Tributaries, sediment sources, and the longitudinal organisation of macroinvertebrate fauna along river systems

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Abstract: Tributary confluences are sites along a main channel where, because of the introduction of water and (or) sediment, the water volume, bed sediment character, and water quality of the mainstream can change abruptly. These shifts ensure that abiotic gradients seldom vary smoothly or continuously for distances of more than 10^0–10^2 km along any river system. The ways in which tributaries and related sediment recruitment points structure longitudinal changes in physical habitat are examined. Variables of importance to stream biota are affected and, in turn, it is suggested that the arrangement of tributaries and related features is an important control on the longitudinal organisation of macroinvertebrate benthos at moderate spatial scales. A new model is presented that stresses the importance of hydrological and sedimentological networks for organising lotic fauna. The link discontinuity concept emphasises the discontinuous nature of lotic ecosystem gradients, addresses the importance of tributaries in unregulated as well as regulated rivers, and extends, to its logical conclusion, the limited recognition of tributary influence in the river continuum concept. A case study from British Columbia, Canada, illustrates the general merit of the new model.

Résumé : Les points de confluence des tributaires avec le cours d'eau principal sont des endroits où, à cause de l'introduction d'eau et/ou de sédiments, le volume d'eau, les caractéristiques des sédiments du fond et la qualité de l'eau changent abruptement. Ces modifications ont comme conséquence que les gradients abiotiques varient rarement de façon graduelle et continue sur des distances de plus de 10^0–10^2 km dans un système hydrographique. On trouvera ici un examen des manières par lesquelles les tributaires, et les points d'apport de sédiments qui en résultent, structurent les changements longitudinaux dans l'habitat physique. Les variables qui sont importantes pour les organismes du cours d'eau sont affectées; nous proposons, en conséquence, que l'arrangement des tributaires, et des caractéristiques qui en dépendent, exercent un important contrôle de la structuration longitudinale des communautés d'invertébrés benthiques à des échelles spatiales intermédiaires. Nous présentons un nouveau modèle qui met l'emphase sur le rôle des réseaux hydrologiques et sédimentologiques dans l'organisation de la faune d'eau courante. Le «concept de discontinuité des maillons» (Link Discontinuity Concept) souligne la nature discontinue des gradients dans l'écosystème lotique; il met en valeur l'importance des tributaires dans les cours d'eau à débit régularisé ou non; il tire les conclusions logiques qu'impose l'influence des tributaires, une influence que reconnaissait déjà, mais de façon restreinte, le «concept du continuum fluvial» (River Continuum Concept). Une étude de cas menée en Colombie-Britannique, Canada, met en relief les qualités du nouveau modèle.

[Traduit par la Rédaction]

Introduction

River systems are characterised by longitudinal changes in various aspects of physical habitat, for example, discharge, channel width, and bed sediment size. Macroinvertebrate fauna and other biota respond to these changes so that downstream trends in ecological processes and community structure are, at least in part, a function of longitudinal changes in key abiotic factors (Botosaneanu 1979; Naiman et al.

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1987; Statzner and Borchardt 1994). Patterns of change are scale dependent. At the largest, drainage basin scales (say 10^2–10^4 km), simple, systematic gradients characterise the variability of physical attributes (Fig. 1a), and models like the river continuum concept (RCC) (Vannote et al. 1980) have been used to relate such patterns to simple biotic gradients. At the finest spatial scales (say 10^{-2}–10^0 km), physical habitat parameters vary in an essentially stochastic manner or are structured by specific bedforms, like the riffle–pool sequence (Fig. 1c), again with implications for the spatial organisation of macrobenthos (e.g., Brussock and Brown 1991).
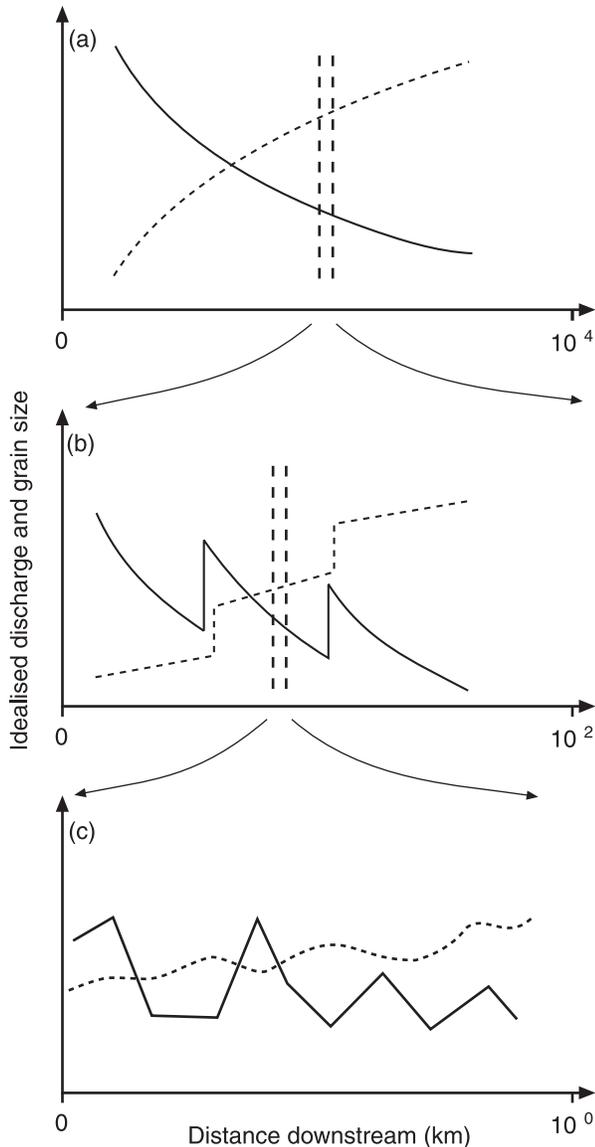
This paper considers changes in physical habitat at intermediate scales (10^0–10^2 km), where noise at larger scales is resolved as a pattern of perturbed downstream change (Fig. 1b). At this scale, longitudinal trends in geomorphological and hydrological attributes are prone to abrupt shifts wherever water and sediment fluxes are modified, for example, by recruitment of water and (or) sediment at tributary confluences or by anthropogenic regulation at dams. The influence of dams has received abundant attention (e.g., Petts 1979, 1984), of-

Fig. 1. Idealised downstream changes in discharge (dashed line) and bed material particle size (solid line) in relation to the scale at which observations are made. Patterns of longitudinal variation change as the observation length scale is reduced from (*a*) the entire drainage basin (0–10^4 km) to (*b*) several consecutive channel network links (0–10^2 km) to (*c*) the pools and riffles within an individual link (0–10^0 km).

wherein the importance of postimpoundment tributary influence is highlighted (Petts and Greenwood 1985; Storey et al. 1991; Stevens et al. 1997; Greenwood et al. 1999). Confluences are recognised as potential sites of continuum disturbance (Vannote et al. 1980), and Minshall et al. (1983, 1985) suggested that tributaries can "reset" longitudinal trends, "sliding" the main channel forward or backward along the nominal downstream gradient. Perry and Schaeffer (1987) regarded tributaries as key elements of their river "discontinuum," and Bravard and Gilvear (1996) argued that tributaries disrupt functional continua to produce a "stepped" ecosystem that reflects drainage network structure.

There is direct evidence of this in Illies' (1953) examination of benthic fauna along the Fulda River, Germany, where community discontinuities (corresponding to shifts between rhithral and potamal zones and their subdivisions) tend to occur at tributary confluences. Observations of this kind support the view that longitudinal patterns of ecological form and process are zonal rather than clinal (cf. Ward 1992). Osborne and Wiley (1992) showed that tributary position within the catchment network is a key control on the diversity of fish communities, such that low-order tributaries connected to high-order, mainstream links have significantly higher diversity than low-order links connected to other low-order links. This suggests that the spatial arrangement of the drainage network is a key control on community organisation in river systems and that conceptual frameworks constrained by linear, upstream–downstream pathways are inherently limited (Osborne and Wiley 1992).

However, empirical assessments of the importance of tributary effects along unregulated rivers are scarce. Bruns et al. (1984) examined macroinvertebrate communities and organic matter parameters around six confluences on the Salmon River, Idaho. They found that tributaries modified some downstream gradients, particularly the composition of functional feeding groups and of transported organic matter. In the context of the RCC, Bruns et al. (1984) suggested that relatively large tributaries tend to set back community development such that functional composition is more like that found upstream, while relatively small tributaries have the opposite effect, accelerating longitudinal community trends. These results are presented without reference to specific causes, although changing substrate texture and canopy separation (leading to increased light penetration) are presented as potential tributary effects.

In fact, the impacts of tributaries on mainstream habitat are potentially numerous and certainly complex, not least because effects will vary between tributaries and in time as a function of the volume and character of the water and sediment that is delivered. The possible, principal effects are abrupt changes in water volume, bed sediment character, and water quality. These, in turn, have implications for a number of important habitat characteristics, in part via the adjustment of channel form (slope, width, depth), bed sediment character (size, sorting, shape), and channel hydraulics (near-bed velocity and shear stress fields) to the imposed changes in water and sediment load (Table 1).

In this paper, we discuss the impacts that tributaries can have on key aspects of physical habitat and contemplate the implications for the downstream organisation of macroinvertebrate fauna. The role that tributaries play along unregulated rivers is

ten within the context of Ward and Stanford's (1983, 1995) exposition of the serial discontinuity concept (SDC), which emphasises the interruption of resource continua by major impoundments. In contrast, and despite their ubiquity, the role of tributaries has received relatively less attention, especially along unregulated rivers.

