LINKING SCALES OF FLOW VARIABILITY TO LOTIC ECO SYSTEM STRUCTURE AND FUNCTION

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ABSTRACT

Obtaining a better knowledge of how flow variability affects lotic biota is of considerable importance to stream and river management. We contend that processes at different hierarchical levels of organization in lotic ecosystems are sensitive to variation in flow at related hierarchical temporal scales. Ecosystem disturbance caused by large-scale events (i.e. infrequent, but high magnitude flow events with a recurrence interval of years to many days) tend to determine high-level characteristics of ecosystem structure (e.g. determining species pools, periphyton versus macrophyte dominance) and function (e.g. balance between auto- and heterotrophy). The high-level ecosystem characteristics then set the stage for processes that are influenced by flow variation that occurs at smaller temporal scale (i.e. minutes to milliseconds) such as colonization, biotic interactions and mass transfer enhancement of production. We contend that large-scale temporal events predominantly affect lotic ecosystems through physical drag processes (‘drag-disturbance’), whereas small-scale flow variations affect ecosystems through mass-transfer processes (including invertebrate and fish food-uptake). Drag-disturbance and mass-transfer related processes mark the opposite ends of a continuum of flow variability controlled processes, with moderate temporal scale flow variability events affecting ecosystems through both drag-disturbance and mass-transfer processes in similar proportions. Flow variability, and associated effects on ecosystems, across these scales is discussed with reference to New Zealand rivers. We suggest that these concepts can be integrated across the full range of temporal scales based on a spectrum of velocity variations. This may provide a unifying conceptual model for how the structure and functioning of lotic ecosystems are linked to flow variability.

INTRODUCTION

While it is acknowledged that biotic interactions such as predation and competition have major influences on community organization at local scales in both time and space, it is the abiotic environment that has probably set the main stage for evolutionary development of specific traits and associated life-history strategies in ecosystems (Lytle and Poff, 2004). It is also the abiotic environment which probably then constrains a large proportion of the subsequent biotic interaction (Hart and Finelli, 1999). An organism must be able to survive, grow and reproduce under a given set of abiotic conditions, before the habitat defined by those conditions can be considered viable for that species. Over evolutionary time, a vast number of different species have gradually become adapted to exploit different permutations of abiotic constraints at different scales of time and space. Through this process of adaptation to specific habitats, species have also sought to increase survivorship by reducing competition for resources and space. In effect, the abiotic environment has ‘forced’ the development of different sets of traits that combine, at some scale, to define life-history strategies. Southwood (1988) terms this the ‘habitat templet’ and the variables that have forced the development, and now select for, particular species and traits the ‘selective forces’.

The abiotic selective forces acting on lotic ecosystems are extremely variable in both time and space (e.g. Palmer and Poff, 1997; Biggs et al., 2001). The need to decompose environmental heterogeneity and associated selective forces into different natural scales as an aid to describing patterns and increasing understanding of ecosystem processes has been widely promoted in the general ecological literature (e.g. Weins, 1989; Levin, 1992).
particular, hierarchical descriptions have been promoted as a method of understanding the characteristics of ecosystems by isolating processes at a single level and by-passing the details of lower organizational levels (e.g. Allen and Starr, 1982; O’Neill et al., 1987; Frissell et al., 1986). In hierarchical descriptions, the system components and processes are described in enough detail to understand the characteristic patterns that occur at particular temporal or spatial scales. The higher-level components and processes provide a more abstract description of the system, and characteristics operating at this organizational level are considered to constrain the organization of lower hierarchical levels.

There have been a number of studies demonstrating the potential value of such hierarchical approaches to description of both characteristics (i.e. structure and function) and causative processes in streams and rivers covering both wide (e.g. Frissell et al., 1986; Biggs et al., 1990; Poff and Ward, 1990; Naiman et al., 1992; Habersack, 2000), and relatively narrow (e.g. Downes et al., 1993), ranges in scale. Poff (1997) has integrated the above concepts into a heuristic framework for understanding and predicting the distribution and categorical abundance of species in river communities. He suggests that the habitat ‘selective forces’ of Southwood (1988) be viewed hierarchically as a set of nested ‘filters’ (ranging from regions down to micro-habitats) with large-scale filters viewed as causative or mechanistic agents that constrain the expression of local selective forces or biotic potential at lower scales. Indeed, many researchers have advocated viewing lotic ecosystem processes in a classic hierarchical framework in relation to flow variability whereby intense, infrequent events drive large-scale (usually long-duration) phenomena and also constrain low magnitude, more frequent events that drive fine-scale (usually short-duration) phenomena, with physical processes being the primary selective forces (Poff and Ward, 1990; Biggs, 1996; Poff, 1997; Snelder and Biggs, 2002). Thus, differences in flow variability (e.g. magnitude and timing of flood events) could explain differences in ecosystem structure and function among, and within, rivers. However, knowledge is still poor of the specific effects of timing and magnitude of flow events, and the implications of flow variability at different temporal scales are still not fully understood.

