**Earth Surface Processes and Landforms**
*Earth Surf. Process. Landforms* **32**, 1693–1704 (2007)
Published online 18 September 2007 in Wiley InterScience
(www.interscience.wiley.com) **DOI:** 10.1002/esp.1594

# Ecosystem expansion and contraction dynamics along a large Alpine alluvial corridor (Tagliamento River, Northeast Italy)

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Received 15 February 2006;
Revised 18 October 2006;
Accepted 20 October 2006

## Abstract

**Riverine floodplains are pulsing ecosystems that expand and contract with changing flow. In this study we quantified large-scale expansion and contraction dynamics of surface waters along a 41·5 km braided section of the last remaining semi-natural large Alpine gravel-bed river (Tagliamento River; NE Italy). To assess surface–subsurface exchange patterns we measured discharge and vertical hydraulic gradients at multiple locations along the corridor. We identified two river sections delineated by distinct geomorphic knickpoints. In the upper 29 km, Section I (losing zone), surface flow decreased on average by $2{\cdot}5 \pm 0{\cdot}8$ m$^3$ s$^{-1}$ per river-km. In the downstream 12·5 km, Section II (gaining zone), surface flow increased on average by $0.3 \pm 0.1$ m$^3$ s$^{-1}$ per river-km. The losing zone experienced frequent and extensive drying and rewetting cycles. The length of the dry river section was measured over a 1·5 year period using differential GPS. Up to 23 km of Section I fell dry at the surface. Frequent and irregular flow pulses led to rapid expansions of the wetted channel at velocities of up to 3 km h$^{-1}$, while the subsequent contraction velocities were less than 0·5 km h$^{-1}$. Water level was linearly regressed against the total length of the dry river section ($r^2 = 0{\cdot}74$; $p < 0{\cdot}0001$). This relationship, in combination with a continuous stage record, was used to evaluate expansion and contraction dynamics over a 4 year period. Timing, frequency, magnitude (spatial extent) and duration of expansion and contraction dynamics reflected the flashy flow regime of the Tagliamento River, including a high intra- and inter-annual variability of surface drying and rewetting. Our study emphasizes that even small changes in flow can cause major increases or decreases of ecosystem size, thereby creating a highly dynamic and harsh environment for both terrestrial and aquatic organisms. Copyright © 2007 John Wiley & Sons, Ltd.**

**Keywords: floodplain; flow regime; ecosystem process; braided river; hydraulic exchange; temporary river; Mediterranean; aquifer**

## Introduction

Riverine floodplains are defined as the entire channel network and valley-bottom area that is capable of flooding (Stanford *et al.*, 2005). As such, they are highly complex and dynamic ecosystems that undergo distinct cycles of expansion, contraction and fragmentation along longitudinal, lateral and vertical dimensions (Malard *et al.*, 2006; Stanley *et al.*, 1997; Ward *et al.*, 2002). Flood pulses exceeding bankfull level and droughts represent two extremes of the flow regime (Lytle and Poff, 2004). Between these extremes, rivers experience frequent instream water level fluctuations (‘flow pulses’ *sensu* Tockner *et al.*, 2000), which lead to expansion and contraction of the channel network. The magnitude, frequency, duration and timing of the expansion and contraction are important variables influencing the size, spatial configuration and connectivity of aquatic and terrestrial habitats of floodplain ecosystems (Junk *et al.*, 1989; Sparks *et al.*, 1990; Ward *et al.*, 2002). These dynamic processes shape floodplain communities and ecosystem functioning (see, e.g., Humphries and Baldwin, 2003; Jones, 1995; Lake, 2000; Langhans and Tockner, 2006; Robertson *et al.*, 1999).

The lateral expansion and contraction of floodplain ecosystems has been studied extensively; examples include the subtropical Ogeechee River in southeastern USA (Benke *et al.*, 2000), the Amazon River (Sippel *et al.*, 1998) and the Alpine Tagliamento River in northeastern Italy (Van der Nat *et al.*, 2002). However, only a few studies focused on large-scale longitudinal expansion and contraction in combination with vertical exchange processes. Notable examples are studies in the proglacial Val Roseg River floodplain in Switzerland (Malard *et al.*, 2002, 2006) and the semi-arid catchment of Sycamore Creek in Arizona, USA (Stanley *et al.*, 1997).

Apart from these studies, information on longitudinal expansion and contraction dynamics is widely lacking. However, such information is essential to understand the effect of changing flow conditions on biogeochemical processes and nutrient transformations, especially in temporary streams (Baldwin and Mitchel, 2000; Dahm *et al.*, 2003; Humphries and Baldwin, 2003; Jakobson *et al.*, 2000). Worldwide, 30% of all rivers are temporary, but our knowledge about their functioning is still in its infancy (Poff, 1992).

