

Vertical hydrological exchange, and ecosystem properties and processes at two spatial scales along a floodplain river (Tagliamento, Italy)

Author(s): M. Doering , U. Uehlinger , and K. Tockner

Source: Freshwater Science, 32(1):12-25. 2012.

Published By: The Society for Freshwater Science

DOI: <http://dx.doi.org/10.1899/12-013.1>

URL: <http://www.bioone.org/doi/full/10.1899/12-013.1>

BioOne (www.bioone.org) is a nonprofit, online aggregation of core research in the biological, ecological, and environmental sciences. BioOne provides a sustainable online platform for over 170 journals and books published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

Vertical hydrological exchange, and ecosystem properties and processes at two spatial scales along a floodplain river (Tagliamento, Italy)

M. Doering^{1,4}, U. Uehlinger^{1,5}, AND K. Tockner^{1,2,3,6}

¹ EAWAG, Swiss Federal Institute of Aquatic Science and Technology, 8600 Dübendorf, Switzerland

² ETH, Institute of Integrative Biology, Swiss Federal Institute of Technology, Zurich, Switzerland

³ IGB, Leibniz-Institute of Freshwater Ecology and Inland Fisheries, Berlin, and Institute of Biology, Freie Universität Berlin, Germany

Abstract. We examined the effect of vertical hydrological exchange on physicochemical variables, periphyton biomass (ecosystem properties), and sediment respiration (ecosystem process) at 2 spatial scales along a large gravel-bed river (Tagliamento River, northeastern Italy). At the regional scale, we investigated a 29-km-long, expanding and contracting, losing (average flow decrease $2.5 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$) and a 12.5-km-long, stable, gaining (average increase $0.3 \text{ m}^3 \text{ s}^{-1} \text{ km}^{-1}$) reach. At the local scale, we sampled riffle head and riffle tail units nested within the losing and gaining reaches. At the regional scale, we characterized vertical exchange by strong downwelling (negative vertical hydraulic gradient; VHG) in the losing and moderate upwelling (positive VHG) in the gaining reach. Nutrients, such as $\text{NO}_3\text{-N}$ and dissolved N (DN), and periphyton biomass (AFDM) showed a significantly ($p < 0.05$) lower concentration in the losing than in the gaining reach. A contrasting pattern emerged for sediment respiration. Expansion and contraction dynamics (i.e., drying and rewetting) in the losing reach negatively affected chlorophyll *a* and AFDM. At the local scale, VHG was negative at riffle heads and positive at riffle tails nested in the gaining reach, but variables did not respond to vertical exchange at riffle heads and riffle tails in the losing or gaining reach. However, averaged data from riffle heads and riffle tails in the losing reach compared to averaged data for riffle heads and riffle tails in the gaining reach showed the same pattern as found in the regional investigation. Vertical exchange was apparently a major factor influencing ecosystem properties and ecosystem processes hierarchically across different spatial scales.

Key words: flood plain, spatial scales, vertical exchange, sediment respiration, periphyton, ecosystem hierarchy.

Floodplain ecosystems can be viewed as a series of spatially and hierarchically organized geomorphic entities constrained within a nested spatial context (Frissell et al. 1986, Lowe et al. 2006, Thorp et al. 2006, Parsons and Thoms 2007). Riffles and pools are nested within river reaches that are nested within stream networks, and stream networks are nested within catchments. In this composite view, bidirectional hydrological exchange between the channel and alluvial aquifer, commonly described as upwelling and downwelling, connects different geomorphic entities. The direction and strength of vertical exchange varies with hydraulic conductivity and the

vertical extent of the alluvial sediments (Malard et al. 2002, Acuña and Tockner 2009), and is scale dependent (Fernald et al. 2001, Kasahara and Wondzell 2003, Poole et al. 2004, 2006). Scales of exchange range from entire river reaches where subsurface water may travel for kilometers and mixes with groundwater before being forced to the surface at distinct geomorphic knickpoints (Poole et al. 2002, 2008, Doering et al. 2007, Larned et al. 2007) to local vertical hydrologic exchange patterns where surface water infiltrates at the riffle head into sediments and exfiltrates at the riffle tail (White 1993, Brunke and Gonser 1997, Franken et al. 2001, Poole et al. 2008).

Vertical hydrologic exchange is an important physical process influencing river ecosystem properties (e.g., algal growth), processes (e.g., respiration), and biodiversity patterns (Valett et al. 1994, Jones

⁴ E-mail addresses: michael.doering@eawag.ch

⁵ urs@uehlinger.info

⁶ tockner@igb-berlin.de

1995, Malard et al. 2006, Boulton et al. 2010). For example, sediment respiration is generally higher in downwelling than in upwelling areas because organic matter derived from the infiltrating surface water fuels respiration (Jones 1995). However, in upwelling areas, algal growth is stimulated by nutrients released by the mineralization of organic matter in the hyporheic zone (Valett et al. 1994, Dahm et al. 1998, Wyatt et al. 2008).

Most studies of hyporheic flow systems have been focused at the fine scale (i.e., riffle–pool sequence), but focus has shifted recently from fine to larger scales (Datry et al. 2007). Despite a few studies in which the variability in vertical exchange and its consequence for ecosystem processes and animal behavior was considered explicitly across different spatial scales (Baxter and Hauer 2000, Dent et al. 2001, Poole et al. 2008), we have yet to understand the role of these interactions across multiple hierarchical scales (Boulton et al. 2010).

The goals of our study were to assess the effect of vertical hydrological exchange on physicochemical habitat variables, periphyton biomass, and sediment respiration at 2 spatial scales and to evaluate the extent to which regional hydrogeomorphic characteristics impose constraints at the local scale. The study system encompasses a 41.5-km-long section of a large gravel-bed river. In a 29-km-long losing reach, water continuously infiltrates into a deep porous aquifer. Major parts of this reach fall dry during base flow. In the adjacent 12.5-km-long gaining reach, some of the water infiltrated upstream emerges. Pool–run–riffle sequences representing the local scale are nested within the losing and gaining reaches at the regional scale. We expected that: 1) the regional (large scale) vertical exchange would shape ecosystem properties and processes in the losing and gaining reaches in a manner similar to what has been observed at the local riffle–pool scale in other studies, i.e., in the losing reach, we expected higher sediment respiration and lower periphyton biomass and nutrient concentrations than in the gaining reach (Valett et al. 1994, Jones et al. 1995, Wyatt et al. 2008); 2) differences in ecosystem properties and processes between riffle head (in-welling) and riffle tail (out-welling) of a pool–riffle sequence would be smaller than differences in ecosystem properties and processes between the losing and gaining reach if the vertical exchange at the regional scale dominated the effect of the vertical exchange at the local scale; 3) longitudinal expansion and contraction dynamics (drying and rewetting) would affect periphyton biomass and sediment respiration because they affect the composition, abundance, and physiology of primary producers and microbial communities (Van Gestel et al. 1993,

Clein and Schimel 1994, Stanley et al. 2004, Marxsen et al. 2010).

Study system

The Tagliamento River (lat 46°12'N, long 12°30'E; Fig. 1) is a 7th-order river that originates in the southern limestone Alps and flows almost unimpeded by dams for 172 km to the Adriatic Sea (catchment area = 2580 km², maximum elevation = 2781 m asl, mean annual discharge = 90 m³/s). The Alpine and prealpine area consist mainly of limestone and flysch, occasionally intermixed with layers of gypsum (Tockner et al. 2003). The lowland Venetian–Friulian Plain consists mainly of carbonate sediments (limestone and dolomites) that form a highly permeable and several-hundred-meter-deep aquifer (Fontana et al. 2008). Flow peaks in spring and autumn, but flow and flood pulses (\geq bankfull discharge) may occur at any time of the year (Arscott et al. 2002). The investigated river corridor along this section is up to 2 km wide and includes gravel (38%), vegetated islands (7%), riparian forest (24%), and developed land (25%). Detailed descriptions of the study section have been given elsewhere by Arcsott et al. (2002), Tockner et al. (2003), and Doering et al. (2007).

The losing and gaining reaches we studied form a 42-km-long river section in the lowland plain. The losing reach extends from the bedrock-constrained knickpoint at river km 85 (Pinzano) to river km 114. In this losing reach, an average 2.5 m³ s⁻¹ river km⁻¹ infiltrate into the highly permeable alluvial aquifer (in total up to 70 m³/s; Doering et al. 2007). At river km 114, the linea delle risorgive (Fig. 1), an aquiclude composed of silt and clay sediments, intersects the alluvial sediments and forces the groundwater to the surface (Fontana et al. 2008). Downstream of this knickpoint, only a small fraction of infiltrated water returns to the river bed (average exfiltration rate: 0.3 m³ s⁻¹ river km⁻¹; Fig. 2A), whereas a larger fraction of exfiltrating Tagliamento water feeds rivers that emerge along the linea delle risorgive east and west of the main stem of the Tagliamento (Doering et al. 2007). Expansion and contraction dynamics in the losing reach are linearly related to the discharge at the upstream knickpoint at river km 85. If discharge at this location is <60 m³/s, the losing reach becomes surface-disconnected from the gaining reach. During the dry summer of 2003, the downstream front of surface water ended at river km 91 (Doering et al. 2007).

