

Spatial patterns in macroinvertebrate assemblages in surface-flowing waters of a glacially-influenced floodplain

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Abstract We examined the spatial structure of macroinvertebrate assemblages in surface-flowing waters of a glacially-influenced floodplain. The floodplain main-channel responded longitudinally to changes in hydrology with evident coarse-scale zones of upwelling and downwelling; the lower floodplain main channel fell dry in late winter. Physico-chemical attributes differed among tributaries and the main channel. The main channel had lower values of conductivity, alkalinity and nitrate–N than tributaries, with right-side (east-facing) tributaries having the highest values. Left-side (west-facing) tributaries flowing over an exposed rock-face had warmer water temperatures than the main channel and right-side tributaries. The biomass of benthic organic matter and periphyton was highest in right-side tributaries, followed by main channel sites then left-side tributaries. Similarly, macroinvertebrate density and richness were higher in right-side tributaries, intermediate in main channel sites, and lowest in left-side tributaries. Macroinvertebrate assemblages clearly differed between main channel sites, right-side tributaries, and left side tributaries based on an NMDS analysis. Minor differences were observed among main channel sites, although most upstream sites showed some structural differences from downstream sites. Ephemeropterans and plecopterans were most common in main channel sites and right-side tributaries, whereas chironomids and trichopterans also were common in right-side tributaries. Although the main

channel changed longitudinally in physico-chemical characteristics, no real patterns of zonation were evident in macroinvertebrate assemblages. Coarse spatial patterns in macroinvertebrate assemblages in the floodplain were reflected in the physico-chemical differences between the main channel and tributaries, and between left-side and right-side tributaries. We conclude that coarse-scale floodplain properties enhance the overall diversity of lotic macroinvertebrates. Consequently, floodplain alterations that reduce surface water heterogeneity/connectivity limits the potential macroinvertebrate diversity of floodplains.

Keywords Stream · Aquatic insects · Glacial · Tributary · Temperature · Hydrology

Introduction

Intact floodplains are dynamic ecosystems that harbor an amazingly diverse flora and fauna (Robinson et al. 2002b). Much of this diversity can be linked to the hydrological complexity that occurs in natural floodplains (Gregory et al. 1991). Spatially, this hydrological complexity is evident in the kinds and numbers of both surface waters and terrestrial habitats (Arscott et al. 2002; Van der Nat et al. 2003). Additional complexity is related to habitat linkages with sub-surface flowpaths that influence coarse-scale patterns in upwelling and downwelling zones (Boulton et al. 2010; Doering 2012b). Hydrological complexity is also demonstrated temporally (daily or seasonally) via changes in event-driven flows or annual discharge regimes. For instance, floods and flow pulses are an inherent feature in the ecology of floodplains (Junk 1989; Tockner et al. 2000), directly influencing the life histories of floodplain flora and fauna. These natural

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changes in flow create and maintain a successional habitat mosaic that ultimately sustains floodplain biodiversity (Stanford et al. 2005). A major concern today is the loss in biodiversity from floodplain regulation resulting in a reduced hydrological complexity and associated loss in floodplain aquatic and terrestrial habitats. Consequently, a greater understanding of the role surface-flowing waters in maintaining macroinvertebrate diversity in floodplains is urgently needed to enhance the recovery potential from floodplain restoration actions.

From a holistic perspective, most floodplain ecosystems can be viewed within a spatio-temporal hierarchical context (sensu Frissell et al. 1986). Floodplain dynamics were also key in respect towards perceiving rivers within a 4-dimensional domain (Ward 1989; Ward et al. 2002) that included the longitudinal, lateral and vertical spatial relationships of rivers within the floodplain landscape along with time as the 4th dimension. Further researchers visualized floodplains as 'beads on a string', suggesting the role of geomorphic knick points in delineating the upper and lower boundaries of floodplains in a hydrological context (Stanford and Ward 1993). In this respect, hydrology across space and time is the primary component integrating the multi-dimensional hierarchy of floodplains, dictating the general habitat template of surface waters in floodplains (sensu Southwood 1977). This relationship allows floodplains to be placed in a more predictive relationship underpinning ecological pattern and process. For example, upwelling and downwelling zones follow a spatial hierarchy as rivers flow through the floodplain landscape. At a coarse-scale, many floodplains exhibit downwelling areas in the upper floodplain and upwelling areas in the lower floodplain with hyporheic boundaries shifting with hydrology (Boulton et al. 2010). At a finer scale, downwelling zones often occur at the heads of riffles and upwelling zones are found at riffle tails (Brunke and Gonser 1997). In the context of this study, an important issue is to determine whether coarse-scale patterns in macroinvertebrate assemblage structure are related to spatio-temporal differences along and among surface-flowing waters embedded in the floodplain landscape, thus being the principal driver, i.e. loss in surface water heterogeneity, of biodiversity loss from floodplain regulation.

Indeed, most natural floodplains contain a variety of surface-flowing waters external to the main channel. These flowing waters comprise side-slope tributaries of varying size, groundwater streams upwelling in the floodplain, side-channels of the main channel, and potentially even ponds of different size and degree of permanence (Tockner et al. 1997; Arscott et al. 2000, Ward et al. 2002, Stanford et al. 2005, Gray and Harding 2007). Under flow and floodplain regulation, many of these other surface waters are lost and spatial heterogeneity of the main channel itself is reduced

as side channels and lateral connectivity of surface waters are eliminated. Frequently, even the tributaries are channelized or placed in culverts to improve the drainage capacity of the system to reduce flow/flood risks and hazards to human dominated landscapes. The overall effect of floodplain regulation is to reduce the spatial heterogeneity of surface-flowing waters in floodplains along with a loss in lateral and vertical connectivity of water bodies, often resulting in an overall loss in the diversity of habitats and their flora and fauna (e.g., Doering 2012a). An overarching question beckons as to the contribution of different surface waters to the gamma diversity of a floodplain ecosystem. For instance, does the enhanced spatial heterogeneity inherent in natural floodplains comprising a variety of surface waters translate into a higher overall aquatic biodiversity, and if so, should management actions take this into account in the restoration of degraded floodplains.