In this paper, we review flow variability in New Zealand rivers from large to small temporal scales. We contend that while the existence of lotic ecosystems is based on the presence of flowing water, community structure, population dynamics and the functional processes are strongly influenced by temporal variations in this flow. Our hypothesis is that ecosystems, described at different levels of organisation (i.e., system levels) are sensitive to flow variability at specific temporal scales. Also, there is a hierarchy of biotic effects whereby infrequent, but high magnitude flow variations influence lotic ecosystem structure and function at high system levels (i.e. communities) through drag processes (resulting in ‘drag-disturbance’) whereas more frequent, but lower magnitude events influence ecosystem structure and function more through mass-transfer processes (controlling growth of individuals). We use the term ‘drag-disturbance’ throughout to mean loss of biomass due to dislodgement by high water velocities and associated abrasion by bed sediments that are also mobilized through high velocity drag, and to distinguish such disturbance from that caused by other agents such as drying or pollution. We use the term ‘mass-transfer’ processes throughout to broadly include uptake of inorganic nutrients by autotrophs, food uptake by invertebrates through grazing and predation, and food uptake by fish through predation. Drag-disturbance and mass-transfer mark the opposite ends of a continuum of flow variability controlled processes in lotic systems with moderate temporal scale flow variability events affecting ecosystems through both drag-disturbance and mass-transfer processes in similar proportions (controlling performance of populations). We first describe some of the key elements of flow variability and ecosystem effects in New Zealand rivers as an example of how flow regimes and ecological structures vary together at different scales. Then we define a spectrum of temporal velocity variations across these scales, and suggest that such spectra could be used to help understand and model the ecological effects of flow variability over the full range of temporal scales in lotic ecosystems.

FLOW VARIABILITY AND ITS ECOLOGICAL EFFECTS IN LOTIC ECOSYSTEMS: THE NEW ZEALAND EXAMPLE

*Hydrological-scale flow fluctuations: years*

Variation in flow over years (i.e. inter-annual variability) in New Zealand rivers is controlled by inter-annual variations in climate. However, the local manifestation of these variations in climate and flow differ within
New Zealand depending on regional topography (e.g. east versus west of the axial mountain ranges) and latitude (Mullan, 1998). Recent climatological studies (Salinger and Mullan, 1999; Salinger et al., 2001) have also demonstrated regional shifts in annual rainfall across New Zealand at the scale of decades that are associated with the Interdecadal Pacific Oscillation (IPO) index. A very significant shift in the IPO occurred around 1977, whereby a wetter, westerly regime commenced which increased the magnitude of high rainfall events in the western and southern regions of New Zealand. Compared with the period 1947 to 1977, consistent decreases in rainfall of up to 8% occurred in the north and east of the North Island and increases in rainfall of up to 8% occurred in the west and south of the South Island for the period 1978–1999. The increased precipitation resulted in an increase of c. 13% in mean flows of rivers in the Southern Alps (McKerchar and Henderson, 2003). While important in terms of understanding and managing water resources and flood hazard issues, it is difficult to determine the effects of such large-scale changes in flows on lotic ecosystems except that they may increase the duration and magnitude of intra-annual high flow events, as discussed below. We note that these temporal scales in the order of many years exceed the life history of most instream biota in New Zealand rivers.

Shifts in the El Niño Southern Oscillation (ENSO) phenomenon are superimposed on IPO events and drive major year-to-year variation in precipitation and flows that are of considerable ecological relevance. El Niño episodes tend to produce greater precipitation and more frequent high flow events in the south and west of the country (McKerchar and Henderson, 2003). Rivers in the east of both main islands of New Zealand tend to experience periods of consistently low precipitation (with few high flow events) for more than a year (i.e. extreme low flows) in El Niño episodes. For example, the Waipara River is located in the southeastern climate region of New Zealand (east coast, South Island) and experienced particularly benign flood conditions during the period between 1998 and mid-1999 (Figure 1). Conversely La Niña episodes that generate more tropical, moist north-easterly derived weather tend to produce more rain in the northeast of the country and less in the south and western regions. The effect of altitude on precipitation may mean that within a climate region, inter-annual effects of the ENSO may be muted for rivers with mountainous watersheds.

Inter-annual variations in flow regime can have major implications for the character of river ecosystems at high system levels due to frequent flood disturbance in some years and extended periods of low flows in other years. Increased flows (particularly flood flows) will lower periphyton biomass and reduce invertebrate production as a result of direct dislodgement with excessive drag-disturbance caused by higher water velocities and indirectly through drag on the bed sediments causing bed movement and crushing/abrasion of individuals (Scrimgeour and Winterbourn, 1989; Biggs et al., 1999a, 2001). Indeed the basis of a shift between heterotrophy, and different types of autotrophy (algal and macrophyte dominance) can be driven by the long-term recurrence interval of bed-moving flood disturbances (Biggs, 1996; Young and Huryn, 1996; Riis and Biggs, 2003). For example, a large proportion of the Taieri River (southeastern South Island) was dominated by heterotrophy in a La Niña high-flow year, but switched to dominance by autotrophic communities in the following El Niño low-flow year (Young and Huryn, 1996). When flow, and associated drag-disturbance, is low for prolonged periods of time, some streams that are normally dominated by diatoms and cyanobacteria can become dominated by a high biomass of green filamentous periphyton or large vascular macrophytes. Scarsbrook et al. (2000) also found differences in macro-invertebrate communities between La Niña and El Niño years. Inter-annual variation in flow can also lead to major year-to-year variation in river nutrient concentrations (e.g. Biggs et al., 1998a) which could further influence the trophic base of some rivers.