Methods

We assessed the effects of vertical exchange on physicochemical variables, periphyton biomass, and

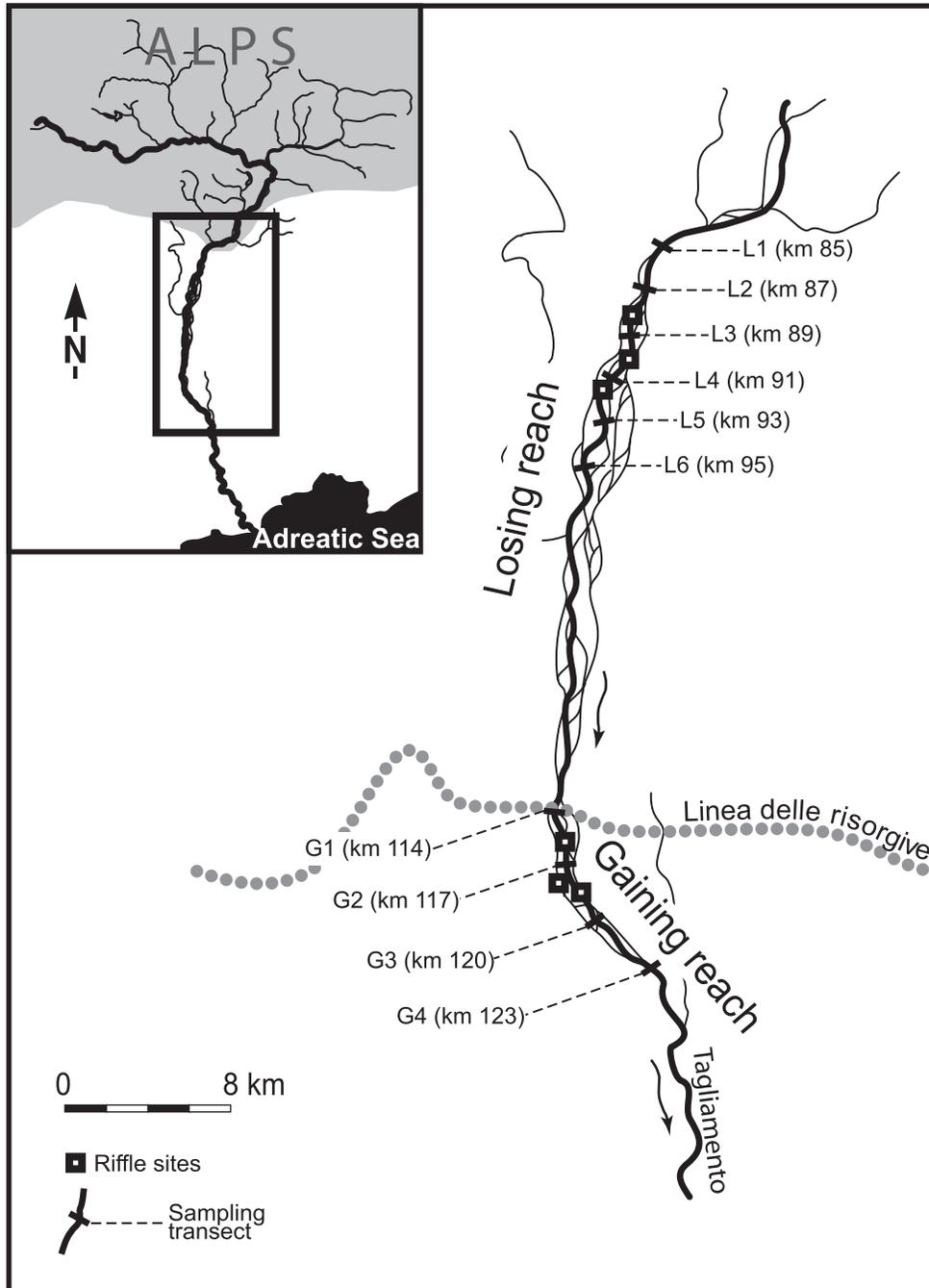


FIG. 1. Map of the study reach with transects in the losing reach (L1–L6) and gaining reach (G1–G4) sampled from July 2003 to April 2004. The open squares indicate riffle sites sampled from October 2004 to July 2005. The insert shows the study area within the drainage of the Tagliamento River.

sediment respiration at 2 nested spatial scales. At the regional scale, we sampled 6 transects in the losing and 4 transects in the gaining reaches (6 times, July 2003–April 2004). The 2 lowermost transects (L5 and L6) in the losing reach were affected by the expanding and contracting river course and mostly were dry at the surface (4 times) in summer 2003 (Fig. 1). The

distance between transects was 2 km in the losing and 3 km in the gaining reach. We placed all transects in runs to minimize the effect of local vertical exchange rates at the riffle–pool scale.

At the local scale, we randomly selected 3 riffles nested in the gaining and 3 riffles nested in the losing reaches (Fig. 1). In each riffle, we sampled 1 transect

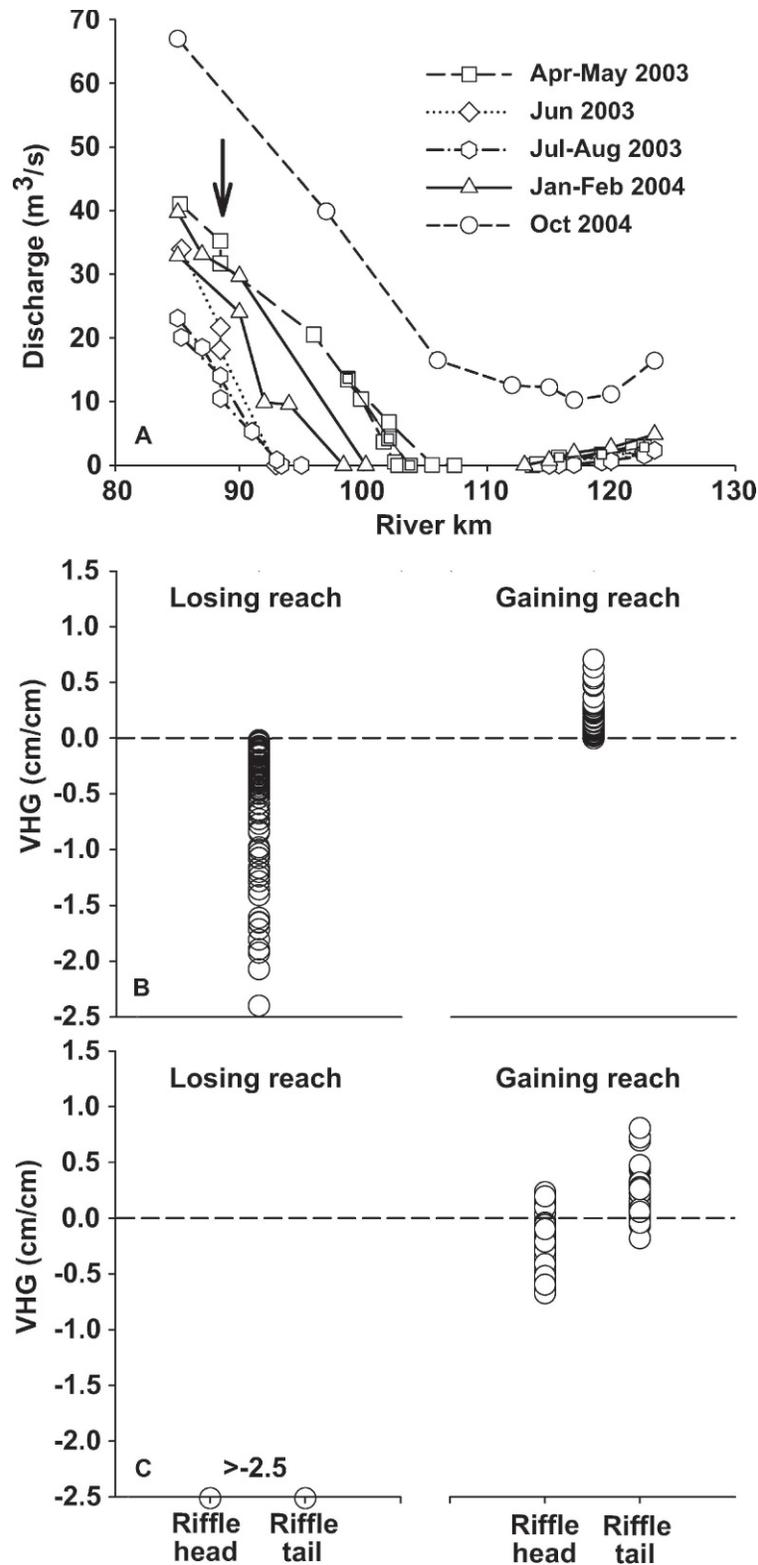


FIG. 2. A.—Surface discharge along the losing and gaining reaches (regional scale; July 2003–April 2004). The arrow marks the location of water abstraction. B.—Vertical hydraulic gradient (VHG) in the losing ($n = 183$) and gaining ($n = 129$) reaches (regional scale; July 2003–April 2004). C.—VHG at riffle heads and riffle tails in the losing (VHG > -2.5) and riffle heads ($n = 60$) and riffle tails ($n = 60$) in the gaining reach (local scale; October 2004–July 2005).

at the riffle head and 1 transect at the riffle tail 4 times from October 2004 to July 2005. The distance between riffle head and riffle tail ranged from 100 to 150 m.

