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Physical modelling of water, fauna and flora: knowledge gaps, avenues for future research and infrastructural needs

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State-of-the-art paper

Physical modelling of water, fauna and flora: knowledge gaps, avenues for future research and infrastructural needs

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ABSTRACT

Physical modelling is a key tool for generating understanding of the complex interactions between aquatic organisms and hydraulics, which is important for management of aquatic environments under environmental change and our ability to exploit ecosystem services. Many aspects of this field remain poorly understood and the use of physical models within eco-hydraulics requires advancement in methodological application and substantive understanding. This paper presents a review of the emergent themes from a workshop tasked with identifying the future infrastructure requirements of the next generation of eco-hydraulics researchers. The identified themes are: abiotic factors, adaptation, complexity and feedback, variation, and scale and scaling. The paper examines these themes and identifies how progress on each of them is key to existing and future efforts to progress our knowledge of eco-hydraulic interactions. Examples are drawn from studies on biofilms, plants, and sessile and mobile fauna in shallow water fluvial and marine environments. Examples of research gaps and directions for educational, infrastructural and technological advance are also presented.

Keywords: Biofilms; biogeomorphology; eco-hydraulics; experimental facilities; flow–biota interactions; macrozoobenthos; vegetated flows

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1 Introduction

The complex interactions between organisms and hydraulics are fundamental to the understanding and management of aquatic environments. The recent growth of the field of eco-hydraulics (Nikora 2010, Rice *et al.* 2010a, 2010b) reflects the imperative of predicting the consequences of current and future environmental change (Parry *et al.* 2007, Solomon *et al.* 2007, Thorne *et al.* 2007). Changes such as sea-level rise, increased storminess and conveyance-related flooding (Parry *et al.* 2007, Thorne *et al.* 2007) can, in turn, be expected to force changes to the dynamic interactions between ecology and hydraulics. Physical modelling provides an essential bridge between field observations and theoretical, stochastic and numerical models that attempt to predict the impact of environmental changes on aquatic ecosystems.

Recent progress in eco-hydraulic experimentation has been relatively rapid (Nikora 2010, Rice *et al.* 2010a; Nepf 2012). However, there are still many aspects of this field that are in their infancy and within this context it is significant that the introduction of biota is impossible in many of our hydraulic facilities. As a result, experiments have to rely on inert surrogates, often plastics or wood, which simplify responses but introduce issues of complexity and representation. Other issues relate to the fact that eco-hydraulic experimental research is truly interdisciplinary, requiring contributions from ecology, environmental sciences and hydraulic engineering/physics. It is challenging to access information across these disciplinary boundaries because of differing research methods, aims and terminology (Rice *et al.* 2010a). Given the problems it is not surprising that our understanding of the interactions between flow and biota is still at an early stage of development.

1.1 *Issues and difficulties associated with understanding the interactions between flows and biota*

The measurement of turbulent fluid flow fields is a challenging problem even before considering their interaction with mobile objects, deformable boundaries and/or biology. Turbulent flows are highly variable in all three spatial dimensions and in time and exhibit a range of spatial and temporal scales and quasi-periodicities from very small lengths (the Taylor or Kolmogorov microscales) and short durations to considerably longer lengths (up to the thickness of the boundary layer) and durations. Thus, velocity measurements should be undertaken at high spatial and temporal resolution, but simultaneously cover a large spatial domain and sample for long periods of time. These dichotomous requirements, compounded by data storage limitations, help to make controlled laboratory environments especially attractive venues for the study of turbulent flows.

However, introducing biological agents, such as biofilms, plants, and sessile and mobile vertebrate and invertebrate animals, into the laboratory presents significant additional challenges. Accounting for the additional degrees of freedom afforded by the interactions of turbulent flows with features immersed within the fluid and with the boundaries within which they are constrained is non-trivial. Aquatic fauna and flora are capable of modifying both time- and space-averaged as well as turbulent fluid flows, but conversely, fluid flows are also capable of changing the form and behaviour of deformable and reactionary biota. Furthermore, there are other, potentially unrelated, factors which may drive or at least modify the behaviour of biota.

This paper documents an eco-hydraulic foresight workshop held in Trondheim on 15 September 2011 that was organized as part of HYDRALAB IV, an Integrated Infrastructure Initiative that is part of the European Community's 7th Framework Programme. This includes PISCES, a joint research activity designed to improve physical modelling of eco-hydraulic systems. The foresight teams aim to identify the probable future infrastructure requirements of the next generation of engineers and scientists working within the broad field of environmental hydraulics. Anticipation of those requirements is essential if we are to respond in a timely fashion to the challenges that face society as freshwater and coastal-marine systems respond to environmental change. In the sections that follow, the dominant issues undermining existing and future efforts to further understand eco-hydraulic interactions are described and discussed:

- *Abiotic factors*: The detection of, reaction to and modification of a number of environmental factors, which may be dependent on or independent of the flow field, by subaqueous plants and animals.
- *Adaptation*: The adjustments made to or by organisms at multiple spatio-temporal scales in response to hydrodynamic forcing, abiotic stimuli or both.
- *Complexity and feedback*: Complex interactions between organisms and the hydrodynamic environment and the role of feedback, whether positive or negative, in amplifying or moderating organism or environmental response, respectively.
- *Variation*: Differences between (parts of) individual organisms or groups of organisms of any species caused either by genetic differences or by the influence of environmental factors (Encyclopaedia Britannica 2013).
- *Scale and scaling*: Is it possible to scale down biological (and biomechanical) processes operating at the large scale, are the variables measured at the large scale pertinent at the small scale and does technology permit us to measure the same variable across scales?