The primary goal of this study was to characterize the distribution and abundance of macroinvertebrates in surface-flowing waters of a relatively intact floodplain ecosystem. Surface waters included the glacial-influenced main channel and various tributaries (and groundwaters) on either side of the floodplain. The floodplain also was longitudinally structured in terms of upwelling and downwelling dynamics directly influenced by catchment hydrology. We expected spatial distribution patterns and abundances of macroinvertebrates to reflect the physico-chemical attributes of the different surface waters (e.g., permanent vs temporary tributaries) and longitudinally along the main channel (coarse-scale upwelling downwelling properties). We predicted that the spatial heterogeneity of surface waters in the floodplain would contribute to the overall biodiversity of the system as assessed through aquatic macroinvertebrates.

Study site description

The Sandey floodplain (790–910 m a.s.l., ca. 125 ha) on the lower Urbach River is situated in the central Alps of Switzerland (46°40'N, 8°12'E) (Fig. 1). The 3.4-km long and up to 600-m wide floodplain is bordered by grassland and forested mountain slopes to the east, a steep (up to 1.6 km high) rock-face confines the floodplain valley to the west, and the floodplain has canyon-constrained knick-points at both ends. The catchment has moderate precipitation (1345 mm year⁻¹) and high seasonal and daily variation in temperature (average annual temperature = 8.8 °C). Geology is mainly characterized by limestone and crystalline rocks. Floodplain vegetation is dominated by alder (*Alnus incana*) and willow (*Salix* spp.). The floodplain contains habitats typical of natural floodplains, including the main channel, side channels, islands,

open gravel bars, and vegetated gravels. Livestock (cows, sheep) grazing occurs in the floodplain in summer.

The discharge regime of the Urbach is melt-water dominated with highest discharge during snow- and glacier-melt in spring/summer, although precipitation events result in frequent high flow pulses (Fig. 2). Various tributaries and groundwater springs enter from both sides of the floodplain. Since 1950, a dam ca. 6 km upstream of the study area allows about 30 % of the average annual discharge to be abstracted from the system, and several levees have been installed throughout the years in the active floodplain area for flood protection. The upper floodplain acts mostly as a downwelling system (range VHG = -0.34 to -0.45), whereas the lower floodplain acts mostly as an upwelling system (range VHG = -0.09 to 0.06) that shifts longitudinally with seasonal melt-waters and precipitation-related high flow events (Fig. 2).

For the study, we divided the main channel longitudinally into four channel segments (called zones hereafter) that corresponded to clearly observed changes in floodplain morphology and hydrology (see Fig. 1). Channel slope of the main channel ranged between 3 and 5 %. Zone 1 was at the head of the floodplain and extended ca. 500 m downstream with mostly downwelling properties (mean VHG = -0.34). Zone 2 was downstream of zone 1 and

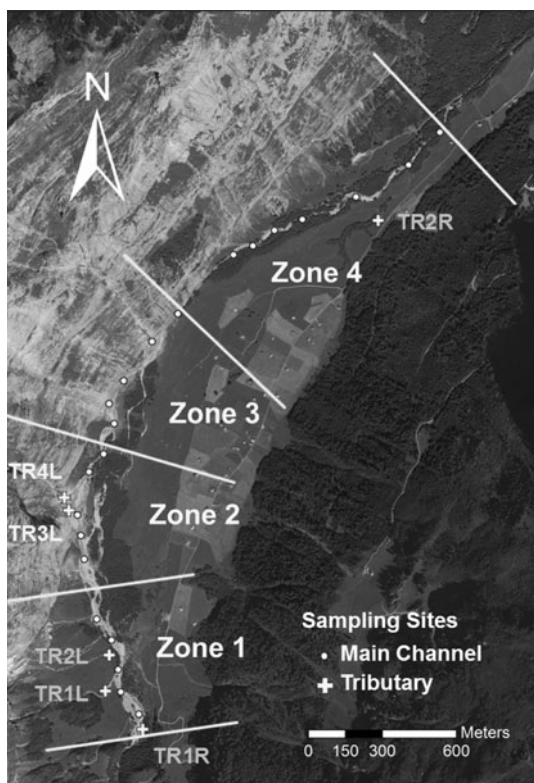


Fig. 1 Schematic map of the Sandey floodplain in central Switzerland with locations of study sites. The river flows downstream from zone 1 to zone 4

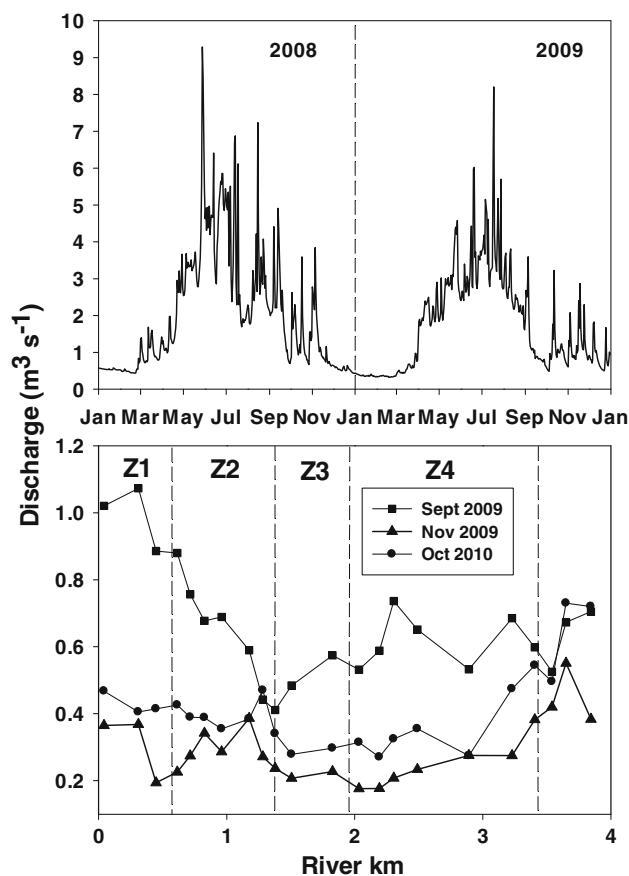


Fig. 2 Annual discharge (top) and seasonal changes in the spatial hydrology of the Sandey floodplain (bottom) with river km beginning at the head of the floodplain

represented a confined channel segment bordered directly with the steep rock-face on the left side. This zone also was in the most downwelling area of the floodplain (mean VHG = -0.45). Zone 3 was located downstream of zone 2 and represented a single channel at the upper most influence of the upwelling area of the floodplain (mean VHG = -0.29). Zone 4 was downstream of zone 3 and represented a mostly intact floodplain channel with mostly upwelling properties (mean VHG = 0.06) and relatively high lateral connectivity. We also sampled four tributaries on the left side of the floodplain that originated from high elevation areas above the steep rock-face. These tributaries below the rock-face had channel slopes up to 30 %. Two intermittent left-side tributaries entered the river in zone 1 (TR1L and TR2L), whereas the other two tributaries entered in zone 2 and were permanent (TR3L and TR4L). Two permanent tributaries were sampled on the right side of the floodplain, a small forest tributary that entered the river in zone 1 and a large side-slope and groundwater-fed tributary that entered the river in zone 4. Channel slopes of these tributaries at the sample reaches were ca. 3 %. All sites were dominated by cobble substrates, but interspersed

with some boulders in the main channel and sand/pebble substrata in right-side tributaries.