The goal of this study was to investigate expansion and contraction dynamics along a large braided corridor and to discuss their potential significance for terrestrial and aquatic communities as well as for ecosystem processes. To achieve this goal we quantified (i) vertical exchange processes and (ii) large-scale expansion and contraction dynamics at different timescales along one of the last remaining semi-natural river corridors in Central Europe, the Tagliamento River in northeastern Italy. Two key questions were asked. First, what is the magnitude of surface–subsurface water exchange along the gravel-bed corridor? Second, what are the magnitude (spatial extent), duration (number of days), frequency (number of drying and rewetting cycles) and timing (season) of surface expansion and contraction along the gravel-bed corridor? To answer these questions we quantified surface discharge and vertical hydraulic gradient at multiple locations along the corridor. Further, we developed a simple model to predict surface drying and rewetting at average daily intervals along the entire study reach. This model is based on the relationship between water level and the spatial extent of ecosystem expansion and contraction. Finally, we discuss potential ecological implications of these large-scale expansion and contraction dynamics that were historically a common feature of braided gravel-bed rivers, particularly in Mediterranean and semi-arid regions (Tockner *et al.*, 2006).

## Study Area

The Tagliamento River in northeastern Italy (46° N, 12°30′ E; Figure 1) is a seventh order river that flows unimpeded by high dams for 172 km to the Adriatic Sea and drains an area of approximately 2580 km$^2$. It is a mountainous catchment, over 70% of which is located in the Alps. The highest peak in the catchment is Mt. Coglians (2781 m a.s.l.). The mean altitude is 987 m a.s.l. The Alpine and prealpine areas consist mainly of limestone and flysch, occasionally intermixed with layers of gypsum (Tockner *et al.*, 2003). The lowland section is part of the Venetian–Friulian Plain, forming a highly permeable aquifer, several hundred meters deep (Fontana *et al.*, in press; Figure 3).

Average annual precipitation is 2150 mm, but precipitation increases from W to E and S to N from 1000 mm to ~3000 mm. The Tagliamento River is influenced by both Alpine and Mediterranean snowmelt and precipitation regimes ($Q_{80} = 72$ m$^3$ s$^{-1}$; Ward *et al.*, 1999). As a result, it exhibits a flashy discharge regime with peaks in spring and autumn. However, flow and flood pulses (≥bankfull discharge) can occur at any time of the year (Arscott *et al.*, 2002). Despite local human impacts, the Tagliamento River is considered to be the last remaining large semi-natural river corridor in Central Europe.

Our main study area (Figure 1) is an unconstrained 41·5 km river segment downstream of the bedrock constrained knickpoint at Pinzano (river-km 85) to the bridge at Varmo (river-km 126·5) situated in the lowland section. Downstream of Pinzano (Section I) the river loses surface water into the highly permeable alluvial aquifer (Figures 2 and 3). A portion of the river in this segment lacks surface flow (maximum dry length: 23 km) under low flow conditions. At river-km 114 the 'linea delle risorgive' (Figure 1) consisting of silt and clay sediments acts as an aquiclude and forces the groundwater to the surface (Fontana *et al.*, in press; Figure 3). This results in a massive upwelling of Tagliamento River water (Section II) (Figure 1). Only a small fraction of this water returns to the Tagliamento river-bed itself, since it also feeds adjacent rivers (Fontana *et al.*, in press), for example the Stella River located to the east of the Tagliamento River. Downstream of the bridge at Varmo the braiding river transforms into a meandering river (geomorphic knickpoint at the downstream end of Section II).

The fluvial corridor of the main study reach is up to 2 km wide and contains exposed gravel (32 km$^2$), surface water (≤5 km$^2$), vegetated islands (6 km$^2$), riparian forest (20 km$^2$) and developed land (21 km$^2$). At river-km 88·5 water is abstracted for fish farming and irrigation ($3{\cdot}3 \pm 0{\cdot}1$ m$^3$ s$^{-1}$; $n = 3$). The Cosa River, the only natural although temporary tributary along the study reach, enters the Tagliamento River at river-km 98·8 (see Figure 1). Surface flow was observed only twice during the study period (20 January 2004, 1·89 m$^3$ s$^{-1}$; 22 October 2004, 2·31 m$^3$ s$^{-1}$).



DOI: 10.1002/esp

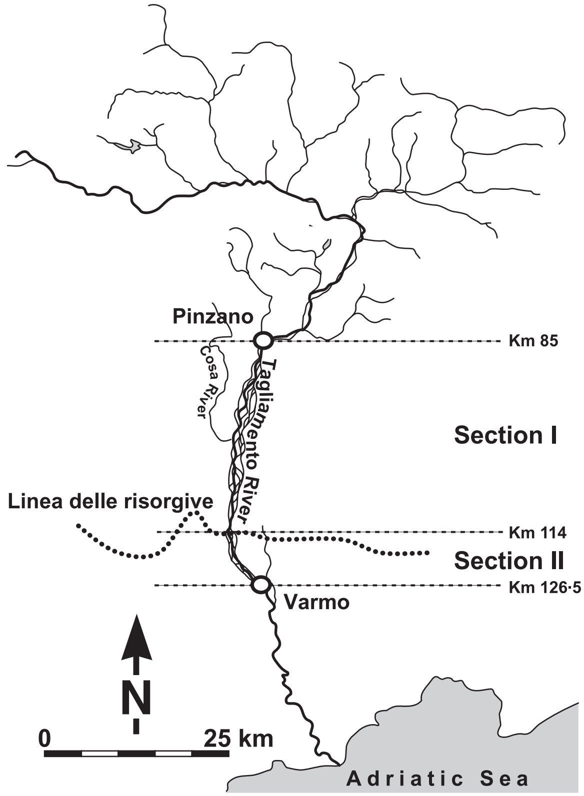


**Figure 1.** Map of the Tagliamento catchment indicating the location of the main study area delineated by distinct geomorphic knickpoints (modified after Ward *et al.*, 1999). Section I extends from the bedrock constrained knickpoint at Pinzano (river-km 85–114) to the knickpoint of the 'linea delle risorgive'. Section II (river-km 114–126.5) extends to the transition between the braiding and meandering sections.

