Ecosystems (2002) 5: 802–814
DOI: 10.1007/s10021-002-0192-7

ECOSYSTEMS

Aquatic Habitat Dynamics along a Braided Alpine River Ecosystem (Tagliamento River, Northeast Italy)

Dave B. Arscott,* Klement Tockner, Dimitry van der Nat, and J. V. Ward

Department of Limnology, Swiss Federal Institute for Environmental Science and Technology (EAWAG/ETH),
133 Überlandstrasse, 8600 Dübendorf, Switzerland

ABSTRACT

Aquatic habitat change caused by flooding was quantified along the Fiume Tagliamento, a morphologically intact gravel-bed river ecosystem in northeast Italy. Five different geomorphic reaches (each around 1.5 km), ranging from near the headwaters at 800 m above sea level (a.s.l.) to near the mouth at 5 m a.s.l., were studied over a 1-year period. All floodplain water bodies in each reach were delineated in August 1999 using a differential global positioning system. Each reach was remapped twice (in December 1999 and August 2000) to investigate the impact of autumn and spring flood seasons on aquatic habitat composition and configuration. A high degree (nearly 62%) of aquatic habitat turnover was documented in a braided headwater floodplain. The degree of aquatic habitat turnover decreased with decreasing elevation to approximately 20% turnover in a meandering reach at 5 m a.s.l. In contrast to turnover, braiding, sinuosity, and aquatic habitat composition changed little in response to flooding in all reaches. Location of aquatic habitats in floodplains changed considerably (turnover), whereas habitat configuration and composition remained relatively stable. These results support the applicability of the shifting mosaic steady-state model to riverine floodplain environments.

Key words: river geomorphology; floodplain; hydrology; flood pulse; flow pulse; fluvioscape; fluvial dynamics.

INTRODUCTION

Disturbances are important determinants of biotic community structure and function (Grime 1977; Stanford and Ward 1983; Junk and others 1989; Pickett and others 1989; Poff and Ward 1990; Townsend and others 1997; Sparks and Spink 1998) and may manifest in a hierarchical manner, affecting several levels of organization, from an individual to an ecosystem and the landscape. Disturbances also rearrange the environment, destroying certain habitats and creating others. According to Pickett and others (1989), to recognize disturbance, the object or entity being influenced needs to be identified; in addition, the conceptual framework should recognize a broad spectrum of effects, ranging from the complete destruction of an entity at one end to subtle but significant changes at the other. White and Pickett's (1985) broad definition of disturbance encompasses what is meant by "disturbance" in this manuscript: "A disturbance is any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources and the physical environment."

Flooding represents the dominant type of natural disturbance along most river corridors (Welcomme 1979; Junk and others 1989; Puckridge and others 1998; Swanson and others 1998; Tockner and others 2000), and it is likely that all stream ecosystems are disturbed by fluvial forces to some degree (Reice 1985; Statzner and Higler 1986; Ward 1989). Moreover, floodplains are disturbance-driven ecosystems

---

Received 12 September 2001; accepted 24 April 2002.
**Corresponding author's current address:* Center for Agriculture and Natural Resources, University of Minnesota, 2900 University Ave., Crookston, Minnesota 56716, USA; *e-mail:* arsco002@mail.crk.umn.edu

(Junk and others 1989). Flood dynamics have been well studied in riverine ecosystems; however, relatively little information is available on the effects of disturbance at a scale large enough (for example, an entire river corridor) to match that operating in nature (Fisher 1987; Pickett and others 1989; Dudgeon 1992), although recent important advances have been made (Michener and Haeuber 1998; Swanson and others 1998; Nakamura and others 2000). Brinson (1993) states that little has been synthesized regarding landscape patterns of wetland/floodplain structure and dynamics along the river continuum, from streamside riparian zones in headwater regions to broad lowland floodplains.

The major physical drivers in river–floodplain systems are fluvial dynamics and temperature (Puckridge and others 1998; Tockner and others 2000; Poole and Berman 2001). The thermal heterogeneity of aquatic water bodies along the Tagliamento River (the system of interest in this study) has been investigated in detail (Arscott and others 2001; Claret and others 2002). However, the influence of flooding on dynamics of aquatic structure has not been examined (but see Kollmann and others 1999; Gurnell and others 2001; van der Nat and others 2002).