Methods

Sampling was conducted monthly from spring to autumn in 2009 (July to October) and 2010 (May to October). Study sites were inaccessible in winter and early spring. Data loggers for temperature (Vemco Inc., Canada) were installed at each study site except TR4L and recorded water temperature at 30 min intervals; loggers were downloaded every 4–6 months. An additional temperature logger was installed at the end of zone 4 as well. Piezometers were installed to measure the vertical hydraulic head at specific locations along the main channel to assess upwelling and downwelling characteristics of the floodplain in late spring/early summer and late summer/early autumn (see Bodmer 2011). In addition, discharge was measured using the standard transect method (Platts et al. 1983) in the main channel at locations near where the piezometers were placed to further examine longitudinal changes in flow. A flow tracker was used to determine flow velocities for estimating discharge.

On each sampling date, spot measures of conductivity, temperature, pH, and turbidity were recorded using portable field meters (WTW GmbH, Weilheim, Germany). In addition, a 1-L grab sample of water was collected and returned to the laboratory in a cooler with ice. The water sample was analyzed in the laboratory for DOC, POC, alkalinity, TIC, nitrate, dissolved nitrogen, particulate nitrogen, phosphorus, dissolved phosphorus and particulate phosphorus using methods detailed in Tockner et al. (1997). Transported organic matter (seston) and drifting macroinvertebrates ($n = 3$, sampling duration = 3 min each) were collected at the head of each zone and tributary on each visit using a 100- μm mesh nylon net (1-m long, aperture = 11 cm). Flow was recorded at the mouth of the net using a MiniAir2 velocity meter (Schiltknecht AG, Gossau, Switzerland) to calculate the volume of water filtered. In the laboratory, invertebrates were handpicked from each sample, identified, and counted. The remaining material was then dried at 60 °C, weighed, ashed at 550 °C, and reweighed for determination of seston as ash-free dry mass (AFDM).

Five 10-m long reaches (7 reaches for zone 4 in 2010) were located longitudinally equidistant (100–150 m apart depending on zone length) within each zone and used for sampling of macroinvertebrates and periphyton. One sample of macroinvertebrates (Hess sampler, 250- μm mesh, 0.04 m² area) was collected at each reach within each zone ($n = 5$ samples total per zone, 7 samples for zone 4 in 2010) on each sample date and preserved with 70 % ethanol.

Three benthic Hess samples were collected from each tributary on each date as well. Study reaches in tributaries were ca. 10–20 m long depending on the size of the tributary. Benthic samples were returned to the laboratory, macroinvertebrates were handpicked from each sample using a microscope at 10 \times magnification, identified to lowest feasible taxonomic unit (mostly genus except chironomids), and counted. The remaining material was used to estimate benthic organic matter (BOM) as AFDM as above.

Two stones were collected from each study reach in each zone ($n = 10$ stones per zone, 14 stones for zone 4 in 2010) on each date for estimates of periphyton biomass as AFDM. Five stones were collected from each tributary on each date as well. Periphyton was scrubbed from a measured area from the stone surface using a metal brush. The slurry was collected and its volume measured. A measured portion of the slurry was filtered (Whatman GFF filters) and returned to laboratory for analysis of AFDM (units = g AFDM m⁻²).

Data analysis

The physico-chemical water measures were assessed using a principal components analysis (PCA) on $\log(x + 1)$ transformed data. Two PCAs were conducted, one comparing all sites among dates and a second comparing the individual zones among dates. The second PCA was used to have a more clear illustration of physico-chemical differences among zones in the main channel. Temperature data from the data loggers were summarized as maximum, minimum, mean, standard deviation and coefficient of variation (CV) for each site. Differences between sites in drift and seston were tested using ANOVA on $\log(x + 1)$ transformed data (Zar 1984). Variation in drift and seston among dates and between sites was assessed using the coefficient of variation (CV). ANOVA was also used to test for site differences in macroinvertebrate density and taxon richness, benthic organic matter, and periphyton AFDM on $\log(x + 1)$ transformed data. Lastly, non-metric dimensional scaling (NMDS) was used to examine for site and date differences in macroinvertebrate assemblage structure using $\log(x + 1)$ transformed density data of the individual taxa collected. Two plots were generated from the data, one comparing all sites and a second with only the zones being illustrated.

Results

Physico-chemistry

Conductivity values were substantially higher in the tributaries (mean = 144 $\mu\text{s cm}^{-1}$) than the main channel (mean = 84 $\mu\text{s cm}^{-1}$), although mean values increased

Table 1 Summary of physico-chemical measures recorded monthly for each site during the study period (n = 10)