For a complete description of the catchment and longitudinal geomorphic features see the work of Arscott *et al.* (2002, 2000), Gurnell *et al.* (2001), Tockner *et al.* (2003) and Ward *et al.* (1999).

## Methods

### Vertical hydraulic gradient and surface discharge

We determined the direction and intensity of groundwater–stream water exchange by measuring the vertical hydraulic gradient (VHG). VHG is defined as

$$\mathrm{VHG} = \frac{\Delta h}{\Delta l}$$

where $\Delta h$ is the difference in hydraulic head between the water level in the piezometer and the level of the stream surface (cm) and $\Delta l$ is the depth from the surface of the streambed to the first opening in the piezometer sidewall (Baxter *et al.*, 2003). Therefore, VHG is a unitless metric. It is positive under upwelling conditions and negative under downwelling conditions.

VHG was measured in five mini-piezometers installed across each of eight to 10 transects equally spaced along Sections I and II (six different dates, July 2003 to April 2004). The number of transects differed with the wetted length of Section I. Differences in VHG among transects were evaluated using Kruskal–Wallis ANOVA.

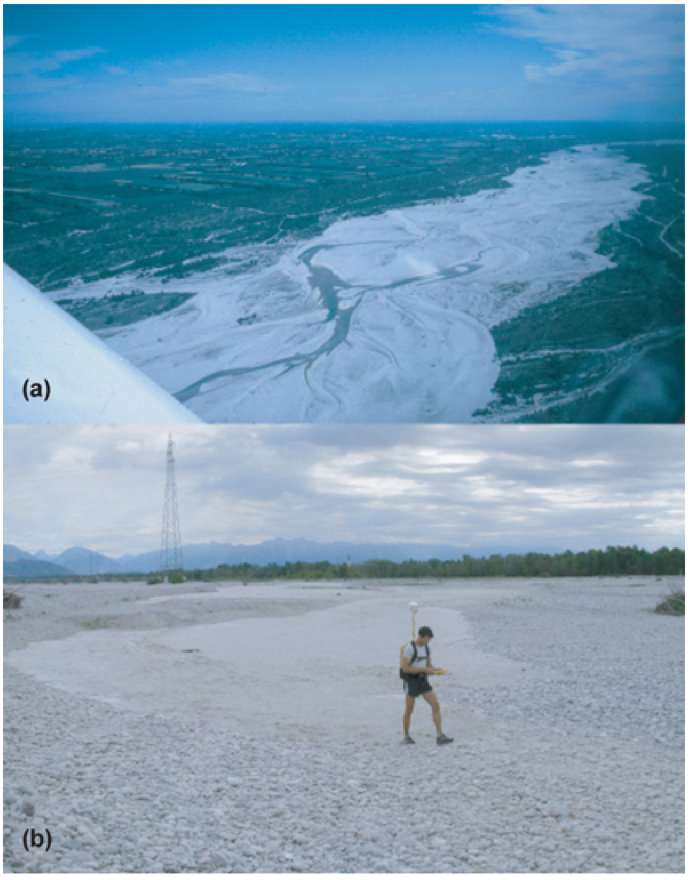


**Figure 2.** (a) Aerial photograph of Section I showing the downstream end of the wetted channel and the dry river corridor. (Photograph: D. Van der Nat.) (b) Flow front of the expanding channel after a headwater storm event (Photograph: A. Rotach). This figure is available in colour online at www.interscience.wiley.com/journal/espl

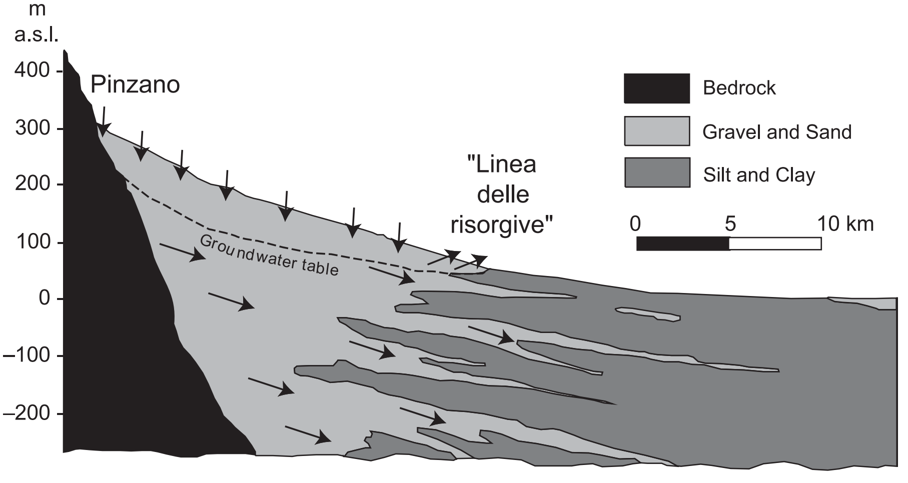


**Figure 3.** Longitudinal–vertical profile of the Venetian–Friulian Plain (modified after Fontana *et al.*, 2004). Arrows mark the direction of the surface and subsurface flows.

