

FLOOD-PULSE AND RIVERSCAPE DYNAMICS IN A BRAIDED GLACIAL RIVER

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Abstract. River ecosystems are increasingly viewed as dynamic riverscapes; their extent, composition, and configuration vary in response to the pulsing of discharge. Although compositional and configurational shifts in riverscapes are thought to control ecosystem processes and biodiversity, attempts to quantify riverscape dynamics of braided rivers are scarce. We measured monthly changes in the length, spatial arrangement, and age distribution of clear (groundwater-fed) and turbid-water (glacial-fed) channels during two annual cycles in a braided glacial river. Biological data from concurrent studies were used to assess the effects of seasonal changes in the size and pattern of the riverscape on local zoobenthic density, standing crop of epilithic algae, and spatiotemporal distribution of the hyporheos. The hydrological processes involved in the expansion–contraction cycle of the riverscape resulted in a complex, albeit predictable, pattern of change in the proportion and spatial arrangement of clear and turbid channels. On average, 30% of the riverscape was renewed at monthly intervals. Surface hydrological connectivity and the length of turbid channels increased logarithmically with increasing discharge. The length of clear channels increased up to a threshold discharge of 1.5 m³/s, above which surface flooding resulted in the contraction and fragmentation of clear water bodies. Turbid channels exhibited a unimodal age distribution, whereas clear channels had two cohorts that appeared during the expansion and contraction phases. The renewal pattern and configuration of the riverscape changed little between years despite differences in discharge and the occurrence of several rainfall-induced spates. The density of benthic invertebrate communities in the main channel decreased with increasing size of aquatic habitats indicating that local zoobenthic density was affected by dilution-concentration effects. The disproportionate increase in the proportion of glacial-fed habitats during summer high flows limited the standing crop of epilithic algae in this braided river. The spatial arrangement of inhospitable glacial-fed habitats probably impeded the colonization of newly created suitable habitats by invertebrates with poor dispersal capacities. Quantification of riverscape dynamics is critical to understanding how changes in size, composition, and configuration of braided rivers affect biodiversity, bio-production, and ecosystem processes.

Key words: algae; benthos; expansion-contraction cycle; flood pulse; glacial water; groundwater; habitat life span; hyporheos; inundation; shifting mosaic; spatial heterogeneity; wetland.

INTRODUCTION

River ecosystems are increasingly viewed as dynamic riverscapes (i.e., spatially and temporally heterogeneous areas made of connected water bodies), their extent, composition, and configuration vary over several temporal scales (Malard et al. 2000, Fausch et al. 2002, Ward et al. 2002; Stanford et al., *in press*). Temporal variation in the discharge of multiple water sources (i.e., river water, direct precipitation, groundwater, and local runoff) not only controls the spatial extent of the riverscape but also modifies the relative areas and spatial arrangement of water bodies, each having distinct hydraulic attributes (e.g., lentic vs. lotic), water

temperatures, and nutrient concentrations. Although compositional and configurational shifts in the riverscape are thought to control ecosystem processes and biodiversity (Junk et al. 1989, Benke et al. 2000, Tockner et al. 2000, Robinson et al. 2002), these relationships are still poorly understood. In river–floodplain systems characterized by nonerosive discharge pulses, the proportional area and spatial arrangement of water bodies fed by different water sources are expected to change in a predictable way as discharge increases (inundation sequence) and decreases (recession sequence) (Lesack and Melack 1995, Tockner et al. 2000). In contrast, changes in the composition and configuration of the riverscape are difficult to predict in braided gravel-bed rivers characterized by frequent erosive floods that continuously reshape their morphology (Arscott et al. 2002, Van der Nat et al. 2003).

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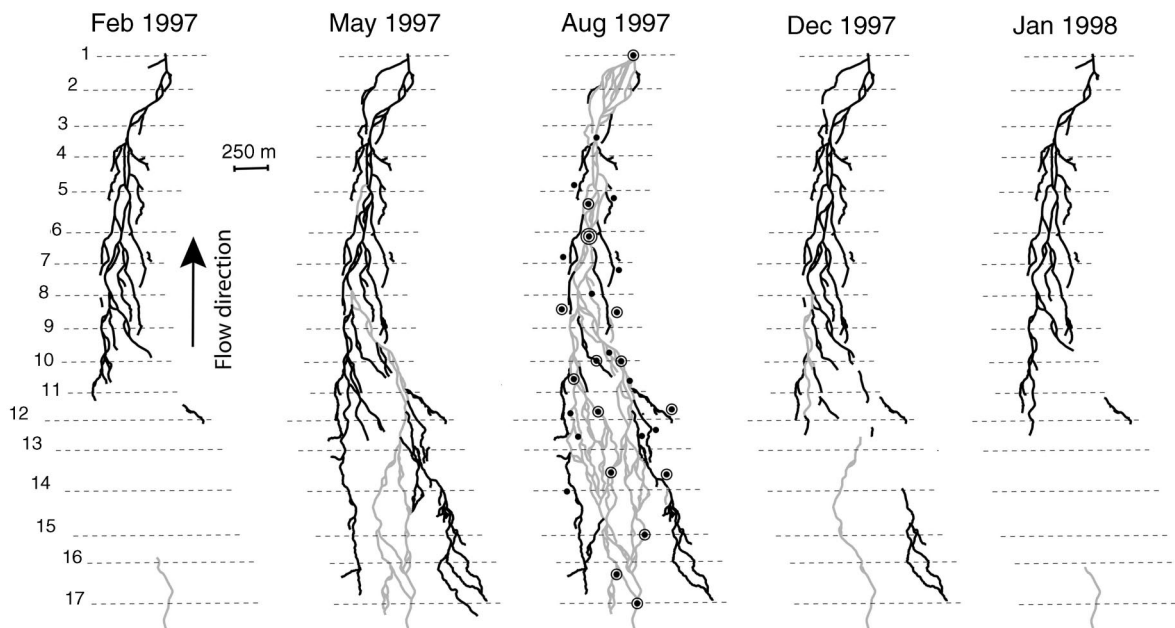


FIG. 1. Expansion-contraction cycle of the channel network in 1997 showing the distribution of clear channels (black lines) and turbid channels (gray lines) for selected months. Dashed lines indicate the sampling transects (numbers along left of figure). Solid circles with two, one, and no rings correspond to sampling sites of the zoobenthos, periphyton, and hyporheos.