Large changes in community composition and age structure can occur when component species with life histories that span these inter-annual time scales (e.g. trout) are strongly affected by large-scale flow variation. For example, Unwin (1997) hypothesized that inter-annual variation in flood frequency influences salmon runs in the Rakaia River as high flows increase the size of the fresh water/salt water mixing zone in the coastal region thereby enhancing acclimation time and consequent survival of the juvenile salmon migrating to sea. Direct flood effects also occur on fish populations. Hayes (1995) reported the loss of an entire year class of brown trout from the Kakanui River (east coast, South Island) when it was subjected to persistent high flows and floods in the spawning season during a La Niña year and McIntosh (2000) reported a strong negative correlation between total fish biomass (mainly galaxiids, eels and trout) and increasing flow variability/bed sediment instability in 24 hill stream reaches, Canterbury, South Island.

Similarly, sustained low flows during some years can also severely reduce fish densities and change community composition. Jowett (2001) found that prolonged low flows over spring, summer and autumn during an El Niño...
year eliminated >70% of native fish numbers in the downstream half of the Waipara River because of a loss of high quality habitat. This did not occur in the years before or after this event when precipitation and flows were more ‘normal’. Floods during the other years of the study appeared to have little effect on the native fish communities, probably because they have evolved to cope with regular flooding. While, in this case, recruitment from the sea replenished juvenile native fish populations in the following year, such effects might impact a river’s ecosystem for many years where the ecosystem contains many species which depend on local recruitment for their persistence (e.g. trout).

**Hydrological-scale flow fluctuations: months**

Within regions of broadly homogenous climate, topography has a strong effect on the amount and timing of local precipitation (Griffiths and McSaveney, 1983). Topography also influences storage mechanisms that modify the river’s response to rainfall inputs (e.g. steep topography increases the rate of change of flow due to rapid run-off). Thus, within the large areas of homogenous climate regions flow variability over months (i.e. intra-annual variability) is further explained by the dominant topography of a river’s catchment. Three primary ‘source of flow’ categories of river are recognized in New Zealand (mountain, hill and low elevation), together with several secondary sources (spring-fed, lake-fed etc.) (Snelder and Biggs, 2002). These source-of-flow categories discriminate intra-annual patterns in flow regimes, including flood and low flow magnitude and frequency (also a product of the

Figure 1. Example hydrographs from mountain, hill, and spring source-of-flow rivers. All rivers are in the Canterbury region, South Island of New Zealand. Note that while there are frequent flow perturbations in the spring-fed Avon River, these are of a relatively low magnitude compared with freshes and floods in the other two rivers and are partly the result of urban runoff from paved surfaces in the Avon catchment.
higher level ENSO events) and provide a context for discussing differences in ecological characteristics that arise from these different flow regimes.

Hydrographs illustrating typical intra-annual variability in flow regimes for three source-of-flow categories (mountain, hill and spring-fed rivers) for the period 1995–2000 are illustrated in Figure 1. Flow variability regimes for each of these three categories will be briefly reviewed in the following sections, together with the ecological implications, to illustrate the large differences in key biophysical characteristics of these river classes which are driven by different intra-annual patterns in flow variability and associated processes of drag-disturbance.

**Mountain rivers.** Mountain rivers in New Zealand have fairly frequent, and moderately intense, high flow events within any one year and these are often quite seasonal (e.g. Figure 1). The lowest flows generally occur in winter when precipitation is locked up as snow (and westerly winds are less frequent), and high flows and flood events dominate in spring and summer as a result of more frequent westerly weather and snow melt (Figure 2). The periods of winter low flows enable high primary production (regardless of low water temperatures) in shallow side channels (braids) where bed sediments are persistently stable (Biggs and Close, 1989). Frequent spring and summer high flows disturb benthic communities through a process of excessive drag-disturbance which usually results in these systems being dominated by ‘weedy taxa’ (e.g. diatoms and highly mobile invertebrates such as the mayfly *Deleatidium* spp.) and a low overall biomass of primary and secondary producers (e.g. Sagar, 1986; Biggs and Close, 1989). Macrophytes (mainly the native species of *Myriophyllum* and *Potamogeton*) are usually only occasionally found in peripheral braids that are protected from most floods and with armoured bed sediments (B.J.F. Biggs, unpublished observations).

Salmonid spawning occurs during the period of stable winter flows in mountain rivers, although salmon usually prefer the most stable spring-fed tributaries in the upper inter-montane basins of these catchments.