We calculated infiltration and exfiltration rates ($m^3\ s^{-1}\ km^{-1}$) along the entire study area by measuring surface discharge across seven to 13 transects (nine dates between July 2003 and October 2004). In shallow channels we used a mini-air flow meter (Schildknecht Messtechnik AG, Gossau, CH) and an acoustic Doppler velocity meter (ADV; Flowtracker, SonTek, San Diego, CA, USA). Discharge was calculated using the area–velocity method (Gore, 1996). In channels deeper than ~1 m, we applied an acoustic Doppler profiler (ADP; SonTek, CA, USA) mounted on an inflatable raft. Detailed information on ADP and ADV applications is provided by Lorang *et al.* (2005).

## Expansion and contraction dynamics

Between April 2003 and October 2004, we monitored expansion and contraction dynamics along the main study area by determining the beginning and end of the wetted river section with a differential global positioning system (dGPS; TCS1, Trimble, Sunnyvale, CA, USA). In total, we measured the downstream end of the wetted channel (Section I) 200 times and the emergence of channels in Section II 22 times. In addition, the expansion and contraction dynamic of a major flow pulse was monitored between 2 and 14 July 2003 (total: 536 measurements). The length of the wetted channel (Section I) was regressed against water level in a linear model (Statistica 5.1; Statsoft Inc., Tulsa, OK, USA).

## Duration, frequency, extent and timing of dry and wet cycles

Duration, frequency, magnitude and timing are important components of the drying and rewetting cycle. We used the calculated relationship between the length of the wetted channel and water level to convert 4 years of daily water level values (from Pinzano station) to daily dry length of Section I. Then we calculated duration of surface drying and wetting distribution, number (frequency) of shifts between surface drying and wetting and magnitude of dry–wet cycles at 1 km distance intervals along the entire 41·5 km study reach.

We limited the application of our predictive regression to four years (2001–2004) for the following reasons. First, the analyses of the hydrograph from 1982 to 2004 indicated that the yearly average stage height declined by 2 cm per year. We could not attribute this decline to changes in morphology (deepening of channels) or hydrology (increased abstraction). Second, the period of 2001–2004 covers a representative range of the hydrologic conditions of the Tagliamento River and includes an extremely dry (2003) and a wet (2002) year.

# Results

## Vertical hydraulic gradient (VHG) and surface discharge

Average VHG was significantly different between Section I and Section II (Kruskal–Wallis ANOVA, $\chi^2 = 129{\cdot}79$, df = 1, $p < 0{\cdot}001$). Average VHG was negative along Section I ($-0{\cdot}67 \pm 0{\cdot}55$) and positive along Section II ($0{\cdot}03 \pm 0{\cdot}23$). However, local down- and upwelling conditions were measured along both sections (Figure 4(a)). Spatio-temporal

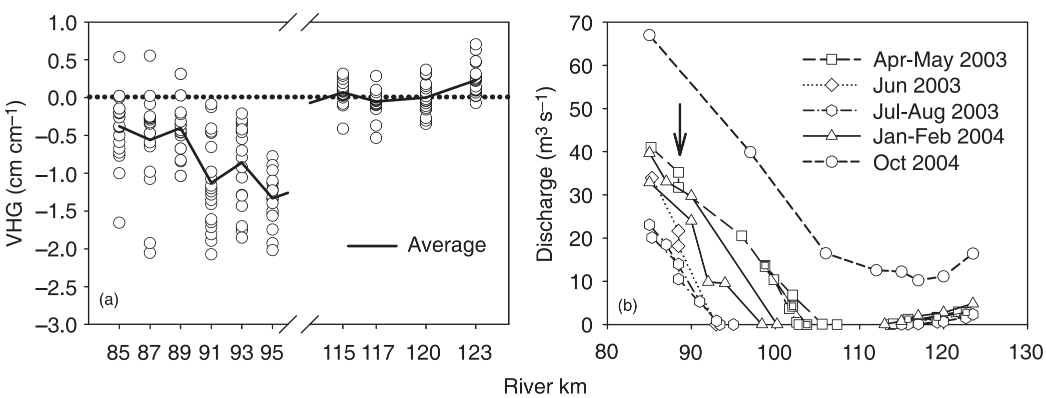


**Figure 4.** (a) Vertical hydraulic gradient (VHG; $cm\ cm^{-1}$) along Section I ($n = 183$) and Section II ($n = 129$) (July 2003–April 2004). (b) Surface discharge ($m^3\ s^{-1}$) along Sections I and II (April 2003–October 2004). The arrow marks the location of water abstraction.