Braided glacial rivers exhibit a highly predictable annual flow pulse caused by the freeze-thaw cycle onto which summer diel discharge fluctuations and unpredictable spates induced by rainfall are superimposed (Röthlisberger and Lang 1987). Glaciers and subsurface aquifers are the main water sources that interact over time and space to produce a dynamic riverscape made of contrasting glacial water fed channels and groundwater-fed channels (Brown et al. 2003). Groundwater-fed channels are more suitable habitats for algae and invertebrates than are glacial-fed channels because they have distinctly lower turbidity and shear stress, and higher temperatures and DOC concentrations (Ward 1994, Milner et al. 2001, Tockner et al. 2002, Burgherr et al. 2002, Bürge et al. 2003, Uehlinger et al. 2003). Understanding riverscape dynamics is of particular importance because the relative proportion, life span, and spatial arrangement of these contrasting water bodies control biodiversity and bioproduction within the braided band.

The main objectives of this paper are to quantify the seasonal dynamics in the extent, composition, and configuration of a headwater glacial riverscape during two annual cycles; and to assess the effects of seasonal changes in the size and pattern of the riverscape on local zoobenthic density, standing crop of epilithic algae, and spatiotemporal distribution of the hyporheos. We hypothesized that seasonal expansion-contraction cycles would result in a predictable trend of change in area, spatial arrangement, and life span of glacial-fed and groundwater-fed habitats. Seasonal changes in aquatic habitat size were expected to produce concom-

itant variation of zoobenthic density in the main channel. We also expected that the rising proportion of glacial-fed habitats during high summer flows would limit primary production and impede the dispersal of non-insect taxa within the riverscape.

STUDY SITE

The Roseg River, Switzerland, is a steep-gradient (1.9–4.8%), braided gravel-bed river. Its geomorphology, hydrology, and ecology have been investigated in exceptional detail (Ward and Uehlinger 2003). The catchment area is 66.5 km², 30% of which is covered by glaciers and 40% of which is bare rock or glacial till without vegetation. The braided band (elevation 1981–2055 m above sea level) begins 1.3 km downstream from a glacier terminus and covers a distance of 2.6 km (total area, 0.67 km²). Morphologically, two sections can be distinguished: an upper band up to 510 m wide (transects 11 to 17 in Fig. 1) and a lower band between 130 and 260 m in width (transects 1 to 11 in Fig. 1). The river has a distinct seasonal flow regime: daily mean discharge peaks during the ice-melt season (from 6 to 10 m³/s in July and August) and is lowest in winter (approximately 0.2 m³/s from January to March) when surface flow is sustained solely by groundwater.

METHODS

Mapping of the channel network

Aerial photographs of the braided band were taken on 5 August 1997 with a hand-held 35-mm camera from

a helicopter (at an altitude of 580 m above the ground) and on 23 June 1999 with a standard aerial camera with color infrared film (WILD 21 NAGIIA-F, focal length 214.74 mm; Leica Geosystems, St. Gallen, Switzerland) from an airplane (altitude, 1181 m above the ground). Additional aerial images taken in summer 1998, in combination with ground control points, were used for the generation of a digital elevation model (DEM) at a precision <0.15 m (Zah et al. 2000). The high-accuracy DEM and color-IR orthophotos from 1998 were used for the spatial correction of images taken in 1997 and 1999. Spatial corrections were performed using OrthoEngine (by PCI-Geomatics, Richmond Hill, Ontario, Canada) on a UNIX-workstation. Using ArcInfo (ESRI 1994), the flow paths of the channels with surface flow in summer 1997 and 1999 (i.e., maximum extent of the channel network) were digitized as line coverages. The channel network coverage consisted of 586 and 922 channel segments in 1997 and 1999, respectively.

Turbidity measurements and monthly mapping of the riverscape

In 1997 and 1999, changes in the pattern of channels with surface flow and water turbidity (nephelometric turbidity units, NTU) were recorded on field surveys carried out at monthly intervals (total, 24 surveys). Mean annual discharge was lower in 1997 ($2.95 \text{ m}^3/\text{s}$) than in 1998 ($3.31 \text{ m}^3/\text{s}$) and 1999 ($3.55 \text{ m}^3/\text{s}$). Moreover, the river was affected by a series of rain-induced spates between 1997 and 1999 (see Fig. 3). Six spates had a recurrence interval of >2.5 yr (i.e., instantaneous peak discharge $>27 \text{ m}^3/\text{s}$). Each month, the presence or absence of water and water turbidity (Cosmos, turbidity meter, Fa. Züllig, Rheineck, Switzerland) were recorded in each channel along 17 perpendicular transects within the braided band (Fig. 1). The number of turbidity measurements for a particular survey varied from 27 to 155 depending on the number of channels with surface flow along each transect ($n = 988$ and 1314 measurements in 1997 and 1999, respectively). Results of the monthly field surveys were used to map the network of channels with surface flow and the distribution of turbidity. Dry channel segments were excluded from the channel network coverage in ArcInfo and a single turbidity measurement was attributed to each channel segment with surface flow. A threshold turbidity value of 9 NTU was used to map the distribution of groundwater-fed channels (hereafter referred to as clear channels, turbidity < 9 NTU) and glacial-fed channels (hereafter referred to as turbid channels, turbidity ≥ 9 NTU). This threshold value was selected because turbidity in the main channel and side channels connected upstream with the main glacial channel was always >9 NTU during the ice-melt season (Malard et al. 1999, 2000). Low temperature ($<5^\circ\text{C}$), high flow velocity (>0.5 m/s), and elevated turbidity (>60 NTU) prevailing in the main channel and upstream connected

channels fed essentially by surface glacial water severely constrained bioproduction and organic matter processing (Robinson et al. 2000, Burgherr et al. 2002, Uehlinger and Zah 2003). Bioproduction hotspots in this braided glacial river corresponded to channels with no upstream connection with the main channel (i.e., downstream connected channels), which were fed either by hillslope or alluvial groundwater.

Sampling of zoobenthos, periphyton, and hyporheos

A full description of methods used for sampling the zoobenthos, periphyton, and hyporheos was provided by Burgherr et al. (2002), Uehlinger and Zah (2003), and Malard et al. (2003), respectively. Zoobenthic density was measured by collecting three Hess samples (0.043 m^2 in area) from randomly selected riffle-run habitats at a main channel site in April, June, August, October, November, and December 1997 (Fig. 1).

Periphyton biomass was measured at 16 channel sites during three low-flow periods (15 April, 10 November, and 15 December 1997; $Q = 0.49 \pm 0.27 \text{ m}^3/\text{s}$ [mean \pm SD]) and three high-flow periods (5 August, 1 and 29 September 1997; $Q = 6.74 \pm 3.80 \text{ m}^3/\text{s}$; Fig. 1). At each site and date, five to 11 rocks (3–12 cm in width) were sampled at random within a 20 m long reach. Length, width, and height of the stones were measured with calipers. Filaments of the chrysophyte *Hydrurus foetidus* were removed with a knife and nonfilamentous algae were scrubbed with a wire brush in a container with water. Aliquots of this periphyton suspension were filtered onto glass fiber filters (Whatman GF/F). Ash-free dry mass of periphyton (AFDM, g/m^2) was determined according to Clesceri et al. (1998) and was standardized on half the surface area of the stones. Surface areas of the stones were calculated according to Graham et al. (1988).