Note that while each of these issues may be viewed as being distinct and different, it is also clear that they overlap and interact with one another. In each section below, each issue is briefly discussed and then some potential avenues for research are described. Examples are drawn from studies upon biofilms, plants, mobile benthic invertebrates and sessile macrozoobenthos that populate shallow water fluvial and marine environments, reflecting the areas of expertise of the contributors to the workshop. The improvements to technologies and infrastructures necessary to tackle these issues are then outlined.

2 Abiotic factors

2.1 *Theme description*

The behaviour of subaqueous plants and animals may be modified by a number of environmental factors that may be dependent on or independent of the flow field around them. Biota may sense and react to variations in acoustic, electro-chemical, optical and thermal stimuli that may be beyond the ability of humans to detect and may presently also be beyond the ability of instruments to detect. Examples of abiotic factors (see the recent review of Bornette and Puijalon 2011) include light, sound, carbon dioxide, oxygen, nutrients (e.g. nitrogen, phosphorus and sulphur), the presence/absence of heavy minerals, salinity, pH, organic matter (both within the substrate and the water column), sediment composition (both within the substrate and the water column), turbidity and temperature. Some of these factors are inter-related. Furthermore, the responses of biota may be physiological and/or chemical rather than physical and thus may also prove difficult to detect.

2.2 *Examples of knowledge gaps*

The impact of biological activity upon substrate and suspended sediment physico-chemical characteristics is presently an under-studied area. For example, while there is an extensive body of literature describing the nutrient and oxygen exchange promoted by passive irrigation and pumping of Thalassinidean shrimp (Aller *et al.* 1983, Suchanek 1983, Ziebis *et al.* 1996, Astall *et al.* 1997, Griffen *et al.* 2004, D'Andrea and DeWitt 2009), few studies have extended to study the chemical composition of the sediment surrounding burrows and the role of chemical exchanges in modifying the chemical balance within the substrate, especially under different wave–current regimes. Furthermore, studies of this type need to be extended to a wider range of species, particularly mobile animals and plants. Macrophytes, for instance, often form in clustered groups of individuals of one or more species on the beds of rivers. The deposition of sediment and organic matter is promoted within these "patches" (Schoelynck *et al.* 2012), making them bio-geochemical hotspots (Schoelynck 2011). There is also growing evidence that Silicon concentration in aquatic species litter is a major factor driving decomposition rates (Schaller *et al.* 2012a, 2012b), which can impact upon ecosystem productivity and nutrient availability and thus affect vascular plant distribution (Bragazza and Gerdol 2002). Unfortunately, laboratory studies on plants face practical constraints. For example, the root networks of some plants are too anoxic for use in the laboratory, while others (e.g. *Posidonia oceanica*) are thought to fix oxygen into the substrate, improving growing conditions. However, it is not currently possible to transplant *P. oceanica*, mainly because the uptake of nitrogen by leaves is insufficient to replenish the N lost during natural leaf decay (Lepoint *et al.* 2004). In addition, although *P. oceanica* may fix oxygen, it is still sensitive to substrate oxygen levels, has deep roots and has high stem densities that are difficult to replicate (Gobert *et al.* 2003). Further research is thus needed to identify and isolate the environmental parameters and tolerance ranges to which *P. oceanica* is sensitive and/or to identify other species that may be more resilient. Such studies are complicated by the difficulties presented by chemical instabilities within the substrate, associated with limited sediment thicknesses, planform areas and ground (pore) and overlying water chemical imbalances within experimental facilities. The latter issue may be ameliorated by using riverside flumes and/or unfiltered water. At a broader spatial scale, the *relative* importance of the decay and exchange of organic and inorganic matter, salinity and hydrodynamics in modifying the spatial distribution of individuals, and/or communities of organisms in estuarine and lagoonal environments is yet to be fully established.

Due to the complex and important controls that environmental variables exert over the behaviour and morphology of living organisms, it is intuitive to assume that organisms will be sensitive to changes in these parameters. Organisms may respond to subtle alterations to environmental variables and at levels below those that may cause stress. However, many aquatic species tolerate a wide range of conditions in the field and thus have global distributions covering a range of climates, habitats and environmental conditions. For instance, signal crayfish (*Pacifastacus leniusculus*) are native to the north-western USA, but now thrive throughout Europe and Japan. Many non-marine aquatic plants also have extremely wide distributions, with climatic factors seemingly having minimal effect on their distribution (Santamaria 2002). This implies that many plants and animals can survive a large range of environmental conditions, potentially lessening the challenge of maintaining organisms in flumes. However, while great ranges of conditions are "survivable", they may still have important consequences for flume work as organism behaviour and morphology can be largely controlled by environmental conditions. For instance, while many species of mollusc have colonies all over the world, those in areas of high hydraulic stress are likely to be morphologically dissimilar to those from sheltered areas (e.g. blue mussels (*Mytilus edulis*): Seed 1969, Jørgensen 1976; limpets (genera *Cymbula* and *Scutellastra*): Branch and Marsh 1978; brown mussels (*Perna perna*): McQuaid and Lindsay 2000, McQuaid *et al.* 2000; Mediterranean mussels (*Mytilus galloprovincialis*): Steffani and Branch 2003, Hammond and Griffiths 2004; fan mussels (*Pinna nobilis*): García-March *et al.* 2007). Similarly, plants within a species can be morphologically very different depending on the environment within which they are growing (Idestam-Almquist and Kautsky 1995, Strand and Weisner 1996, Doyle 2001, Puijalon and Bornette 2006, Puijalon *et al.* 2008a). It would be useful to establish the extent to which these morphological adaptations benefit an individual and also influence the hydraulics within the surrounding fluid. Likewise, at the annual scale, external factors other than hydrodynamics may trigger changes to biofilm composition (de Brouwer *et al.* 2000). The effects of light attenuation, clogging of pore spaces, abrasion and fluid drag on biofilm dynamics have still not been isolated. Consequently, there is a need for research that identifies important organism stresses, beyond just the tolerable range, and a discussion of which environmental conditions need to be replicated. In addition, consideration needs to be given to organisms with a wide spatial distribution and the implications this has for the selection of experimental parameters. For example, when using blue mussels should the characteristics of the water (e.g. temperature, salinity, pH) in Norway or Chile be replicated? Much relevant information could be gained from existing biological literature and the answers to many such questions will depend on the specific aims of the study. For most studies, replicating the conditions at the site of interest would be sufficient, but an understanding of which conditions need to be replicated in flumes to ensure organism behaviour is analogous to field equivalents would be beneficial to experimental design.