DOI: 10.1002/esp

**Table I.** Average, minimum and maximum water level (cm) at the knickpoint Pinzano (river-km 85). Percentage and days of disconnection between Sections I and II, and average length (km) and relative proportion (%) of Section I that falls dry at the surface (2001–2004; based on average daily water level records provided by the Direzione Centrale dell'Ambiente)

| Year | Average stage (cm) | Minimum stage (cm) | Maximum stage (cm) | Disconnection (% of year) | Average length (km) and proportion (%) that falls dry |
|---|---|---|---|---|---|
| 2001 | 157 | 90 | 286 | 59 (215 days) | 6·1 km (21%) |
| 2002 | 167 | 100 | 361 | 49 (179 days) | 4·9 km (17%) |
| 2003 | 121 | 73 | 279 | 96 (350 days) | 13·1 km (45%) |
| 2004 | 142 | 85 | 307 | 85 (310 days) | 8·1 km (28%) |
| **Average** | **147** | **87** | **308** | **73 (266 days)** | **(8·1 km) (28%)** |

variation, expressed as the maximum range of VHG across individual transects, was higher in Section I (range: –2·07 to +0·55) than in Section II (range: –0·59 to +0·70) (Figure 4(a)).

Discharge decreased (Section I) and increased (Section II) linearly along the study reach. In Section I discharge decreased on average by $2{\cdot}5 \pm 0{\cdot}8$ $m^3$ $s^{-1}$ ($n = 9$) per river-km. In Section II discharge increased on average by $0{\cdot}3 \pm 0{\cdot}1$ $m^3$ $s^{-1}$ ($n = 9$) per river-km (Figure 4(b)). Along Section I up to 60 $m^3$ $s^{-1}$ downwelled into the expansive aquifer. However, along the 12·5 km long Section II less than 13 $m^3$ $s^{-1}$ re-emerged to the surface of the Tagliamento River bed. There was no significant correlation between total discharge, measured at the knickpoint in Pinzano, and the relative rate of infiltration and exfiltration.

## Expansion and contraction dynamics

Between 2001 and 2004 average daily water level at the knickpoint at Pinzano (river-km 85) ranged from 73 to 361 cm. The corresponding calculated discharge ranged from 20 to >200 $m^3$ $s^{-1}$. Average annual water level ranged from 121 cm (2004) to 167 cm (2002) (Table I).

Sections I and II became surficially connected when river discharge at the knickpoint at Pinzano reached 60 $m^3$ $s^{-1}$ (water level: 165 cm). Below this threshold, water level at the downstream end of Section II (river-km 126·5) remained very constant despite a pulsed hydrograph at the upstream end of Section I (Figure 5(a)). During dry summer conditions the upstream end of the wetted channel in Section II moved from river-km 113·6 slowly downstream to river-km 114·5 before it moved 1·5 km upstream again with the onset of autumnal rain events. In Section I, the uppermost 6 km (river-km 85–91) carried surface flow during the entire study period. However, downstream of river-km 91 the dry channel rapidly expanded and contracted with changing water levels. During the main investigation period (April until August 2003), we calculated a maximum expansion velocity of 2·9 km $h^{-1}$ and a contraction velocity of up to 0·5 km $h^{-1}$ (Figure 5(b)).

The length of the dry river-bed was significantly related to the water level (and discharge) at the knickpoint at Pinzano (Figure 6(a)). The maximum length of the dry river-bed was 23·5 km. During a single flow pulse, beginning on 2 July 2003, the wetted channel expanded by 19·9 km within four days and contracted by 21·7 km during the subsequent nine days (Figure 6(b)). This flow pulse exhibited a distinct hysteresis effect, with fast expansion and delayed contraction of the wetted channel. For example, at a water level of 140 cm the length of the dry river-bed was 20 km during the expansion phase but 5 km during the contraction phase (Figure 6(b)).

## Duration, frequency and timing of dry and wet cycles

We used the relationship between water level and length of the dry channel to model expansion and contraction dynamics over a four year period (2001–2004; average daily values). This simple model was based solely on the average length of the dry channel. It did not take into account potential hysteresis effects (Figure 6(b)) or the area of wetted surface. The output of the model suggested a substantial inter-annual variability in duration, frequency and timing of surface drying and rewetting (Figure 7). The average annual length of the dry reach varied from 5 km (2002) to 13 km (2003) (Table I). Maximum contraction was calculated either in late summer (2001, 2003) or in early spring (2002, 2004), with frequent and often rapid expansion and contraction cycles at any given time of the year (Figure 7).



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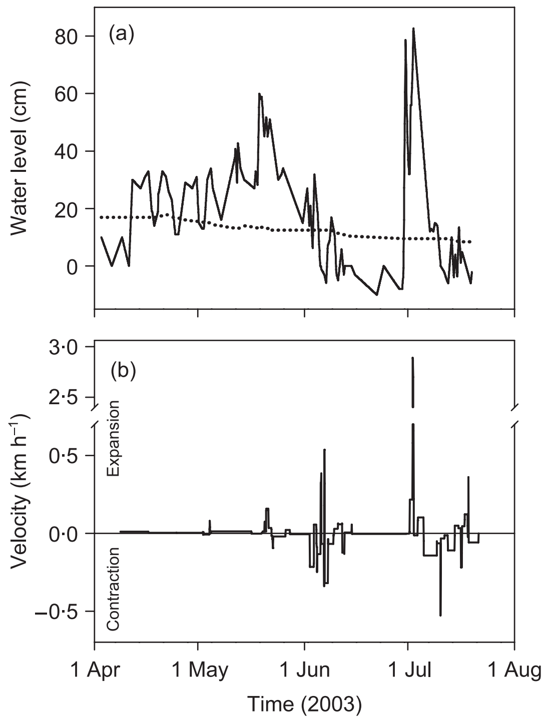


**Figure 5.** (a) Average daily water level (cm) records at Pinzano (river-km 85; solid line) and at the bridge at Varmo (river-km 126·5; dotted line) from April to August 2003. (b) Expansion and contraction velocities (km h$^{-1}$) of the wetted channel in Section I from April to August 2003.