Across each transect at the regional and local scale, we measured vertical hydraulic gradient (VHG), hydrochemistry of surface and subsurface water, periphyton biomass, sediment respiration, and sediment organic matter content.

Vertical hydraulic gradient (VHG) and surface discharge

VHG characterizes groundwater–stream water exchange direction and potential intensity. VHG is defined as

$$\text{VHG} = \Delta h / \Delta l \quad [1]$$

where Δh is the difference in head between the water level in the piezometer and the level of the stream surface (cm), and Δl is the depth from the streambed surface to the first opening in the piezometer sidewall (Baxter et al. 2003). VHG is a dimensionless metric that is positive under upwelling and negative under downwelling conditions. We measured VHG in 5 equally spaced minipiezometers driven to a depth of ~ 50 cm into the bed sediments across each transect.

We calculated infiltration and exfiltration rates ($\text{m}^{-3} \text{s}^{-1} \text{ river km}^{-1}$) along the entire study area by measuring surface discharge across 7 to 13 transects with the area–velocity method and acoustic Doppler techniques (9 dates between July 2003 and October 2004). A detailed description of discharge measurements was given by Doering et al. (2007).

Temperature and water chemistry

We recorded surface-water temperature hourly at river km 88.5 (losing reach) and river km 126.5 (gaining reach) from August 2004 until July 2005 with temperature loggers (TR Minilog; VEMCO, Halifax, Nova Scotia). We also measured temperature at the end of each respiration experiment (spot measurements; see below).

We collected surface and interstitial water with polyethylene bottles (1 sample per date and transect). We pumped interstitial water from a depth of ~ 50 cm from a piezometer in the middle of each transect. We measured conductivity of surface water and pumped interstitial water in situ with a portable conductivity meter (LF 320; WTW, Weinheim, Germany). We used analytical methods identical to those used by Tockner et al. (1997) for $\text{NH}_4\text{-N}$, $\text{NO}_2\text{-N}$, $\text{NO}_3\text{-N}$, dissolved N (DN), particulate N and P (PN, PP), soluble reactive P ($\text{PO}_4\text{-P}$), dissolved P (DP), dissolved and particulate organic C (DOC, POC), and ash-free dry mass

(AFDM) of suspended solids (SS). We used analytical methods identical to those used by Malard et al. (1999) for total inorganic C (TIC), SO_4^{2-} , and SiO_2 . We used ion chromatography to measure Cl^- and an inductively coupled emission spectrometer (SPECTRO; Analytische Geräte, Kleve, Germany) to measure Ca^{2+} , Mg^{2+} , Na^+ , and K^+ . We analyzed interstitial water for dissolved components only.

Periphyton biomass

We quantified periphyton biomass on 5 randomly collected rocks along each transect. We placed rocks in plastic storage bags and kept them frozen until processed. We scrubbed the rocks with a wire brush to remove algae into a bucket with water. We measured the length and width of each rock with a caliper. We filtered subsamples of the algal suspension through glass-fiber filters (Whatman GF/F) for measurement of chlorophyll *a* (chl *a*) and ash-free dry mass (AFDM). We quantified chl *a* by high-performance liquid chromatography after extraction in hot ethanol (Meyns et al. 1994). We calculated mean areal values of chl *a* for each site as described by Uehlinger (1991).

Sediment respiration and particulate organic matter (POM)

We measured respiration of aquatic sediments as change in O_2 concentration over time in Plexiglas® tubes (5.2 cm diameter, 32 cm long) sealed with rubber stoppers (Uehlinger et al. 2002). We sampled sediments (0–20-cm sediment depth) at 3 sites along each transect after removing the uppermost sediment layer with epilithic algae. We presieved sediments to exclude particles > 8 mm. We half-filled each tube with sediment, added water from the sampling site, and incubated the tubes in situ for ~ 4 h. We measured O_2 concentrations and temperature with a portable O_2 meter (Oxi 340/bset; WTW, Weilheim, Germany). After incubation, we kept sediments frozen until we analyzed them for organic-matter content and grain-size distribution. Based on the rate of O_2 consumption in the chamber water (r ; $\text{g O}_2 \text{ m}^{-3} \text{ h}^{-1}$), we calculated respiration per kg sediment (R ; $\text{g O}_2 \text{ kg}^{-1} \text{ h}^{-1}$) as

$$R = rV_w / G_w \quad [2]$$

where V_w is the volume of water in a tube (m^3) and G_w is the mass of the sediment in the tube. We normalized respiration rates at a reference temperature of 20°C with the Arrhenius equation:

$$R_{20^\circ\text{C}} = R_T 1.072^{T-20^\circ\text{C}} \quad [3]$$

where $R_{20^{\circ}\text{C}}$ is the respiration rate ($\text{g O}_2 \text{ kg}^{-1} \text{ h}^{-1}$) at 20°C and T is temperature in the tube at the end of the incubation (Naegeli and Uehlinger 1997).

Sediment analysis

We elutriated POM with deionized water (Zah 2001), and separated it by sieving into size fractions >1 , $1-0.25$, and <0.25 mm. For the smallest fraction, we filtered an aliquot through a preweighed glass-fiber filter (Whatman GF/F; diameter = 47 mm). We dried POM fractions at 60°C for 24 h, weighed them, combusted them at 500°C for 3 h, and reweighed them. After elutriating POM, we measured the mass of the POM strongly attached to sediment particles >0.025 mm (SOM) by combusting the sediments at 500°C for 3 h. We expressed POM as AFDM/kg sediment. We measured total N content of the 3 POM fractions as DN and PN components quantified as $\text{NO}_3\text{-N}$ after digestion of filtrates with $\text{K}_2\text{S}_2\text{O}_8$ at 121°C . We measured total dissolved P (TDP) as $\text{PO}_4\text{-P}$ after digestion with $\text{K}_2\text{S}_2\text{O}_8$ at 121°C (Ebina et al. 1983). We calculated the molar C:N ratio of different POM fractions assuming C content of organic matter was 50%.

Statistical analysis

We $\log(x + 1)$ -transformed all data to meet assumptions of normality (Sokal and Rohlf 1995). We ran analyses separately for the regional-scale and the local-scale data because of the difference in sampling dates. We evaluated differences in VHG between the losing and gaining reach and between riffle heads and riffle tails with Kruskal–Wallis analyses of variance (ANOVAs). We applied 1-way ANOVAs to test for differences in R , periphyton chl a and AFDM, and physicochemical variables among sampling sites. We used Student t -tests to evaluate differences in physicochemical variables, periphyton chl a and AFDM, and R between intermittent and permanent wetted sites (losing reach). All variables were tested separately. We subjected biogeochemical variables to principal component analysis (PCA) to assess general spatiotemporal habitat factors separating sampling sites. Frequently, chemical variables (NH_4^+ , $\text{NO}_2\text{-N}$, $\text{PO}_4\text{-P}$, and DP) were below detection limits of the analytical methods (Table 1) and, therefore, we excluded them from statistical analysis. We deleted data gaps on a case-wise basis. We ran all analyses with Microsoft Excel 2003 (Microsoft, Redmond, Washington) and Statistica 7.0 for Windows (StatSoft, Tulsa, Oklahoma).

Results

Regional-scale ecosystem properties and processes

VHG in runs differed between reaches (Kruskal–Wallis, $p < 0.001$) and averaged -0.67 ± 0.55 (mean \pm SD; $n = 183$) in the losing reach (average infiltration rate: $2.5 \text{ m}^3 \text{ s}^{-1} \text{ river km}^{-1}$) and 0.03 ± 0.23 ($n = 129$) in the gaining reach (average exfiltration rate: $0.3 \text{ m}^3 \text{ s}^{-1} \text{ river km}^{-1}$; Fig. 2B). A detailed description of the surface discharge dynamics was given by Doering et al. (2007). Diel temperature amplitude from data loggers ranged from 0.4 to 12.6°C in the losing reach (river km 88.5) and from 0.4 to 6.2°C in the gaining reach (river km 126.5). The respective mean annual temperatures were 11.5 and 12.9°C .