The objective of this study was to investigate the spatial/temporal dynamics of aquatic habitat composition and configuration along the Tagliamento River (northeast Italy) in response to flooding. Habitat, in this study, refers to different geomorphic units across the floodplain (that is, main channel, side channel, backwaters, isolated pool) where different aquatic invertebrate (see Arscott 2001) and algal communities (D. B. Arscott unpublished) occur. Because of its morphologically intact nature, the Tagliamento River, is considered to represent a reference condition for many of the rivers draining the European Alps (Ward and others 1999), thereby offering an excellent opportunity to study the influence of hydrology (particularly flooding) on geomorphology and biology. This research was conducted to determine the extent to which aquatic habitat morphodynamics were influenced by hydrological factors operating at the scales of the entire corridor (172 km length) and reach (1–2 km length). We hypothesized (a) that aquatic habitat turnover following a single flood season is greater than the amount of aquatic habitat that is unchanged, (b) that the composition and abundance of habitat types do not change over time despite high habitat turnover rates, and (c) that fluctuations in habitat composition and abundance are caused primarily by water-level changes rather than morphological change related to flooding.

SITE DESCRIPTION

The Tagliamento River in northeast Italy (Friuli-Venizia Giulia; 46°N, 12°30′E) (Figure 1) is a gravel-bed river characterized by a diverse array of geomorphic units (Ward and others 1999; Gurnell and others 2000a). Seventy percent of the catchment is located within the southern edge of the Alps (dominated by limestone–dolomite). In its lower reaches, the river traverses a coastal plain to the Adriatic Sea. The river arises at 1195 m a.s.l. in an alpine climate and flows for approximately 172 km, crossing into a Mediterranean climate in its lower reaches (85–172 river km). Five distinct geomorphic reaches along the main-stem corridor were selected for further study (see Arscott and others 2000) (Figure 1 and Table 1): headwater island-braided floodplain (reach II), bar-braided floodplain (reach III), lower island-braided floodplain (reach IV), braided-to-meandering transition floodplain (reach V), and meandering channel floodplain (reach VI). Reach I, constrained headwaters (Arscott and others 2000), was not included in this study.

Along the main-stem corridor of the Tagliamento, the level of direct engineering (that is, levees, dams, embankments) is remarkably low, and the common recurrence of floods (three to four times per year) regularly resets floodplain morphology. Owing to the low level of human control and frequent flooding, the river has been described as the last morphologically intact river corridor draining the European Alps (Müller 1995; Ward and others 1999).

The spatial distribution of precipitation in the catchment is highly variable (Tockner and others forthcoming). In general, precipitation is lowest in the lower reaches (around 1200 mm y^{-1}); peaks to the north, where the flat coastal plain gives way to the Alps (around 2600–3200 mm y^{-1}); and declines again at the northern border of the catchment (around 1600 mm y^{-1}). The wettest month in the catchment is November (160–240 mm); the driest is February (60–100 mm).

The hydrograph is described as a flashy pluvionival flow regime (Figure 2a) defined by peak flows in autumn because of torrential rains and smaller peak flows in spring from snowmelt runoff and precipitation. Despite the seasonal periodicity, individual flood events are stochastic and can occur any time during the year. Average discharge at river-km 59 (seventh order) is 90 $m^3 s^{-1}$ with 2-, 5-, and 10-year return period floods estimated to be 1100, 1500, and 2150 $m^3 s^{-1}$ (Gurnell and others 2000b). From field observations, it was estimated that geomorphic work (that is, bed-load transport, avulsion, and visible cut-and-fill alluviation) occurred at discharges below the 2-year return interval. Based on