The hydraulic, morphological, and sedimentological characteristics of tributary confluences have been widely studied (Best 1987; Roy and Bergeron 1990), and their impacts on longitudinal river morphology and sedimentology are generally acknowledged. Tributary impacts on macroinvertebrate fauna have been examined in the context of channel recovery below impoundments and as part of direct tests of the SDC,

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Table 1. Possible tributary and dry LSS impacts on lotic macroinvertebrate habitat. Impacts, adjustments, and consequences that are anticipated at nontributary (dry) lateral sediment sources (LSSs) (as well as tributaries) are italicised.

Primary impacts on	Hydrogeomorphological adjustments of	Habitat consequences for
		Wetted area (total available resources, space resources)
	Channel dimensions	Illumination and heating (primary productivity, phototaxis, life cycle controls)
Water volume	*Channel slope*	*Substrate stability* (attachment of sessile feeders, crushing and abrasion)
Sediment characteristics	*Bed material size and sorting*	*Bed microtopography* (patchiness of hydraulic microhabitats, trapping of organic material)
Water quality	*Channel planform*	*Near-bed hydraulics* (refugia, entrainment of fauna, corrasion, gas exchange)
	Boundary hydraulics	Food supply and nutrient sources (seston flux, drift, grazing opportunities)
		Water chemistry (pH, toxins, O_2, hardness)

considered rather than the specific role that tributaries play downstream of major impoundments. Furthermore, dry sources of sediment called lateral sediment sources (LSSs) (e.g., points of significant bank erosion and landslides) are included because, like tributaries, they can be associated with a step change in sediment characteristcs.

We begin with a general discussion of the ways in which tributaries affect environmental gradients and speculate about the implications for macroinvertebrate fauna. A model is proposed in which longitudinal structure is related to the framework of hydrosedimentary links and nodes that are defined by tributaries and LSSs. Our hope is that this model will facilitate wider consideration of the network-related physical habitat structures that influence biotic organization at moderate scales in lotic ecosystems (cf. Osborne and Wiley 1992; Johnson et al. 1995). To assess the general merit of our model, macroinvertebrate communities are examined along two tributary-affected, gravel-bed rivers in British Columbia, Canada.

Tributary impacts on longitudinal abiotic gradients

As a starting point, we consider the impacts that tributaries can have on the downstream gradients of the physical habitat attributes listed in the first two columns of Table 1. Discussion is limited to coarse-grained alluvial channels in mountain or piedmont settings. Local-scale variability is not considered by focussing on riffle habitats throughout. Where possible, arguments are illustrated using data from the same rivers that are subsequently used to empirically examine macroinvertebrate responses.

It is unlikely that each of these factors is affected at all confluences, or even that any one factor is affected at every confluence. Impacts will vary between confluences as a consequence of the character and volume of the water and sediment that different tributaries introduce. This, in turn, is largely a function of tributary size relative to the mainstream and the biophysical characteristics (land use, vegetation, lithology, hydroclimate, geomorphology) of the subbasins that they drain. For example, not all tributaries disrupt longitudinal patterns of bed sediment maturation, and the characteristics of those tributaries that do have an effect are difficult to

specify (Rice 1998). It is therefore likely that abiotic impacts and biotic responses are complex, such that individual or composite habitat changes occur at different confluences and at individual confluences at different times.

Water volume and channel dimensions

Downstream changes in discharge and channel dimensions occur in response to the recruitment of water along a drainage line. Although transmission losses and throughflow inputs can be relevant in certain environments, net seepage along the hydrological links between tributaries is usually negligible in comparison with the volumes of water supplied by tributaries. Channel capacity therefore varies relatively little within links (typically varying stochastically about some link average value) but undergoes a step increment from one link to the next (Richards 1980). Field data to illustrate this pattern are limited because measurements are usually derived from gauging stations that are spaced many channel links apart or on different drainage lines. However, discharge Q is typically scaled by basin area A so that with a suitable regional relation, incremental increases in contributing basin area, derived from topographic maps, can be used to estimate discharge values. This method is used in Fig. 2a to estimate longitudinal changes in the 2-year flood discharge along Sukunka River in northeastern British Columbia. In turn, changes in width (Fig. 2a) can be estimated using regional hydraulic geometry relations. These estimates only approximate the actual changes along Sukunka River, but they are useful because they illustrate the "stepped" (Bravard and Gilvear 1996) pattern of change that exists along all river systems.

Several methods have been proposed for predicting changes in channel dimensions at confluences. Richards' (1980) approach recognises the typically strong relation between channel dimensions and link magnitude (N). The change at a given junction in, for example, channel width (w) is then given by

(1) $w_D = w_U (N_D/N_U)^k$

where D and U denote the downstream and upstream channels, respectively, and k is an empirical constant. Richards (1980) found $k = 0.65$ for the River Fowey in Cornwall, such that the percentage increases in mainstream width where a

Fig. 2. Habitat discontinuum on the Sukunka River. (*a*) Impact of the hydrological network on discharge (solid line) and channel width (dashed line). Estimated 2-year flood discharge is based on a regional basin–area relation ($Q_2 = 0.155A^{0.96}$, $R^2 = 0.96$, $n = 21$) where increments in contributing area at confluences were determined from 1 : 50 000 mapping. Estimated changes in channel width are based on a regional downstream hydraulic geometry relation ($w = 7.59Q_2^{0.39}$, $R^2 = 0.98$, $n = 8$) based on local gauge records. (*b*) Punctuated downstream fining. Note the fining trends separated by abrupt discontinuities where significant LSSs (dashed lines) adjoin the mainstream. (*c*) Punctuated downstream sorting. Inclusive graphic sorting index for surface bed materials. (*d*) Punctuated local channel gradient determined by field survey. Smoothing has been performed using a five-point running mean.
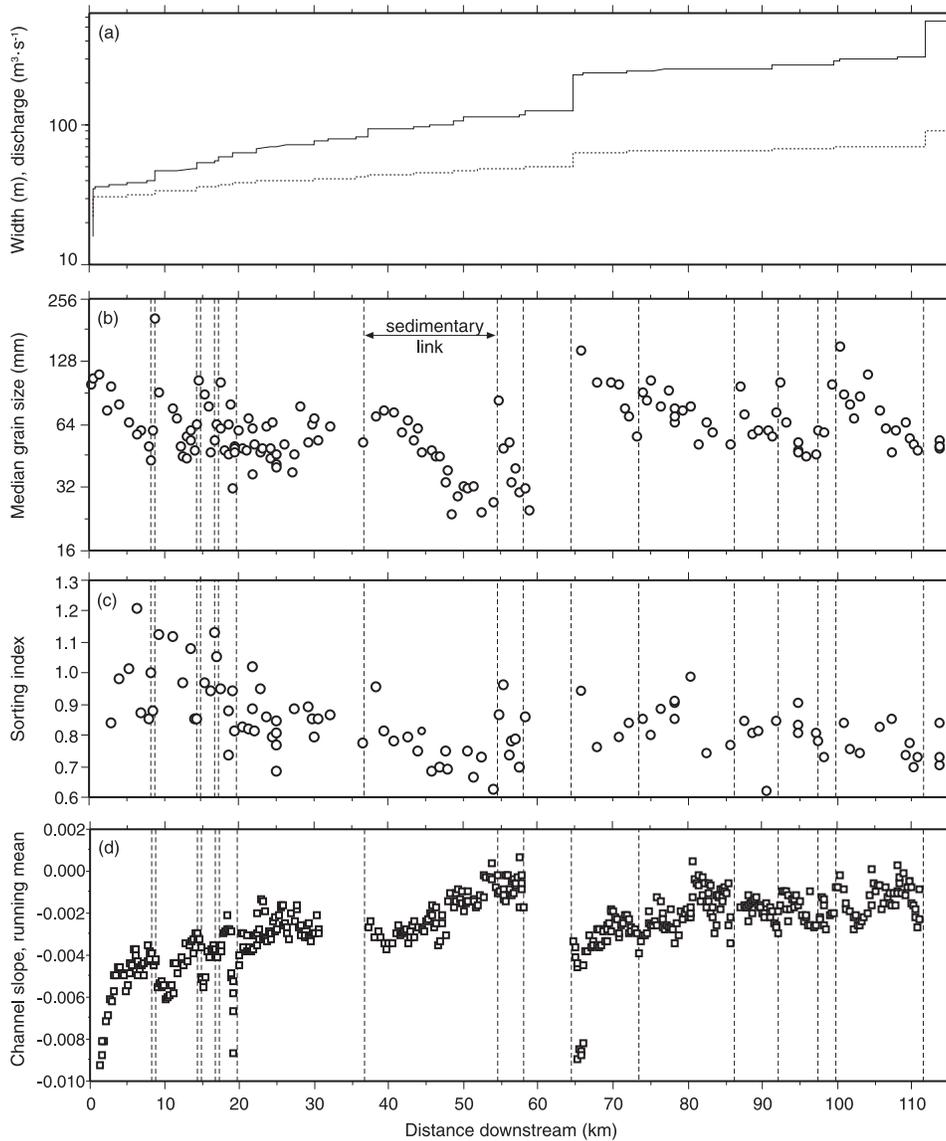
tributary of equal, half, and one-tenth magnitude joins the mainstream are 56, 30, and 6%, respectively.