Site	Conductivity ($\mu\text{S cm}^{-1}$)	Turbidity NTU	pH	DOC (mg C L^{-1})	POC (mg C L^{-1})	Alkalinity mmol L^{-1}	TIC mg C L^{-1}	$\text{NO}_3\text{-N}$ (mg N L^{-1})	DN (mg N L^{-1})	PN (mg P L^{-1})	$\text{PO}_4\text{-P}$ (mg P L^{-1})	DP mg P L^{-1}	PP (mg P L^{-1})
Zone 1													
Mean	77.1	30.3	7.9	0.58	0.30	0.55	6.55	0.29	0.46	0.03	4.42	5.23	7.10
SD	26.7	32.8	0.5	0.14	0.19	0.07	0.80	0.07	0.10	0.03	4.99	4.63	5.96
CV	0.3	1.1	0.1	0.24	0.64	0.13	0.12	0.24	0.21	0.97	1.13	0.88	0.84
Zone 2													
Mean	82.0	19.0	7.9	0.51	0.41	0.55	6.58	0.26	0.44	0.02	3.22	3.70	12.68
SD	35.7	11.4	0.4	0.09	0.28	0.07	0.80	0.07	0.12	0.02	1.65	1.25	15.50
CV	0.4	0.6	0.1	0.17	0.69	0.13	0.12	0.28	0.27	0.70	0.51	0.34	1.22
Zone 3													
Mean	85.4	18.4	8.1	0.51	0.39	0.59	7.12	0.27	0.42	0.02	3.25	3.90	7.67
SD	34.2	19.7	0.4	0.13	0.24	0.08	0.92	0.08	0.12	0.02	2.08	1.81	8.75
CV	0.4	1.1	0.0	0.25	0.63	0.13	0.13	0.29	0.29	0.79	0.64	0.46	1.14
Zone 4													
Mean	93.2	39.3	8.2	0.78	0.32	0.70	8.41	0.29	0.45	0.02	2.46	3.49	4.15
SD	35.6	43.8	0.3	0.97	0.29	0.13	1.57	0.08	0.10	0.02	1.72	1.21	4.11
CV	0.4	1.1	0.0	1.24	0.92	0.19	0.19	0.27	0.22	0.82	0.70	0.35	0.99
TR1L													
Mean	139.7	22.8	8.4	0.58	0.54	1.46	17.53	0.24	0.40	0.06	2.80	3.73	3.80
SD	38.3	29.5	0.3	0.13	0.43	0.20	2.33	0.06	0.16	0.08	1.77	1.02	2.67
CV	0.3	1.3	0.0	0.23	0.80	0.13	0.13	0.26	0.40	1.31	0.63	0.27	0.70
TR2L													
Mean	153.9	17.2	8.3	0.50	0.82	1.42	17.08	0.23	0.39	0.03	3.11	4.00	5.44
SD	54.0	14.1	0.3	0.11	1.13	0.18	2.17	0.04	0.15	0.02	2.02	1.72	7.48
CV	0.4	0.8	0.0	0.22	1.38	0.13	0.13	0.18	0.38	0.86	0.65	0.43	1.37
TR3L													
Mean	144.6	20.6	8.4	0.93	1.15	1.45	17.41	0.22	0.39	0.05	1.83	3.06	3.19
SD	36.1	17.7	0.2	0.20	0.51	0.25	3.00	0.10	0.19	0.06	1.48	1.36	2.39
CV	0.2	0.9	0.0	0.21	0.45	0.17	0.17	0.45	0.50	1.17	0.81	0.45	0.75
TR4L													
Mean	101.7	20.0	8.3	0.65	1.19	1.19	14.22	0.21	0.46	0.03	2.32	3.62	1.92
SD	14.1	20.8	0.2	0.19	0.64	0.20	2.37	0.07	0.10	0.03	2.09	1.08	1.26
CV	0.1	1.0	0.0	0.29	0.54	0.17	0.17	0.34	0.22	1.00	0.90	0.30	0.66
TR1R													
Mean	160.7	6.9	8.1	0.53	2.39	1.48	17.71	0.91	0.93	0.16	3.17	3.83	14.69
SD	39.3	7.4	0.3	0.07	3.07	0.03	0.36	0.18	0.17	0.36	1.74	1.04	30.45
CV	0.2	1.1	0.0	0.13	1.29	0.02	0.02	0.20	0.19	2.19	0.55	0.27	2.07
TR2R													
Mean	162.9	5.1	7.9	0.44	0.24	1.57	18.83	0.64	0.68	0.02	2.86	3.93	2.90
SD	45.2	7.2	0.3	0.11	0.09	0.04	0.56	0.10	0.09	0.02	1.88	1.01	5.35
CV	0.3	1.4	0.0	0.24	0.39	0.03	0.03	0.15	0.12	0.91	0.66	0.26	1.85

SD Standard deviation, CV coefficient of variation

from zone 1 to zone 4 (Table 1). Alkalinity had a similar pattern with low values in the main channel (mean range 0.55–0.70 mol L⁻¹, increasing downstream) and higher values in the tributaries (mean range 1.19–1.57 mol L⁻¹). Turbidity values ranged from 17 to 40 NTUs at most sites except for the right-side tributaries with mean values <7.0 NTUs. Mean values for pH ranged from 7.9 to 8.4, and DOC from 0.44 to 0.93 mg C L⁻¹. Mean POC values were lower in the main channel (mean range 0.30 to 0.41 mg C L⁻¹) than in the tributaries (mean range 0.54–2.39 mg C L⁻¹) except for TR2R (mean = 0.24 mg C L⁻¹). TIC values also were lower in the main channel (mean range 6.55–8.41 mg C L⁻¹, increasing downstream) than tributaries (mean range 14.2–18.8 mg C L⁻¹).

Mean nitrate concentrations ranged from 0.21 to 0.29 mg N L⁻¹ except for right-side tributaries with higher mean values of 0.64 and 0.91 mg N L⁻¹ (Table 1). Dissolved N values showed a similar pattern, ranging from 0.39 to 0.46 mg N L⁻¹ except for right-side tributaries with mean values of 0.68 and 0.93 mg N L⁻¹. Particulate N, in contrast, was low at all sites, ranging from 0.02 to 0.16 mg N L⁻¹. Phosphorus values were similar among sites, ranging from 1.83 to 4.42 mg P L⁻¹. Values decreased downstream in the main channel from 4.42 mg P L⁻¹ at zone 1 to 2.46 mg P L⁻¹ at zone 4. Dissolved phosphorus values ranged from 3.06 to 5.23 mg P L⁻¹, with the highest values found at zone 1 in the main channel. Particulate phosphorus values ranged from 1.92 (at TR4L) to 14.69 mg P L⁻¹ (at TR1R) with no clear patterns evident between sites.