3 Adaptation

3.1 *Theme description*

Living organisms adapt to the natural environment in which they are immersed at temporal scales ranging from supra-millennial (genetic mutation or evolution) to sub-second (reconfigurations or behavioural adjustments). Adjustments may be classified as avoidance or tolerance and may take the form of changes to growth, movement, feeding and reproduction strategies. Adaptations may be in response to hydraulic drivers (i.e. the mean current, whether unidirectional or multidirectional; waves; turbulence; boundary and/or wall effects) or they may be predominantly in response to abiotic drivers (see Section 2). Alternatively, adaptations may result from the superimposition of abiotic drivers on hydraulic drivers. In addition to the adaptations made by individuals, some species also form colonies that may enable both the individuals within the colony and the colony as a whole to obtain a collective advantage (e.g. within colonies the ascidians *Botryllus schlosseri* inhale water independently but exhale into a common exhalant cavity, increasing the flow rate and enhancing the efficiency of waste removal; Vogel 1994). Furthermore, some groups of species tend to associate with each other because of either an observed or a presumed competitive advantage afforded by cohabitation (e.g. goose barnacles (*Capitulum mitella*) require a firm substrate, which may be supplied by the shells of mussels (*Septifer virgatus*). This increases the roughness of shells, reducing wave-induced shear stress and thus decreasing mussel entrainment; Kawai and Tokeshi 2004). The challenge faced by the scientific community is to observe and measure these adaptations in an objective manner, both for individual specimens and entire colonies.

3.2 *Examples of knowledge gaps*

Without detailed biological and ecological knowledge of organism activity and behaviour in field situations, it is impossible to assess the extent to which the behaviour exhibited by an organism removed from its natural habitat is abnormal. Thus, although it is difficult to assess what constitutes a natural behaviour of a wild organism in an undisturbed field situation, a first goal must be to obtain baseline information on natural behaviours. Incorporating a field validation component to flume experiments is also an effective way of assessing the realism of the response of biota to stimuli in laboratory flumes, as field experiments integrate across biological interactions. Once this information has been obtained for the organism of interest, a second goal is to assess how analogous the behaviour of organisms in flume environments is to field equivalents. In addition, it would be beneficial to understand whether organisms respond differently to a “natural stress”, such as a flood event, than to an “unnatural stress” that is specifically associated with artificial environments, such as a lack of space or the imposition of a diurnal signature through pausing experiments each night. If tell–tale signs of these stresses could be identified it would be extremely beneficial to future studies.

Acclimatizing organisms to experimental conditions is important so as to avoid mistakenly believing the response of an organism to the new environment is actually the organism response to experimental variables (Barmuta *et al.* 2001, Battin *et al.* 2003, Hurtado *et al.* 2011, National Research Council Committee for the Update of the Guide for the Care and Use of Laboratory Animals 2011). However, the life-history of an organism partially dictates its response to environmental and biological conditions. Therefore, the environment in which the organism has been kept prior to experimentation is likely to impact upon experimental results. This has a number of implications. First, organisms used in experiments may either be obtained from the field, raised in a laboratory or collected in the field and kept in a laboratory environment until used in experiments. There is evidence that the behaviour of animals raised in laboratories differs from field-collected equivalents (Tiselius *et al.* 1995) but further research is needed to determine whether organisms raised in these different manners behave and respond to environmental stimuli in the same way. Second, maintaining organisms in experimental conditions for extended periods may increase the likelihood of unnatural behaviours. Signal crayfish (*P. leniusculus*) that had been collected from the field but maintained in laboratory conditions rapidly altered their behaviour (Rice *et al.* 2012), presumably due to the standardization of conditions and lack of biological interactions (e.g. lack of predation and/or competition). Research is needed to determine whether these findings are applicable to other species.

In addition to research on individual organisms, the impact of communities of organisms, rather than descriptions of the impact of individuals and/or single species on near-bed hydraulics, needs to be explored. For example, growing evidence (Amyot and Downing 1997, Rowden *et al.* 1998, Widdows *et al.* 1998, 2000a, 2000b, 2004, Andersen 2001, Widdows and Brinsley 2002, Fortino 2006) suggests that communities of animals can control substrate stability, with seasonal cycles in community structure controlling seasonal cycles in substrate stability.