Sampling of the hyporheos was carried out at 28 channel sites during the expansion phase (2–6 June 1997; $Q = 3.78 \pm 0.51 \text{ m}^3/\text{s}$), the maximum expansion phase (28 July–2 August, $Q = 7.85 \pm 0.49 \text{ m}^3/\text{s}$), the contraction phase (22–27 September, $Q = 3.19 \pm 0.13 \text{ m}^3/\text{s}$), and one week prior to the drying of most channels in the upper part of the braided band (10–14 November, $Q = 0.65 \pm 0.10 \text{ m}^3/\text{s}$; Fig. 1). Hyporheic samples were collected by driving a mobile pipe (0.025 m internal diameter with 0.005-m holes at the base) to a depth of 30 cm below the streambed. Ten liters of interstitial water and sediment were immediately extracted using a Bou-Rouch pump (Bou and Rouch 1967). Zoobenthic and hyporheic samples were filtered through a 100- μm mesh net and preserved in 4% formaldehyde. In the laboratory, invertebrates were sorted, counted, and identified to the lowest practical taxonomic level using a dissecting microscope.

Data analysis

Extent and composition of the riverscape.—We examined changes in the length of the total channel net-

work, turbid channels, and clear channels and surface hydrological connectivity as a function of river discharge. Surface hydrological connectivity was defined as the percentage of the total channel length having an upstream surface connection with the main channel.

Relative change of the riverscape.—To quantify changes in the riverscape between two consecutive months, channels were placed into eight categories: 1, clear channels that stayed clear channels; 2, turbid channels that stayed turbid channels; 3, dry channels that became clear channels; 4, dry channels that became turbid channels; 5, clear channels that became turbid channels; 6, turbid channels that went dry; 7, turbid channels that became clear channels; and 8, clear channels that went dry. The relative change in the riverscape was defined as the percentage of the total channel network length that was modified between two consecutive months, and was calculated as follows:

$$\text{relative change} = \frac{\sum_{i=3}^{N=8} L_i}{\sum_{i=1}^{N=8} L_i}$$

where L_i = length of channels in category i .

Temporal changes in the fragmentation of clear channels were assessed by measuring their patchiness (PA) defined as the number of clear patches divided by the total length of clear channels. A clear patch was defined as a group of contiguous channels carrying clear water.

Life span distribution of channels.—Monthly changes in the life span distribution of clear and turbid channels were examined by attributing a life span to each channel segment. The life span of a channel segment was defined as the continuous time this segment carried either clear or turbid water. Segment life span was reset to zero each time that a channel segment went dry. For example, the life span of a clear segment flowing from May to September was 1, 2, 3, 4, and 5 mo in May, June, August, and September, respectively. If this channel segment went dry or became fed by turbid water in July, its life span was 1, 2, 1, and 2 mo in May, June, August, and September, respectively.

Functional classification of habitats.—Based on this detailed analysis of riverscape dynamics, we developed a functional classification of aquatic habitats. The duration of the aquatic phase and duration of clear water flow were used to distinguish between five habitats: I, permanent habitats fed exclusively by clear water; II, permanent habitats fed by clear water in winter and by turbid water during the ice-melt season; III, temporary habitats fed exclusively by clear water; IV, temporary habitats fed by clear water in spring and/or autumn and by turbid water in summer; and V, temporary habitats fed exclusively by turbid water.

Zoobenthic density, periphyton biomass, and distribution of the hyporheos.—We examined the relationship between zoobenthic density at the main channel

site and total aquatic area using linear and nonlinear functions. Channel areas with surface flow in summer 1997 (i.e., maximum area of the channel network) were digitized as a polygon coverage. Then, seasonal variations in the total aquatic area were obtained by modifying the area of polygons each month using discharge–channel-width relationships measured in multiple channels (data from Burgherr 2000).

Measurements of periphyton biomass at 16 channel sites were used to estimate the standing crop of epilithic algae in the braided band during periods of low and high flow ($n = 3$ dates per period). At each date, main channel segments, upstream connected channels, and clear water channels were assigned an average biomass value for each channel type ($4 \leq n \leq 7$ sampling sites per channel type). The standing crop of epilithic algae was then obtained for each date by multiplying the area covered by each channel type by their respective average biomass values.

We tested the relevance of our functional habitat classification for explaining spatial variation in the density of two taxonomic groups differing in their dispersal capacities. Repeated-measures analysis of variances was used to test for differences in the density of Chironomidae and Oligochaetes among habitats. The design was a two (habitat effect) by four (date) analysis of variance. The sampling date was introduced as a repeated measures factor in the analysis and its statistical significance was tested using Wilks' lambda multivariate test. Post hoc Tukey's hsd tests were performed to determine pairwise differences among habitats.

RESULTS

Seasonal changes in the extent and composition of the riverscape

The riverscape exhibited a distinct expansion/contraction cycle in response to the annual pulse in river discharge (Fig. 1). Total channel length and the length of turbid channels increased logarithmically with river discharge (Fig. 2A). Surface hydrological connectivity (SC) followed a similar pattern ($SC = 0.11 \times \ln(Q) + 0.35$; $r^2 = 0.86$, $n = 24$). About 60% of the channel network length became connected upstream with the main channel when river discharge exceeded $5.5 \text{ m}^3/\text{s}$. The relationship between length of clear channels and discharge was best explained with a discontinuous logarithmic function (Fig. 2B). The length of clear channels increased with river discharge up to a threshold of $1.5 \text{ m}^3/\text{s}$, above which the extent of clear channels decreased again.