**Hill rivers.** High flows and floods in hill rivers in New Zealand tend to occur predominantly in winter and spring and low flows in summer and early autumn (Figures 1 and 2). This is opposite to the seasonal regime of mountain rivers (e.g. Waipara and Rangitata Rivers, Figures 1 and 2). The annual frequency of flood events for hill rivers is dependent on the climate region and ranges from an average of 27 events/year where floods exceed three times the median flow (southwestern climate region; Snelder and Biggs, 2002) to 11 events/year (southeastern climate region; Snelder and Biggs, 2002). These strong within-year variations in high flow events in hill
rivers cause dramatic short-term shifts in ecosystem structure and function (e.g. Biggs et al., 1998a; Townsend et al., 1997).

Intra-annual variability in flows is most closely linked with characteristics at a community level, through processes such as dispersal, sloughing/sediment crushing and stranding. Drag-disturbance associated with high flow perturbations and sediment movement during floods can severely disturb benthic communities re-setting them to a ‘pioneer’ successional stage (e.g. Scarsbrook and Townsend, 1993). Such re-set events may be an important process maintaining the diversity of invertebrate communities (Townsend et al., 1997), but the effects on periphyton diversity are more complex and strongly interlinked with resource supply (Biggs and Smith, 2002). If flood disturbances occur at an intermediate frequency in relation to the time required for community re-development, then diversity is expected to be highest in such streams (e.g. Death and Winterbourn, 1995) because communities are generally composed of a mixture of pioneer and climax taxa (the ‘intermediate disturbance’ hypothesis; Grime, 1979).

Recently, Riis and Biggs (2003) demonstrated a shift from periphyton- to macrophyte-dominated autotrophic production in rivers where the intra-annual flood frequency dropped to <5/year. No macrophytes are expected in streams which have >13 floods/year (many New Zealand streams have >50 bed-moving floods/year; Biggs et al., 1999a). This has major implications for variations in invertebrate communities and secondary production among hill rivers as macrophyte-dominated systems are expected to be structurally and functionally quite different from periphyton-dominated systems.

Intra-annual flow variability in hill streams is also an important process influencing the structure and function of fish communities (Matthews, 1986). During stable flow conditions fish populations in streams may be highly organized. For instance, in New Zealand, giant kokopu (Galaxias argenteus) have been shown to form size (weight-related) dominance hierarchies within stream pools with individual fish defending defined territories (David and Stoffels, 2003). Such organization and residency (of the same individuals) can persist for indeterminate periods providing there are no major changes in flow (David and Closs, 2003). High discharge events, however, can radically disrupt this stability by providing opportunities for fish restricted during base flow conditions to move to other stream locations (David and Closs, 2002). A high flow event does not necessarily mean fish will move, however. Giant kokopu have been shown to display a variety of behaviours during floods, with some individuals staying within their home reach (by making micro-movements less than 5 m to a refuge location), others moving and settling elsewhere and others moving but homing back as flows subside (David and Closs, 2002). This variable behaviour indicates that movements during floods are complex and may not necessarily be related to flood magnitude. Irrespective of individual fish behaviours, high flow events are particularly important in ‘re-setting’ stream organization and function and enabling fish habitats that may have been vacated during base flows (e.g. through death) to be re-occupied.

The relatively higher resistance of native fish to prolonged and/or intense high-flow events compared with trout appears to be an important factor driving fish community structure in many New Zealand rivers. McIntosh (2000) reported that highly disturbed hill rivers in the Canterbury high country (South Island) had few large trout, but contained native galaxiid populations, whereas more stable rivers were dominated by trout to the exclusion of galaxiids. Co-existence predominantly occurred where there was a moderate degree of instability and trout densities were low.

Spring streams. Spring-fed regimes display weak intra-annual variations and seasonality in flow (e.g. Figure 2; Avon River). While the frequency of high flows is usually most significantly influenced by climate, the resultant effect on flow variation in spring-fed streams is often muted compared with mountain and hill rivers because of a much flatter catchment topography and greater storage in the underlying valley bottom or plains gravels. Thus, following from the above discussion on hill rivers, a defining ecological characteristic of spring-fed rivers (and many rivers with low elevation catchments) is that they are biologically and physically often dominated by large beds of aquatic macrophytes because high magnitude flood disturbance events are very rare. This, in turn, has implications for invertebrate habitat and fish. Such vegetation creates a much more extensive, three-dimensional habitat for some animals, but effectively removes available habitat for a large number of other periphyton and invertebrates that require clean stones for living space (e.g. mayflies, stoneflies and many caddisflies; Biggs, 2000; Death, 2000). Thus, this category of river is usually quite distinct from hill or mountain rivers in flow variability regime and associated ecosystem structure.
Hydrological-scale flow fluctuations: days