In addition, sessile animals such as ascidians, barnacles and anemones are associated with many organisms that attach to, or live within, reefs and aggregations (e.g. algae, molluscs and sponges) that may significantly increase the projected area and hence increase the drag acting on their hosts. Also, the presence of other organisms will increase competition, which could lead to behavioural and physiological alterations. For example, dense communities of epiphytes (e.g. black fly larvae) may weigh down the leaves of plants and thus deprive their hosts of light, reduce dissolved gas exchange, affect their biomechanics and thus modify how they respond to forcing. Plant structure and morphology is known to change over the order of days/weeks in response to hydrodynamic forcing (Puijalon and Bornette 2004, 2006, Puijalon *et al.* 2005, 2008a, 2008b), but the extent to which these changes provide potential competitive advantages and/or disadvantages (e.g. the invasion of other species if plant size reduces) is yet to be established. Each of these points emphasises that the interactions between communities of organisms and environments are complex and variable and require the expertise of biologists and physical scientists to unravel the complex bi-directional impacts. Organisms respond and react to each other through purely biological interactions, in addition to interactions with each other based on habitat modification (ecosystem engineering). These interactions control the community structure and, consequently, the impacts on the physical environment. However, the nature of the physical environment will also impact the biological interactions between organisms.

4 Complexity and feedback

4.1 *Theme description*

Natural systems are inherently complex. Complexity arises in many different and sometimes unexpected ways, through the myriad interactions between biofilms, plants and animals, and the aquatic environment, including water and sediment physico-chemistry. These often non-linear interactions are further complicated by feedback, whether positive or negative. King (1970: 147) describes the two types of feedback:

> … positive feedback results in the operating process further extending the change it has induced in the dependent variable … Negative feedback, on the other hand, causes a self-regulating effect that reverses the change induced by the action of the process. The first effect is self-generating, the second is self-regulating.

In recent years, much work has been done on feedbacks in “biogeomorphology” and/or “ecogeomorphology” (Fisher *et al.* 2007, Darby 2010, Hession *et al.* 2010, Reinhardt *et al.* 2010, Rice *et al.* 2010b, Wheaton *et al.* 2011, Schoelynck *et al.* 2012.

4.2 *Examples of knowledge gaps*

Feedback operates at a range of spatial and temporal scales. For example, most biofilms, plants and benthic animals reconfigure in response to hydrodynamic loading. Changes in the projected areas of organisms then reduce the hydrodynamic loading upon the organisms (negative feedback) and simultaneously impact upon the flow field. Adjustment mechanisms and the effects of those mechanisms vary by species, and furthermore, vary dynamically in response to turbulent fluctuations (Hedden *et al.* 1995). Thus, as argued by Lauder (2011), in order to properly quantify the interactions between turbulent fluid flows and the biota immersed in them, we must make simultaneous measurements of the flow field and the four-dimensional motion of biota. To date, most concurrent measurements of biological motion and velocities have been made around fish. For example, Sakakibara *et al.* (2004) used both conventional two-dimensional (2D) and stereoscopic three-dimensional (3D) particle image velocimetry (PIV) to quantify the flow field and shedding vortex structures around the tail fin of a goldfish, while employing a 3D shape identification technique to estimate the location and shape of the fish relative to the measurement planes. Very recently, Cameron *et al.* (accepted) developed a 3D PIV system to quantify the flow field and coupled it with a weighted cross-spectral density-based algorithm to detect the 2D motion of a *Ranunculus penicillatus* patch in the field. Nevertheless, it is not easy to reconstruct organism topologies or 3D turbulent flow fields from planar data. Recent advances in high-speed camera and synchronization technologies to capture hundreds of positions at 5–10 times the frequency of organism motion, allied to advances in tomographic, holographic, defocusing (Arroyo and Hinsch 2008) and scanning (Albagnac *et al.* 2013) 3D/3C PIV systems should help circumvent this problem. Scanning techniques, which measure temporal variations of all three velocity components within a finite volume, are particularly well-adapted for high-resolution hydraulic measurements and do not impose additional optical access constraints.

At a broader scale, mobile animals alter the topographic roughness of the bed (Jones and Jago 1993, Ziebis *et al.* 1996), which in turn alters the velocity profile. Evidence suggests (Wright *et al.* 1997, Peine *et al.* 2009) that in most low-energy, fine-grained substrates, animals are the principle phenomenon altering roughness. However, the hydrodynamic impact of the roughness generated by mobile animals has rarely been quantified. For example, it has been widely noted that deposition of fine-grained sediment is promoted in pits that are constructed by a range of animals, including worms, bivalves, crustaceans and gastropods (Yager *et al.* 1993), but to our knowledge, no study details the alteration to flow characteristics created by biogenically constructed pits. Similarly, Thalassinidean shrimp burrows can cover large areas in cones and funnels with diameters hundreds of millimetres wide (Dworschak 1987). Each burrow is also subject to both passive irrigation and pumping by resident shrimp. Therefore, it seems likely that the hydrodynamic conditions over shrimp colonies are altered, but little is known of this alteration, especially in comparison to the biological literature focusing on nutrient and oxygen transfers, ecosystem engineering and functional behaviour of Thalassinidean shrimp.

At an even broader scale, vegetation colonizing the intertidal zone has been found to reduce erosion, enhance deposition and stabilize the coastline, thus improving growing conditions (Bouma *et al.* 2009). Bouma *et al.* (2009) described both areal density (stems m^{-2}) and scale-dependent feedbacks that were manifest through altered sedimentation patterns. However, in some circumstances (Fonseca and Fisher 1986, James and Barko 2000), transfer of results across species is limited and thus work needs to be expanded to a broader range of species, with targeted studies to identify organism characteristics that allow comparison of eco-hydraulic interactions across species. Whether living plants or dead leaves, seagrass meadows act as ecosystem engineers (*sensu* Jones *et al.* 1994, van der Heide *et al.* 2007). In the Mediterranean, leaf litter commonly gets washed up on beaches, with up to 2 m of vertical accumulation, significantly reducing wave impact and erosion caused by waves and currents (Simeone and De Falco 2012). However, it remains unclear whether (i) flow and turbulence fields are always modified in a way that reduces erosion and/or enhances deposition and (ii) there are particular species, assemblages of species, stem, leaf and stand configurations and/or areal extents needed to sustain or attenuate hydrodynamic forcing (Coops *et al.* 1996). In addition, further study is needed to document and quantify the complex response of the coastal ecosystem when leaf litter is removed. To what extent do these actions promote the erosion of beaches, increase sedimentation down-current, and in turn reduce the density of sea grass meadows?