The only chemical variable that differed in concentration between surface and subsurface water was SiO_2 (1-way ANOVA, $p < 0.001$). Temperature (spot measurements) and concentrations of $\text{NO}_3\text{-N}$, DN, TIC, SiO_2 and K^+ were higher in the gaining than in the losing reach, whereas specific conductance and the concentrations of O_2 , PP, POC, SO_4^{2-} , Cl^- , Na^+ , TSS, and AFDM were higher in the losing than in the gaining reach (1-way ANOVAs, $p < 0.05$; Table 1). The molar C:N ratio of sediment POM >1 mm was higher in the losing than in the gaining reach (1-way ANOVA, $p < 0.001$). The molar C:N ratio and N and P content of POM $1-0.025$ mm were higher in the gaining than in the losing reach (1-way ANOVAs, $p \leq 0.007$; Table 2). The PCA separated the losing and gaining reach (Fig. 3A, B). SiO_2 , POM $1-0.025$ mm, Na^+ , SO_4^{2-} , N <0.025 mm, N $1-0.025$ mm, P $1-0.025$ mm, and O_2 accounted for most of the definition of axis F1 (factor loadings $\geq 60\%$). P <0.025 mm, TSS, POM <0.025 mm, Mg^{2+} , and conductivity accounted for most of the definition of axis F2 (factor loadings $\geq 60\%$).

Concentrations of chl a were $19.7 \pm 33.7 \text{ mg/m}^2$ in the losing reach and $20.1 \pm 33.2 \text{ mg/m}^2$ in the gaining reach and did not differ between reaches (1-way ANOVA, $p > 0.05$; Fig. 4A). Periphyton AFDM was significantly lower in the losing ($12.0 \pm 12.2 \text{ g/m}^2$) than in the gaining reach ($21.3 \pm 18.9 \text{ g/m}^2$) (1-way ANOVA, $p < 0.001$; Fig. 4B). $R_{20^{\circ}\text{C}}$ was significantly higher in the losing ($0.42 \pm 0.19 \text{ mg O}_2 \text{ kg}^{-1} \text{ sediment h}^{-1}$) than in the gaining reach ($0.26 \pm 0.15 \text{ mg O}_2 \text{ kg}^{-1} \text{ sediment h}^{-1}$) (1-way ANOVA, $p < 0.001$; Fig. 4C).

Chl a and periphyton AFDM differed between permanent (L1–L4) and intermittent (L5, L6) sites in the losing reach (Fig. 1) (t -tests, $p \leq 0.001$; permanent sites: $12.1 \pm 25.6 \text{ mg chl } a/\text{m}^2$ and $7.1 \pm 10.1 \text{ g AFDM/m}^2$; intermittent sites: $7.9 \pm 11.3 \text{ mg chl } a/\text{m}^2$ and $5.8 \pm 4.2 \text{ g AFDM/m}^2$). Temperature (spot measurements), chemical variables, POM, and sediment respiration did

TABLE 1. Mean (± 1 SD) physicochemical variables in the losing (LR) and gaining (GR) reaches, and pooled data from riffle heads and riffle tails in the losing (RLR) and gaining (RGR) reaches. Significant differences between LR and GR and between RLR and RGR are indicated in bold. * indicates values only from surface-water samples.

Variable	LR <i>n</i> = 56	GR <i>n</i> = 48	RLR <i>n</i> = 24*	RGR <i>n</i> = 48
Temperature ($^{\circ}$ C)	15.3 \pm 4.97	17.3 \pm 5.4	13.5 \pm 7.41	15.1 \pm 4.72
O ₂ (mg/L)	10.9 \pm 1.97	8.91 \pm 1.96	11.5 \pm 1.57	10.1 \pm 1.25
Specific conductance (μ S/cm)	559.9 \pm 39.2	513.1 \pm 50.9	562.2 \pm 35.1	477.8 \pm 37.9
NH ₄ -N (mg/L)	<0.001	<0.001	<0.001	<0.001
NO ₂ -N (mg/L)	<0.001	<0.001	<0.001	<0.001
NO ₃ -N (mg/L)	0.75 \pm 0.05	1.03 \pm 0.32	0.69 \pm 0.06	1.13 \pm 0.34
Dissolved N (mg/L)	0.94 \pm 0.12	1.25 \pm 0.42	0.83 \pm 0.08	1.36 \pm 0.41
Particulate N (mg/L)*	0.02 \pm 0.02	0.01 \pm 0.01	6.50 \pm 11.60	2.47 \pm 5.00
PO ₄ -P (μ g/L)	<5	<5	<5	<5
Dissolved P (μ g/L)	<5	<5	<5	<5
Particulate P (μ g/L)*	2.65 \pm 2.26	1.70 \pm 2.28	4.80 \pm 4.71	2.11 \pm 1.46
Dissolved organic C (mg/L)	0.80 \pm 0.26	0.73 \pm 0.35	0.64 \pm 0.16	0.41 \pm 0.21
Total inorganic C (mg/L)	35.0 \pm 4.29	39.7 \pm 10.8	28.1 \pm 4.97	35.4 \pm 3.94
Particulate organic C (mg/L)*	0.50 \pm 0.34	0.22 \pm 0.14	0.98 \pm 0.89	0.32 \pm 0.23
SiO ₂ (mg/L)	3.03 \pm 0.33	4.08 \pm 1.14	2.83 \pm 0.30	3.55 \pm 0.40
SO ₄ ²⁻ (mg/L)	144.8 \pm 20.25	101.3 \pm 10.06	153.3 \pm 15.9	85.8 \pm 11.3
Cl ⁻ (mg/L)	3.55 \pm 0.39	3.31 \pm 1.23	3.20 \pm 0.67	3.11 \pm 0.45
Ca ²⁺ (mmol/L)	77.3 \pm 11.9	70.8 \pm 7.78	84.6 \pm 11.2	71.3 \pm 6.43
Mg ²⁺ (mmol/L)	19.9 \pm 1.33	20.1 \pm 2.63	19.9 \pm 1.55	19.4 \pm 1.43
K ⁺ (mg/L)	1.03 \pm 0.16	1.13 \pm 0.28	1.12 \pm 0.20	1.28 \pm 0.47
Na ⁺ (mg/L)	3.39 \pm 0.41	3.00 \pm 0.38	3.37 \pm 0.53	2.93 \pm 0.43
Total suspended solids (mg/L)	4.10 \pm 4.29	1.65 \pm 1.70	2.54 \pm 3.82	1.39 \pm 2.07
Ash-free dry mass (mg/L)*	2.89 \pm 1.07	1.94 \pm 0.91	3.55 \pm 1.44	2.95 \pm 0.93

not differ between permanent and intermittent sites in the losing reach.

Local-scale ecosystem properties and processes in the losing and gaining reaches

In the losing reach, piezometers were dry beneath the wetted surface, i.e., VHG was more negative than the difference in piezometer depth (> -2.5) and could not be quantified. In the gaining reach, VHG was more negative at the riffle heads (-0.20 ± 0.24 , $n = 60$) than at the riffle tails (0.18 ± 0.19 , $n = 60$; Fig. 2C) (Kruskal–Wallis, $p < 0.001$).

Temperature (spot measurements), chemical variables, and POM (Tables 1, 2) did not differ between riffle heads and riffle tails in the losing or gaining reaches (1-way ANOVAs, $p > 0.05$). PCA only slightly separated riffle heads and riffle tails but strongly separated the losing and gaining reaches (Fig. 3C, D). Axis F1 was mostly defined by SO₄²⁻, conductivity, NO₃-N, DN, Na⁺, Ca²⁺, PP, SiO₂, and POC (factor loadings $\geq 60\%$). Axis F2 was mostly defined by P 1–0.025 mm, N 1–0.025 mm, N > 1 mm, C:N ratio 1–0.025 mm, P > 1 mm, C:N ratio < 0.025 , and TSS (factor loadings $\geq 60\%$).

Chl *a*, periphyton AFDM, and $R_{20^{\circ}\text{C}}$ did not differ between riffle heads and riffle tails in the losing or gaining reaches. In the losing reach, chl *a*, periphyton

AFDM, and $R_{20^{\circ}\text{C}}$ averaged 15.1 ± 20.8 mg chl *a*/m², 10.3 ± 9.18 g AFDM/m², and 0.46 ± 0.36 mg O₂ kg⁻¹ sediment h⁻¹ at riffle heads and 10.5 ± 16.8 mg chl *a*/m², 14.1 ± 15.8 g AFDM/m², and 0.48 ± 0.34 mg O₂ kg⁻¹ sediment h⁻¹ at riffle tails (1-way ANOVA, $p > 0.05$; Fig. 4D–F). In the gaining reach, chl *a*, AFDM, and sediment respiration averaged 31.4 ± 56.6 mg chl *a*/m², 17.3 ± 23.3 g AFDM/m², and 0.35 ± 0.15 mg O₂ kg⁻¹ sediment h⁻¹ at riffle heads and 30.2 ± 65.2 mg chl *a*/m², 19.1 ± 12.2 g AFDM/m², and 0.24 ± 0.12 mg O₂ kg⁻¹ sediment h⁻¹ at riffle tails (1-way ANOVA, $p > 0.05$; Fig. 4D–F).