Relative change of the riverscape

The annual pulsing of river discharge resulted in a complex renewal of the channel mosaic (Fig. 3). The relative change between two consecutive months averaged 30% and 38% in 1997 and 1999, respectively,

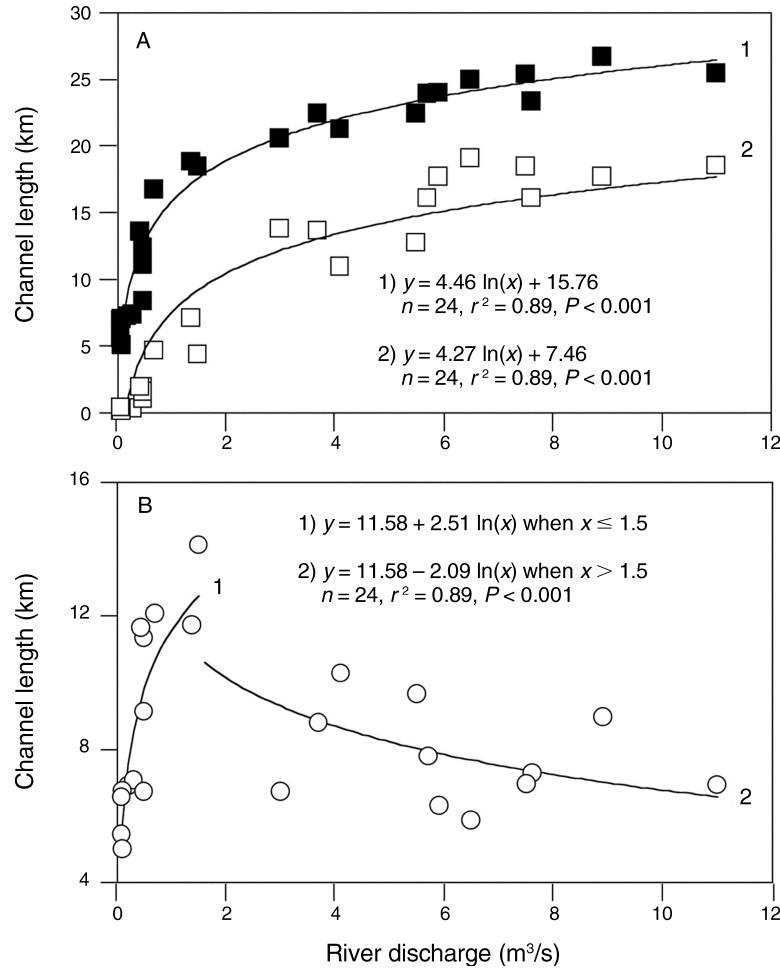


FIG. 2. (A) Relationships between the total length of the channel network (solid squares, line 1) and river discharge and the length of turbid channels (open squares, line 2) and river discharge (data from 1997 and 1999, $n = 24$). (B) Relationships between the total length of the clear-water channels (open circles) and river discharge. A discontinuous logarithmic function was used to fit this relationship. The length of clear-water channels increased with river discharge up to a threshold of $1.5 \text{ m}^3/\text{s}$ (line 1) and decreased above a discharge of $1.5 \text{ m}^3/\text{s}$ (line 2).

and was markedly higher during the expansion and contraction phases (April–June, 41%; October–January, 41%) than during the phases of minimum and maximum extension of the channel network (February–March, 2%; July–September, 12%). Changes in the composition and configuration of the mosaic of clear and turbid channels operated in a specific order as river discharge increased and decreased (Fig. 3). Increase in river discharge resulted in the successive appearance of new clear channels, flooding of clear channels with turbid water, and flushing of clear channels with turbid water. During the recession of flow, some turbid channels began to dry while others became clear channels. Finally, some clear channels went dry. The patchiness (PA) of clear channels increased logarithmically with river discharge ($\text{PA} = 0.49 \times \ln(Q) + 1.55$, $r^2 = 0.71$, $n = 24$). Whereas clear channels were aggregated in the lower part of the braided band during base flow,

flooding resulted in the isolation of many small clear patches along the band margin (Fig. 1).

Life span distribution of clear and turbid water channels

Turbid channels exhibited a unimodal life span distribution (Fig. 4). The flood pulse resulted in a single cohort of turbid channels that appeared in June and then fell dry or became clear channels during the contraction phase (November). The life span distribution of clear channels was bimodal and more complex than turbid channels. The first cohort of clear channels appeared during the expansion phase (April), whereas the second began during the contraction phase (November). About 9 km of clear channels were produced in April and May. However, about half of these clear channels persisted for only one or two months before they became turbid channels. The remaining clear channels

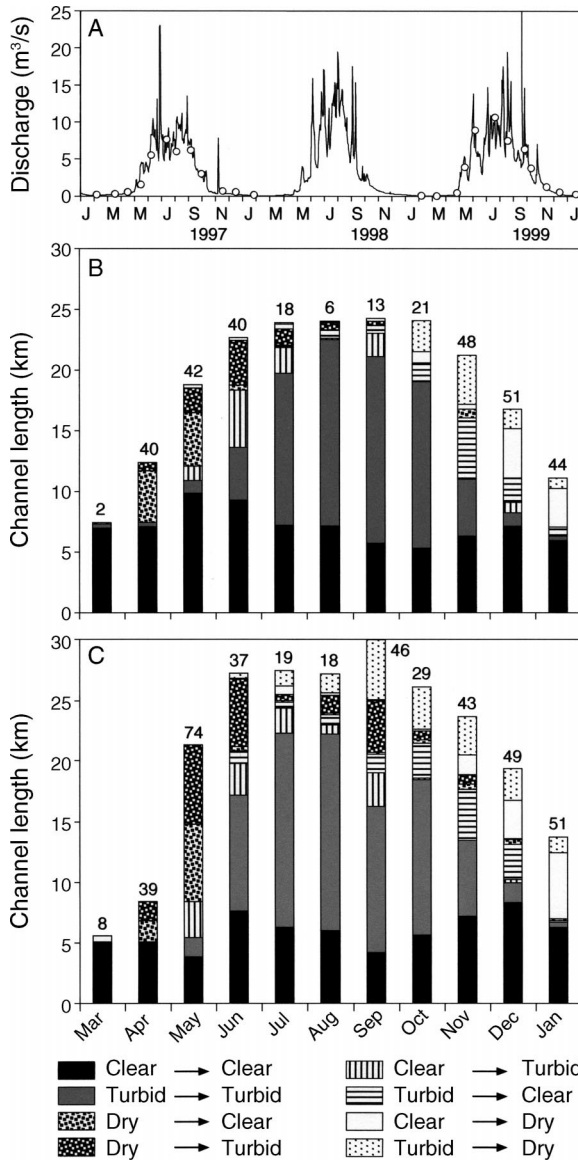


FIG. 3. (A) Daily discharge of the Roseg River in 1997, 1998, and 1999 (open circles indicate the sampling surveys) and changes in the composition of the riverscape between two consecutive months in (B) 1997 and (C) 1999. Numbers at the top of each bar indicate the relative change (%) of the riverscape between two consecutive months.

remained clear until they went dry during the contraction phase (December). Similarly, about 60% of the 8 km of clear channels created during the contraction phase (November and December) went dry within the following two months. The remaining clear channels persisted throughout the winter until they became turbid channels in the next expansion phase (May and June). There were no differences in the seasonal pattern of life span distribution of clear and turbid channels between years 1997 and 1999.