5 Variation

5.1 *Theme description*

Unless (part of) an individual of a particular species has been reproduced asexually (i.e. cloned), it cannot be expected to be either physically or behaviourally identical to another (part of an) individual of the same species. For example, the structure and function of the stems and leaves of individual *R. penicillatus* plants vary depending upon the extent of submergence. Seagrasses exhibit spatio-temporal variations in stem areal density at the scale of entire meadows (Kelly *et al.* 2001) but are also formed of heterogeneous patches of variable size and shape that may force spatio-temporal variability in the mean and turbulent flow fields (Maltese *et al.* 2007). Likewise, while many landscape features appear to look and behave in the same manner, and indeed may share physical characteristics, none can be expected to be identical. In the 1:80 scale braided river experiments of Tal and Paola (2007, 2010), alfalfa seeds were initially distributed uniformly across a flume bed composed of uniform sediment with a constant water table elevation and with constant, uniform lighting. However, the resulting shoot growth patterns, and the behaviour of the braided channels, were highly variable; morphological variation emerged from apparent homogeneity or, at most, subtle heterogeneities (e.g. elevation or seed location differences of the order of a few grains in size) because of heterogeneity in process (flow and sediment dynamics). Variation may thus arise in a number of different ways, but a key challenge is how experimentalists account for it not only within experimental design but also while interpreting experimental results.

5.2 *Examples of knowledge gaps*

To date, laboratory experiments on the hydrodynamics of vegetation have generally been performed under constant flow depths with spatially uniform vegetation patterns in a monoculture or with artificial plants where all surrogates are identical. Similarly, the hydrodynamics of polychaete tube lawns has mainly been studied using surrogate tubes arranged on a regular grid (Friedrichs *et al.* 2000) in contrast to natural lawns that form clumps and irregular patterns, creating a more heterogeneous environment. This approach has the advantage that the number of variables is reduced and input parameters can be controlled more easily. Conversely, it has the disadvantage that it does not replicate the natural variability in morphology and dynamic behaviour between individuals within a species or between different species that make up a community. For example, plant morphology is variable in time (seasonality) and space and the structure of vegetation patches varies (e.g. in height, density, vitality, number of leaves per shoot) even within species depending on their locations (Puijalon *et al.* 2008a). The combination of this variability, both at the scale of the individual and at the scale of the community, with the unsteadiness of the hydrodynamic regime, makes analysing flow-organism interaction a very complex scientific problem. While variation has been recognized and investigated in detail from a biological perspective (Neumeier 2005, Harder *et al.* 2006, Möller 2006, Stewart 2006, Puijalon *et al.* 2008a, Feagin *et al.* 2011, Möller *et al.* 2011, Miler *et al.* 2012), its effect on the physical environment has not yet been fully addressed. It is therefore uncertain whether variation needs to be taken into account or whether the use of a representative morphology is sufficient for studies of organism–flow interactions.

In nature, the aquatic environment at a particular location and at an instant in time is controlled by many interacting external factors. A change to one of those factors, such as variability in upstream or downstream flow conditions induced by diurnal, seasonal or annual changes in tides, waves and/or currents, results in changes to the local hydraulics. Conversely, within a laboratory flume these external factors, or boundary conditions, are imposed depending upon the specific aims of the experimental study. Boundary conditions imposed at the inlet, outlet, bed and flume walls propagate and dissipate within flumes. At the inlet, biases introduced by pumps and incompletely removed by dampers may bear little resemblance to real world conditions and may render experimental results meaningless. Likewise, in contrast to the real world, secondary currents of the second kind (Prandtl 1952) are generated adjacent to where the flume walls meet the flume bed. Thus, a key question is how imposed or inherited boundary conditions propagate and dissipate and what impact they have upon the validity of experimental results.

6 Scale and scaling

6.1 *Theme description*

This theme encompasses two key ideas: first, do biological (and biomechanical) processes scale in the same way as geomorphological and hydraulic processes? i.e. can biological processes operating at the large scale in the real world be scaled such that behaviours are replicated in physical experiments conducted at smaller scales? Second, are we measuring the correct variables at the most appropriate scales? To what extent are the variables we measure at the large scale the pertinent variables at a smaller scale? Do present technologies permit us to measure the same variable across scales? The answers to these questions are dependent upon which parameters can be controlled and measured in both the field and in the experimental set up. This presents us with difficulties because, for example, biocosms enable researchers to have good control of abiotic variables but poor control of hydraulic variables while experimental flume facilities enable there to be good control of hydraulic variables but not abiotic variables. Furthermore, velocity measurement techniques have finite sampling volume sizes and at smaller scales, the amount of spatial averaging incorporated within a velocity measurement may be so large as to smear significant spatio-temporal patterns. For example, a modern laboratory acoustic Doppler velocimeter (ADV) has a typical sampling volume of 85 mm^3. This corresponds to a cylinder of 6 mm in diameter and 3 mm in height (Nortek AS 2009) and is probably too coarse for measurements in turbulent flows with integral length scales of the same order as found near the vicinity of biofilms or in vegetal canopies with thin stems (see for instance the criticism of the interpretation of ADV measurements of López and García 2001 by Barkdoll 2002). Even hot-film anemometry is generally limited to spot measurements within 2 mm of the object of interest (Biggs *et al.* 1998).