For completeness, two caveats are relevant. First, abrupt changes in channel dimensions are most probable at those confluences where bankfull flows tend to be coincident. Asynchronicity in the flood response of contributing catchments will limit the extent to which channel morphology reflects an increase in contributing area. Second, the complexity of the fluid and sedimentary processes operating in confluences may preclude simple step increments of width and depth in the reach immediately downstream of a junction (Gippel 1985). For example, Roy and Roy (1988) found that channel capacity tends to decline immediately downstream of

most confluences, which is consistent with the observed development of flow separation bars in postconfluence channels (Best and Reid 1984). Conservation of flow implies that average channel velocity must therefore increase, and such increases have been documented in both flume and field studies (Best and Reid 1984; Roy et al. 1988).

Bed sediment characteristics

At the largest spatial scales, bed material size shows a progressive decline from boulders or cobbles to gravels and then to sands along most river systems and is appropriately modeled as an uninterrupted, systematic phenomenon (e.g., Robinson and Slingerland 1998). This downstream fining is

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Fig. 3. Downlink changes in sediment characteristics for the sedimentary link highlighted in Fig. 2*b*. The pairs of photographs are of the bed and channel (*a*) 2 km (top), (*b*) 11 km, and (*c*) 15 km down the link. Median surface grain size declines from 75 to 39 to 24 mm. (*d*) Pair of photographs showing the bed and channel at the head of the subsequent sedimentary link, 250 m downstream of a major (dry) sediment input and approximately 2 km downstream from Fig. 3*c*. Median surface grain size here is 83 mm.
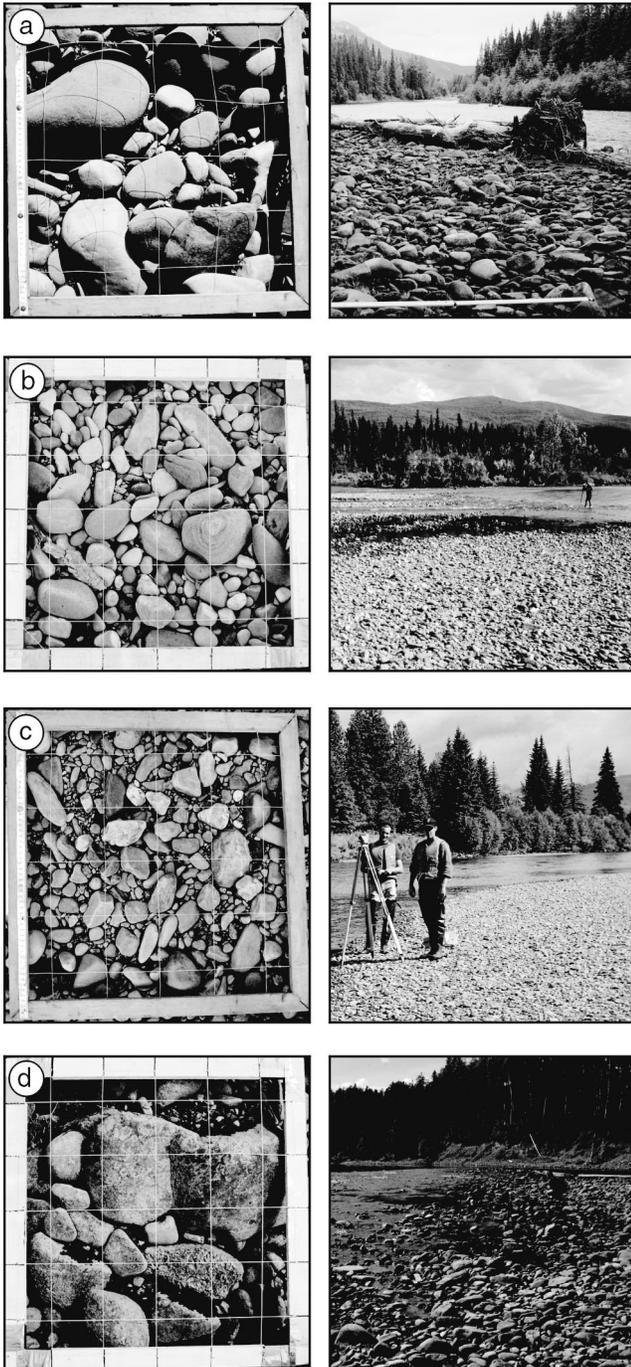
perturbed, sawtooth pattern of punctuated downstream fining is typically observed, with relatively short fining sequences separated by large, step increases in average particle size at confluences (Church and Kellerhals 1978; Knighton 1980). These tributary discontinuities reflect the adulteration of the mainstream bedload population by an influx of sediment that is sufficiently voluminous and (or) sedimentologically distinct to redefine the bed material characteristics of the main channel. Sorting and, to a lesser extent, abrasion processes then produce fining trends along the reaches between tributaries (Rice and Church 1998), and particle size (parameterised by a distribution percentile) typically declines exponentially (for reviews, see Morris and Williams 1999; Rice 1999).

Particle size discontinuities are also common where sediment is supplied by dry sources, such as bedrock outcrops, points of significant bank erosion, and landslides. If such inputs are abundant, for example, in headwater areas characterised by strong hillslope–channel coupling, then the sawtooth pattern of punctuated fining may be replaced by a stochastic pattern (Miller 1958; Rice and Church 1996). Otherwise, dry sources have the same impact as tributaries. Step decreases in average particle size have been observed at tributaries and dry sources, but they are relatively rare because an input that is finer than the resident material must be relatively more mobile and is therefore unlikely to persist.

Rice and Church (1998) referred to significant sediment recruitment points, whether wet or dry, as LSSs and to the intervening channel reaches as sedimentary links. Figures 2*b* and 3 illustrate the pattern of punctuated downstream fining for bed materials along the sedimentary links of Sukunka River. Data and photographs are for a single facies, the coarse bar head, such that local-scale variability associated with the riffle–pool sequence and bar-scale sorting is screened out.

Characteristics other than size also change along links. Sorting by size leads to a reduction in the heterogeneity of bed materials so that "sorting" coefficients typically decline downstream (e.g., Rhoads 1989). LSSs disrupt longitudinal sorting trends (Figs. 2*c* and 3) so that abrupt shifts from fine, homogeneous bed sediments to coarse, heterogeneous beds are common (Knighton 1980; Ichim and Radoane 1990).

Particle roundness tends to improve downstream because abrasion smoothes edges during transport and rounder materials have lower friction angles and are therefore more mobile than their angular counterparts. Again, inputs of less-traveled, fresher material at LSSs may disrupt these trends by increasing the average angularity of the bed material (Brewer and Lewin 1993). Longitudinal shape gradients are more difficult to characterise because the relations between particle mobility and shape are complicated by the lithological mix of the particles present and by confounding relations with size, density, and roundness (e.g., Frostick and Reid 1980). Other factors being equal, spherical particles have lower friction angles, tend to generate stronger lift and drag forces than platy shapes (Hattingh and Illenberger 1995), and, unlike platy shapes, do not form imbricate surface fabrics. This suggests that spheres are more mobile than rods, which are, in turn, more mobile than blades or discs (Krumbein 1942; Hattingh and Illenberger 1995). This can result in longitudinal sorting by shape, but LSSs may disrupt shape gradients, most obviously where material of a distinct lithology is added to the mainstream.

a consequence of size-dependent sorting processes and the abrasion of individual clasts during transport. At moderate spatial scales, however, the decline is seldom systematic. A

Longitudinal profile, channel slope, and planform

Bed gradient typically declines along alluvial rivers to produce a concave-up longitudinal profile, but the decline is rarely smooth. It is clear, on purely theoretical grounds, that step variations in discharge, sediment load, or sediment size at tributaries or dry sediment sources necessitate slope adjustments that must produce changes in gradient (Rice and Church 2001). For example, the accumulation of coarser, relatively immobile sediment downstream of LSSs will lead to a steepening of channel slope until the gradient is sufficiently high to facilitate mobilisation of the majority of the sediment supplied. In an aggradational system with downstream fining, equivalent adjustments are expected along each sedimentary link so that the composite result is a sequence of concave-up link profiles. Similarly, tributaries that supply a significant amount of water but little sediment may cause an increase in main channel slope as discharge and entrainment stresses undergo a step change.

There is little empirical data to illustrate the impact of LSSs on channel slope because most published data are derived from maps that are at too large a scale to be useful. Nevertheless, tributary-related steepening is apparent in map-derived long profiles of the Siret River, Romania (Ichim and Radoane 1990), and the Kootenay River in British Columbia (Galay et al. 1998). A ground survey of a small section of Sunwapta River, Alberta, reveals steepening downstream of tributary fans (Dawson 1988) and, along 100 km of the Sukunka River, local gradient increases below several LSSs (Fig. 2*d*), and individual links tend to exhibit concave profiles (Rice and Church 2001). In contrast with these results and the general expectation, Miller (1958) noted that slope declined below approximately half of the 16 confluences along the steep, mountainous channels that he examined.

Controls on channel planform are complex, involving the interplay between contemporary hydrology, contemporary sedimentology, and inherited morphologies. Important variables that consistently appear in attempts to distinguish amongst channel patterns are discharge, sediment supply, sediment caliber, and channel slope. By changing these variables, tributaries and LSSs may instigate changes in channel pattern. For example, coarse sediment supply and attendant increases in channel slope at tributaries have been associated with a shift from single-thread, meandering planforms to braided patterns on various large rivers in British Columbia (Desloges 1990; Galay et al. 1998). Such transformations are important because they are realised as changes in the proportion of different bedforms (point, diagonal, lateral, and midchannel bars) and hydraulic features (pools, riffles, glides), each of which may generate different biotic associations.