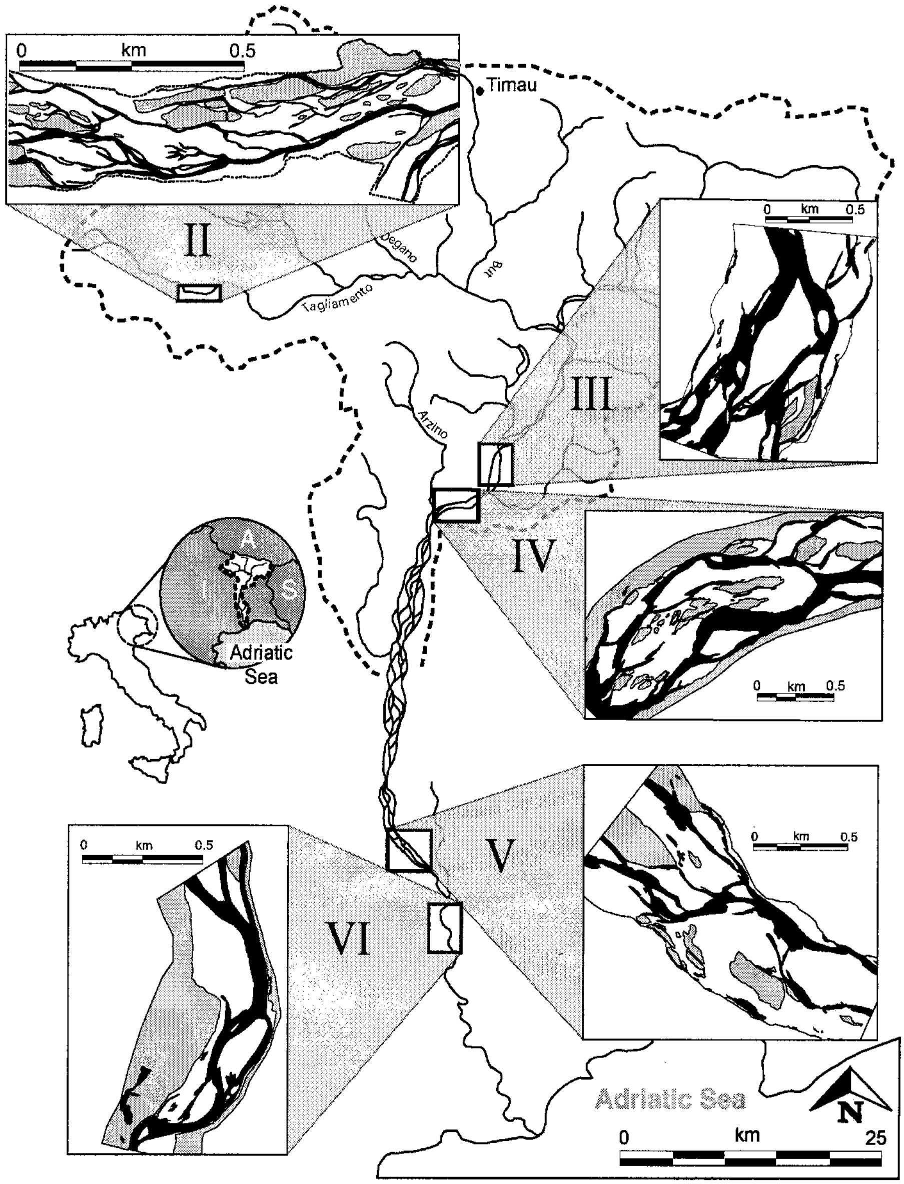

Figure 1. Tagliamento catchment (northeast Italy) and five study reaches along the river corridor.

these observations, we estimated that partial floodplain inundation and initiation of geomorphic work occurred at a discharge of approximately 2.5 times the average or approximately 225 m^3 s^{-1}. This threshold value was used to assess flood risk to benthic development times of 10, 21, 35, and 50 days (Figure 2b) so that flood probability could be related to biological communities. Our choice of 2.5 times the average discharge represents only a benchmark to assess "flood" probability and timing. Two "ecological windows," indicating when there was low risk from bed-moving spates, were identified for summer and winter periods. The winter window (low flood risk) occurs from December until the end of March; the summer window is much shorter, lasting only 1 month (July). Consequently, changes in aquatic habitat configuration and composition were assessed before and after two flood periods (see Methods).

METHODS

A Trimble model TSC1 Pathfinder differential Global Position System (dGPS) receiver was used to collect spatial data from approximately 1.5-km–long reaches of five different floodplains along the Tagliamento River. A second dGPS receiver was installed at a fixed position near the study sites to simultaneously record the variability of the dGPS signal. This stationary data set was then used for

Table 1. Characteristics of Five Geomorphic Floodplain Types, as Measured from Maps Created in the Field using dGPS and Field Observations

Metric	II Headwater Island-Braided Floodplain	III Bar-Braided Floodplain	IV Lower Island-Braided Floodplain	V Braided-to-Meandering Floodplain	VI Meandering Floodplain
Location of study reach (km)	13.3	73.7	80.3	120	127.5
Elevation (m.a.s.l.)	705	165	140	20	5
Slope (%)	1.65	0.4	0.35	0.18	0.07
Active floodplain width (m)	106–263	611–832	670–999	449–834	138–254
Active floodplain area delineated (ha)	36.4	109.9	108.2	55.1	15.4
Dominant sediment class	boulder/cobble	cobble/gravel	cobble/gravel	gravel	gravel/sand
Estimated base-flow discharge (m^3s^{-1})	4	40	45	7	20
Vegetation	riparian/island	riparian	riparian/island	riparian/island	riparian

postprocessing procedures to correct field data, resulting in two-dimensional (that is, latitude–longitude) accuracy of less than 0.30 m for most points (approximately 85%).