Comparisons of physicochemical variables, chl *a*, AFDM, and $R_{20^{\circ}\text{C}}$ between riffle heads and riffle tails in the losing reach with values in riffle heads and riffle tails nested in the gaining reach yielded almost the same pattern as observed at the regional scale (Table 1, Fig. 4G–I). $R_{20^{\circ}\text{C}}$ was related to chl *a* and periphyton AFDM (chl *a*: $R^2 \leq 0.23$, $p < 0.046$; AFDM: $R^2 \leq 0.49$, $p < 0.036$) but not to sediment organic matter ($p \geq 0.068$).

Discussion

We quantified the effect of vertical exchange on ecosystem properties and processes at 2 spatial scales along the large gravel-bed Tagliamento River. At the

TABLE 2. Mean (± 1 SD) biomass (mg ash-free dry mass [AFDM]/kg sediment), N ($\mu\text{g N/kg}$ sediment), P ($\mu\text{g P/kg}$ sediment), and molar C:N ratio of particulate organic matter (POM) in 3 different size fractions (>1 mm, 1–0.25 mm, <0.25 mm) and POM strongly attached to sediment particles > 0.025 mm (SOM; g/kg sediment). Data are shown for the losing (LR) and gaining (GR) reaches and as pooled data for riffle heads and riffle tails in the losing (RLR) and gaining (RGR) reaches. Significant values are highlighted in bold.

Site	LR <i>n</i> = 84	GR <i>n</i> = 72	RLR <i>n</i> = 72	RGR <i>n</i> = 72
POM >1 mm				
AFDM	94.2 \pm 116.4	78.2 \pm 83.4	51.8 \pm 63.2	82.2 \pm 150.2
N	866.3 \pm 1074	1201 \pm 1857	1005 \pm 1371	1099 \pm 1396
C:N	51.8 \pm 23.1	38.3 \pm 30.0	39.3 \pm 42.45	37.5 \pm 36.2
P	46.2 \pm 82.5	72.4 \pm 148.0	68.1 \pm 122.4	46.6 \pm 59.6
POM 1–0.025 mm				
AFDM	129.8 \pm 154.8	208.2 \pm 219.2	140.0 \pm 256.6	156.4 \pm 144.8
N	3544 \pm 5549	6608 \pm 8289	3082 \pm 4612	3452 \pm 4978
C:N	31.5 \pm 57.8	32.6 \pm 29.3	120.5 \pm 258.6	131.1 \pm 288.9
P	791.0 \pm 1131.5	1260 \pm 1461	1302 \pm 2824	955 \pm 1284
POM <0.025 mm				
AFDM	872.4 \pm 585.0	923.0 \pm 620.0	912.2 \pm 505.7	990.5 \pm 572.2
N	12469 \pm 10534	11479 \pm 7267	11645 \pm 8810	13772 \pm 17766
C:N	55.8 \pm 33.8	56.7 \pm 45.1	56.6 \pm 32.5	59.9 \pm 39.1
P	7227 \pm 6233	7054 \pm 5612	6499 \pm 4823	7267 \pm 7353
SOM	6.0 \pm 1.5	5.9 \pm 1.1	7.0 \pm 3.81	5.7 \pm 1.4

regional scale, physicochemical variables, chl *a*, periphyton AFDM, and $R_{20^\circ\text{C}}$ reflected vertical-exchange patterns in losing and gaining reaches similar to those observed in other river systems at the small (riffle-pool) scale. At the local scale, i.e., at riffle heads and riffle tails nested in the losing and gaining reach, variables did not respond to vertical exchange. However, averaged data for riffle heads and riffle tails in the losing reach compared to averaged data for riffle heads and riffle tails in the gaining reach revealed almost the same pattern of response to vertical exchange as observed at the regional scale. Chl *a* and periphyton AFDM showed negative responses to drying and rewetting conditions within the expanding and contracting losing reach.

An integrative view of ecosystem properties and processes at different spatial scales

At the regional scale, the losing reach was characterized by a substantial loss of surface flow into the highly permeable and deep alluvium that led to rapid expansion and contraction dynamics. The average infiltration rate of $2.5 \text{ m}^3 \text{ s}^{-1} \text{ river km}^{-1}$ was comparable to the rates observed in the Middle Fork of the Flathead River (Montana; $1.3 \text{ m}^3 \text{ s}^{-1} \text{ river km}^{-1}$; Stanford et al. 2005) and Homestead Creek (Australia; $1.1 \text{ m}^3 \text{ s}^{-1} \text{ river km}^{-1}$; Dunkerley and Brown 1999). Doering et al. (2007) showed that average infiltration rates per river km in the losing reach (Tagliamento)

were independent of the discharge measured at the upstream end of the reach (for discharge range 20–70 m^3/s). In the gaining reach, the exfiltration rate was, on average, only $0.3 \text{ m}^3 \text{ s}^{-1} \text{ river km}^{-1}$ because most of the upstream infiltrated river water emerges outside of the Tagliamento River corridor and feeds numerous springs (Fontana et al. 2008). Thus, average vertical hydraulic gradient (VHG) was highly negative in the losing reach but only slightly positive in the gaining reach (Fig. 2B).

At the local scale, along the losing reach, an ~ 0.5 -m-deep saturated sediment layer covered an unsaturated layer between the stream bed and the shallow water table (perched hyporheic zone). Similar conditions have been reported for the upper proglacial Val Roseg floodplain (Switzerland) where only the uppermost 20 to 40 cm of the sediments were saturated (Malard et al. 2000, 2002). In our study reaches, ground water was not reached until a depth of 1.7 m below the bed surface, although within 10 cm of the shoreline in the wetted channel area. Duration and magnitude of floods influence sediment permeability of bed sediments (Dunkerley and Brown 1999, Gasith and Resh 1999, Doering et al. 2007) and presumably depth and vertical extent of the saturated reach. We lack direct evidence from VHG measurements in the losing reach of the Tagliamento, but we hypothesize that at the local scale in the losing reach, downwelling marginalizes or prevents local upwelling (e.g., at riffle tails). In the gaining reach, VHG indicated approximately equal intensity