Functional classification of aquatic habitats

Permanent habitats (types I and II) represented only 27% and 17% of the maximum length of the channel network in 1997 and 1999, respectively (Table 1). Permanent habitats fed exclusively by clear water (type I) had a cumulative length of only about 2 km, and represented <10% of the maximum length of the channel network. Temporary habitats III, IV, and V had similar flow duration (i.e., from 6 to 7 mo) but carried clear water for 7, 3, and 0 mo, respectively. The relative proportion of habitat types I, II, and III was lower in 1999 than in 1997, whereas that of types IV and V increased.

Habitat mapping revealed that specific habitat types were distributed distinctly along the longitudinal and lateral dimensions of the braided band (Fig. 5). Permanent habitats (types I and II) were mostly restricted to the lower part of the braided band. Type I was located along band margins and type II in the central part of the band. Most temporary habitats were located in the upper part of the braided band. Type III was located at the margins of the upper band, type IV occurred in the center of the upper band between transects 9 and 13, whereas type V occupied the center and uppermost part of the band (i.e., between transects 13 to 17). There were few differences in the distribution pattern of habitat types between years. However, habitat type IV extended to the upstream end of the lower band (i.e., between transects 6 and 10) as well as to the right margin in the upper band (i.e., between transects 10 and 14) in 1999.

Ecological effects of changes in system size and spatial pattern

The relationship between zoobenthic density at the main channel site and total aquatic area was best explained using a power function (Fig. 6). Differences in the aquatic area among sampling dates explained 94% of the variation in zoobenthic density.

The biomass of epilithic algae was about three to eight times lower in the main channel and upstream connected channels fed by turbid water than in clear channels during high flow periods (ANOVA, channel type effect, $P < 0.001$; Tukey test, $P < 0.01$; Fig. 7). Our estimates indicated that the standing crop of epilithic algae in the braided band was higher during high-flow periods than during low-flow periods, but the difference was not statistically significant (t test, $P = 0.056$). The total periphyton biomass increased in average only twofold during high flow periods despite a threefold increase in the aquatic area.

Chironomid larvae were more abundant in hyporheic sediments of both permanent and temporary habitats fed exclusively by clear water (I and III) than in glacial-fed habitats (II, IV, and V) (ANOVA, habitat effect, $P < 0.001$; Tukey tests, $P < 0.03$; Fig. 8). There were no differences in density between permanent (I) and

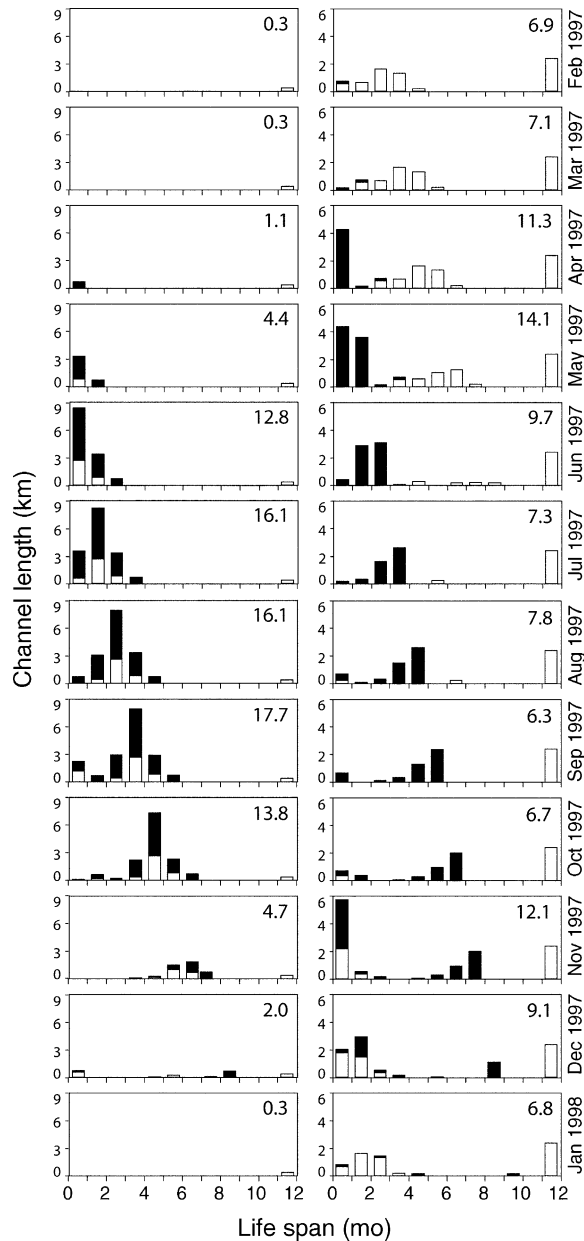


FIG. 4. Monthly changes in the life span distribution of turbid channels (left-hand panels) and clear channels (right-hand panels) in 1997. Open parts of bars correspond to permanent channels and solid parts of bars to temporary channels. Numbers in the upper right corner of each panel indicate the length of channels (km).

temporary clear habitats (III). The density of Chironomidae increased from June to November in clear habitats I and III (ANOVA, time effect, $P = 0.003$). Oligochaeta were significantly more abundant in permanent clear habitats (I) than in other habitats (Tukey tests, $P < 0.05$) but there were no differences in density between temporary groundwater habitats (III) and glacial water habitats (II, IV, and V).

DISCUSSION

Expansion–contraction cycle

Natural riverscapes alternatively expand and contract over multiple temporal scales (Stanley et al. 1997). At the annual scale, the channel network in the Roseg River varied three- to fivefold in length (i.e., from 7.1 to 24 km and from 5.1 to 26.7 km in 1997 and 1999, respectively). Although not documented in this study, the size of the riverscape changed at a daily scale in summer and in response to unpredictable rainfall-induced spates. Zah et al. (2001) demonstrated that the area of the braided band has continuously increased over the last 50 years, probably in response to higher sediment availability and transport caused by the retreat of the glaciers (Ward and Uehlinger 2003). Because the Val Roseg is a high-gradient, deep, braided, gravel-bed river with well-defined thalwegs, water flow was mostly confined to stream channels during the annual expansion–contraction cycle (Uehlinger et al. 2003). Only at river discharge exceeding $25 \text{ m}^3/\text{s}$ did water spill over the main channel banks to inundate a relatively small area of the braided band (i.e., a 30–60 m wide inundated corridor; Uehlinger et al. 2003). Fenn and Gurnell (1987) showed that the Tsidjiore Nouvelle proglacial stream, Switzerland, shifted from a single channel to multiple braids as it progressively reoccupied dry channels during the ice-melt season (a process known as secondary anastomosis). In contrast, Van der Nat et al. (2002) showed that the complete inundation of the braided band of the Tagliamento River, Italy, occurred three to four times per year. Mosley (1983) emphasized variations in flooded areas as a function of discharge among braided rivers of New Zealand and concluded that it was not feasible to predict changes in the channel character of braided rivers in response to discharge variation. The seasonal expansion of the Roseg riverscape was caused ultimately by an increased flux of snow and ice-melt water, however, melting water moved throughout the braided plain via surface and subsurface pathways (Malard et al. 1999). The simultaneous occurrence of two hydrological pathways maintained the complex mosaic of clear and turbid channels throughout the expansion phase.