Most rivers also experience significant variability in flow at time scales of months down to days, but the magnitude of this variation (i.e. magnitude of events) is considerably less than occurs at the larger time scales (e.g. the occurrence of ‘freshes’ rather than ‘floods’). A section of the hydrograph from the Waipara River in North Canterbury from mid-December 1997 to the end of January 1998 is expanded in scale in Figure 3 to illustrate this. What appears as a period of stable flow at annual time scales (Figure 3A) actually varied over a six-fold range at the scale of days (Figure 3B). While these variations are small relative to the variability seen at inter-annual and intra-annual time scales, they are still likely to be important to some stream ecosystem characteristics through drag-disturbance related processes, as discussed for the larger temporal scales, but with much less magnitude (Figure 4). Theoretical considerations and empirical studies suggest that drag-disturbance, and thus population level responses, will vary greatly depending on the traits of different organisms such as shape and size of body structure, and orientation to the flow. These ultimately interact with the tensile and attachment strength of the organism to determine susceptibility to removal and resultant spatial patchiness. Thus, drag-disturbance effects at this scale tend to be much more complex and ‘sub-catastrophic’ compared with the simple ‘catastrophic’ effects of large-scale events. Events at the scale of days are most likely to be affected by anthropogenic activities such as landuse change, abstraction and flow

Figure 3. (A) Typical annual hydrograph of mean daily flows for the hill-fed Waipara River, North Canterbury, and (B) a six-week subsection of the hydrograph of instantaneous flows in early summer
regulation by damming. As a result, flow–biota interactions at this scale (and smaller) are now of considerable ecological and management interest in New Zealand.

One of the first empirical studies in New Zealand rivers to address the effects of moderate to high frequency fresh events (that have moderate to low magnitude) was that of Biggs and Close (1989) on periphyton in the gravel-bed rivers of Canterbury, South Island. Here it was demonstrated that flow variations in the order of 2.5 to 6 times the average daily flow of the preceding week could result in quite variable effects on periphyton biomass, from up to a 90% increase to a 100% decrease. These results were verified, and explored further, in laboratory experiments by Biggs and Thomsen (1995) where it was shown that the taxonomic composition of the mat (and associated physical structure/drag) strongly influenced the extent of removal of biomass by moderate to low magnitude events. As could be expected, the most disturbance-resistant communities were dominated by low profile, prostrate or adnate diatoms with large celled filamentous green algae being least resistant. Biggs et al. (1999b) also demonstrated that the physiological status of diatom mats, as controlled by different light and nutrient levels, also influenced susceptibility to freshes. The most resistant mats were those that were nutrient replete, but light stressed. The least disturbance-resistant mats were light and nutrient stressed.

Of particular significance has been the finding that these moderate to high frequency (moderate to low magnitude) flow events could influence the relative balance between autotrophic and non-autotrophic organic matter in the periphyton mat whereby such flow events can cause a relative increase in the autotrophic component of the mats through a loss of the non-autotrophic component (presumably weakly attached heterotrophs and organic detritus) (Biggs and Close, 1989). Our laboratory has recently commenced experiments to investigate the implications of such effects on higher trophic levels (particularly macroinvertebrates). In the initial experiments, we have found that moderate magnitude drag-disturbance events can result in large increases in macroinvertebrate diversity and almost double mayfly growth rates compared with intense, catastrophic disturbances or no drag disturbance (B. J. F. Biggs, unpublished data). These preliminary results have important implications for how we view the significance of moderate to high frequency flow events.

In contrast to periphyton, macrophytes appear to be much less sensitive to drag-disturbance from high flow events at the temporal scale of months to days. As noted above, infrequent, but intense events appear to be a primary selective force controlling macrophyte establishment and biomass. But in outdoor flume experiments, Riis

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**Figure 4.** Physical and physiological processes in plant communities on the bed of rivers affected by micro-scale and meso-scale velocity variability (i.e. multi-scale eddy impacts). $U$ is the time-averaged downstream velocity, $U'$ is the deviation from the mean of the downstream velocity, and $W'$ is the deviation from the mean of the vertical velocity.
and Biggs (2003) recently demonstrated that <1% of biomass was removed from macrophyte beds covering a wide range of species and morphologies by moderate magnitude flood events (velocities up to 1.5 m/s with no bed sediment movement). These results reinforce earlier discussion on hill rivers that higher magnitude, longer return interval, flow events that cause significant bed sediment movement appear to be required to disturb lotic macrophyte communities significantly.

While low frequency, high magnitude flood events are very destructive to benthic macroinvertebrates (as discussed earlier), what effects do the moderate to high frequency, lower magnitude events have on macroinvertebrates? In a series of flume experiments, Holomuzki and Biggs (2000) demonstrated that several common New Zealand invertebrate species could ‘feel’ the increasing skin friction as velocities increased with higher flows which caused them to rapidly migrate into the hyporheos (the common mudsnail *Potamopyrgus* and the mayfly *Deleatidium*) or, in the case of the common caddisfly larvae *Pycnocentrodes*, to attach themselves to bed sediments using silk-like ‘draglines’. The dragline was then unreeled until the caddisfly larvae located a more sheltered patch on the streambed. Such behavioural responses help explain why many New Zealand streams and rivers incurring moderate to frequent sub-catastrophic freshes can retain high densities of macroinvertebrates (e.g. Quinn and Hickey, 1990).