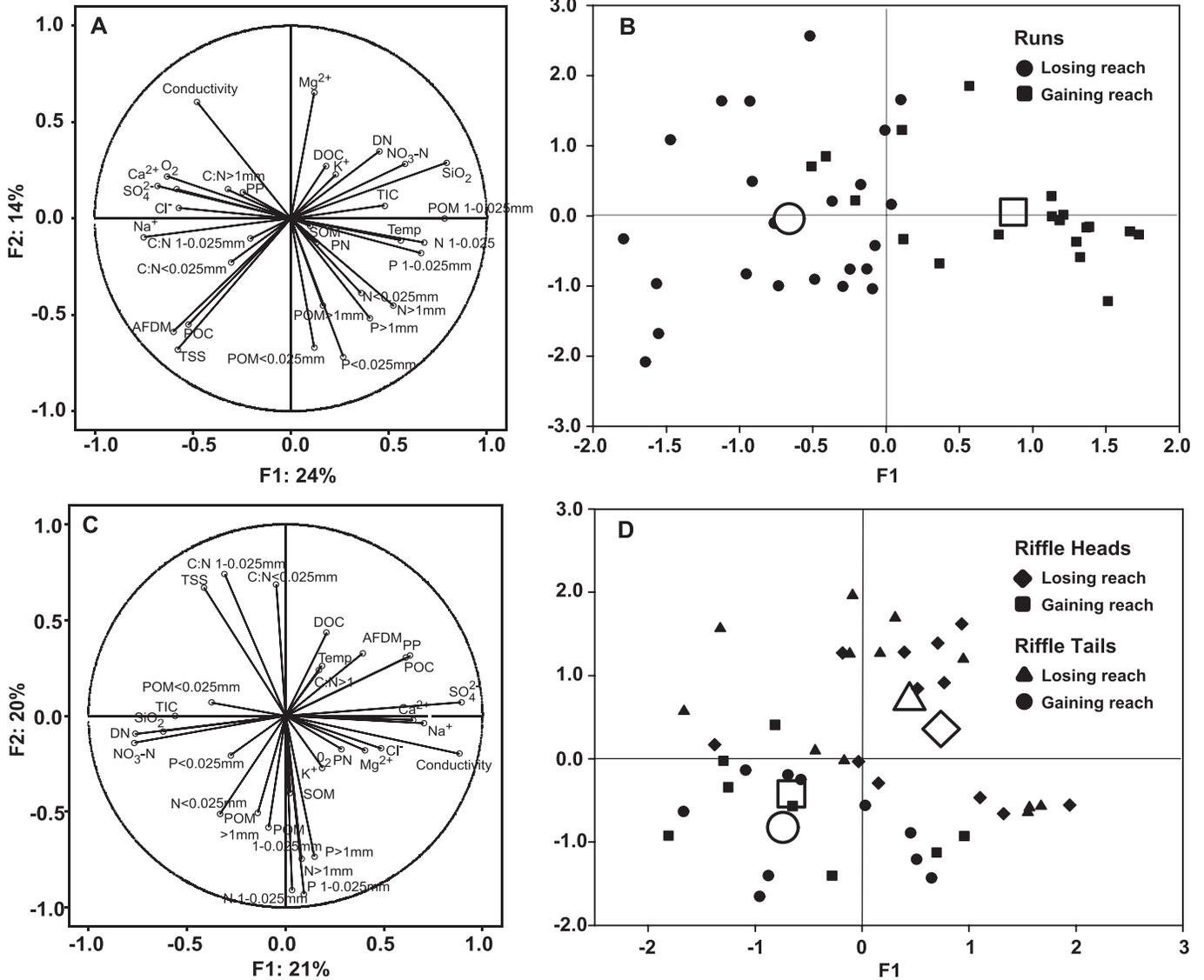


FIG. 3. Principal components analysis of physicochemical variables excluding subsurface hydrochemical data (see text) showing the correlation circle (A) and factor map (axes F1 and F2; percentages are % variance explained) (B) for physicochemical variables sampled in runs from July 2003 to April 2004 in the losing and gaining reach, and correlation circle (C) and factor map (D) for physicochemical variables, excluding subsurface hydrochemical data, sampled from October 2004 to July 2005 at riffle heads and riffle tails in the losing reach and at riffle heads and riffle tails in the gaining reach. Large open symbols represent centroids of respective sites. AFDM = ash-free dry mass, DN = dissolved N, DP dissolved P, PN = particulate N, POC = particulate organic C, POM = particulate organic matter (size classes: >1 mm, 0.025–1 mm, <0.025 mm), PP = particulate P, SOM = soluble organic matter, Temp = temperature, TIC = total inorganic C, TOC = total organic C, TSS = total suspended solids.

of down- and upwelling at riffle heads and riffle tails, respectively. In contrast to the losing reach, the hydrogeomorphic settings apparently impose minor constraints on local vertical exchange.

Overall, physicochemical habitat variables differed between the losing and gaining reaches (regional scale) but not between riffle heads and riffle tails (local scale). Changes in water chemistry are apparently related to the length of the subsurface flow path

and discharge. They were evident at the regional scale, but discharge was too high and flow paths too short to exert a major influence on the chemical milieu at the local scale. In gravel-bed rivers, flow paths are not isolated (Poole et al. 2008). Surface water mixing with shallow hyporheic and phreatic ground waters from long flow paths at the regional scale may result in water chemistry in upwelling locations influenced mainly by water composed of many different ages

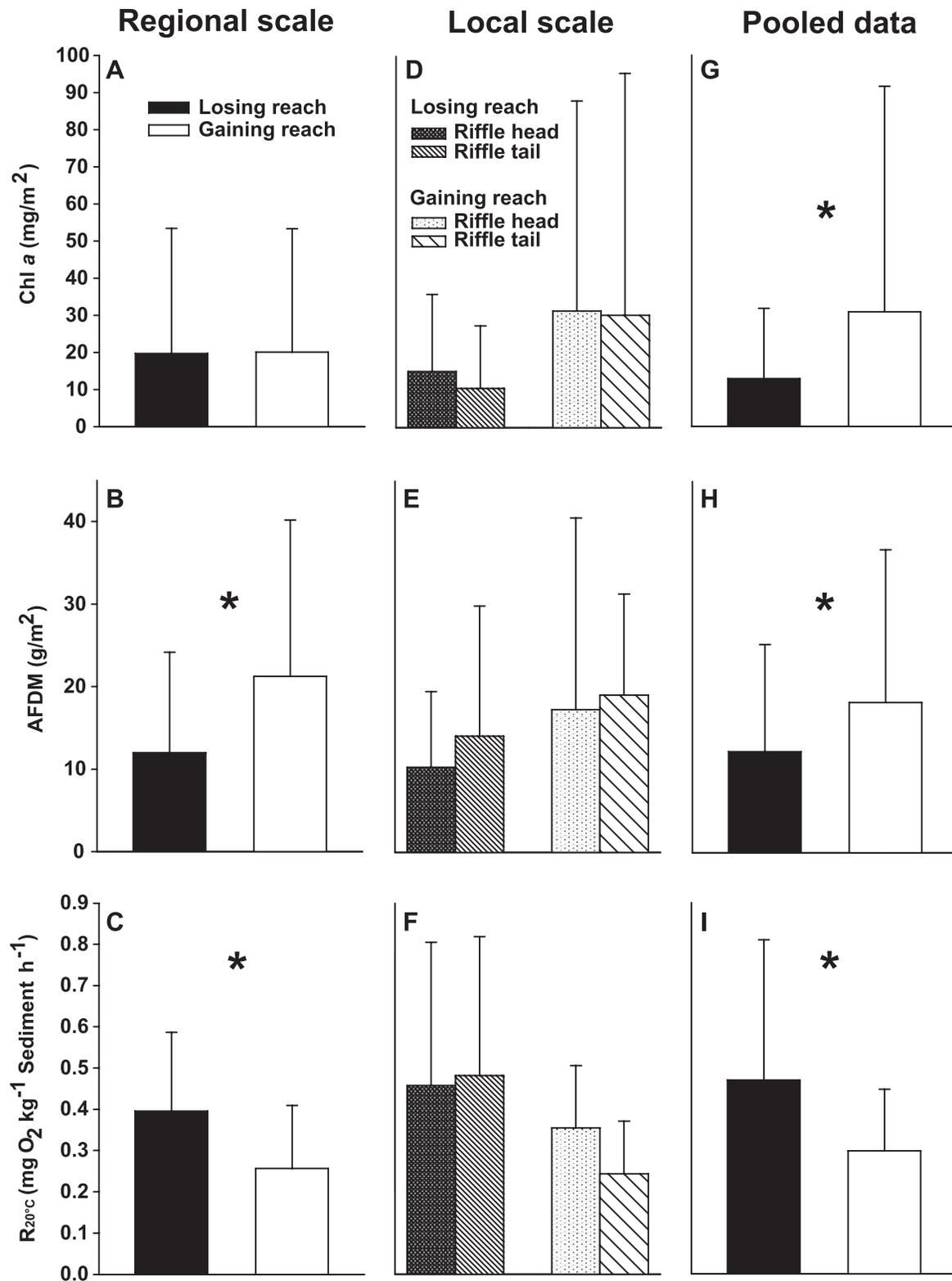


FIG. 4. Mean (± 1 SD) chlorophyll *a* (chl *a*) (A, D, G), periphyton ash-free dry mass (AFDM) (B, E, H), and hyporheic respiration per kg sediment particles < 8 mm normalized to 20°C ($R_{20^{\circ}\text{C}}$) (C, F, I) in runs of the losing and gaining reach at the regional scale (July 2003–April 2004) (A–C), in riffle heads and riffle tails of the losing and gaining reach at the local scale (October 2004–July 2005) (D–F), and pooled data for riffle heads and riffle tails in the losing and gaining reach (G–I). Asterisks mark significant differences.

rather than by biogeochemical processes acting over time along a short flow path. In small streams, local vertical or lateral vertical exchange may strongly influence surface-water chemistry, in particular nutrient concentrations (e.g., Hendricks 1993, Valett et al. 1994, Dahm et al. 1998, Dent et al. 2001). For example, in Sycamore Creek (Arizona, USA), surface NO_3^- concentrations were 2 to $3\times$ higher in local upwelling areas than in corresponding downwelling reaches (Valett et al. 1994). In general, downwelling areas are locations where suspended organic matter is expected to be retained in the uppermost sediments and subsequently processed. In the Tagliamento, differences in sediment organic matter between down- and upwelling areas were not significant at the regional or local scale and corresponded to a low POM load during base flow. Retained POM, such as sloughed algae, is presumably subject to fast decomposition. In particular, POM loads during floods are retained in downwelling areas. Jones et al. (1995) found that sediment POC was higher in downwelling than in upwelling areas after floods in Sycamore Creek, but these differences disappeared during interspate periods. This result suggests that floods, rather than the continuous POM supply during base flow, may account for differences in sediment organic matter between down- and upwelling areas.