Riverscape composition and configuration

Detailed analysis of the shifting mosaic of clear and turbid channels supported our first hypothesis: the hydrological processes involved in the expansion–contraction cycle resulted in a predictable trend of change in the composition and configuration of the riverscape as discharge increased and declined. We quantified a pattern that was expected from concepts in glacial river hydrology (Röthlisberger and Lang 1987), but we acknowledged that the exact proportion and location of clear and turbid channels remained difficult to predict because of local geomorphic and hydrologic processes. Whereas increased subsurface expansion of snow and

TABLE 1. Characteristics of habitat types on the Roseg River.

Characteristic	Habitat types [†]				
	I	II	III	IV	V
Life span (mo) [‡]					
1997	12.0	12.0	7.2 ± 1.5	6.9 ± 2.0	5.6 ± 2.3
1999	12.0	12.0	7.7 ± 1.0	6.6 ± 1.9	4.4 ± 2.2
Duration of clear water flow (mo) [§]					
1997	12.0	6.4 ± 1.2	7.2 ± 1.6	2.6 ± 1.8	0.0
1999	12.0	6.0 ± 1.6	1.4 ± 1.1	2.9 ± 1.7	0.0
Length (m)					
1997	2382	4315	4352	6140	7550
1999	1425	3781	3354	10 596	11 923
Percentage of total					
1997	9.6	17.4	17.6	24.8	30.5
1999	4.6	12.2	10.8	34.1	38.4

Note: Error measurements shown are SD.

[†] Habitat types: I, permanent habitats fed exclusively by clear water; II, permanent habitats fed by clear water in winter and by turbid water during the ice-melt season; III, temporary habitats fed exclusively by clear water; IV, temporary habitats fed by clear water in spring and/or autumn and by turbid water in summer; and V, temporary habitats fed exclusively by turbid water.

[‡] Channel segments belonging to permanent habitat types I and II all have a life span of 12 months; thus, their standard deviation is zero.

[§] Channel segments belonging to habitat types I and V all have a duration of clear water flow of 12 and 0 months, respectively. Thus, their standard deviation is zero.

ice-melt waters (via hillslope and alluvial aquifers) first generated new clear channels in the upper braided band, the increased glacial surface water runoff then led to the flooding of dry channels and pre-existing clear channels with turbid water. This dual flooding process resulted in an almost complete change in the proportion of clear and turbid channels and spatial arrangement of clear channels within a short time (<2 mo). The recession sequence began with a reduction in surface glacial water that resulted in a decrease in the extent of turbid channels and a concomitant increase in the extent of clear channels. Clear channels then progressively decreased as the recharge of hillslope and alluvial aquifers ceased. In their qualitative floodplain inundation model, Lewin and Hughes (1980) emphasized that distinct water sources and hydrological processes operated in a specific order as discharge rose and receded. Mertes (1997) demonstrated, using remote-sensing and field data from several reaches of large rivers around the world, that the early filling of floodplains with clear local water restricted the lateral expansion of turbid river water.

Differences in discharge between the years 1997 and 1999, and the occurrence of several rainfall-induced spates, including one with a recurrence interval of 50 years (peak discharge of 63 m³/s on 20 September 1999), did not modify the seasonal sequence of clear and turbid channel replacement. Although there were noticeable changes in the respective proportions of the five habitat types between 1997 and 1999, the composition and spatial configuration of the riverscape was more stable than predicted earlier by Malard et al.

(2000:693). However, these results conform to more recent findings by Zah et al. (2001) who demonstrated that the structure of the channel network (i.e., sinuosity and braiding indexes) remained relatively constant over the last 50 years. They are also consistent with long-term observations of channel change in other upland braided rivers (Warburton et al. 1993, Fenn and Gurnell 1987). The braiding pattern of the Roseg River probably reflects the occurrence of prior channels with high contemporaneous flows insufficient to override their imprint in the morphology of the braided band (Warburton et al. 1993). Interannual morphological changes involve local erosion or deposition in the main channel leading to localized changes in the distribution of glacial flow within the braided band. For contrast, Van der Nat et al. (2003) measured a relative spatial change of aquatic habitats of 86% over a period of only 2.5 yr in a bar-braided reach of the Tagliamento River, Italian Alps. Because scouring spates reconfigured the spatial arrangement of aquatic habitats without modifying their relative proportion within the riverscape, Van der Nat et al. (2003) concluded that the dynamics of the braided band of the Tagliamento River conformed to the shifting mosaic steady-state model proposed by Borman and Likens (1979; see also Arscott et al. 2002). Longer periods of study are required to test whether this type of dynamic equilibrium also applies to the Roseg riverscape in response to the lateral movement of the main channel.

Age distribution of clear and turbid water channels

Flow variation in river systems not only controls the duration of the aquatic phase, but also the timing when

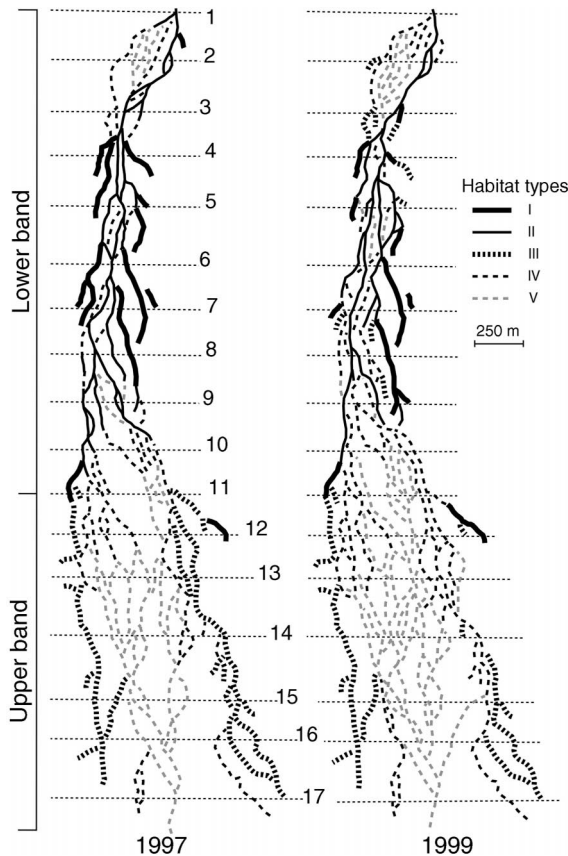


FIG. 5. Simplified maps of the braided band showing the distribution of five habitat types in 1997 and 1999. Habitat types are described in Table 1.