Water temperature displayed strong spatial patterns in the floodplain. Although mean temperatures ranged from 5.4 to 7.2 °C, highest maximum values were found for

left-side tributaries (20.6–25.9 °C) and lowest maximum temperatures were for right-side tributaries (10.1 and 15.5 °C) (Table 2). Maximum temperatures in the main channel increased downstream from 16.2 °C at zone 1 to 18.1 °C at the end of zone 4 (mean values increased by 1 °C between these sites). Variation in temperature was highest for left-side tributaries (CV = 86 to 94 %), lowest for right-side tributaries (CV = 10 and 37 %), and ranged from 70 to 80 % for main channel sites (except at the end of zone 4 where CV = 44 %). Some sites showed negative minimum temperatures, indicating the sites went dry during winter. Negative values were found for zones 3 and 4 in the main channel and the left-side tributaries TR1L and TR2L.

Table 2 Temperature characteristics for the various study reaches based on logger data from October 2009 to April 2011

	Temperature (°C)				
	Maximum	Minimum	Mean	SD	CV
Main channel					
Zone 1	16.2	0.4	5.4	3.8	70.1
Zone 2	16.6	0.4	5.4	3.9	71.8
Zone 3	17.2	-3.6	5.4	4.3	78.9
Zone 4	17.4	-1.7	5.6	4.5	80.1
End Z4	18.1	0.8	6.4	2.8	44.1
Tributaries					
TR1L	22.6	-1.2	5.4	4.7	86.3
TR2L	20.6	-3.6	5.4	4.7	87.2
TR3L	25.9	0.4	6.1	5.7	93.6
TR1R	15.5	0.4	6.6	2.4	36.7
TR2R	10.1	5.2	7.2	0.7	9.6

Negative values indicate channel was frozen or dry in winter
SD Standard deviation, CV coefficient of variation

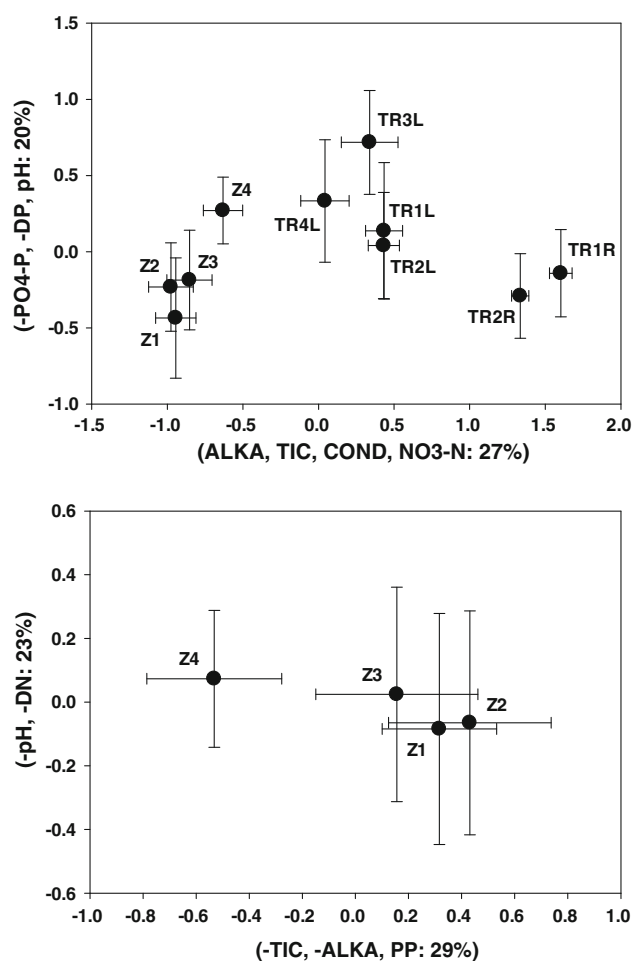


Fig. 3 Principal components analysis based on the water chemistry from each site taken over the study period. *Top* graph is for all sites combined and *lower* graph is for main channel sites. A *minus* sign before a parameter indicates that parameter has a negative relationship along that particular axis. *Errors bars* are standard errors. *ALKA* Alkalinity, *TIC* total inorganic carbon, *PP* particulate phosphorus, *DP* dissolved phosphorus, *COND* conductivity, *DN* dissolved nitrogen. Only factors with loadings greater than 0.70 are labeled on each axis

The PCA results clearly separated sites spatially in terms of physico-chemistry (Fig. 3). Main channel sites were situated to the left, left-side tributaries were intermediate, and right-side tributaries were placed on the right side of the scatterplot along axis 1. Axis 1 was best explained by differences in alkalinity, conductivity, TIC and nitrate. Axis 2 was best explained by values of phosphorus, dissolved phosphorus and pH. Right-side tributaries and zones 1–3 were separated from left-side tributaries and zone 4 on axis 2 with higher values for these parameters. Both axes combined explained 47 % of the variation among sites. Error bars were of similar magnitude for all sites, suggesting a similar temporal variability was found at all sites in physico-chemistry from late spring to late autumn (excluding winter because of access). The second PCA using just the zone data grouped zones 1–3 from zone 4 along axis 1 (Fig. 3). Axis 1 was best explained by values of TIC, alkalinity and particulate phosphorus (PP), with zone 4 showing lower TIC and alkalinity and higher PP than zones 1–3. No major groupings were evident along axis 2, which explained some 23 % of the variation among the zones. Temporal variation, as shown by the error bars, was higher for zones 1–3 than for zone 4.

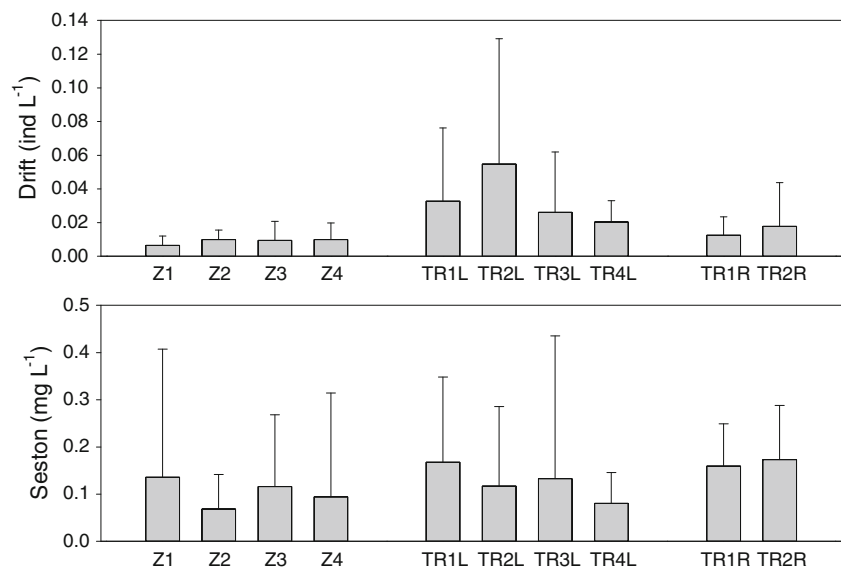
Seston concentrations were non-significantly different among sites with mean values ranging from 0.07 mg L⁻¹ (zone 2) to 0.17 mg L⁻¹ (TR2R) ($F = 0.826$, $p = 0.569$) (Fig. 4). However, temporal variation was lower for right-side tributaries (56 and 66 %) than for left-side tributaries and main channel sites (mean = 154 %). The mean number of drifting invertebrates was higher in left-side tributaries (T1L, T2L) (range 0.03–0.06 ind L⁻¹) than right-side tributaries (0.013 and 0.018 ind L⁻¹) and main channel zones (range 0.007–0.01 ind L⁻¹) ($F = 4.38$,