Using the dGPS, major floodplain features (water, gravel, vegetated islands, and banks of the active floodplain) in study reaches II, III, IV, V, and VI (Figure 1) were delineated by walking each feature's perimeter. Reach I (constrained headwater streams) was not mapped with dGPS because of dense canopy cover and incised channels that prevented reception of the satellite signal. For reaches II, III, V, and VI, mapping occurred on three dates (in August and December 1999 and August 2000); reach IV was mapped twice (in June 1999 and May 2000). Between the August and December 1999 mappings, three flood pulses occurred. Each event exceeded 225 $m^3 s^{-1}$ (Figure 2), thus surpassing the predicted threshold limit for significant geomorphic work. Between December 1999 and August 2000, only four small "flow pulses" (that is, events below bank full discharge) occurred.

Spatial data from each map were analyzed using both MapInfo Professional 4.1 (MapInfo Corporation, Troy, NY, USA, 1996) and ArcView GIS 3.1 (Environmental Systems Research Institute, Inc., Redlands, CA, USA, 1969). All floodplain features were treated as polygons, and each map was examined to determine the areal extent of each feature. Aquatic features were categorized, based on field observations while mapping, as either up- and downstream surface-connected channels (two-way connected channels), downstream surface-connected alluvial channels (that is, one-way connected channels with flowing water), backwaters (one-way connected with standing water [BW]), or isolated water bodies (ISO). Two-way and one-way connected channels were further subdivided into primary (1°), secondary (2°), or tertiary (3°) braided channels based on the ordering system discussed by Bristow (1987). Degrees of braiding and meandering were assessed for each map using a braiding parameter, B, and a sinuosity parameter, P, as reported in Friend and Sinha (1993). The braiding parameter is:

$$B = L_{ctot}/L_{cmax}$$

where L_{ctot} is the sum of the midchannel lengths of all the segments of upstream connected channels in a reach, and L_{cmax} is the midchannel length of the widest channel through the reach. The sinuosity parameter is:

$$P = L_{cmax}/L_R$$

where L_R is the overall length of the channel-belt reach measured along a straight line. Finally, the time series maps (either two or three dates) for each reach were overlaid to quantify floodplain change. Specifically, aquatic polygons were assessed for their spatial similarity between two dates by calculating the spatial extent of overlap. This produced two classes of aquatic area for the more recent map in the comparison—aquatic area of no change and new aquatic area. The amount of new aquatic area occurring in each floodplain was expressed as percent new aquatic area and was considered to be an estimate of aquatic habitat turnover between the two dates in question.

The eight aquatic habitat categories were then considered as habitat types; their total area divided by the active floodplain area in each reach was