Upwelling can enhance periphyton accrual (e.g., chl *a* is positively correlated with VHG). This effect has been demonstrated at the riffle–pool scale (100–140 m) in a small desert stream (Valett et al. 1994) and at a larger scale (500–1000 m) in a medium-sized floodplain river (Stanford et al. 2005, Wyatt et al. 2008). At the regional scale in the Tagliamento, periphyton AFDM was significantly higher in the gaining than in the losing reach, but did not differ between riffle heads and riffle tails (both reaches) at the local scale. The spatial pattern of chl *a* was quite different. No difference was observed between reaches at the regional scale, but distinct differences between losing and gaining reaches in pooled data from riffle heads and riffle tails were found at the local scale. Enhanced nutrient availability in riffle heads and riffle tails of the gaining reach may account for the observed higher chl *a* content of the periphyton community in the gaining reach. However, chl *a* is less suitable than periphyton AFDM as a biomass variable because the chlorophyll content of algae depends on environmental conditions. The chlorophyll content of algae can decline with increasing N or P limitation (Healey and Hendzel 1975, Rhee 1978, Uehlinger 1981) and with decreasing light intensity (Hill and Boston 1991). Both chl *a* and AFDM were higher at permanently wetted sites. Fast contraction–expansion cycles triggered by

local convective rain events limit primary producers from developing desiccant-resistant structures or physiological adjustment. During flow recession, the downstream end of the wetted channel in the losing reach may move upstream at rates as high as 0.5 km/h (Doering et al. 2007). Algae are expected to die within hours after they fall dry (Agrawal and Singh 2002, Stanley et al. 2004).

At the regional scale, vertical exchange was apparently a major factor controlling sediment respiration. At the local scale, differences between downwelling and corresponding upwelling areas were not significant, although $R_{20^\circ\text{C}}$ tended to be slightly higher at riffle heads than at riffle tails (Fig. 4F). The correlations between $R_{20^\circ\text{C}}$, chl *a*, and periphyton AFDM indicate that autochthonous production of organic matter, which includes release of extracellular organic matter by algae and sloughed algal cells, may be an important energy source fueling sediment respiration (Jones et al. 1995). In the wide, braided channel of the Tagliamento, allochthonous inputs from riparian forests and upstream areas presumably are of minor importance as an energy source for aquatic communities (Langhans et al. 2006). In desert streams, autochthonous energy supply can support $>80\%$ of the respiration in the hyporheic reach (Jones et al. 1995), whereas in forested streams, allochthonous organic matter input serves as the primary energy source (Pusch and Schwoerbel 1994, Naegeli et al. 1995). Respiration rates were several times higher in the Tagliamento than in the Alpine floodplain of the Roseg River but 2 to $3\times$ lower than in desert streams (Table 3), a pattern that is most likely a function of temperature and the source and quality of organic matter as described above.

Conclusion

Our results supported our expectations. The observed spatial pattern in ecosystem properties and processes at the regional, large scale in the losing and gaining reach of the Tagliamento River matches findings from other investigations at the scale of channel bedform units (riffle–pool) (e.g., high biomass in upwelling areas and high respiration in downwelling areas; Valett et al. 1994, Jones et al. 1995). Vertical exchange was apparently a major factor controlling ecosystem properties and ecosystem processes across spatial scales. High infiltration and exfiltration rates at the regional scale impose constraints on the vertical exchange at the local, small scale (riffle–pool). Furthermore, relatively high discharge (e.g., 5–60 m^3/s at river km 91), including potential mixing of surface, phreatic, and hyporheic groundwater, presumably reduced the effect of nutrient regen-

TABLE 3. Mean (± 1 SD) respiration rates in hyporheic sediments (0.1 m sediment depth) of the Tagliamento River compared to rates in other streams (Jones et al. 1995, Uehlinger et al. 2002, Uehlinger and Zah 2003). All respiration rates were quantified in respiration chambers at a depth of 0.1 m.

River	Respiration (mg O ₂ kg ⁻¹ h ⁻¹)
Tagliamento (Italy; low elevation Alpine floodplain; July 2003–June 2005; monthly average rate)	
Losing reach	0.42 \pm 0.19
Gaining reach	0.26 \pm 0.15
Val Roseg (Switzerland; high elevation Alpine floodplain; March–October; monthly average rate)	
Main channel	0.02 \pm 0.02
Surface connected channels	0.04 \pm 0.03
Surface-disconnected channels	0.08 \pm 0.06
Sycamore Creek (USA; desert stream; annual mean rate)	
Downwelling zones	1.12
Upwelling zones	0.46
Hassayampa River (desert stream; autumn)	0.96 \pm 0.11

eration along the relatively short subsurface flow path between riffle heads and riffle tails. Both factors are finally responsible for the lack of response in ecosystem properties and ecosystem processes at the local scale. Expansion and contraction dynamics (drying and rewetting) affected periphyton accrual negatively as shown in other studies (Stanley et al. 2004). We demonstrated the hierarchical nature of floodplain systems with respect to vertical exchange, ecosystem properties, and ecosystem processes across different spatial scales. These hierarchical scales cannot be uncoupled, and understanding their interaction is essential in understanding the function and complexity of riverine ecosystems.

Acknowledgements

We are very grateful to the many people who helped in the field and with logistics, especially C. Cruciat, S. Blaser, and Y. Schwill, and C. T. Robinson for comments on earlier versions of this manuscript. The comments of 3 referees improved the manuscript. This work was supported by the European Union project tempQsim (EVK1-CT2002-00112; www.tempqsim.net) and by the Staatssekretariat für Bildung und Forschung (SBF) (No. 02.0072).

Literature Cited

- ACUÑA, V., AND K. TOCKNER. 2009. Surface–subsurface water exchange rates along alluvial river reaches control the thermal patterns in an Alpine river network. *Freshwater Biology* 54:306–320.
- AGRAWAL, S. C., AND V. SINGH. 2002. Viability of dried filaments, survivability and reproduction under water stress, and survivability following heat and UV exposure in *Lyngbya martensiana*, *Oscillatoria agardhii*, *Nostoc calcicola*, *Hormidium fluitans*, *Spirogyra* sp., and *Vaucheria germinata*. *Folia Microbiologica* 47:61–67.
- ARSCOTT, D. B., K. TOCKNER, D. VAN DER NAT, AND J. V. WARD. 2002. Aquatic habitat dynamics along a braided alpine river ecosystem (Tagliamento River, Northeast Italy). *Ecosystems* 5:802–814.
- BAXTER, C., AND F. R. HAUER. 2000. Geomorphology, hyporheic exchange, and selection of spawning habitat by bull trout (*Salvelinus confluentus*). *Canadian Journal of Fisheries and Aquatic Sciences* 57:1470–1481.
- BAXTER, C., F. R. HAUER, AND W. W. WOESSNER. 2003. Measuring groundwater–stream water exchange: new techniques for installing minipiezometers and estimating hydraulic conductivity. *Transactions of the American Fisheries Society* 132:493–503.
- BOULTON, A. J., T. DATRY, T. KASAHARA, M. MUTZ, AND J. A. STANFORD. 2010. Ecology and management of the hyporheic zone: stream–groundwater interactions of running waters and their floodplains. *Journal of the North American Benthological Society* 29:26–40.
- BRUNKE, M., AND T. GONSER. 1997. The ecological significance of exchange processes between rivers and groundwater. *Freshwater Biology* 37:1–33.
- CLEIN, J. S., AND J. P. SCHIMMEL. 1994. Reduction in microbial activity in birch litter due to drying and rewetting events. *Soil Biology and Biochemistry* 26:403–406.
- DAHM, C. N., N. B. GRIMM, P. MARMONIER, H. M. VALETT, AND P. VERVIER. 1998. Nutrient dynamics at the interface between surface water and groundwaters. *Freshwater Biology* 40:427–452.
- DATRY, T., S. T. LARNED, AND M. R. SCARBROOK. 2007. Responses of hyporheic invertebrate assemblages to large-scale variation in flow permanence and surface–subsurface exchange. *Freshwater Biology* 52:1452–1462.
- DENT, C. L., N. B. GRIMM, AND S. G. FISHER. 2001. Multiscale effects of surface–subsurface exchange processes between rivers and groundwater. *Journal of the North American Benthological Society* 20:162–181.