$p < 0.0001$) (Fig. 4). The temporal variation in drift was similar among sites, ranging from 55 to 146 %.

Periphyton biomass was greater in right-side tributaries (mean > 6.3 g m⁻²) than in left-side tributaries (except T2L) and main channel sites (mean < 3.2 g m⁻²) ($F = 22.79$, $p < 0.0001$) (Fig. 5). The amount of benthic organic matter (BOM) also was highest in right-side tributaries (mean > 590 g m⁻²) than in left-side tributaries and main channel sites (mean < 120 g m⁻²) ($F = 13.10$, $p < 0.0001$). The benthic density of macroinvertebrates was highest in right-side tributaries (mean = 3,730 ind m⁻²), intermediate in main channel sites (mean = 1,375 ind m⁻²), and lowest in left-side tributaries (mean = 452 ind m⁻²) ($F = 21.51$, $p < 0.0001$) (Fig. 5). In main channel sites, mean density increased from 1,124 ind m⁻² in zone 1 to 1,541 ind m⁻² in zone 4. Similarly, taxon richness was highest in right-side tributaries (mean = 11 taxa), intermediate in main channel sites (mean = 6.2 taxa), and lowest in left-side tributaries (mean = 4 taxa) ($F = 19.92$, $p < 0.0001$).

The NMDS clearly separated right-side tributaries, left-side tributaries, and main channel sites based on taxon densities (Fig. 6). In general, right-side tributaries had greater abundances of chironomids, nematodes and trichopterans than left-side tributaries and the main channel sites (Table 3). Main channel sites and right-side tributaries had greater abundances of mayflies and stoneflies than the left-side tributaries, and Blephariceridae were absent from right-side tributaries. The NMDS based on taxon densities in the zones of the main channel showed zone 2 to be somewhat separated from the other zones, but all zones overlapped. This latter analysis indicated little difference in macroinvertebrate assemblages between the zones.

Fig. 4 Mean (+SD error) drifting organisms (ind L⁻¹) and seston (mg L⁻¹) collected at each site over the study period. Z zones in the main channel, TL left-side tributary, TR right-side tributary



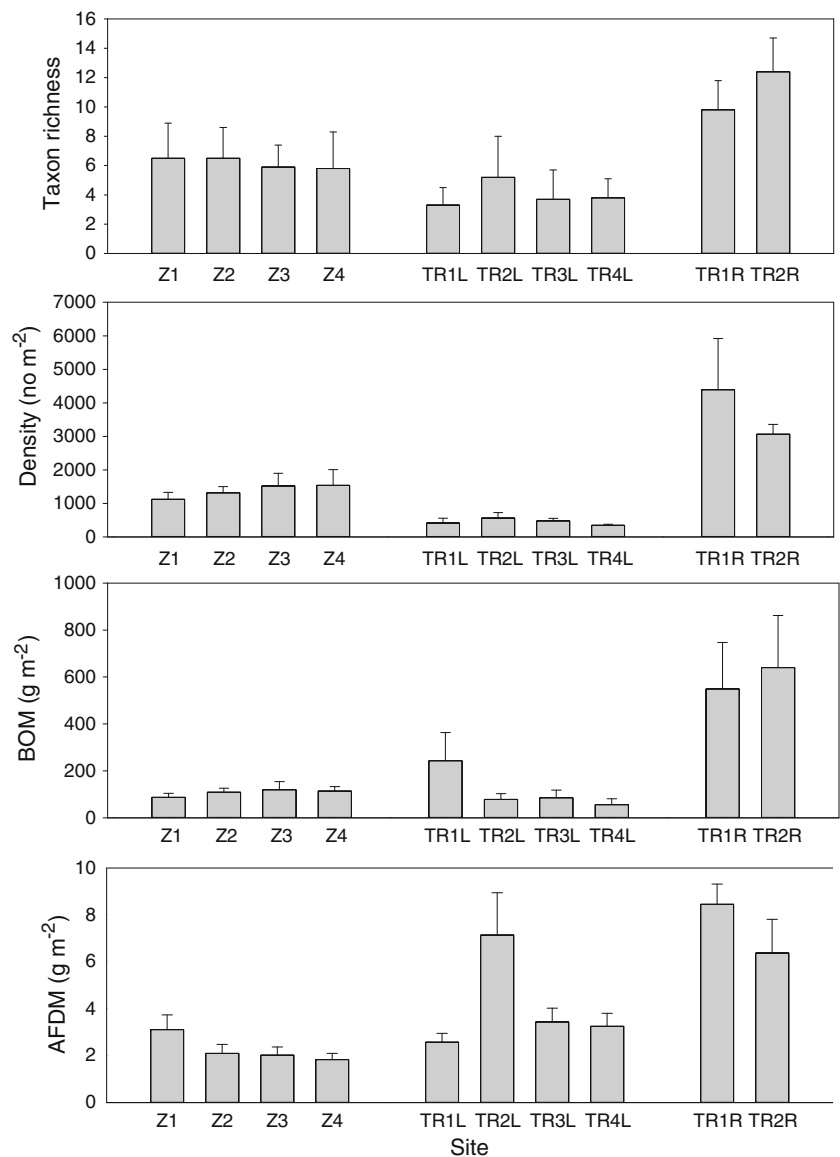
Discussion

An ongoing question in ecology concerns factors that influence the biodiversity of organisms in ecosystems. Riverine floodplains are ecosystems that display strong spatio-temporal linkages between terrestrial and aquatic habitats through the direct effects of hydrological exchange properties (Paetzold et al. 2005, Tockner et al. 2010). Annual aquatic habitat turnover in natural floodplains can be as high as 60 % of the landscape area (Arscott et al. 2002), a dynamic referred to as the shifting habitat mosaic (Stanford et al. 2005). This dynamic maintains a successional diversity of floodplain habitats (aquatic and terrestrial) that sustains the relatively high biodiversity found in natural floodplains (Stanford et al. 2005). Better knowledge regarding the distribution patterns of organisms

