experiments in Fluids* **20**: 68–83.

Roy AG, Buffin-Belanger T, Lamarre H, Kirkbride AD. 2004. Size, shape, and dynamics of large-scale turbulent flow structures in a gravel-bed river. *Journal of Fluid Mechanics* **500**: 1–27.

Sand-Jensen K. 2003. Drag and reconfiguration of freshwater macrophytes. *Freshwater Biology* **48**: 271–283.

Sand-Jensen K. 2008. Drag forces on common plant species in temperate streams: consequences of morphology, velocity and biomass. *Hydrobiologia* **610**: 307–319.

Sand-Jensen K, Pedersen ML. 2008. Streamlining of plant patches in streams. *Freshwater Biology* **53**: 714–726.

Statzner B. 2008. How views about flow adaptations of benthic stream invertebrates changed over the last century. *International Review of Hydrobiology* **93**(4–5): 593–605.

Statzner B, Gore JA, Resh VH. 1988. Hydraulic stream ecology: observed patterns and potential applications. *Journal of the North American Benthological Society* **7**: 307–360.

Statzner B, Borchardt D. 1994. Longitudinal patterns and processes along streams: modelling ecological responses to physical gradients. In *Aquatic Ecology: Scale, Pattern, and Process*, Giller PS, Hildrew AG, Raffaelli DG. (eds). Blackwell Scientific Publications: Oxford; 113–140.

Statzner B, Lamouroux N, Nikora V, Sagnes P. 2006. The debate about drag and reconfiguration of freshwater macrophytes: comparing results obtained by three recently discussed approaches. *Freshwater Biology* **51**: 2173–2183.

Stevens CL, Hurd CL. 1997. Boundary-layers around aquatic macrophytes. *Hydrobiologia* **346**: 119–128.

Stevens CL, Hurd CL, Smith MJ. 2004. Interaction between fronds of the large intertidal seaweed Durvillaea antarctica. *Journal of Marine System* **49**(1–2): 145–157.

Sukhodolov A, Sukhodolova T. 2006. Evolution of mixing layers in turbulent flow over submerged vegetation: Field experiments and measurement study. *Proceedings of the International Conference on Fluvial Hydraulics River Flow 2006* September 6–8, 2006 Lisbon, Portugal, Taylor and Francis, London, v. **1**: 525–534.

Townsend AA. 1976. *The Structure of Turbulent Shear Flow*. Cambridge University Press: Cambridge.

Usherwood JR, Ennos AR, Ball DJ. 1997. Mechanical and anatomical adaptations in terrestrial and aquatic buttercups to their respective environments. *Journal of Experimental Botany* **48**: 1469–1475.

Vogel S. 1994. *Life in Moving Fluids*. Princeton University Press: Princeton.

Wainwright B, Biggs WD, Currey JD, Gosline JM. 1976. *Mechanical Design in Organisms*. Edward Arnold: London, UK.

DOI: 10.1002/rra