6.2 *Examples of knowledge gaps*

It is often necessary to scale biota and hence employ surrogates because in some situations it is not feasible to use 1:1 scale physical models. Many studies have scaled physical processes using Froude or Reynolds numbers as the basis for comparison (ASCE 1942, Yalin 1971, Peakall *et al.* 1996, Julien 2002, Wilson *et al.* 2003). However, when researching at the interface with ecology, it is also necessary to scale biological factors. The studies of Gran and Paola (2001) and Tal and Paola (2007, 2010) scaled the stem diameter of live surrogate riparian trees (alfalfa), but the cohesive and frictional components of sediment shear strength do not scale linearly (Peakall *et al.* 2007) and neither do the tensile and frictional components of plant root strength (Pollen and Simon 2006). It may also be necessary to scale other parameters such as root-mass and stem or population density (see Nikora 2010 for some suggestions of appropriate similarity numbers). Many biological parameters may not scale linearly and for others, the concept of scaling is difficult to envisage. For instance, when scaling population density of live surrogates is it necessary to scale competition and how can that be achieved? Does a direct relationship even exist between population density and competition (between either individual organisms or species), and/or is it possible to identify other reasonable metrics for competition? If not, it may be necessary to neglect some biological parameters, with implications for the reliability of experimental conclusions.

Eco-hydraulic processes and hydraulic-organism interactions operate over a wide range of spatio-temporal scales. While linkages between microscale turbulence and biological response (i.e. avoidance or tolerance through sheltering, reconfiguration and/or streamlining) can be expected to be present, the extent to which this is the case is still unknown. Thus, if our interest is in organism response, to what extent is a detailed description of turbulence needed? The answer to this question is a function of the ability of the organism to reconfigure (i.e. its stiffness or flexibility), the scale of interest and also the scientific approach of the investigator (e.g. reductionist or holistic). If our interest concerns inflexible organisms at the channel- or coastline-scale, then presumably the answer is that a detailed description of turbulence is not warranted and only a relative time-averaged value is needed (e.g. turbulent fluctuation normalized by the time-averaged velocity; Nikora *et al.* 2003). However, if our interest concerns very flexible structures at the patch scale, the converse is likely to be true and microscale turbulence may have a significant impact upon the behaviour of individual organisms. The ideal spatio-temporal resolution of measurements is also related to the scale of interest and, indeed, to the approach of the investigator. Given presently available technologies, perhaps the key question is how to up-scale detailed measurements of turbulence signals at a single place in space and over relatively short periods of time (of the order of minutes to hours to adequately characterize the full range of turbulent fluctuations; Soulsby 1980), first to describe the response of individual organisms and second to describe higher level responses of the ecosystem as a whole.

There has been a great deal of research on the impacts of (especially) sessile animals on the physical environment. However, much of this previous research has a biological focus at a scale of relevance to organisms. Research at intermediate- and large-scales is largely missing from the existing literature. This is of importance both because of the bioengineering potential of aggregations of bivalves for protecting coasts and for assessing the significance of sessile animals at larger scales. For instance, mussels have been found to significantly alter near-bed hydraulics in flumes with a maximum flow depth of 1 m (Butman *et al.* 1994, Peine *et al.* 2005, van Duren *et al.* 2006), but the significance of mussel beds in natural flows that can be 10s of metres deep is unknown. There is also significant uncertainty associated with upscaling bioturbation fluxes obtained from laboratory experiments on a small number of organisms to the broader ecosystem scale, and the significance of bioturbation (in terms of sediment, nutrient and other fluxes) relative to physical processes remains largely unknown. In one exception, Grant (1983) found that, during high ebb flow, rays disturbed up to 24.2 $\text{cm}^3\,\text{m}^{-2}$ of sediment, worms displaced 1.8 $\text{cm}^3\,\text{m}^{-2}$ and amphipods disturbed 60–70 $\text{cm}^3\,\text{m}^{-2}$. These are significant quantities, especially when accumulated; however they are minor compared with tidal sediment displacement which was measured to be between 6.1×10^3 and $1.2 \times 10^4\,\text{cm}^3\,\text{m}^{-2}$ during the high ebb flow. Similar studies need to be developed for other animal-related processes in order to assess their significance in comparison to acknowledged physical processes.

Most studies investigating the impact of vegetation on coastal hydrodynamics have been performed over short durations and in the summer months, when above-ground biomass is high and incident wave conditions are slight to moderate (Paul and Amos 2011, Jadhav and Chen 2012). Field studies on unidirectional and channelled flows have also tended to focus on low or moderate discharges, due to difficulties associated with planning field campaigns to measure highly unpredictable events (Bakry *et al.* 1992 and references therein). Results obtained from such studies cannot easily be extrapolated to the annual scale for perennial species (Widdows *et al.* 2008a, 2008b) and it is questionable whether results obtained in this manner can be up-scaled to extreme or catastrophic events (Feagin *et al.* 2009, Koch *et al.* 2009). Attempts have been made to investigate the effect of vegetation on extreme events in laboratory studies, but these experiments have been performed in small-scale model basins, a fact which raises doubts as to how well they express field conditions due to distorted scaling and edge effects (Lynett 2007). It is therefore desirable to undertake full-scale laboratory or field studies under extreme conditions to establish how present knowledge can be transferred to extreme events such as large magnitude, low frequency floods or storm surges (e.g. see Rueben *et al.* 2011 or Song and Irish in preparation).

7 Technological and infrastructural needs

In order to address the outstanding issues identified above, the participants of the Trondheim workshop noted a series of limitations of existing infrastructures and measurement technologies and made a number of suggestions for infrastructural and technological development. It was recognized that technological developments tend to be stepwise and therefore it is necessary to anticipate the refinement of existing techniques and technologies. However, it was also recognized that there must be an awareness of potentially new and/or ground-breaking technologies and techniques that may lead to a revolution in our understanding, rather than evolution.