Flow velocity and hydraulic stresses

At the largest spatial scales, downstream hydraulic geometry exponents for velocity relations are typically in the range 0.1–0.2, indicating that longitudinal increases in mean velocity are small. The main controls on this pattern are a downstream reduction in channel gradient and, as depth increases and particle size declines, a reduction in effective grain roughness. The changes in channel slope and relative roughness that occur between tributaries can be similar to the large-scale pattern (declining gradient, declining particle

size), but empirical data are not available to assess within-link patterns of velocity variation — we can, therefore, only speculate about the net effect in links. Downlink variations in mean velocity are probably small, especially at high flows when the effects of grain roughness are drowned out and the relation between water surface slope and bed slope weakens. It is unlikely that tributaries cause step changes in mean velocity along the receiving channel, at least beyond the local effect (discussed above) associated with channel narrowing immediately downstream.

It is likely, however, that longitudinal patterns of shear stress are affected by tributaries, especially those that produce mainstream changes in both channel slope and water depth. Shear is likely to increase immediately below tributaries and decline downlink as channel slope lessens. Once again, there is a lack of direct evidence, but the suggestion is supported by observed patterns of perturbed downstream fining because maximum bed material particle size is generally correlated with average shear stress (Church 1978; Wilcock 1993).

Changes in reach or even water column averaged hydraulic conditions are less important to macroinvertebrates than local, near-bed patterns of stress and velocity (Nowell and Jumars 1984; Davis and Barmuta 1989). Consideration of the relations between flow characteristics and roughness element density (Morris 1955; Nowell and Church 1979) suggests that near-bed hydraulic conditions are apt to change at tributaries and LSSs in response to changes in substrate texture. The introduction of relatively coarse, poorly sorted bed material leads to an increase in relative roughness and, in turn, a propensity for highly turbulent, chaotic flows. Complex velocity fields characterised by multidirectional accelerations and decelerations of the flow and significant local variations in water surface elevation create microzones of both very high and extremely low velocity and shear stress. A wide array of hydraulic habitats may therefore be apparent immediately downstream of tributary junctions. In turn, as effective grain roughness declines and the bed material becomes better sorted, there is likely to be a shift toward less turbulent, quasi-smooth or skimming flows. The hydraulic heterogeneity exhibited by upstream riffles may then be replaced by more homogeneous hydraulic environments downlink in which maximum velocities and shear stresses are generally lower.

Water quality characteristics

At the drainage basin scale, water quality varies across the drainage network as a function of the biophysical characteristics of individual subcatchments (for a review, see Walling and Webb 1992). For example, differences in total dissolved and suspended solids typically reflect variations in catchment geology, land use, and precipitation–evapotranspiration ratios (Walling and Webb 1975; Grayson et al. 1997; Meybeck et al. 1999), while catchment size and altitude and the character of riparian vegetation are responsible for differences in water temperature (Smith 1979) and the amount and size distribution of organic particles (Minshall et al. 1983). Differences in the composition of the dissolved load are important because they determine the water's nutrient status, acidity, and salinity and may reflect the presence of toxic metals, pesticides, and herbicides (for a review, see Webb and Walling 1992). Mixing of water from sub-

catchments with distinct biophysical characteristics may, then, modify water quality at confluences so that tributaries have, for example, been associated with significant changes in mainstream turbidity (Grayson et al. 1997; Stevens et al. 1997), nutrient status (Grayson et al. 1997; Marneffe et al. 1997), seston character (Minshall et al. 1992), and metal concentrations (Wilby and Gibert 1996; Axtmann et al. 1997).

As a mainstream channel aggregates the contributions of numerous tributaries, the structure of the channel network becomes increasingly important for explaining water quality changes. Oversimplification of network structure and poor information about tributary flow and load characteristics limit the success of longitudinal water quality modeling (Eatherall et al. 1998). Downstream from mixing points, a suite of complex processes including dilution, aeration, reaction, deposition, and degradation may modify physical and chemical constituents (Wilby and Gibert 1996) so that longitudinal changes, even within individual links, are difficult to model and predict.

It is clearly impossible to make generalisations about tributary impacts on water quality. Impacts will vary from tributary to tributary as a function of the properties of their catchments and from time to time as a function of catchment hydrology, runoff, and stream discharge. What is important here is simply to recognise that, like other aspects of physical habitat, water quality can be affected by tributaries and, in turn, affect stream biota. For example, along the Clark Fork River in Montana, longitudinal patterns of mining-related metal concentrations (Cd, Cu, Pb) in silt-sized bed sediments and macroinvertebrate fauna are tightly controlled by patterns of dilution and dispersion at tributary inflows (Axtmann et al. 1997).

Some implications for macroinvertebrate fauna of tributary effects on habitat gradients

The links between the physical variables on the right in Table 1 and macroinvertebrate fauna are the subject of very extensive literatures that are not reviewed here. Rather, we aim to draw out some of the potential impacts that tributaries and LSSs might have for benthic habitat along river systems and contemplate the implications for the longitudinal organisation of benthic communities. Discussion is inevitably speculative in the absence of field data and provocative in the hope of exciting interest in tributary effects. Each factor is considered in isolation, although, in reality, various effects are likely to be coincident.

Illumination

The penetration of light energy for heating and photosynthesis is controlled by water depth, channel width (via riparian shading), and turbidity. Greater light penetration occurs where channels are shallow, wide, and clear. As discharge increases downstream, depth increases at a slower rate than width so that, in the absence of significant suspended sediment contributions, increases in channel width are likely to dominate at confluences and lead to increased illumination as the riparian canopy separates. At some point downstream, depth becomes a limiting factor as a function of the attenuation of light energy as it passes through the water column.

Width-related changes in illumination are a key element of the RCC.

Increases in light penetration are associated with greater primary production by periphyton (McIntire and Phinney 1965), macrophytes (Westlake 1975), and phytoplankton (Lewis 1988) and, in turn, greater availability of autochthonous food resources. Several experimental field studies have shown changes in macroinvertebrate community composition in response to increased or reduced illumination. Thus, in artificially shaded reaches, Towns (1981) and Fuller et al. (1986) observed a reduction in collector–gatherers (e.g., chironomids) as food supplies dwindled and an increase in sessile filter feeders (e.g., hydropsychid caddisflies) as clean rock surfaces became available for attachment (Ward 1992). Similarly, canopy removal by clearcut logging along two streams in the southeastern United States was associated with an 18-fold increase in the abundance of diatom-feeding *Baetis* mayflies (Wallace and Gurtz 1986), and in Fuller et al.'s (1986) work, *Baetis* mayflies were more abundant and of larger body size in uncovered stream sections. Where tributary-related increases in channel width and illumination are large, for example, where two relatively small, heavily shaded streams of similar size meet, a step increase in autotrophy and a consequent step increase in the abundance of herbivorous collector–gatherers and scrapers might be expected.

Where a tributary delivers a significant suspended sediment load, increased turbidity in the main channel may reduce benthic illumination and affect macroinvertebrate fauna. Stevens et al. (1997) reported a "stairstep," 37-fold reduction in algal food production at the confluence of the turbid Paria River with the regulated Colorado River. Food resources for some macroinvertebrates were reduced and total invertebrate standing mass declined (Stevens et al. 1997).

Substrate stability and bed microtopography

Changes in size, sorting, roundness, and shape affect the stability and microtopography of the mineral substrate — the primary component of the substrate upon which macroinvertebrates move, rest, find shelter, and feed. Bed sediments also moderate hyporheic fluxes of water and nutrients and, through their role in defining channel slope and roughness, affect the hydraulic conditions that benthic fauna must tolerate. The effects of mineral substrate on macroinvertebrate communities are therefore profound (for reviews, see Minshall 1984 and Ward 1992), and spatial variations in bed material character are known to elicit macroinvertebrate responses at a variety of scales.

At our scale of interest, bed material change is characterised by punctuated downstream fining that is structured by LSSs and sedimentary links and accompanied by step changes in sorting, roundness, and (with less certainty) sphericity. Relations between particle stability and bed material characteristics are complex (Death and Winterbourn 1994; Buffington and Montgomery 1997; Downes et al. 1997), but it is reasonable to assume that stability will be relatively high at the upstream end of sedimentary links and decline downstream as inertial controls (size), hiding factors (sorting), and pivot angles (sorting, roundness, shape) are reduced. Furthermore, as particle size and sorting coefficients decline downlink, bed microtopography becomes less complex, offering a restricted range of particle sizes, flow condi-

tions, and interstitial opportunities and possibly limiting the diversity and abundance of trapped particulate organic matter and algae (Ward 1992).

Reductions in size, stability, and bed heterogeneity are generally associated with a shift from lithophilous to psephophilous and, ultimately, psammophilous faunal assemblages. Many of the species found in boulder–cobble substrates are also found in gravels (e.g., many stonefly and heptageneiid mayfly families), in part because of widespread substrate patchiness in gravel-bed rivers. The distinction between lithophilous and psephophilous faunal classes has therefore been questioned (cf. Ward 1992). However, the dramatic changes in bed texture that can occur at confluences and LSSs (Fig. 3) suggest that some response is likely. Thus, caddisfly larvae that attach their cases to bed particles (several brachycentrids, for example) are most successful where the available bed material is stable and the effort involved in construction is rewarded by longevity. In contrast, mobile animals that do not require stable attachment points or vermiform animals that can exploit the narrow interstices of gravelly substrates (e.g., members of the family Chloroperlidae) may find greater feeding or cover advantages in downlink locations. Lithophilous species are therefore more likely to be found immediately downstream, rather than upstream, of LSSs, and a downlink trend from lithophilous to psephophilous fauna may be apparent.