in floodplains in relation to habitat properties could assist in the current trend of floodplain restoration that is occurring globally. Our primary goal in this study was to examine the distribution patterns of macroinvertebrates in surface waters of a floodplain that has been regulated by levees to reduce local flood risks. The floodplain system was delineated by upstream and downstream knick points, giving it the characteristic ‘bead’ on the string in river floodplain structure (Ward et al. 2002).

We found distinct differences in the physico-chemical properties among surface waters in the floodplain. Tributary waters differed from both the main channel and between each side of the floodplain. The main channel was directly influenced by glacial waters from the upper watershed, whereas left-side tributaries were mostly snow-melt and precipitation fed and right-side tributaries were

Fig. 5 Mean (+SD error) macroinvertebrate taxon richness and density, benthic organic matter (BOM), and periphyton biomass (AFDM) collected at each site over the study period. *Z* zones in the main channel, *TL* left-side tributary, *TR* right-side tributary



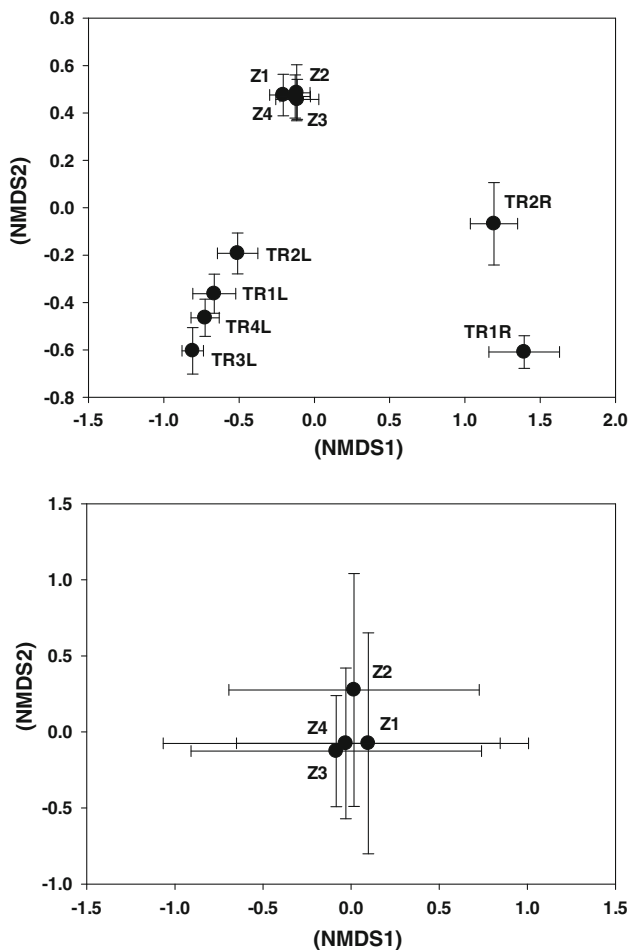


Fig. 6 NMDS results based on the density of taxa collected at each study site. *Top* graph shows all sites combined (stress = 0.10) and *bottom* graph shows the results only for the zones in the main channel (stress = 0.15)

mostly slope and groundwater fed. Temperature patterns also differed significantly among the 3 groups of surface waters with right-side tributaries showing lower but less variable temperatures than other surface waters. Left-side tributaries flowed over an exposed and high (1,000 + m) rock face that allowed considerable solar warming, with maximum temperatures of over 20 °C. However, these left-side tributaries were prone to drying, whereas right-side tributaries were permanent. This coarse-scale heterogeneity in physico-chemistry of surface waters has been observed in other glacial floodplain systems (Tockner et al. 1997; Malard et al. 2006; Robinson and Matthaei 2007; Brown et al. 2007).

The floodplain demonstrated a high degree of hydrological complexity. Surface waters comprised both permanent and temporary systems, particularly between right- and left-side tributaries. The main channel also displayed significant longitudinal differences in physico-chemistry with temperatures generally increasing downstream. Furthermore, the

upper floodplain acted mostly as a downwelling system and the lower floodplain as an upwelling system. These properties fluctuated longitudinally with increases in seasonal and event-driven discharge. The lower main channel upstream of the major right-side tributary confluence (lower zone 4), as a consequence, was prone to river drying during low flow periods such as in winter when glacial sources are minimal and most precipitation falls as snow. In severe cases, even flows from permanent right-side tributaries are insufficient to maintain flows in the main channel in the downwelling segment (authors, personal observation). These permanent tributaries, in turn, may act as important refugia for surface-dwelling aquatic organisms during extreme low flow periods. Robinson and Matthaei (2007) noted that surface waters of glacial floodplains undergo extreme contraction periods during late autumn and early winter with over 60 % of surface waters potentially falling dry. Main channels also have been shown to fall dry during low flow periods such as found for the Tagliamento River in northern Italy (Doering et al. 2007). How important these dry periods influence the distribution of riverine biota is still an open question. For example, the Selway River in New Zealand follows a seasonal contraction period that directly affects the longitudinal distribution of macroinvertebrates (Larned et al. 2007).