Recent experiments also indicate that the intensity of fish effects on invertebrates can be influenced by sub-catastrophic, drag-disturbances with implications for longer-term benthic community structure. In experimental channels, Nyström and McIntosh (2003) found that trout had a significantly higher effect on invertebrates following sub-catastrophic disturbance compared to undisturbed channels, and this resulted in a progressive decline in invertebrate densities (and commensurate increase in periphyton biomass) during the post-disturbance resilience phase. The mechanism for this was by direct consumption of invertebrates and increased emigration (to avoid predation) by the ‘weedy’ colonists arriving in the disturbed channels. These invertebrate colonists (e.g. mayflies) are also more vulnerable to predation by virtue of their drifting and stone-surface grazing habits. Conversely, the channels without trout or with native galaxiids were rapidly recolonized by invertebrates, and periphyton biomass was low, with overall densities of invertebrates returning to pre-disturbance levels within 2 weeks.

Physiological processes are progressively becoming more important features of lotic ecosystem functioning with flow events having return intervals at the scale of days. These physiological processes predominantly relate to mass-transfer (e.g. nutrient delivery to autotrophs), but also include individual species performance and competition (Figure 4). These will be discussed in more detail in the following section.

**Hydraulic-scale flow fluctuations: minutes to milliseconds**

If sections of the time–flow plot, such as that shown in Figure 3, are further differentiated, high frequency variations in velocity (the more ecologically relevant aspect of flow at this scale) can be demonstrated, such as up to a two-fold variation in the downstream velocity component at intervals of seconds (Figure 5A). These variations in velocity are commonly known as ‘turbulence’. Most cobble streambeds also generate complex velocity fields with high temporal (and spatial) variability in the lateral and vertical plains with length scales from channel depth to the size of the bed sediment particles (Figures 5B, C). Thus, at this scale, geomorphology of the channel is a factor that strongly controls velocity variability and flows in the immediate vicinity of benthic organisms and these flows will often be highly turbulent due to vortices created by upstream roughness elements. While it is still difficult to determine exactly what degree of turbulence different organisms can sense at this scale, and what velocity statistic of the turbulent eddies they are responding to (e.g. minimum, mean or maximum), we anticipate that the variations would have to be at least commensurate with the length scale of the individual organisms (i.e. 0.01–10 times the body length) to be ‘felt’. We also anticipate that turbulent eddies at this scale would tend to mix resources (e.g. nutrients) in the water column, be of vital importance to skin friction, and greatly erode the thickness of the viscous sublayer of the boundary layer surrounding autotrophs and therefore influence rates of molecular diffusion across external membranes (Nikora et al., 2002; S. Larned, unpublished data) (Figure 4). These flow fields may be a primary determinant of the patchy distributions of benthic organisms (e.g. Hart et al., 1996).

Until recently, there has been little empirical data on the biological importance of flow variations in streams at the scale of minutes to milliseconds. In part, this is because of past difficulties in measurement methodology (Hart and Finelli, 1999). However, some progress is now being made following the introduction of new
technologies (e.g. acoustic Doppler anemometers). Much of the evidence supporting the above concepts has been generated from experiments where the near-bed flows have been quantified in terms of fixed, time-averaged velocities over a given experimental range (a ‘time for space’ replacement analysis) and this might be satisfactory for many studies as mean velocity and turbulence intensity are usually significantly correlated at these scales.

Borchardt (1996) and Larned et al. (2004) have demonstrated increases in inorganic nutrient uptake and growth rates of nutrient-limited periphyton over wide ranges in near-bed velocities, such as occur when parts of the streambed are swept with turbulent eddies. The biomass and growth form of periphyton patches is also influenced by the magnitude of velocity variations at such scales whereby the biomass of dense, mucilaginous diatom mats increase with increasing near-bed velocities while the biomass of loosely aggregated filamentous green algal mats declines over such gradients (Biggs and Hickey, 1994; Biggs et al., 1998b). These effects are a result of a balance between mass-transfer enhancement of growth at progressively higher microscale velocities, and detachment of biomass with the onset of higher drag at higher velocities and as biomass increases.

The above concepts are also relevant to understanding the biomechanics and hydraulic habitat requirements of fish in turbulent flows. As an example, our research into fish swimming performance of the New Zealand native fish Galaxias maculatus (Nikora et al., 2003a, b) has shown that the degree of fish–turbulence interaction may depend on both the turbulence energy and size of fish. Indeed, within the same turbulent flow, fish of different sizes will experience different effects (e.g. skin friction) from turbulent eddies. A fish of a given length will probably not sense or respond to turbulent eddies much smaller than (or comparable with) its length, but will respond to eddies appreciably larger than it. Our data and theoretical considerations suggest that the turbulence impact on fish should increase with a decrease in the ratio of fish length to length of turbulent eddies which are, in general, comparable with the flow sizes (i.e. depth and width). If our model is correct, then a proper understanding of turbulence effects on fish behaviour should involve, in addition to turbulence energetics, recognition of fish dimensions in relation to the spectrum of turbulence scales. Overall, the effects of turbulence on stream fish swimming performance are not yet clear and require further study covering a wider range of fish sizes and turbulence scales.