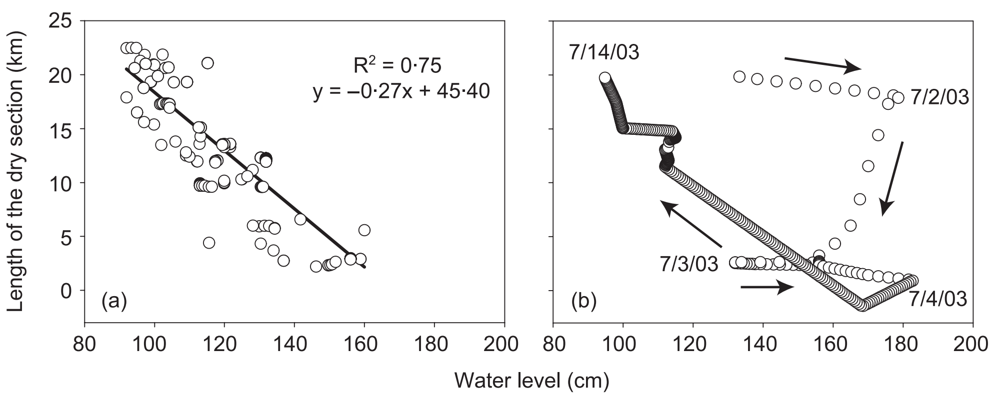


**Figure 6.** (a) Relationship between water level (cm) at Pinzano (river-km 85) and length of the dry channel in Section I (April 2003–October 2004; $n = 200$). (b) Relationship between water level (cm) at Pinzano (river-km 85) and length of the dry channel in Section I during a single flow pulse from 2 July to 14 July 2003. Data points represent a linear interpolation (hourly interval) of the length of the dry river corridor and the stage at Pinzano.

Along Section I, the relative duration (% of time) of surface flow decreased continuously downstream of river-km 91. At the downstream end of the temporary section (river-km 114), the number of days with surface flow ranged from 16 (2003) to 185 (2002) (Figure 8(a)). Frequency of dry and wet cycles exhibited a unimodal distribution. The maximum number of drying and rewetting cycles ranged from 33 (2002) to 53 cycles per year (2003), and the location with highest frequency differed among years (Figure 8(b)).



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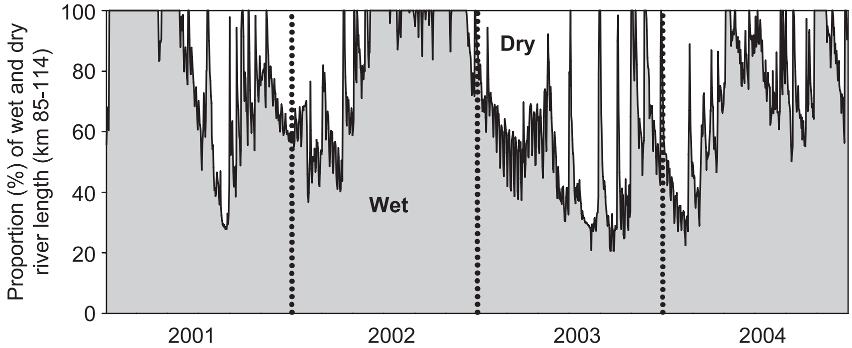


**Figure 7.** Relative proportion (%) of wet (gray area) and dry (white area) channel length along Section I from 2001 to 2004 (daily averages).

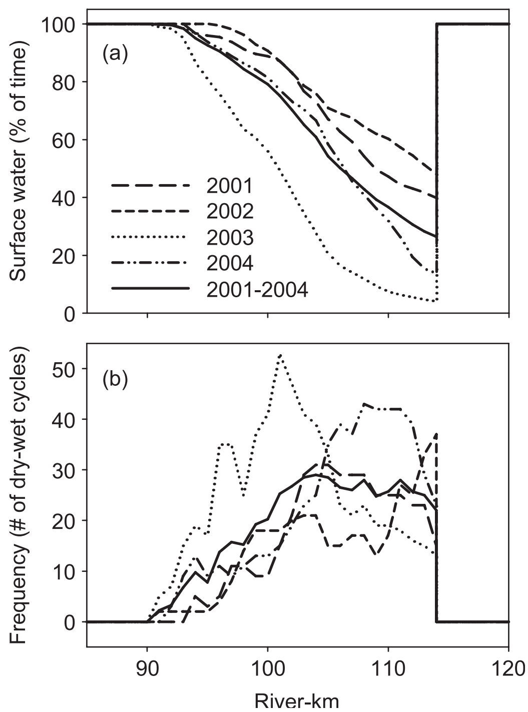


**Figure 8.** (a) Spatiotemporal distribution of surface flow duration (% of time) along Section I and the upper part of Section II (average of 2001–2004 and average of all individual years). (b) Number of dry–wet cycles (frequency) along Section I and the upper part of Section II (average of 2001–2004 and average of all individual years).