In addition to the preferences of individual species, downlink changes in bed material characteristcs may elicit a predictable biotic response by causing changes in habitat heterogeneity. Species diversity is generally higher in heterogeneous environments (Minshall 1984), and positive relations between sediment sorting and taxa diversity have been reported (Williams 1980; Dudgeon 1982). The relative importance of particle sorting, rather than attendant changes in food availability, hydraulic complexity, and changes in particle size, remains unclear (e.g., Erman and Erman 1984), but the implication is clear — species diversity is likely to decline downlink and increase at significant LSSs. This tendency may be reinforced by reported strong relations between habitat stability and faunal diversity (Death and Winterbourn 1995).

Near-bed hydraulics

Near-bed hydraulic conditions determine the potential for entrainment of resident fauna and the associated substrate, moderate rates of food supply via seston delivery, and affect other relevant processes such as corrasion, gas exchange, and the ability to escape predators or hunt prey. Macroinvertebrate taxa therefore exhibit morphological (Statzner and Holm 1989) and behavioural (Lancaster 1999) adaptations to hydraulic stress that lead to strong associations between local hydraulic conditions and community composition.

Tributary junctions are associated with the generation of more chaotic and heterogeneous near-bed flow conditions, where local velocities and shear stresses attain a maximum range. With distance downlink, boundary Reynolds numbers are apt to decline, maximum shear and velocity will be reduced, and flow characteristics are likely to become less diverse within given morphological units, for example, within riffle sites. Areas of high hydraulic diversity offer a variety of feeding and resting opportunities that, as with substrate

variability, potentially support more diverse communities than relatively simple sites with less functional complexity.

Hydraulic conditions both define and are defined by local substrate characteristics so that disentangling substrate and hydraulic effects is problematic under natural conditions (Erman and Erman 1984; Minshall 1984). It is therefore difficult to identify field studies that uniquely relate faunal diversity to hydraulic complexity, but it seems reasonable to suppose that a positive relation exists. Community diversity at complex sites may be further enhanced by the greater provision of numerous low-stress microhabitats that promote the survival, recovery, and persistence of benthic communities at those locations. Thus, patches of low hydraulic stress and high substrate stability, for example, in the lee of stable boulders (de March 1976), may be utilised as flow refugia during spates and subsequently act as nodes of recruitment or recolonisation afterwards (Lancaster and Hildrew 1993; Winterbottom et al. 1997; Rempel et al. 1999). We therefore speculate that faunal diversity is apt to increase at confluences and other LSSs and to decline downlink.

Although many macroinvertebrate taxa are found across a wide range of hydraulic conditions, many preferentially select a fairly narrow range of shear stress or velocity. In turn, downlink hydraulic gradients may promote a longitudinal biotic response, particularly in animals that show strong hydraulic preferences such as filter feeding caddisflies of the families Brachycentridae and Hydropsychidae (e.g., Wetmore et al. 1990; Voelz and Ward 1996) and the Diptera family, Simuliidae (e.g., Chance and Craig 1986; Morin 1991).

Biotic gradients may be apparent at the level of functional feeding groups rather than individual taxa. For example, abundances of filter-feeding insects have been positively correlated with velocity and Reynolds number in a number of field studies (Orth and Maughan 1983; Wetmore et al. 1990). This probably reflects greater seston supply in turbulent environments (Quinn and Hickey 1994), and filter feeders may therefore be more prevalent in the turbulent, high-stress, high-velocity environments immediately downstream of confluences. In contrast, browsers and collector–gatherers rely on the availability of abundant fine detritus, which is unlikely to persist in highly turbulent settings. Thus, Quinn and Hickey (1994) found strong negative correlations between collector–gatherers and boundary Reynolds numbers in New Zealand streams, and a shift toward greater abundance of this functional group may be expected downlink. In light of this example, it is informative that Bruns et al. (1984) found an increase in the abundance of filter feeders downstream of large tributaries that they attributed to elevated supplies of particulate organic matter.

Model development: the link discontinuity concept

Various aspects of river channel form and function are often modeled as smooth, continuous functions of distance downstream, for example, bed elevation (e.g., Ohmori 1991), channel geometry (e.g., Leopold and Maddock 1953), bed material particle size (e.g., Morris and Williams 1999), and lotic habitat structure (Vannote et al. 1980). However, the sediment and water fluxes ultimately responsible for longitudinal change in physical habitat do not vary smoothly or

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continuously downstream but often change abruptly where a tributary stream or other point source adds water and (or) sediment to the main channel. Patterns of discontinuity and repeated adjustment therefore characterise downstream changes in bed elevation (e.g., Rice and Church 2001), channel geometry (e.g., Richards 1980), bed particle size (e.g., Church and Kellerhals 1978), and, we propose here, ecosystem structure.

Within every drainage basin, there is a hydrological network that routes water and a sedimentary network that routes sediment. The sedimentary links of Rice and Church (1998) are analogous to hydrological network links but reflect the supply and transfer of sediment rather than water. These two networks are not always equivalent because sediment production and delivery is discontinuous in the landscape (not all tributaries are important sources of sediment) and many sources of sediment lie outside the hydrological network (dry, nontributary LSSs). Thus, along the Sukunka River, there are 78 perennial tributaries but only 17 LSSs, of which only 11 are tributaries (Rice 1998). The sequence of sedimentary links structures some aspects of physical habitat (substrate characteristics, channel slope, near-bed hydraulics). The hydrological network provides additional structure, in terms of changes in discharge and water quality with all of the attendant implications for habitat (channel dimensions, nutrient status, etc.). We suggest that stream biota respond to these changes so that, notwithstanding the role of biotic processes, macroinvertebrate community characteristics are apt to change significantly and suddenly at tributaries and related features while exhibiting less remarkable, systematic gradients or unstructured variation along the intervening links.

Not all tributaries and LSSs are important. Rather, a subset of them adds water and (or) sediment of sufficient quantity or sufficiently distinct character to cause changes in mainstream habitat that exceed local, within-link noise. This subset of significant tributaries and LSSs delineates a sequence of links that are connected together but that function semi-independently as internally integrated units. There is a degree of longitudinal continuity because the outputs from one link (water, sediment, nutrients, pollution, drift) are part of the input to the downstream link, but perturbation, physical adjustment, and biotic reaction repeatedly preclude extended continuous gradients. In a very long sequence of links, progressive changes in link-averaged conditions are expected (e.g., an increase in channel width or decrease in slope), but the degree to which this is true depends on the channel network pattern and the pattern of sediment supply from the landscape. In turn, the form and existence of large-scale biotic gradients depend on processes occurring at the link scale. Each link is a relatively simple abiotic system, free of lateral perturbation and characterised by the adjustment of physical parameters to inputs at the head of the link. Links then become a useful spatial unit for examining, understanding, and modeling the response of aquatic biota to abiotic gradients and disturbances.

In short, at moderate spatial scales, as a result of their impact on physical habitat, the pattern of significant water and sediment sources along a river system configures a fundamental abiotic framework within which biotic communities are organised. We refer to this model as the link discontinuity concept (LDC). It represents an attempt to (*i*) more rigorously develop previously published expositions about the discontinuous nature of lotic ecosystems (e.g., Perry and Schaeffer 1987; Bravard and Gilvear 1996), (*ii*) address the importance of tributaries in unregulated as well as regulated rivers (cf. the SDC of Ward and Stanford 1983, 1995), and (*iii*) extend, to its logical conclusion, the limited recognition of tributary influence within the RCC (Minshall et al. 1983, 1985; Bruns et al. 1984). Lateral sources of water and sediment are not exceptional features that temporarily reset inevitable, systematic, downstream changes in physical conditions (cf. Vannote et al. 1980); rather, by defining patterns of water and sediment flux, they are entirely responsible for moderate- and large-scale variations in physical habitat along all river channels.

The LDC provides an alternative perspective on the influence of geomorphological and hydrological variables for the spatial organisation of biotic communities in lotic ecosystems. It emphasises the fundamental importance of water and sediment fluxes at moderate spatial scales rather than large-scale patterns of energy partitioning (RCC) or local-scale habitat patchiness (Townsend 1989). It recognises the complexity of fluvial systems and the importance of geomorphic context and in this regard shares common ground with the process domain concept of Montgomery (1999). We suppose that the LDC is a useful adjunct to these habitat models that can improve understanding of the spatial organisation of lotic communities (cf. Johnson et al. 1995). It is intended to facilitate further exploration of the ideas discussed above and is easily tested by examining tributaries and other LSSs for significant ecological discontinuities and the intervening links for biotic gradients.

Case study: sedimentary links and macroinvertebrate organisation on the Pine and Sukunka rivers, British Columbia

To assess the general merit of the LDC, macroinvertebrate communities along two mountain rivers in British Columbia were examined. Two study reaches where tributaries and dry LSSs cause significant changes in bed sediment characteristics but have relatively minor impacts on discharge and water quality were selected. This deliberate focus on sediment changes and sedimentary links allows us to comment on the general model and to examine, in a semicontrolled field situation, the role of shifts in sediment character alone.