channels are fed by distinct water sources. In addition to drying, changes in the physical environment (e.g., flow velocity, temperature) and in resource availability (e.g., periphyton biomass) caused by a shift in water source also can be considered a disturbance (sensu White and Pickett 1985). Burgherr et al. (2002) showed that the density and composition of zoobenthic assemblages in braided channels fluctuated drastically in response to changes in the relative contribution of glacial water to surface flow. In the Roseg River, surface flow was permanent in about 20% of the channel network and persisted on average 6 mo in the remaining temporary channels. However, the average time a flowing channel remained continuously fed either by clear or turbid water was only 4.4 mo (excluding the permanent groundwater-fed channels that represented <10% of the riverscape). Interestingly, the results showed that channels fed by distinct water sources could be viewed as cohorts that appeared, maintained, and disappeared during particular phases of the expansion–contraction cycle. As expected, the successive expansion and recession of glacial water resulted in a single cohort of turbid channels. In contrast, clear channels had a summer cohort and a winter cohort that appeared during

the expansion and contraction phases of the riverscape, respectively. These two cohorts may either be used by invertebrate species with dissimilar life cycles or by the same species at different stages of its life cycle. Van der Nat et al. (2003) demonstrated that the half-life of aquatic habitats in braided reaches of the Tagliamento River was less than 7 mo. They suggested that the short time span of most habitats constrained species with long life cycles.

Ecological effects of riverscape dynamics

The extremely dynamic nature of natural riverscapes provides ideal settings to examine the consequences of changes in system size and spatial pattern on ecological processes and biodiversity. Change in aquatic habitat size is a fundamental feature of river systems that potentially affects all aspects of the ecosystem (Stanley et al. 1997, Benke 2000, Tockner et al. 2000). Despite the widespread occurrence of glacial river shrinkage during flow recession, almost no studies have considered that the autumnal increase in local zoobenthic density might reflect the concentration of individuals in the shrinking aquatic habitat (but see Burgherr et al. 2002). Distinct seasonal shifts in the density of zoobenthos were previously attributed to variation in temperature, channel stability, and food resources (Milner et al. 2001). In the Roseg River, the strong relationship between local zoobenthic density and total aquatic area strongly suggested that dilution–concentration effects were in part responsible for seasonal variations in the density of benthic invertebrates in the main channel. Previous studies of glacial rivers which ignored the effect of changing stream size might have attributed a disproportionate importance to ecological factors for explaining density variations.

Bed sediment movement is a primary factor limiting periphyton biomass in gravel-bed rivers (Biggs et al. 1999, 2001). In glacial rivers, the growth of algae is

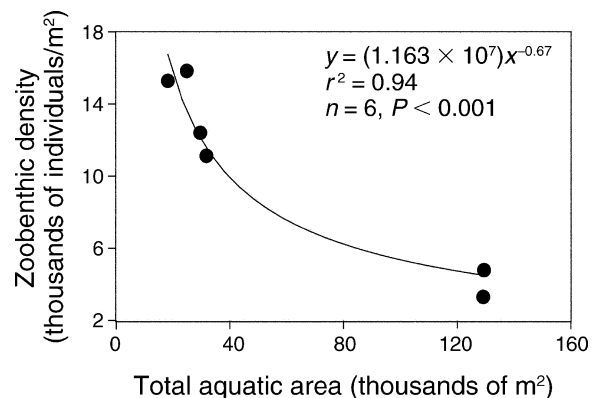


FIG. 6. Relationship between zoobenthic density at a main channel site (transect 6 in Fig. 1) and total aquatic area (data from Burgherr et al. [2002]). Zoobenthos were collected in April, June, August, October, November, and December 1997 ($n = 3$ replicate samples per date).

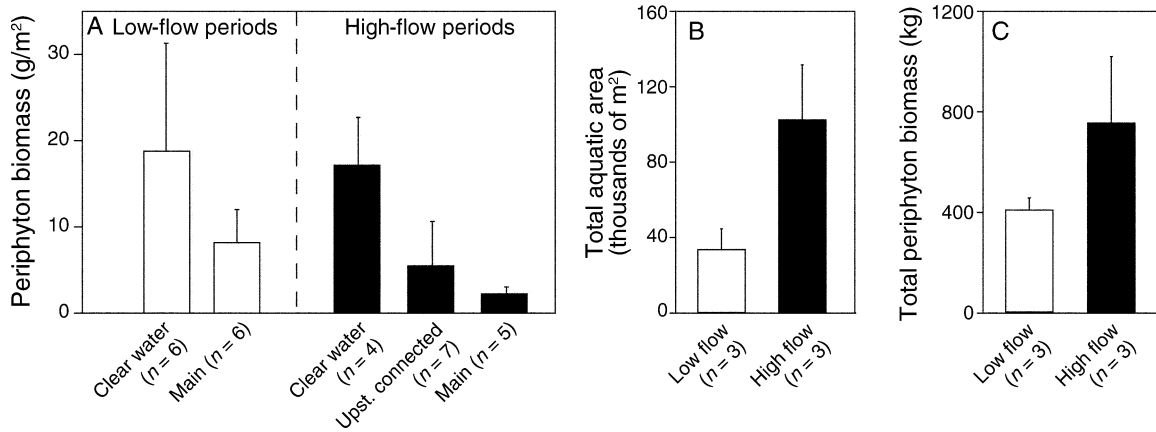


FIG. 7. (A) Characteristic pattern of periphyton biomass (ash-free dry mass, AFDM) among channel types (clear-water, main, and upstream connected) during low-flow (open bars) and high-flow (black bars) periods (data from Uehlinger and Zah [2003] for 15 December and 1 September 1997, respectively). (B, C) Differences in total aquatic area and total estimated biomass (AFDM) of epilithic algae in the braided band between periods of low flow (data from 15 April, 10 November, and 15 December 1997) and high flow (data from 5 August and 1 and 29 September 1997). Error bars show SD.