## Discussion

Rapid changes in ecosystem size are a well known phenomenon in Mediterranean and semiarid rivers although quantitative data are very scarce (Gasith and Resh, 1999; Stanley *et al.*, 1997; Tockner *et al.*, 2000). In this study we quantified longitudinal expansion and contraction dynamics of surface water and vertical hydraulic exchange (infiltration and exfiltration rates) along the 41·5 km braided river corridor of the Tagliamento River, NE Italy. The Tagliamento River offers the rare opportunity to study large-scale hydrologic, geomorphic and ecological processes under near-natural conditions; therefore, it serves as a model ecosystem of European importance (Tockner *et al.*, 2003). It still contains the complexity and dynamics that most Alpine rivers had prior to river regulation and dam construction.

## Underlying mechanisms of large-scale expansion and contraction dynamics

The rapid expansion and contraction dynamics along the Tagliamento River corridor is primarily a function of high infiltration rates and distinct flow variations. The average infiltration rate of $2{\cdot}5\ m^3\ s^{-1}$ was much higher than in the Middle Fork of the Flathead River (USA, NW Montana) ($\sim 1{\cdot}3\ m^3\ s^{-1}$ per river km; Stanford *et al.*, 2005) or the semi-arid Homestead Creek (Australia) ($\sim 1{\cdot}1\ m^3\ s^{-1}$; Dunkerley and Brown, 1999). High negative vertical hydraulic gradients in Section I exceeded reported maximum negative values of up to $-0{\cdot}37$ cm $cm^{-1}$ (Baxter *et al.*, 2000; Vallet *et al.*, 1994). Infiltration rates are expected to be influenced by water temperature, which affects viscosity, sediment permeability affected by grain size distribution and porosity, and wetted channel area (Brunke and Gonser, 1997; Constantz, 1998). Temperature is subject to seasonal and daily variation but also changes along the river continuum. For a losing reach in the Ohio River, Constantz (1998) reported a doubling of the infiltration rate for a temperature increase from 0 to 25 °C. For the Tagliamento River we found no seasonal variation of the infiltration rate, an indication that other factors mask potential temperature effects. During flow or flood pulses deposition or removal of fine sediments affects the permeability of surface bed sediments (Dunkerley and Brown, 1999; Gasith and Resh, 1999). For example, we observed temporary clogging of the bed sediments in the Tagliamento River after an extremely flashy flood event in August 2003. A subsequent flood restored high permeability. Although not measured, we assume that the wetted area increases linearly with flow as shown by Van der Nat *et al.* (2002) for two floodplain segments located upstream of our study reach. In our main study reach the number of wetted channels across a transect ranged from 1 to a maximum of 11 channels at mean flow conditions (Ward *et al.*, 1999). However, we did not find a relationship between discharge, which reflects channel area, and specific infiltration rate.

We observed an abrupt transition from the losing section (Section I) to the permanent gaining section (Section II). A layer of impermeable fine sediments forces infiltrated Tagliamento River water to emerge to the surface starting at approximately river-km 114. The gaining zone is characterized by relatively stable flow conditions, except during high flow, when Sections I and II are connected at the surface. The large alluvial aquifer serves as a major transient storage zone that stabilizes flow in the gaining zone (Baxter *et al.*, 2000; Malard *et al.*, 2002). However, even Section II experienced a slow seasonal expansion and contraction of surface waters (maximum length: ~1·5 km), most likely as a consequence of the slow emptying and refilling of the large alluvial reservoir. The continuous contraction during summer was most likely enhanced by groundwater extraction for irrigation and high evapotranspiration loss. Based on geochemical tracers (i.e. lower sulfate and strontium concentrations in Section II compared to Section I) we think that the recharging of the alluvial reservoir primarily occurs during high autumnal precipitation and spring snowmelt (K. Tockner, unpublished data).

In Section I infiltration rates were more than 10 times higher than exfiltration rates in Section II. Apart from groundwater abstraction, the vast alluvial aquifer expands laterally beyond the study area and therefore feeds rivers outside of the main corridor (Fontana *et al.*, in press).

## Spatio-temporal characteristics of expansion and contraction dynamics

To evaluate lateral and longitudinal expansion and contraction dynamics in streams and rivers, simple models were used relating discharge or stage with inundated area or channel width (Benke *et al.*, 2000; Malard *et al.*, 2006; Van der Nat *et al.*, 2002; this study). The relationship between the Pinzano stage and the length of the dry channel (Figure 6(a)) exhibited some scatter of the data resulting from the hysteretic relationship between the stage and the dry channel length (Figure 6(b)). Furthermore, the Tagliamento River is subject to some regulation upstream and to water abstraction downstream of the Pinzano stage. These factors imposed some uncertainties on the spatial extent of wetted channel length, which may have been over- or underestimated.

The model output indicates that the losing and gaining reaches became disconnected at the surface between 179 and 350 days per year. In the losing section (Section I), spatio-temporal distribution of dry and wet episodes is highly unpredictable. The river can fall dry at any time of the year, and the location of the maximum frequency of wet and dry cycles is shifting up- and downstream as a result of interannual flow variability. In contrast to the Tagliamento River, highly predictable expansion and contraction cycles of the wetted channel network were reported for the proglacial floodplain of the Roseg River (Malard *et al.*, 2006), which are driven by seasonal snow and ice melt.