Study area and physical habitat

The Pine and Sukunka rivers drain the eastern flank of the northern Rocky Mountains, with respective drainage areas of approximately 2500 and 2750 km^2. At hydrometric station 07FB003 (Water Survey of Canada), located near the mouth of the Sukunka River, mean flow is 54 m^3·s^{-1} and the mean annual flood is 480 m^3·s^{-1}. Maximum flows occur in May and June in response to river ice breakup and regional snowmelt. Tributaries, relict Pleistocene landforms, and Holocene fans are important sources of coarse sediment for the contemporary rivers, which have a wandering planform characterised by irregular sinuosity, few vegetated islands, and complex arrangements of gravel bars. Spruce and cottonwoods are the dominant floodplain vegetation types. In gen-

Fig. 4. Pine and Sukunka study reaches showing LSSs (arrowed), sedimentary links (dashed lines), and macroinvertebrate sampling positions (circles). Sample sites are coded according to their position beside a lateral input ("us' for upstream, "ds" for downstream) or their sequential position within a link so that, for example, P1.3 is the third site along link 1 on the Pine River. The symbol that identifies the position of Rocky Creek fan is different from those identifying the other LSSs because it is a dry input.
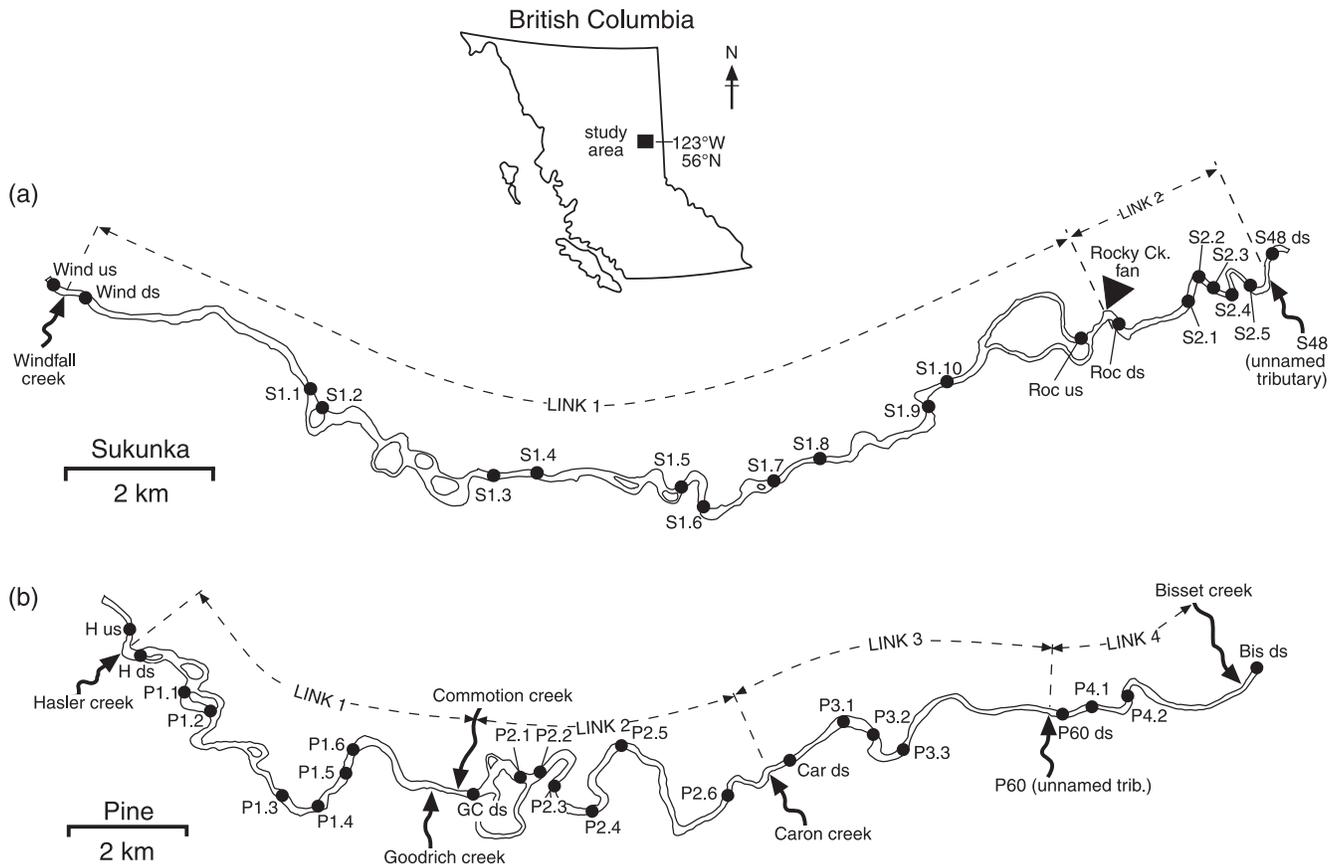
eral, the riparian zone is natural and unmanaged and neither river is regulated in any way.

Previous work has established a detailed picture of bed material particle size trends along each river (Rice and Church 1998). In turn, major LSSs (those associated with significant particle size discontinuities and the instigation of new fining trends) have been identified and examined. These LSSs demarcate 33 sedimentary links, most of which exhibit exponential, downstream particle size decline and concave longitudinal profiles (Rice 1999; Rice and Church 2001). For this study, one 26.2 km reach of the Pine River consisting of four sedimentary links and one 20.6 km reach of the Sukunka River consisting of two sedimentary links were selected (Fig. 4). On the Sukunka River, a dry LSS separates the two links. Note that the photographs of bed material in Fig. 3 were taken along these two links. The Sukunka reach is at a slightly higher elevation (700 versus 560 m) and has a higher average gradient than the Pine reach.

Along both study reaches, the primary influence of tributaries and the dry LSS is on sediment characteristics (Fig. 5). There are clear, step increases in particle size and reductions in sorting at each input point, followed by downlink reductions in size and improvements in sorting. Sorting data along the Pine reach are insufficiently frequent to allow identification of a clear pattern (the 400-stone samples used to calculate these sorting coefficients are difficult to collect), but

photographic data confirm that the bed materials do become more homogeneous downlink. In contrast, downlink changes in channel dimensions and in water quality parameters are relatively minor. Both river channels are already very wide at the upstream end of the respective study reaches and estimated downstream changes in discharge are small. Estimated channel width increases from approximately 42.5 to 49.0 m on the Sukunka (a 15% increase) and from approximately 60.0 to 65.6 m along the Pine reach (a 10% increase). It is therefore unlikely that individual tributaries significantly affect riparian shading or markedly increase available habitat area. Similarly, only minor, unstructured changes in water temperature and pH are observed along both study reaches. Conductivity does increase downstream in both cases, indicating a general downstream increase in total dissolved solids. However, absolute values are low and longitudinal variations (210–310 μS) are relatively minor.

Macroinvertebrate sampling

Consistent with our focus on larger-scale, longitudinal trends, sampling was limited to riffle sites and does not, therefore, incorporate any assessment of local-scale variability associated with the riffle–pool sequence or other within-link patches. Samples were collected in the upstream and downstream mainstream riffles closest to each sediment input point (Fig. 4) and at pairs of consecutive riffle sites in

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Fig. 5. Physical habitat variables of Pine and Sukunka study reaches. Dashed lines indicate the positions of LSSs. Median grain size (D_{50}, squares) and maximum grain size (D_{max}, circles) are for the bed surface particle size distribution.
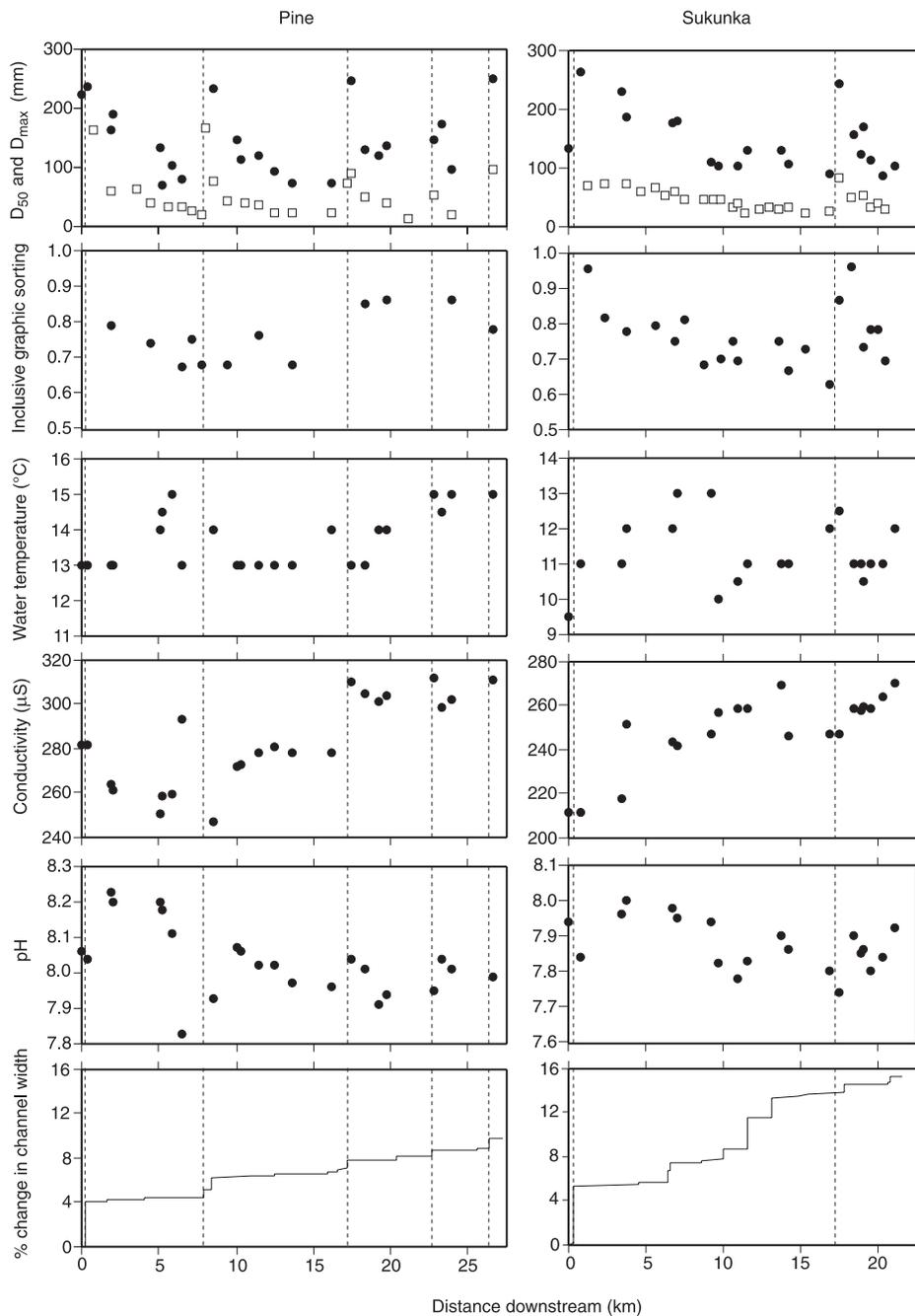

the intervening links. A total of 43 mainstream samples were collected over a 12-day period in late July and early August.