7.1 *Importance of interdisciplinary research*

Perhaps the most obvious starting point for progress is the improvement of "human technology". Crucially, to date, there has been a dearth of truly interdisciplinary studies (and interdisciplinary discussions) involving engineers, applied mathematicians, microbiologists, ecologists and fluid dynamicists. Disciplinary backgrounds lead scientists in disparate fields to ask fundamentally different questions (see Rice *et al.* 2010a and references therein). For example, microbiologists may focus on biofilm microbial or algal composition and succession, and relate it to biomass and function (nutrient degradation, carbon, nitrogen and/or phosphorus cycles), but may provide very little quantitative information on either the properties of the flow or the mechanical properties (3D structure, elasticity and porosity) of the biofilm. Hydraulics and fluid mechanics researchers provide a better description of the local flow conditions but ignore those variables studied by microbiologists and struggle to describe the properties of the turbulent boundary layer and mass transfer due to the lack of information on the biomechanical properties of the underlying biofilms. The characterization of these biomechanical properties will likely require the application of existing techniques developed in other fields or scientific communities (e.g. cryosections or confocal laser-scanning microscopy used by Battin *et al.* 2003 or 3D X-ray tomography used by Iltis *et al.* 2011) or the development of new techniques (e.g. the use of rotating electrodes by Boulêtreau *et al.* 2011 to make biofilm thickness and elasticity measurements). Furthermore, these biomechanical data are required for input into numerical models that may help to develop a more complete understanding of scale-dependent interactions and feedbacks. High-resolution small-scale models can then be used to parameterize large-scale models to bridge gaps between processes operating at different scales (see also Section 6.2). However, numerical models are limited without adequate parameterization and validation datasets. Many experimental programmes suggest such data as an anticipated outcome, but few consider the spatio-temporal resolution of the model mesh during experimental design. To minimize the need for interpolation and extrapolation, measurements should be undertaken at a resolution and precision that is commensurate with that of the numerical model and at positions in space and instants in time that are coincident with the model mesh.

Disciplinary backgrounds also lead scientists in disparate fields to take different approaches to physical modelling. For example, replication helps add confidence that the independent variable consistently drives response (or a range of responses) in the dependent variable and that this response is not caused by bias or chance. In hydraulic experiments, replication typically consists of collecting sufficient independent velocity samples in space and time to ensure convergence of mean and turbulent quantities (i.e. to increase confidence that those quantities accurately describe the flow field; Soulsby 1980). Conversely, in ecological experiments, replication typically consists of monitoring the responses of different individuals while changing only the independent variable (i.e. to increase confidence that a particular state or behaviour is broadly representative of the target (sub-)population). One approach to reconcile these different perspectives may be to place physical modelling within a Monte

Carlo framework and use a large number of replicates covering the parameter space of interest, while simultaneously sampling velocities over sufficient space and time, to identify a "most likely" organism response. However, although selection based on similarity may limit variance caused by intraspecies variation (e.g. gender, life-cycle stage, size, fitness, etc.), variance will generally be large because of a range of interacting limiting factors (Hart and Finelli 1999). Often, it is dominated by ecological interactions and variability in organism response rather than measurement error (Lancaster and Downes 2010). Crucially, the resources necessary to adopt a Monte Carlo framework for experimental design generally make it impracticable. A more pragmatic approach may be to accept that experimental aims and objectives need to be specific and realistic and that trade-offs and compromises will be needed to explore the desired range of parameter space while performing sufficient replicates to ensure confidence in results.

Thus, interdisciplinary discussion and collaboration, within and between research institutes, consultancies and management agencies, are key first steps for identifying and understanding the essential behaviours of flora and fauna under hydraulic stress. The result of such discussion and collaboration should be the identification and development of common themes, problems, questions and approaches across disparate fields and applications.

7.2 *Limitations of existing facilities*

Before describing potential areas for improvement, it is perhaps beneficial to first outline some basic limitations of existing technologies and facilities. Some of these limitations follow directly from the lack of interdisciplinary collaboration during the design and construction of experimental facilities. For example, most studies conducted in fluid dynamics laboratories have been geared towards investigating responses to hydrodynamic forcing and have ignored behavioural changes and longer-term responses triggered by abiotic stresses (perhaps due to toxic effects or long term fitness effects). Therefore, many experimental facilities can only house species that are relatively insensitive to abiotic stimuli and do not permit researchers to control some key abiotic factors that are needed for healthy organisms and/or natural behaviours (e.g. temperature or oxygen content). Furthermore, most hydraulics facilities have little control over the source of water – many use domestic or commercial water supply networks that have been chemically treated to alter or reduce the bio-geochemical activity that is crucial for the natural function of ecological systems. Changing the bio-geochemical constituents of the water, whether ground- or surface-water, may also have implications when sediment is incorporated in experiments. Adding sediment to a flume is not trivial and ensuring that it is adequately recirculated, without artificially sorting it, through pumps is already challenging even before one considers the control of nutrient fluxes and biotically-mediated interactions between the water and the sediment. These fluxes are sensitive to the chemical signatures of the surface-water, pore-water and the constituent components of the sediment bed itself. Adequately studying these fluxes, behaviours and responses requires large, deep facilities where key parameters can be controlled for long periods of time. Such facilities are often prohibitively expensive to construct and run and so an additional consideration is another human factor: funding.