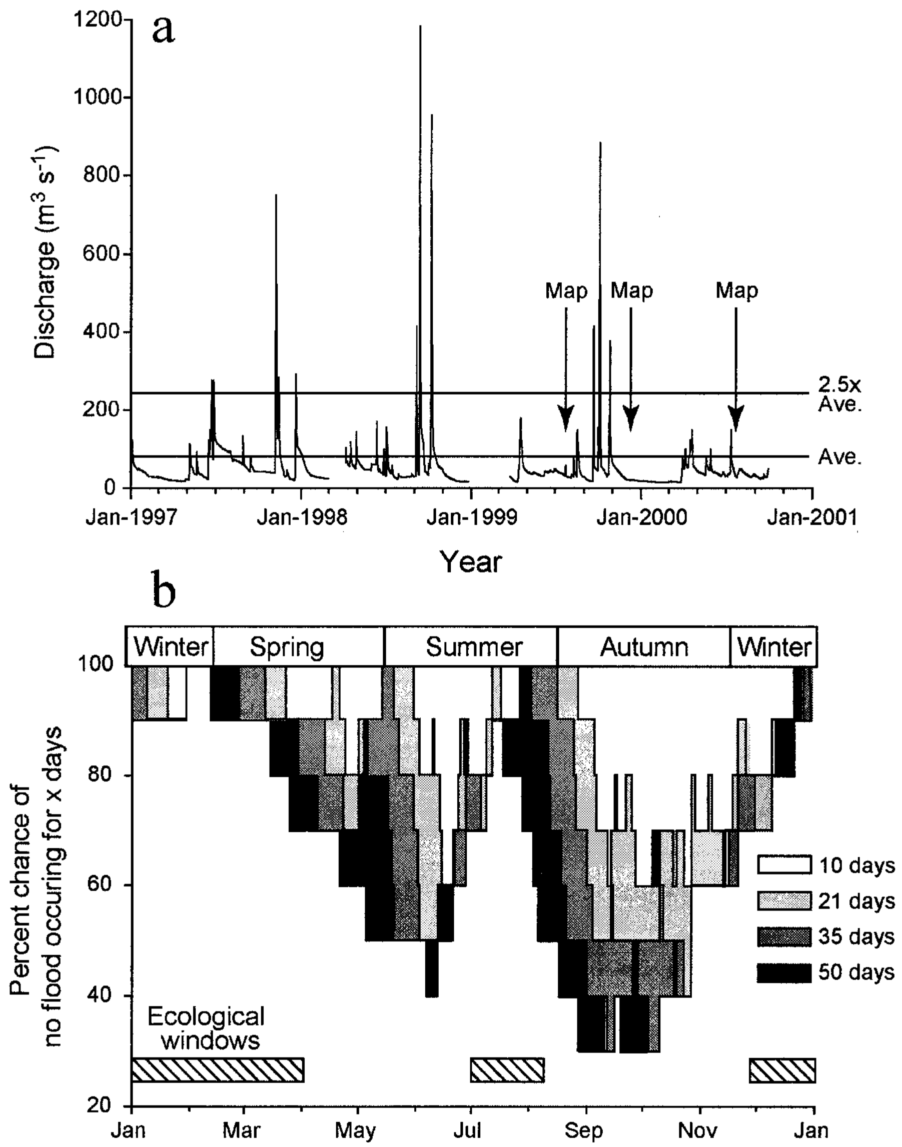

Figure 2. The Tagliamento hydrograph at river-km 59 (seventh order) from 1997 to 2001 (**a**). The lower panel (**b**) shows flood risk to development times of aquatic biota over a year, expressed as the percent chance of no flood occurring for 10, 21, 35, and 50 days, based on a 10-year record and a flood defined as 2.5 times the average flow.

considered as habitat abundance. Habitat diversity was quantified by considering the specific habitat types as "species" and their abundances as representing "species abundance" values and then calculating Shannon's diversity (H′) for each map (each reach and date), similar to Arscott and others (2000). Significant differences ($P < 0.05$) in H′ were assessed using bootstrapping techniques to determine 95% confidence intervals for each estimate of H′ and comparing indexes using a randomization test for computing significant differences in diversity between two samples (Solow 1993). Reach IV was eliminated from this analysis because of different mapping dates. Pearson's product-moment correlation analyses were used to investigate relationships between habitat variables and water level.

RESULTS

Aquatic habitat turnover (represented in Figure 3) between the first two mapping dates (August and December 1999), as well as between the first and third mapping dates (August 1999 and August 2000), was highest in the headwater island-braided reach (reach II) (61.5%) and decreased downstream (Figure 4a). The magnitude of aquatic habitat turnover between the second and third mapping dates was lower than that of other comparisons but followed the same downstream pattern. Comparison of reach IV maps, created over a different time period (June 1999 and May 2000), yielded a turnover estimate of nearly 40%, closely following the downstream trend observed for other reaches despite different numbers and magnitudes