At each site, two 10-min kick samples were collected concurrently by two operators, who each moved to 10 locations within the riffle, stopping for 1 min at each point to gather macroinvertebrate benthos. The path taken by each operator encompassed as much of each riffle as could safely be sampled and incorporated both lateral and streamwise variations in flow and substrate characteristics. We are confident that observed differences in abundance are real, despite the use of kick sampling, because sampling areas and duration were

consistent between sites. Where the substrate was particularly coarse, hand searching preceded kick sampling.

The macroinvertebrate community on the Pine and Sukunka rivers was dominated by the insect orders Ephemeroptera (four families, 18 taxa), Plecoptera (five families, 17 taxa), and Trichoptera (six families, 19 taxa). Other families together constitute a relatively small proportion of total abundance at each site, less than 7% on average, and are therefore considered as a single taxon in subsequent analysis. Of the mayflies, the family Ephemerellidae, all collector–gatherers, was the most diverse (eight taxa), together with Baetidae (five taxa),

Fig. 6. Longitudinal variations in community diversity (taxa richness and Simpson's index) on the (*a*) Pine River and (*b*) Sukunka River. Dashed lines indicate the positions of LSSs.
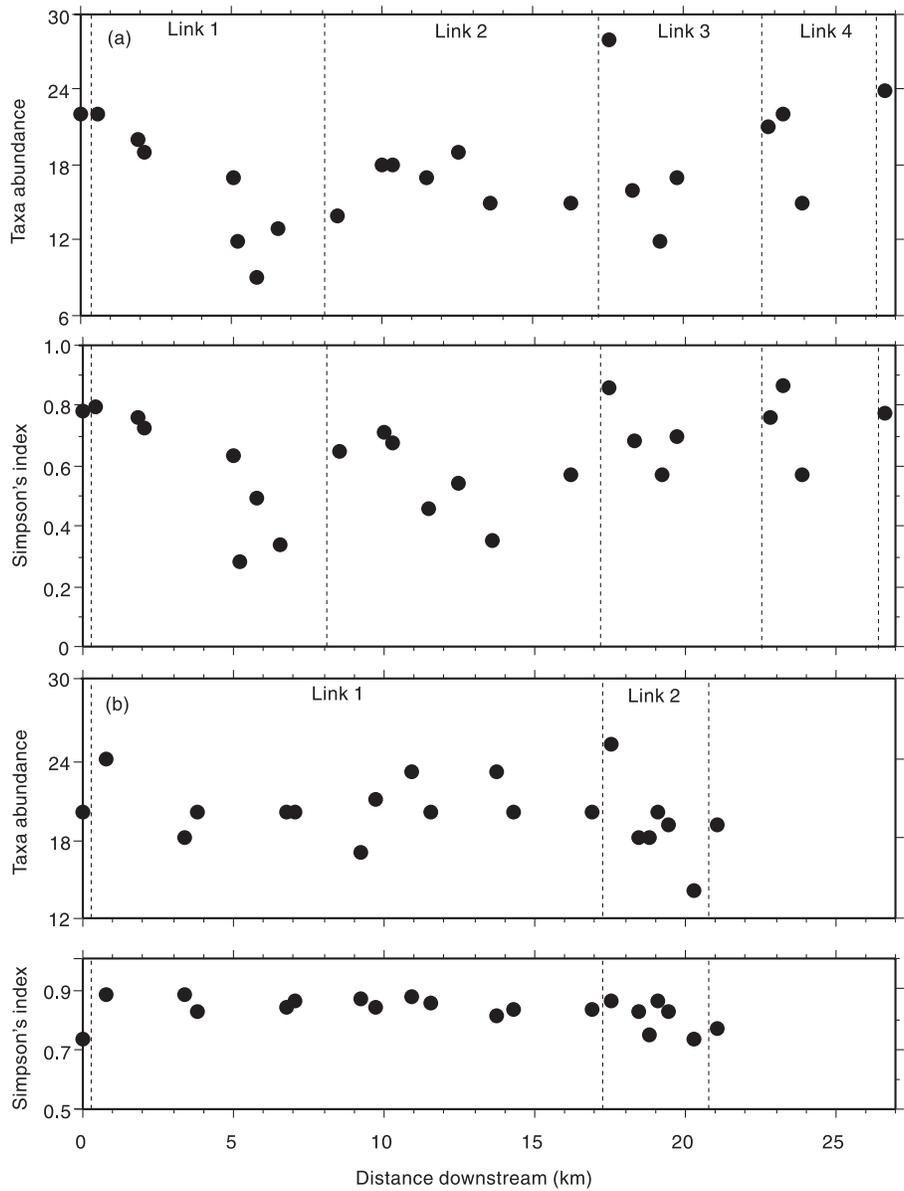
Heptageniidae (four taxa), and Siphlonuridae (one taxon). The stonefly community was represented by five families: Perlodidae (five taxa), Nemouridae (four taxa), Perlidae (four taxa), Pteronarcyidae (two taxa), and Chloroperlidae (two taxa). Most taxa were predatory, with some described as shredders–detritivores (Merritt and Cummins 1996). Caddisflies were represented by the families Rhyacophilidae (eight taxa), Hydropsychidae (four taxa), Limnephilidae (three taxa), Lepidostomatidae (two taxa), Glossosomatidae (one taxon), and Brachycentridae (one taxon). Predatory species of *Rhyacophila* dominated the community, together with collector–filterers from the family Hydropsychidae.

Results and discussion

Results presented elsewhere (S.P. Rice et al., unpublished data) show that coarse sediment sources along the two study reaches are associated with abrupt changes in the composition of macroinvertebrate communities. First, comparison of several dissimilarity indices, calculated for pairs of samples collected around LSSs and pairs of samples collected within links, shows that changes in the absolute abundance and relative proportions of each taxa tend to be greater between sites that straddle an LSS than between sites within links. This is true of wet and dry LSSs. Second, abrupt changes in taxa abundance and community diversity are apparent at most LSSs. Third, TWINSPAN classification identifies those communities found downstream of LSSs as a distinct ecological group on both rivers.

These results support the idea that tributaries and LSSs can cause large changes in community composition, but they do not address the issue of whether lateral inputs affect longitudinal biotic gradients. Complementary lines of investiga-

Fig. 7. Longitudinal variations in the abundance of the two key taxa on the (*a*) Pine River and (*b*) Sukunka River. *Leucrocuta* sp. (Heptageniidae) indicated by circles and *Brachycentrus* ?*americanus* (Brachycentridae) indicated by squares. Dashed lines indicate the positions of LSSs.
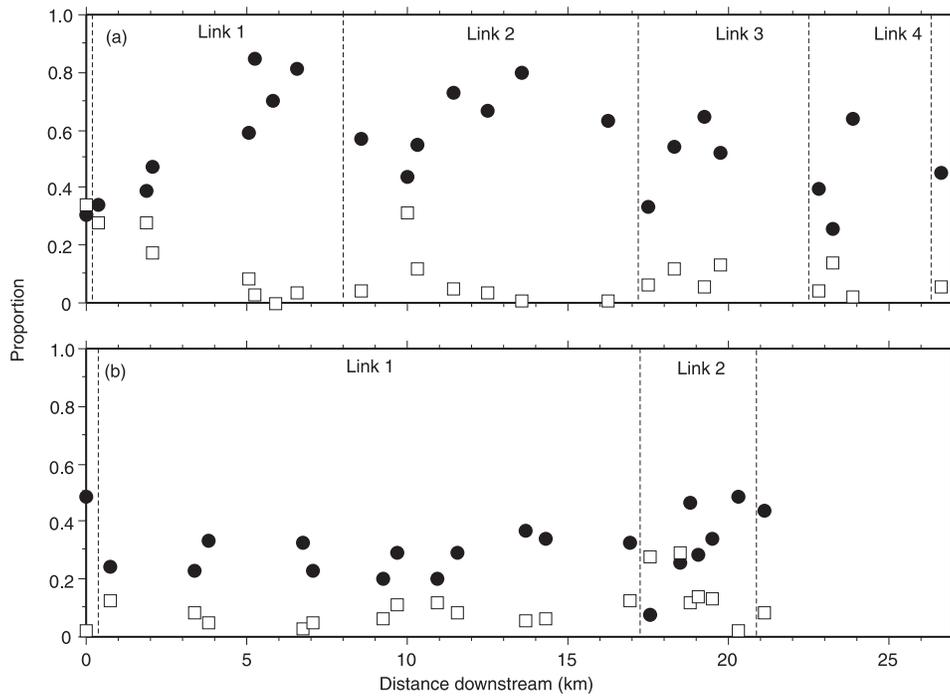