Some benthic autotrophs also change their growth form in response to velocity variability at scales of minutes to milliseconds (i.e. there is dynamic feedback). This is most clearly observed in the spatial domain. For example, the growth form of some macrophyte leaves and some filamentous green algae appears different in high velocity areas (e.g. Bergey et al., 1995; Sand-Jensen and Mebus, 1996). Biggs et al. (1998b) demonstrated that the taxonomic composition and growth form of periphyton communities during stable periods between flood disturbances was also a product of fine-scale velocity effects. This work demonstrated that the conflicting effects of drag-disturbance...
and resource acquisition through mass-transfer at these scales can be exploited by different taxa for niche separation. In turn, this can lead to considerable patchiness in streambed periphyton communities. It has also been suggested that flow-dependent phenotypic plasticity occurs in the morphology of feeding appendages of some invertebrates to maximize the balance between drag-disturbance and resource capture at these fine scales (Hart et al., 1991). Thus, temporal (and associated spatial) variability in velocities would be expected to control the spatial distribution of such taxa.

There is also a considerable feedback effect of biotic structures on flow patterns and variations at the scale of minutes to milliseconds. Filaments of periphyton and stems of mosses can cause major changes to near-bed flow conditions, particularly turbulence. Growth of mosses on stones can cause a reduction in average stream-wise velocity, Reynolds stress, and total turbulent energy, whereas relative velocity variations can be much higher in the presence of moss (Nikora et al., 1997, 2002; Nikora and Goring, 1998). An internal boundary layer around the moss has also been observed which was then destroyed behind the moss clumps as a result of turbulent mixing in the roughness sublayer. These results provide some explanation for why mosses (and periphyton) can provide such good refugial habitat for invertebrates (and enable a high diversity of invertebrates to be maintained) in harsh environments such as steep, highly turbulent rivers prone to large-scale flood disturbance events (e.g. Suren, 1991). However, whether this is achieved through reductions in turbulence intensity or mean velocity within the mats has yet to be determined.

**CONCEPTUAL SYNTHESIS BASED ON A SPECTRA OF FLOW VELOCITY VARIABILITY**

It is clear from the above discussion that flow variability occurs over a wide range of temporal scales in rivers and these variations are strongly linked to different aspects of the structure and function of lotic ecosystems. Most lotic research in the past has not explicitly recognized that flow variation at these different temporal scales affects different ecosystem components and processes. Furthermore, it has not been explicitly recognized that there may be a hierarchical relationship between time scales of flow variability and related physical processes, the effect of these physical processes on biological processes and, ultimately, the organization of ecosystem characteristics (Table I).

We propose for our model that linked physical and biological processes are the dominant influence on these ecosystem characteristics and that these processes are largely controlled by flow variations that occur at specific time scales. The effect of flow variability on stream ecosystem character changes in a continuous fashion from high flow events at large temporal scales (i.e., ‘hydrological scales’) that structure community composition and function by catastrophic disturbance, to more frequent and less intense flow changes that influence mass-transfer dominated processes that affect the growth rates of individual plants and animals at small scales (i.e., ‘hydraulic scales’). In other words, drag-disturbance related processes decline in relative importance with decreasing time scales, but mass-transfer related processes steadily increase until they become dominant at very high frequencies of low magnitude events during periods of stable flow. This concept is depicted simply on a hydrograph in Figure 6 in relation to the temporal sequence of high and low flow events.

Table I. Summary of the hierarchy of organization and associated physical processes, biological processes, ecological characteristics, and time scales of flow variability in lotic ecosystems. Linked physical and biological processes are the dominant influence on the ecological characteristics and these processes are largely controlled by flow variations that occur at the specified time scales

<table>
<thead>
<tr>
<th>Organizational level</th>
<th>Physical processes</th>
<th>Biological processes</th>
<th>Ecological characteristics</th>
<th>Time scale</th>
</tr>
</thead>
<tbody>
<tr>
<td>High</td>
<td>Catastrophic disturbance</td>
<td>Re-set/biomass loss</td>
<td>'Community': composition, trophic state</td>
<td>Years–months</td>
</tr>
<tr>
<td>Medium</td>
<td>Sub-catastrophic disturbance &amp; mass-transfer</td>
<td>Colonization, biotic interactions, reproduction</td>
<td>'Population': densities, physiological condition</td>
<td>Days</td>
</tr>
<tr>
<td>Low</td>
<td>Mass-transfer</td>
<td>Oxygen/nutrient/food uptake, photosynthesis, respiration</td>
<td>'Individual': biomass accrual, growth form</td>
<td>Minutes–milli-seconds</td>
</tr>
</tbody>
</table>
We believe that it would be useful to integrate this understanding even further by developing a conceptual model that explicitly links the naturally defined scales of flow variability with the aforementioned processes and characteristics. One approach to this is to develop a spectrum of velocity variability covering the full range of time scales that are ecologically relevant (Figure 7). Although we have not developed the ideas here we also believe that there are space scales that are relevant to our hierarchical model. This spectrum is a combination of flow variability/turbulence data from many studies of rivers with different morphologies and bed roughness (e.g. Nikora, 1991,
1999; Nikora and Goring, 1998). Although morphologies and bed roughness may change locally, and these may influence the ordinates of the spectrum, the overall shape will remain among rivers.