further constrained by light limitation due to high turbidity and by low supply of growth-limiting nutrients (Lloyd et al. 1987, Bürgi et al. 2003). During high-flow periods, the combining effect of bed instability, reduced light availability, and low temperature severely limited the accrual of benthic algae in the main channel and upstream connected channels fed by glacial water. The rising proportion of these low-productivity habitats in the braided band mitigated the beneficial effect of the summer increase in aquatic habitat size on the total biomass of epilithic algae. The disproportionate increase in the proportion of unfavorable habitats during flooding presumably prevents braided rivers from sustaining high standing crops of algae and invertebrates (Tockner et al., *in press*). The moderate increase in algal biomass caused by the shift in riverscape composition might also restrict secondary production in the Roseg River. Rempel et al. (2000) suggested that high turbidity and fine sediment deposition in the Fraser River, Canada, limited algal and grazer productivity and accounted for the low representation of grazers in the zoobenthos. Mosley (1983) examined changes in the aquatic area usable by fishes as a function of discharge in several New Zealand braided rivers. The weighted usable area index (a function of water depth, flow velocity, and species preference) generally increased with river discharge but there were large differences in the shape of the relationship among rivers.

From a landscape perspective, biodiversity patterns in streams reflect the differential responses of organisms with distinct biological traits to the composition and spatial configuration of the riverscape (Townsend and Hildrew 1994, Wiens 2002). However, most predictive models of invertebrate community structure in streams including the disturbance-productivity-diver-

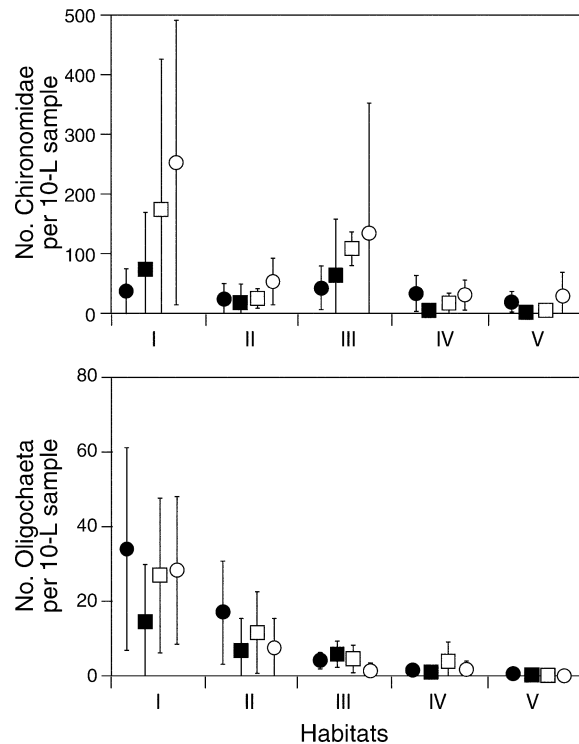


FIG. 8. Differences in hyporheic density of Chironomidae and Oligochaeta among habitats (see Table 1 and Fig. 5 for the definition of habitats). Solid circles, solid squares, open squares, and open circles correspond to sampling surveys carried out in June, August, September, and November 1997, respectively ($3 \leq n \leq 7$ replicate samples per habitat and date). Data are from Malard et al. (2003). Error bars represent SD.

sity model (Hildrew and Townsend 1987) and the habitat templet model (Townsend and Hildrew 1994) largely ignored the ecological significance of the spatial arrangement of habitats. Most invertebrates in this harsh braided riverscape are expected to preferentially select suitable clear water habitats (I and III) because they provide flow refugia with high substrate stability and high algal productivity during the summer expansion of glacial water. Flow refugia strongly contribute to the diversity of invertebrate communities in unstable graded-bed rivers although they often represent a small proportion of the total aquatic area (Rempel et al. 2000, Biggs et al. 2001; Tockner et al., *in press*). Temporary clear water habitats (III) may however be inaccessible flow refugia to species with poor dispersal capacities, because they are separated from permanent source areas of colonizers (I) by inhospitable glacial-fed channels (II, IV, and V). Differences in the spatiotemporal pattern of Chironomidae and Oligochaeta in shallow hyporheic sediments of the braided band support this hypothesis. Because of their high dispersal capacities (Robinson et al. 2004), chironomids equally colonized habitats I and III. Oligochaetes were abundant in permanent clear-water habitats (I) but they failed to colonize temporary clear-water habitats (III) in great numbers despite suitable environmental conditions and long flow duration (7 mo in habitat III). High flow velocity and bed instability in glacial-fed channels impeded the dispersal of oligochaetes via upstream migration (Malard et al. 2001). Vertical migration from groundwater was also severely limited by the weakness of hydrological connections between groundwater and hyporheic sediments in the upper braided band (Malard et al. 2003). Biodiversity patterns in expanding-contracting aquatic systems may not only reflect the spatial heterogeneity of environmental conditions but also the constraints imposed by the riverscape configuration on the dispersal of organisms.

CONCLUSIONS

Landscape ecology is being recognized as a promising approach for developing a truly holistic perspective of river structure and function (Fisher et al. 2001, Ward et al. 2002; Stanford et al., *in press*). Conversely, riverscapes provide excellent arenas for testing landscape ecological theory (Wiens 2002). Variation in the flux of distinct water sources and hydrological pathways in a catchment makes riverscapes extremely dynamic over multiple temporal scales. In this braided glacial river, seasonal variation in the flux of melting water and surface and subsurface flow paths resulted in a predictable pattern in riverscape composition and configuration. This seasonal pattern and resulting diversity of habitats which recurred among years despite contrasting annual flow (but see also Zah et al. 2001) might facilitate the development of adaptations among invertebrates for exploiting the natural flood regime (Lytle and Poff 2004). Quantifying the dynamics of

riverscapes among natural river systems differing in their hydrology is a critical step in understanding their functions and to restore regulated riverine corridors. A next important step is to obtain quantitative estimates for determining how temporal changes in the size, composition, and configuration of riverscapes affect biodiversity and bioproduction of river systems.

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APPENDIX A

A photo of the lower braided band of the Roseg River (length, 1.6 km) (*Ecological Archives* E087-041-A1).

APPENDIX B

A table providing compositional and configurational characteristics of the riverscape (*Ecological Archives* E087-041-A2).

APPENDIX C

A figure showing the totality of the expansion–contraction cycle in 1997 and 1999 (*Ecological Archives* E087-041-A3).

APPENDIX D

A figure showing monthly changes in the age distribution of turbid channels and clear channels in 1999 (*Ecological Archives* E087-041-A4).

APPENDIX E

Detailed color maps showing the distribution of habitat types in 1997 and 1999 (*Ecological Archives* E087-041-A5).