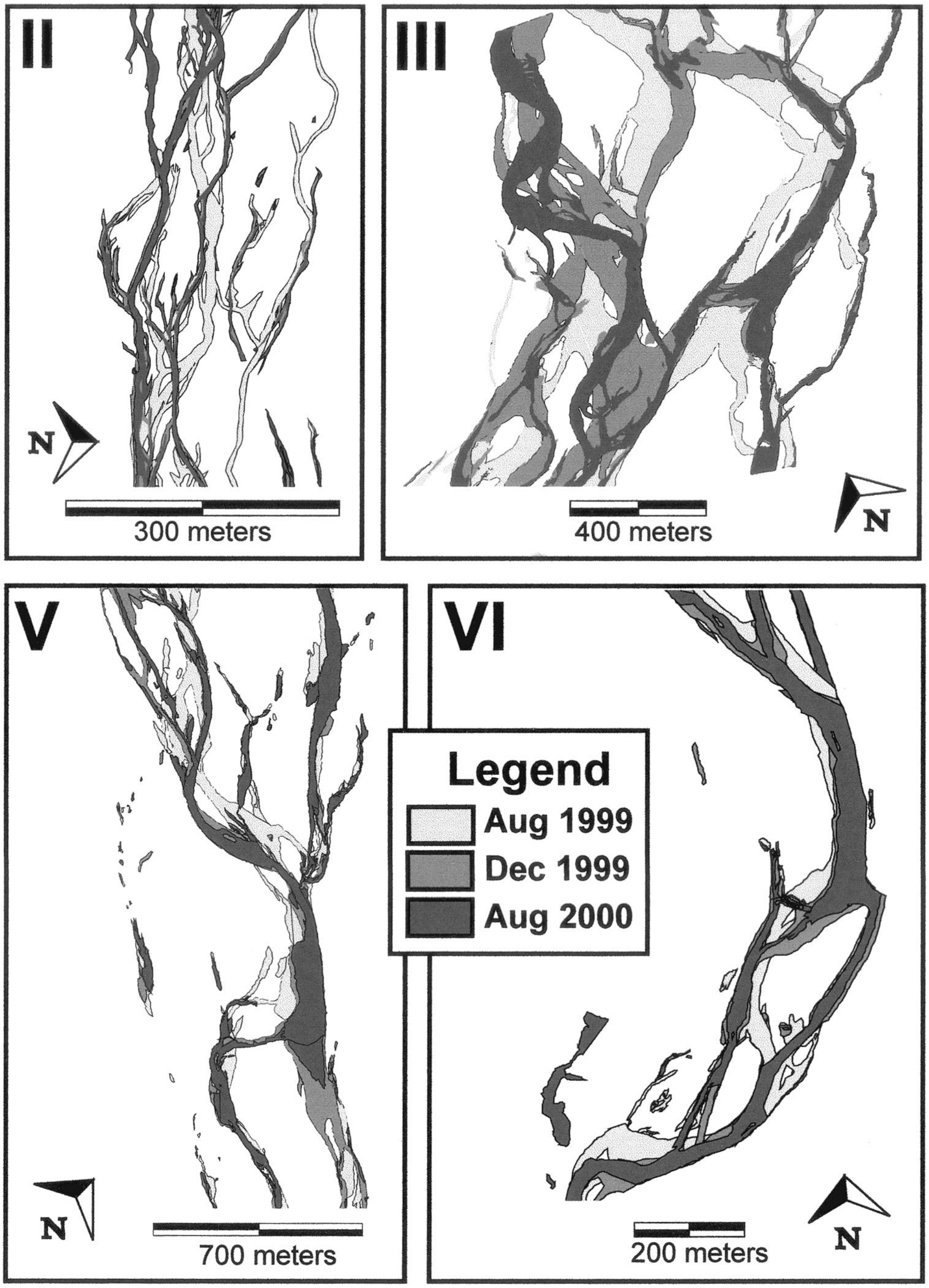

Figure 3. Results of mapping reaches II, III, V, and VI on three dates using dGPS.

of flow/flood pulses between mapping dates (see Figure 2a). The magnitude of aquatic habitat turnover was higher after the autumnal flood season when flood magnitudes were high (peak discharge, approximately 1150 m^3 s^{-1}). However, aquatic habitat turnover was not additive among seasons (Figure 4a). This indicated that some aquatic habitats reoccupied abandoned channels and pools.

Comparison of the braiding index B and the sinuosity index S in Figure 4b and c indicated no consistent and very little change in these variables between dates. The braiding index correlated significantly with water level ($P = 0.04$), but variance explained was low ($r^2 = 0.31$). Reach III had the highest degree of braiding (average, 4.89). Sinuosity was low in reaches II–V (average, 1.1), but it doubled in reach VI (2.06).