This spectrum measures the relative amount of kinetic energy that biota are subjected to as a product of the different intensities of high flow events at the different scales and thus how energy is much higher with events at large scales than at smaller scales (e.g. Nikora, 1991, 1999; Nikora and Goring, 1998). The spectrum provides a context for linking the magnitude of the flow/velocity variability with different physical and biological processes in lotic ecosystems. The ranges of these scales are separated by discontinuities in the slope of the frequency spectrum of velocity variability. As noted earlier, the large scale variability in flow/velocity over time periods of years are often associated with phenomena such as the El Niño Southern Oscillation index, whereas the intra-annual flow/velocity variability are a result of seasonal variations in flow regimes and short-term periods of intense precipitation or drought that occur reasonably infrequently. These spectral ranges display peaks associated with medium term phenomena (every 2–7 years for the inter-annual sector and 2–7 months for the intra-annual sector). Little is known of the shape of the spectrum in the transition from periods of months to periods of days. In the smaller scale, hydraulic, region of the spectrum the magnitude of velocity variability is also influenced by the heterogeneity of channel bed form and bed sediment heterogeneity. Velocity variations over periods of minutes down to seconds are constrained in size by the width and depth of the channel. At these scales there is insignificant change in the amplitude of velocity variations with decreasing time intervals. These larger eddies contain smaller eddies (microscale) that have higher frequency velocity variations (seconds down to a second) and sizes between the depth of the water and height of the roughness elements on the bed. Over this temporal range there are three distinct sub-scales where the amplitude of velocity variability decreases at different rates with decreasing period. In the inertial sub-range, the variations reduce sharply with time (following Komolgrov’s $-5/3$ law; Grinvald and Nikora, 1988). At the range of dissipative eddies, which occur with periods in the millisecond range, there is a very sharp decline in magnitude of the velocity variability as the movement of water is strongly controlled by viscosity.

**PROSPECTS**

We believe that the ecological effects of hydrological variability at different temporal scales in rivers are nested hierarchically according to classic hierarchy principles. Thus, the effects of flow variation on community composition at large temporal scales constrain the influence of smaller scale flow variation at lower levels of ecosystem organization. We also think it is likely that some aspects of these temporal scales can be linked directly through to concordant spatial scales. Further, we hypothesize that this hierarchy in flow variability is probably the underlying reason for (or at least contributes strongly to) many temporal and spatial patterns of biological characteristics at different scales in lotic ecosystems. To date there has been only poor appreciation of these linked hierarchies in both lotic research and environmental flow allocation.

Infrequent, high energy flow events are generally catastrophic to lotic ecosystem structure and function for periods of time that vary depending on the resistance and resilience of the different populations. These ‘re-set’ events comprise predominantly drag-disturbance processes and help determine the high-level character of the ecosystem including the broad composition and functioning. This high-level character sets the context for mass-transfer processes which dominate between the high magnitude events. For a portion of the year, most lotic ecosystems are subject to a balance between both drag-disturbance and mass-transfer related processes. Of particular importance are the moderate to high frequency (i.e. moderate to low magnitude/energy) events. It appears that these might strongly influence processes that act at the population level of ecosystem organization and, therefore, be fundamental to maintaining healthy and diverse lotic ecosystems. At sequentially smaller temporal scales, mass-transfer processes become progressively more important and control growth and performance of individual plants and animals.

The value of the above conceptual model is to allow explicit recognition of how flow variability varies greatly in magnitude (and thus kinetic energy) at different temporal scales and how these scales can be explicitly linked to lotic ecosystem structure and function at multiple scales. At present the model is proposed as a descriptive tool to better understand and explain the magnitude and ecological effects of different levels of energy associated with different scale hydrological/hydraulic events. However, eventually it may be possible to parametrize such a model to
explicitly link the physical and biological processes thereby providing a unifying approach to predicting the effects of flow variability, and anthropogenic changes in this variability, in lotic ecosystems. A first step might be to calibrate/validate for specific reaches in some rivers the transition from drag-disturbance to mass-transfer control of ecosystem processes in relation to the magnitude of variation in flows (i.e. calibrate/validate Figure 6). In the meantime, considerably more research will be required that directly measures the magnitude of flow fluctuations, together with the associated biotic response variables, at different scales.

ACKNOWLEDGEMENTS

This paper was prepared under funding provided by the New Zealand Foundation for Research, Science and Technology (‘Water Allocation: effects on instream values’ programme, Contract C01X0308). We are grateful for the use of hydrological data provided by Environment Canterbury, the assistance of Kathy Walter and Mark Weatherhead in the preparation of the hydrographs, material provided by Bruno David, and stimulating discussions with Ian Jowett and Dave Hart that have influenced the ideas that went into this paper. Thanks to two anonymous reviewers who provided very useful comments that helped clarify the depiction of our concepts.

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