7.3 *Desirable improvements to facilities*

Addressing the limitations identified in Section 7.2 will first require many of the issues and themes described in Sections 2–6 to be tackled by the scientific community. For example, while there is undoubtedly a need for new facilities that are flexible and capable of employing ranges of widths and depths and with holding facilities, etc. that ensure organism integrity, what range of widths and depths is required? It is known that boundary and territorial conditions are important for animals and plants, but how wide does a flume need to be to house a certain number of individuals and/or species? To answer this question, it will be necessary to improve direct observations of animals and plants in the natural environment, perhaps exploiting microsensors and nanotechnologies to develop location sensors, or using smaller tracers for plants and animals. Alternatively, perhaps it is possible to use chemical indicators to detect and measure the stress caused to organisms by different stimuli. Whichever methodologies are adopted, it will also be necessary to develop behavioural screening devices to identify and isolate organism responses to specific stimuli. In addition, the depth of the flume is a key limiting factor, both from the perspective of maximum water depth, but also maximum sediment thickness. Benthic organisms are likely to be sensitive to hyporheic flow, and thus a flume must be deep enough to ensure flow through the porous bed, not preferential flow along the flume floor.

While hydraulic flume facilities have excellent control over flow rates and velocity fields, they generally have limited control over abiotic factors. Conversely, the biocosms employed in aquaculture research have greater control over abiotic factors, but have little or no control over flow/wave conditions. Biocosms are generally installed *in situ* as an enclosure within the field environment. Therefore, problems associated with modifications to the bio-geochemical properties of the ground- and surface-water are minimized. There are a handful of facilities across the world (e.g. the St. Anthony Falls Laboratory, Minneapolis, USA; the Silverstream Flume near Christchurch, New Zealand and the Stroud Water Research Center, Pennsylvania, USA) that extract natural stream water to ensure that bio-geochemical properties are unchanged, but more hydraulic flumes need to be built with this provision. It is thus desirable to transfer knowledge and technologies to produce hybrid facilities capable of ensuring control over both hydraulic and abiotic variables. This should make it possible to study the behaviour of sensitive species, such as sponges, that need better control of abiotic factors. In addition, almost all fish species and many aquatic invertebrates are sensitive to underwater sounds and vibrations. Although acoustic ecology is a well-established area of research, relatively little is known about the response of aquatic organisms to environmental noises. However, animals are known to respond to anthropogenic sounds and noise is regularly and successfully used to manipulate the movement of fish in rivers in relation to engineered features, such as turbines and fish passages (Knudsen *et al.* 1994, Popper and Hastings 2009). Therefore, it is likely that aquatic organisms will be sensitive to the vibration and noise produced by pumps and also ambient laboratory noise. Improvements are thus needed to reduce these disturbances, either through improvements to pump technologies and/or by sound-proofing flume walls.

However, in all likelihood, the single most important factor limiting advancement of eco-hydraulic experimentation is time. It is presently not feasible for researchers to adequately control key parameters, run experiments and take detailed measurements for prolonged periods of time. First, it is not straightforward to ensure continuous, reliable operation of complex equipment such as pumps, lasers, high-speed cameras, etc. Furthermore, measurement techniques such as laser Doppler anemometry and PIV are incredibly memory intensive and have associated high data storage requirements (of the order of 80 GB of data per minute with a modern 100 Hz, 5 MP camera) and it is difficult to prevent memory buffers from becoming full, causing data loss. After image acquisition and storage, PIV requires significant computing power to process images, cross-correlate between images and extract velocity fields. Thus, improvements also need to be made to computing facilities in order to extract and post-process the resulting data. Solutions to all these issues are necessarily expensive. This has implications for funding streams. In particular, the transnational access components of HYDRALAB IV, whereby the European Commission provides funds to large or unique affiliated laboratories to enable researchers from other countries to perform experiments in those installations, may provide a model for new funding mechanisms. Within each member state, funding bodies may provide funds such that researchers from other institutions within the member state can gain access to facilities that are capable of performing experiments for prolonged periods of time.

8 Conclusion

This review has described the outcomes of discussions between contributors to the PISCES work package of HYDRALAB IV and a panel of invited experts to identify coherent themes undermining existing and future efforts to further understand eco-hydraulic interactions. Five dominant issues were defined and discussed: abiotic factors, adaptation, complexity and feedback, variation, and scale and scaling. Examples of areas where knowledge is currently lacking, and thus of avenues for future research, have been presented, with reference to biofilms, plants, and sessile and mobile fauna in shallow water fluvial and marine environments. Finally, limitations in existing practices and experimental facilities have been identified and suggestions for future improvements have been made.

It is our contention that physical modelling, informed by interdisciplinary discussion and collaboration, will play a crucial role in advancing our knowledge of organism–fluid interactions. The exploitation of infrastructural and technological advances will be central to this advance. Results obtained from studies performed over short durations and under low to moderate hydraulic forcing (e.g. incident wave conditions or discharges) cannot be easily extrapolated to the seasonal or annual scale, nor up-scaled to extreme or catastrophic events. There is therefore a desperate need for large, deep and flexible hydraulic facilities that can permit the study of bio-geochemical, biological, ecological and sedimentary interactions under extreme conditions (e.g. floods or storm surges) for extended periods. Furthermore, knowledge and technology will need to be transferred between disparate fields to design and construct hybrid facilities capable of ensuring control and measurement of both hydraulic and abiotic variables. For maximum flexibility, such a facility should be capable of sourcing natural stream and/or unfiltered water to ensure that biogeochemical properties are unchanged and simultaneously also be capable of using salt water. Because of construction, maintenance and staffing costs, it is likely that this would inevitably be a shared facility and would require the implementation of imaginative funding mechanisms, such as the transnational access components of HYDRALAB IV that enable researchers from European countries to perform experiments in large or unique affiliated laboratories.

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