The surface drying of the Tagliamento River is not restricted to the large alluvial corridor. A preliminary investigation in five headwater subcatchments showed that the proportion of temporary stream segments ranged from 6 to 62% per subcatchment (K. Tockner, unpublished data). For the entire catchment we calculated that approximately 46% of the drainage network falls dry at the surface (Table II). Extensive headwater surface drying reflects the catchment geology (dolomite and limestone), topography (i.e. steep slopes) and highly variable precipitation patterns.



DOI: 10.1002/esp

**Table II.** Tagliamento catchment: total number and length (km) of stream segments, and proportion (%) of temporary sections calculated for each stream order. n.d. = not determined

| Stream order | Number of stream segments | Average stream segment length (km) | Total stream segment length (km) | Relative proportion (%) that falls dry |
|---|---|---|---|---|
| 1 | 1663 | 0·8 | 1405 | 62 |
| 2 | 416 | 1·5 | 631 | 51 |
| 3 | 90 | 3·6 | 320 | 6 |
| 4 | 21 | 7·4 | 155 | n·d |
| 5 | 6 | 14·1 | 85 | 32 |
| 6 | 2 | 8·0 | 16 | 0 |
| 7 | 1 | 114·0 | 114 | 20 |
| **Total** | **2199** | **–** | **2726** | **ca. 46%** |

## Ecological implications

World-wide, about one-third of all streams and rivers are temporary (Poff, 1992). In the near future their relative proportion will increase further due to increasing flow variability and increasing water consumption. Temporary streams are also unique because they provide habitats for characteristic aquatic and terrestrial biota. However, we are not aware of a single study that has investigated simultaneously aquatic and terrestrial communities along temporary rivers.

This study provided important quantitative information about drying and rewetting cycling along a large gravel-bed river over a multi-year period. Small alterations of the flow regime can lead to major changes in duration, frequency, timing and extent of drying and rewetting, with probably severe consequences for terrestrial and aquatic communities and ecosystem processes.

The abrupt losses of aquatic and terrestrial habitats lead to stranding and inundation of the resident biota (Stanley *et al.*, 1994). Unpredictable and rapid changes between dry and wet periods are more difficult for organisms to deal with through evolved adaptations (Lake, 2003). For example, for primary producers, rapid drying does not provide sufficient time for production of desiccation-resistant structures or physiological adjustment. Consequently, algae die typically within a short period after drying (Stanley *et al.*, 2004). Stranded organisms such as macroinvertebrates and fish will perish or, if trapped in pools, will suffer from enhanced competition and predation (Boulton, 2003; Matthews and Marsh-Matthews, 2003; Schlaepfer and Rotach, 2003; M. Doering, personal observation). Aquatic and terrestrial communities are expected to react differently to expansion and contraction cycles. While terrestrial organisms can rapidly recolonize exposed channels, recolonization of wetted channels by aquatic organisms is often delayed. Recovery of aquatic organisms, for example from drought, depends on the extent of desiccation and on the fashion in which water returns, i.e. by a slowly increasing water level or by floods associated with scouring (Blinn *et al.*, 1995; Stanley *et al.*, 1994). Both characteristics are part of the expansion and contraction dynamic of the Tagliamento River.

Drying and rewetting influence ecosystem processes such as nutrient cycling and respiration. As sediments dry out, bacterial biomass and activity decline. In contrast, rewetting flushes nutrients and enhances bacterial activity (Baldwin and Mitchel, 2000; Fierer and Schimel, 2002; JaapBloem *et al.*, 1992). Frequent drying and rewetting cycles alter the composition of microbial communities by selecting for microbes that can survive rapid changes in water potential (Fierer *et al.*, 2003; Schimel *et al.*, 1999), which subsequently affects respiration rates (Clein and Schimel, 1994; Van Gestel *et al.*, 1993). In highly permeable vast aquifers water can travel exclusively in the hyporheic zone, where its chemistry can change substantially, for example by nitrification, for kilometers. At upwelling sites, nutrient-enriched water can stimulate algal primary production (Grimm *et al.*, 1981; Schlaepfer and Rotach, 2003; Stanley *et al.*, 1997) and affects tree growth (Harner and Stanford, 2003). At downwelling sites organic matter is trapped in the hyporheic zone, and respiration rates increase (Jones, 1995).

This study provides important quantitative information about longitudinal changes of drying and rewetting patterns along a large gravel-bed river. How the different components of the expansion and contraction cycles control aquatic and terrestrial communities as well as ecosystem processes is a major challenge for future research.

## Acknowledgements

The authors thank Dr. N. Surian and one anonymous reviewer for comments that resulted in considerable improvements to this paper. We also thank many people who helped in the field and with logistics especially C. Cruciat, Y. Schwill, W. Doering, M. Kiefer,

A. Marin, G. Morro and S. D. Langhans. Special thanks to Direzione Regionale dell'Ambiente and A. Marin for providing hydrological data. This work was supported by the EU project tempQsim (EVK1-CT2002-00112; http://www.tempqsim.net) and by SBF (No. 02.0072).

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DOI: 10.1002/esp