- DOERING, M., U. UEHLINGER, A. ROTACH, AND D. R. SCHLAEPPER. 2007. Ecosystem expansion and contraction dynamics along a large alpine alluvial corridor (Tagliamento River, Northeast Italy). *Earth Surface Processes and Landforms* 32:1693–1704.
- DUNKERLEY, D., AND K. BROWN. 1999. Flow behaviour, suspended sediment transport and transmission losses in a small (sub-bank-full) flow event in an Australian desert stream. *Hydrological Processes* 13:1577–1588.
- EBINA, J., T. TSUTSUI, AND T. SHIRAI. 1983. Simultaneous determination of total nitrogen and total phosphorus in water using peroxodisulfate oxidation. *Water Research* 17:1721–1726.
- FERNALD, A. G., P. J. WIGINGTON, AND H. L. DIXON. 2001. Transient storage and hyporheic flow along the Willamette River, Oregon: field measurements and model estimates. *Water Resources Research* 37:1681–1694.
- FONTANA, A., P. MOZZI, AND A. BONDESAN. 2008. Alluvial megafans in the Venetian-Friulian plain (North-Eastern Italy): evidence of sedimentary and erosive phases during late Pleistocene and Holocene. *Quaternary International* 189:71–90.
- FRANKEN, R. J. M., R. G. STOREY, AND D. D. WILLIAMS. 2001. Biological, chemical and physical characteristics of downwelling and upwelling zones in the hyporheic zone of a north-temperate stream. *Hydrobiologia* 444: 183–195.
- FRISSELL, C. A., W. J. LISS, C. E. WARREN, AND M. D. HURLEY. 1986. A hierarchical framework for stream habitat classification: viewing streams in a watershed context. *Environmental Management* 10:199–214.
- GASITH, A., AND V. H. RESH. 1999. Streams in Mediterranean climate regions: abiotic influences and biotic responses to predictable seasonal events. *Annual Review of Ecology and Systematics* 30:51–81.
- HEALEY, F. P., AND L. L. HENDZEL. 1975. Effect of phosphorus deficiency on two algae growing in chemostats. *Journal of Phycology* 11:303–309.
- HENDRICKS, S. P. 1993. Microbial ecology of the hyporheic zone: a perspective integrating hydrology and biology. *Journal of the North American Benthological Society* 12: 70–78.
- HILL, W. R., AND H. L. BOSTON. 1991. Community development alters photosynthesis-irradiance relations in stream periphyton. *Limnology and Oceanography* 36:10–23.
- JONES, J. B. 1995. Factors controlling hyporheic respiration in a desert stream. *Freshwater Biology* 34:91–99.
- JONES, J. B., S. G. FISHER, AND N. B. GRIMM. 1995. Vertical hydrologic exchange and ecosystem metabolism in a Sonoran desert stream. *Ecology* 76:942–952.
- KASAHARA, T., AND S. M. WONDZELL. 2003. Geomorphic controls on hyporheic exchange flow in mountain streams. *Water Resources Research* 39:1005–1019.
- LANGHANS, S. D., S. D. TIEGS, U. UEHLINGER, AND K. TOCKNER. 2006. Environmental heterogeneity controls organic-matter dynamics in river floodplain ecosystems. *Polish Journal of Ecology* 54:675–680.
- LARNED, S. T., T. DATRY, AND C. T. ROBINSON. 2007. Invertebrate and microbial responses to inundation in an ephemeral river reach in New Zealand: effects of preceding dry periods. *Aquatic Sciences* 69:554–567.
- LOWE, W. L., G. E. LIKENS, AND M. E. POWER. 2006. Linking scales in stream ecology. *BioScience* 56:591–597.
- MALARD, F., K. TOCKNER, M. J. DOLE-OLIVER, AND J. V. WARD. 2002. A landscape perspective of surface–subsurface hydrological exchanges in river corridors. *Freshwater Biology* 47:621–640.
- MALARD, F., K. TOCKNER, AND J. V. WARD. 1999. Shifting dominance of subcatchment water sources and flow paths in a glacial floodplain, Val Roseg, Switzerland. *Arctic, Antarctic and Alpine Research* 31:135–150.
- MALARD, F., K. TOCKNER, AND J. V. WARD. 2000. Physico-chemical heterogeneity in a glacial riverscape. *Landscape Ecology* 15:679–695.
- MALARD, F., U. UEHLINGER, R. ZAH, AND K. TOCKNER. 2006. Flood-pulse and riverscape dynamics in a braided glacial river. *Ecology* 87:704–716.
- MARXSEN, J., A. ZOPPINI, AND S. WILCZEK. 2010. Microbial communities in streambed sediments recovering from desiccation. *FEMS Microbiology Ecology* 71:374–386.
- MEYNS, S., R. ILLI, AND B. RIBI. 1994. Comparison of chlorophyll *a* analysis by HPLC and spectrophotometry: where do the differences come from? *Archiv für Hydrobiologie* 132:129–139.
- NAEGELI, M. W., U. HARTMANN, E. I. MEYER, AND U. UEHLINGER. 1995. POM dynamics and community respiration in the sediments of a floodprone prealpine river (Necker, Switzerland). *Archiv für Hydrobiologie* 133:339–347.
- NAEGELI, M. W., AND U. UEHLINGER. 1997. Contribution of the hyporheic zone to ecosystem metabolism in a prealpine gravel-bed river. *Journal of the North American Benthological Society* 16:794–804.
- PARSONS, M., AND M. C. THOMS. 2007. Hierarchical patterns of physical-biological associations in river ecosystems. *Geomorphology* 89:127–146.
- POOLE, G. C., S. J. O'DANIEL, K. L. JONES, W. W. WOESSNER, E. S. BERNHARDT, A. M. HELTON, J. A. STANFORD, B. R. BOER, AND T. J. BEECHIE. 2008. Hydrologic spiralling: the role of multiple interactive flow paths in stream ecosystems. *River Research and Applications* 24:1018–1031.
- POOLE, G. C., J. A. STANFORD, C. A. FRISSELL, AND S. W. RUNNING. 2002. Three-dimensional mapping of geomorphic controls on flood-plain hydrology and connectivity from aerial photos. *Geomorphology* 48:329–347.
- POOLE, G. C., J. A. STANFORD, S. W. RUNNING, AND C. A. FRISSELL. 2006. Multiscale geomorphic drivers of groundwater flow paths: subsurface hydrologic dynamics and hyporheic habitat diversity. *Journal of the North American Benthological Society* 25:288–303.
- POOLE, G. C., J. A. STANFORD, S. W. RUNNING, C. A. FRISSELL, W. W. WOESSNER, AND B. K. ELLIS. 2004. A patch hierarchy approach to modeling surface and subsurface hydrology in complex flood-plain environments. *Earth Surface Processes and Landforms* 29:1259–1274.
- PUSCH, M., AND J. SCHWOERBEL. 1994. Community respiration in hyporheic sediments of a mountain stream (Steina, Black Forest). *Archiv für Hydrobiologie* 130:35–52.

- RHEE, G. Y. 1978. Effects of N:P atomic ratios and nitrate limitation on algal growth, cell composition, and nitrate uptake. *Limnology and Oceanography* 23:10–25.
- SOKAL, R. R., AND F. J. ROHLF. 1995. *Biometry: the principles and practice of statistics in biological research*. 3rd edition. Freeman, New York.
- STANFORD, J. A., M. S. LORANG, AND F. R. HAUER. 2005. The shifting habitat mosaic of river ecosystems. *Verhandlungen der Internationalen Vereinigung für theoretische und angewandte Limnologie* 29:123–136.
- STANLEY, E. H., S. G. FISHER, AND J. B. JONES. 2004. Effects of water loss on primary production: a landscape-scale model. *Aquatic Sciences* 66:130–138.
- THORP, J. H., M. C. THOMS, AND M. D. DELONG. 2006. The riverine ecosystem synthesis: biocomplexity in river networks across space and time. *River Research and Applications* 22:123–147.
- TOCKNER, K., F. MALARD, P. BURGHERR, C. T. ROBINSON, U. UEHLINGER, R. ZAH, AND J. V. WARD. 1997. Physico-chemical characterization of channel types in a glacial floodplain ecosystem (Val Roseg, Switzerland). *Archiv für Hydrobiologie* 140:433–463.
- TOCKNER, K., J. V. WARD, D. B. ARSCOTT, P. J. EDWARDS, J. KOLLMANN, A. M. GURNELL, G. E. PETTS, AND B. MAIOLINI. 2003. The Tagliamento River: a model ecosystem of European importance. *Aquatic Sciences* 65:239–253.
- UEHLINGER, U. 1981. Ecology of the planktonic blue-green alga *Aphanizomenon flos-aquae* in Alpine lakes. *Schweizerische Zeitschrift für Hydrologie – Swiss Journal of Hydrology* 43:69–88.
- UEHLINGER, U. 1991. Spatial and temporal variability of the periphyton biomass in a prealpine river (Necker, Switzerland). *Archiv für Hydrobiologie* 123:219–237.
- UEHLINGER, U., M. W. NAEGELI, AND S. G. FISHER. 2002. A heterotrophic desert stream? The role of sediment stability. *Western North American Naturalist* 62:466–473.
- UEHLINGER, U., AND R. ZAH. 2003. Organic matter dynamics. Pages 199–215 in J. V. Ward and U. Uehlinger (editors). *Ecology of a glacial floodplain*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
- VALETT, H. M., S. G. FISHER, N. B. GRIMM, AND P. CAMILL. 1994. Vertical hydrologic exchange and ecological stability of a desert stream ecosystem. *Ecology* 75:548–560.
- VAN GESTEL, M., R. MERCKX, AND K. VLASSAK. 1993. Microbial biomass and activity in soils with fluctuating water contents. *Geoderma* 56:617–626.
- WHITE, D. S. 1993. Perspectives on defining and delineating hyporheic zones. *Journal of the North American Benthological Society* 12:61–69.
- WYATT, K. H., F. R. HAUER, AND G. F. PESSONEY. 2008. Benthic algal response to hyporheic-surface water exchange in an alluvial river. *Hydrobiologia* 607:151–161.
- ZAH, R. 2001. Patterns, pathways, and trophic transfer of organic matter in a glacial stream ecosystem in the Alps. PhD Thesis, ETH, Zurich, Switzerland.

Received: 1 February 2012

Accepted: 26 September 2012