The hydrological complexity of the floodplain was reflected in the spatial distribution of aquatic macroinvertebrates among surface waters. The temporary nature of left-side tributaries clearly constrained the number and kinds of macroinvertebrates inhabiting these streams. Temporary flowing waters are known to harbor a distinct and less diverse assemblage of macroinvertebrates than permanent waters (Williams 1996; Rüegg and Robinson 2004). Taxon richness and densities were substantially lower in left-side intermittent tributaries than in right-side tributaries and main channel sites. Permanent right-side tributaries housed the highest densities and most taxa of surface waters examined in the floodplain. In particular, these systems harbored the greatest numbers and taxa of trichopterans. The glacial influence in the main channel also was evident in the macroinvertebrate assemblages found at the different sites. Here, mayflies and stoneflies commonly found in other glacial streams were present (see Milner et al. 2001; Robinson et al. 2001; Hieber et al. 2005). Although the floodplain was below 1,000 m in elevation, there was still a strong glacial signature influencing the distribution of macroinvertebrates in the main channel. The NMDS showed that the three groups of surface waters had different macroinvertebrate assemblages present.

No differences in macroinvertebrate assemblages were evident between the examined main channel zones. The influence of upwelling and downwelling properties delineated by the different zones was not apparent in

Table 3 Mean density (no. m⁻²) and standard deviation (SD) of common macroinvertebrate taxa at the various sites using all dates combined (N = 10)

Site	Ephemeroptera	Plecoptera	Trichoptera	Chironomidae	Simuliidae	Psychodidae	Limoniidae	Empididae	Blephariceridae	Diptera	Hydracarina	Ostracoda	Turbellaria	Oligochaeta	Nematomorpha	Other
Z1																
Mean	702.2	203.7	11.0	121.5	23.1	2.2	49.3	43.0	32.7	3.5	8.8	0.0	41.8	13.2	0.0	1.8
SD	413.7	163.3	8.9	128.9	23.4	7.0	28.0	53.2	28.3	4.5	11.4	0.0	132.2	15.4	0.0	3.1
Z2																
Mean	817.5	255.6	10.6	150.8	63.8	2.2	49.6	35.9	27.8	5.3	6.6	4.4	0.0	13.2	2.2	0.9
SD	473.2	301.3	12.7	124.2	156.1	7.0	36.2	26.0	24.2	6.8	10.6	13.9	0.0	17.8	7.0	1.9
Z3																
Mean	865.0	502.9	8.4	108.9	4.4	4.4	36.0	8.8	20.9	4.8	11.0	2.2	0.0	9.4	0.0	1.3
SD	471.4	937.0	9.8	115.3	9.3	9.3	17.0	11.4	16.8	8.4	11.6	7.0	0.0	12.2	0.0	2.1
Z4																
Mean	814.4	609.7	15.3	74.6	28.6	0.0	27.1	14.3	22.7	1.3	16.0	9.9	0.0	13.2	0.0	2.2
SD	525.5	1213.6	12.0	43.9	46.4	0.0	12.2	12.8	21.7	1.6	18.4	13.2	0.0	15.4	0.0	4.2
TR1L																
Mean	70.9	55.0	9.8	243.2	7.3	12.2	3.7	11.0	3.7	4.9	7.3	0.0	37.9	11.0	0.0	8.6
SD	111.8	74.6	17.1	246.6	11.4	13.7	9.0	18.4	9.0	6.0	18.0	0.0	82.5	12.0	0.0	8.6
TR2L																
Mean	143.4	103.5	7.3	279.1	33.0	0.0	7.3	9.8	12.2	0.8	2.4	0.0	25.7	9.8	4.9	0.0
SD	216.0	105.2	12.2	238.3	46.0	0.0	15.6	11.6	19.4	2.4	7.3	0.0	31.1	11.6	9.7	0.0
TR3L																
Mean	19.6	11.4	8.1	344.7	26.9	14.7	12.2	4.9	2.4	9.0	4.9	0.0	36.3	58.3	0.0	0.8
SD	25.1	11.1	9.3	460.8	14.7	22.0	22.3	9.7	7.3	7.1	9.7	0.0	49.3	48.2	0.0	2.4
TR4L																
Mean	24.4	30.6	7.3	201.7	7.3	0.0	18.3	3.7	0.0	2.4	11.0	0.0	29.3	65.4	0.0	2.4
SD	20.6	34.5	6.6	198.0	11.4	0.0	21.6	9.0	0.0	6.0	12.0	0.0	45.4	71.7	0.0	3.8
TR1R																
Mean	532.4	1078.0	78.5	1869.3	36.3	199.5	29.3	27.9	0.0	16.9	49.5	122.5	17.6	394.9	60.9	38.9
SD	652.3	703.8	87.2	1840.4	53.1	132.8	23.2	44.2	0.0	24.0	39.6	101.7	34.1	541.3	114.8	94.7
TR2R																
Mean	775.9	717.6	195.8	873.4	24.2	33.0	52.1	46.2	0.0	2.9	114.8	129.8	60.9	108.2	59.0	13.2
SD	682.5	345.3	145.1	753.9	39.4	35.5	44.6	25.0	0.0	5.1	59.9	148.6	92.2	59.4	59.0	29.3

macroinvertebrate assemblage structure. Even the potential influence of channel drying was not evident in the macroinvertebrate results. Larned et al. (2007) showed a strong longitudinal effect of river drying on the distribution of macroinvertebrates, albeit at a much greater stream length (>25 km) than in this study (<4 km). We suggest that the glacial signature, and relatively flashy flow regime, was strong enough to mask the effects of upwelling and downwelling properties on macroinvertebrates during surface flow periods. For instance, little difference was observed in physico-chemical properties among the main channel zones, except for a slight increase in temperature downstream. Furthermore, the short channel length between zones (100 s of meters) may have facilitated a continual redistribution of organisms in the main channel that overrode any subtle effects in physico-chemistry or periodic channel drying. For instance, macroinvertebrate drift can be quite substantial in glacial streams, influencing the colonization by macroinvertebrates between floodplain surface waters (Robinson et al. 2002a, 2004; Hieber et al. 2003).

The results clearly show the importance of coarse-scale habitat heterogeneity on floodplain biodiversity. Even under some floodplain regulation (e.g., levees), surface water heterogeneity was reflected strongly in the degree of hydrological complexity, and this complexity was evident in macroinvertebrate distributions and abundances. Regulation of floodplains and floodplain surface waters homogenizes aquatic habitats (Doering 2012a) and likely are principal causes for losses in floodplain biodiversity. These results suggest that floodplain restoration should attempt to reconnect floodplain surface waters and increase the hydrological complexity associated with natural floodplains. The increased hydrological complexity would add coarse-scale habitat heterogeneity (i.e. greater variety of floodplain surface waters) that should translate into a higher biodiversity over time.

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