Fig. 8. (*a*) CCA of sample sites and environmental variables from the Pine and Sukunka rivers. Macroinvertebrate abundance data (number of individuals, transformed using natural logarithms) were used in the CANOCO programme (Ter Braak 1991). Sample sites are coded as per Fig. 4 with different symbols for different links and sequential position indicated by the number beside the symbol. Environmental variables are represented by arrows. (*b*) Representation of main diagram highlighting overall spatial trends in relation to sediment size.
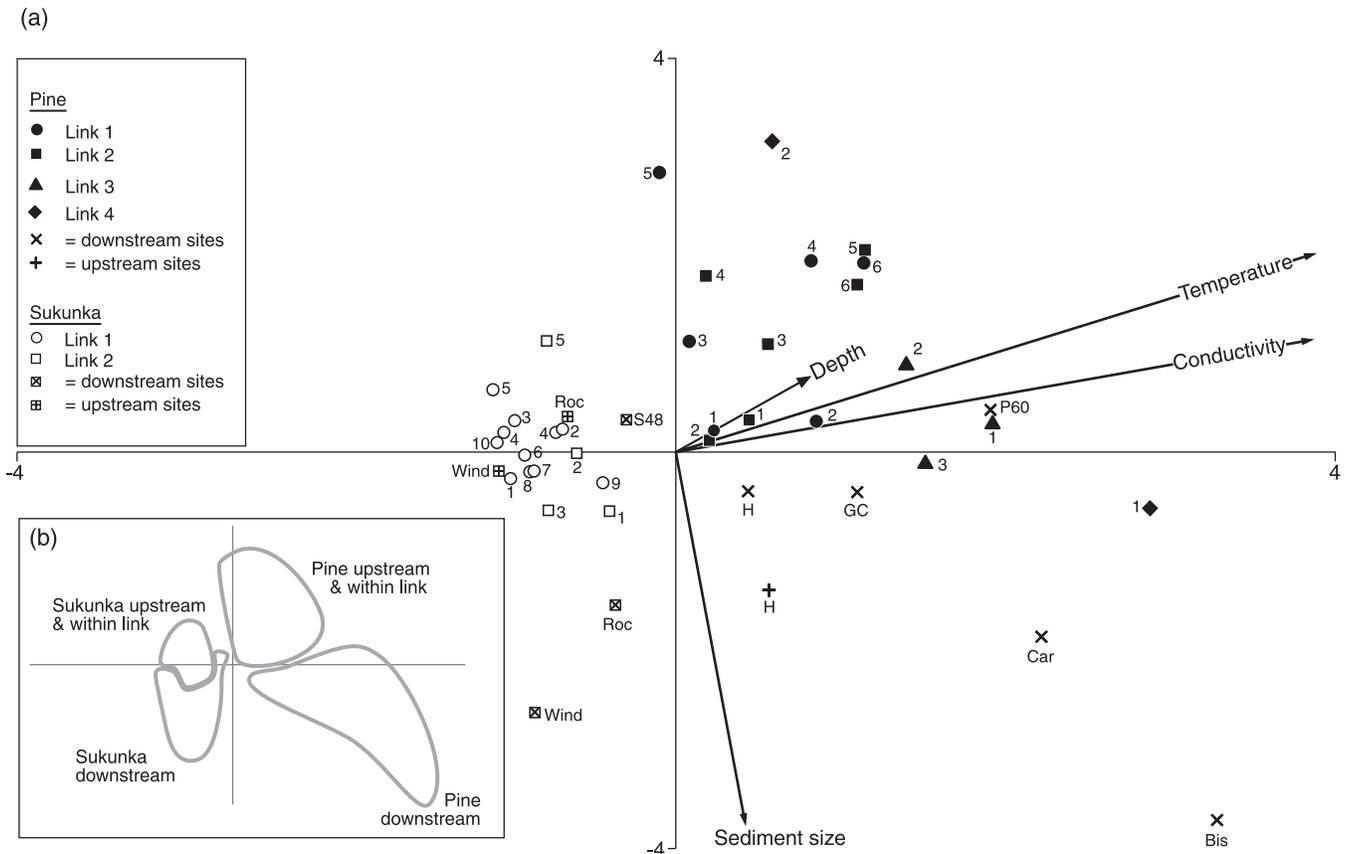
tion, reported here, suggest that community organisation is, at least in part, controlled by lateral sediment inputs and thence the sedimentary network.

Variations in community diversity (measured using taxa richness and Simpson's index (Simpson 1949)) exhibit negative downlink trends with positive steps at LSSs, particularly on the Pine River (Fig. 6). On the Sukunka River, diversity is generally greater and within-link trends and LSS steps are less clear. Nevertheless, they do mimic those on the Pine River, with declining diversity along each link and 20, 25, and 36% increases in taxa richness at the three LSSs. It was suggested above that near-bed hydraulics and substrate become more heterogeneous at LSSs and therefore provide a wider array of habitat possibilities that may support a greater range of taxa. We did not examine this hypothesis explicitly, but the suggestion is supported by these observations.

There is a clear tendency for the proportion of order Ephemeroptera to increase downlink and then to decline abruptly at LSSs along both rivers. This reflects changes in the abundance of one common taxon, *Leucrocuta* sp. (Heptageniidae), which, on average, accounts for 76 and 43% of all mayfly individuals on the Pine and Sukunka rivers, respectively. Generally positive within-link trends in the proportion of *Leucrocuta* sp. are reversed by large negative steps at all Pine and Sukunka LSSs (Fig. 7). Less clear variations are apparent in certain other common taxa. For example, the proportion of the caddisfly *Brachycentrus ?americanus* (Brachycentridae) declines along link 1 on the Pine River and along link 2 on the Sukunka River (Fig. 7), and marginal step increments in its proportion occur at each Sukunka LSS. This pattern is consistent with literature, reviewed above, which suggests that sessile, filter-feeding caddisflies, like *Brachycentrus ?americanus*, show a preference for large and stable substrates where roughness is high and food sources (seston) are plentiful.

While these results are not unequivocal, there is strong evidence that changes in macroinvertebrate community composition are framed by the pattern of sedimentary links. Without the structure provided by the dashed lines in Figs. 6 and 7, the plots would exhibit little more than some vague cyclicity. With the LSSs indicated, it is clear that sedimentary links are associated with relatively directional, systematic changes, while lateral inputs are important sites of discontinuity that abruptly reverse or reset within-link trends.

Canonical correspondence analysis (CCA) of macroinvertebrate abundance data using CANOCO with Monte Carlo tests (Ter Braak 1991) shows that community composition, although different in the Pine and Sukunka rivers, is significantly impacted by sediment size ($p = 0.001$) in both rivers (Fig. 8). Moreover, the pattern of community change in relation to sediment size is organised within links rather than at the larger study reach scale. Thus, within-link sites tend to be positioned sequentially along a gradient of sediment size, with sites immediately downstream of LSSs characterized by large sediment size and distal downstream sites having progressively finer sediments. This trend is particularly evident in the Pine data set, which is more variable than Sukunka, but in the latter river, two of the three invertebrate communities at sites immediately downstream of LSSs are also clearly differentiated on the basis of the sites' larger sediment size.

CCA also reveals that macroinvertebrate community variation in the two rivers is significantly related to water conductivity ($p = 0.001$) and temperature ($p = 0.009$) and that depth has a minor influence (Fig. 8). However, the longitudinal pattern of community change in relation to these variables is not interrupted by LSSs, indicating that the macroinvertebrate communities respond to the downstream increases in conductivity and temperature (and depth) sustained along the study reach as a whole (Fig. 5).

The CCA clearly shows that link-scale changes in sediment texture are an important control on the spatial organisation of benthic communities along these study reaches. The reaches were chosen for their strong sedimentary patterns, and so the general result is not wholly surprising. Nevertheless, these results illustrate, for the first time, the potential importance of sedimentary networks for structuring longitudinal biotic patterns.

A process that has not been considered in this case study, but that may nevertheless be important, is ex-tributary colonisation. Drift out of a tributary into the channel immediately downstream of a confluence may lead to a distinct change in mainstream fauna, especially as some conditions in the postconfluence channel (e.g., bed material particle size) may be similar to those in the tributary and therefore viable for drifting animals. The potential importance of this mechanism is illustrated by the work of Cellot (1996) who found that drift from side channels affects main channel community structure along the Upper Rhone River. However, our results suggest that significant changes can occur in the complete absence of such affects because the dry LSS (Rocky Creek fan on the Sukunka River) exhibits changes similar to the other, wet LSSs, but there is no possibility that drift is involved.

Conclusion

Along all rivers, the introduction of water and (or) sediment at tributaries and LSSs causes steplike adjustments in a variety of physical habitat variables. These changes may, in turn, elicit responses in the macroinvertebrate community, and we have made some speculative suggestions as to what these might include. In turn, we suggest that the hydrological and sedimentary networks that organise the movement of water and sediment through a drainage basin are ecologically important structures that can usefully inform attempts to explain the spatial organisation of macroinvertebrate fauna. This is especially true at moderate spatial scales, above which network structure is apparent as noise and below which patchy geomorphological structures dominate. Our case study supports the LDC model proposed and our arguments regarding tributary influence on benthic diversity and the distribution of sessile filter feeders.

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