Habitat composition was assessed by examining changes in the area of each geomorphic type among dates in relation to water level. Percent inundation of

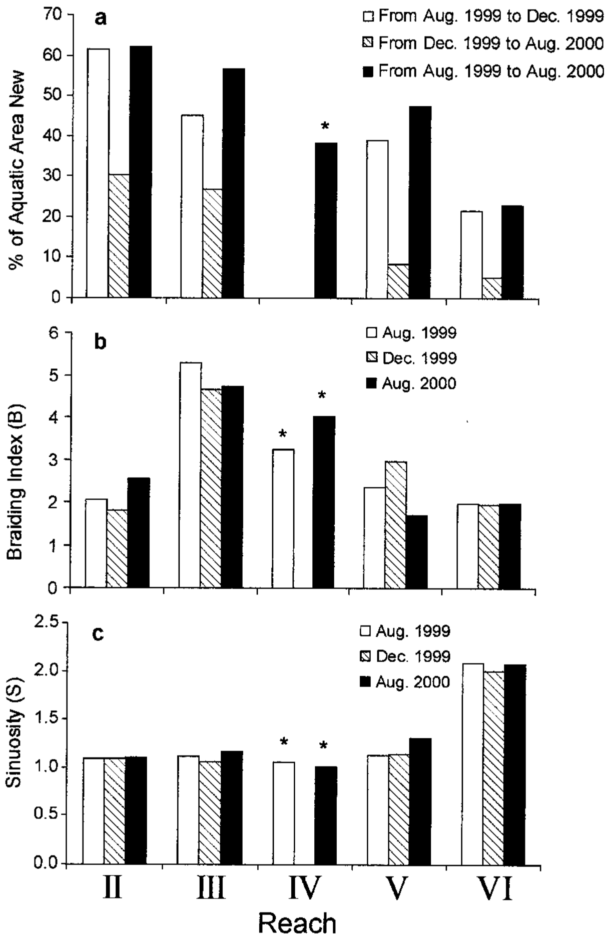

Figure 4. Percent of new water area (a), braiding index (b), and sinuosity (c) from reaches along the main-stem corridor as calculated from maps (Figure 3). Stars indicate different dates of maps for calculations from reach IV (June 1999 and May 2000).

the active floodplain and the total area of all two-way connected channels (1°, 2°, and 3° combined) correlated significantly with water level (Table 2). Standing water area (backwaters and isolated water bodies) was marginally negatively correlated ($P = 0.06$) with water level. Total area of one-way connected channels (1°, 2°, and 3° combined) did not correlate with water level (Table 2). All correlations in Table 2 included reach II water bodies except for standing water. The analysis was repeated for standing water bodies after excluding reach II because the relatively steep floodplain slope favors flowing rather than standing water conditions and causes inundation to occur via upstream movement of emerging groundwater rather than overbank or lateral flooding.

The greatest changes in the percent of flowing channels were observed in reach II, where two-way connected 1° channels (August 1999) were replaced by two-way connected 2° channels and one-way connected 1° channels (Figure 5a and b) on the subsequent mapping dates (December 1999 and August 2000). This change was partly explained by the significant negative correlation between water level and percent of aquatic area as two-way connected 2° channels (Table 3), particularly when all reaches were included in the model (as opposed to excluding reach II). Reach III had no two-way connected 1° channel on the last two mapping dates, as compared to approximately 10% coverage in August 1999 (Figure 5a). In general, percent of two-way connected 3° channels correlated positively with water level, while percent of aquatic area as standing water (BW and ISO) in reaches III, V, and VI was significantly negatively correlated with water level (Table 3) when reach II water bodies were eliminated from the analysis. Percent standing water (BW and ISO) varied to a greater degree over time than did flowing water channels (Figure 5c).

Diversity of geomorphic habitat types, assessed using Shannon's H′, indicated that change in H′ among dates was significant ($P < 0.05$) for one of the three dates for each reach (Figure 5c). Aquatic habitat diversity (H′) did not correlate with water level.

DISCUSSION

Natural rivers are highly dynamic in space and time, with aquatic habitat characteristics being variable, but predictable, along lateral, longitudinal, and temporal dimensions (Townsend 1989; Ward 1989; Spink and others 1998). The occurrence of bed-moving floods is especially important in sustaining the functional integrity of many natural rivers. These floods represent the primary mechanism by which a river interacts with the lateral fluvioscape (Junk and others 1989; Benke and others 2000). Flooding constrains autogenic and favors allogenic processes by, for example, removing the buildup of living and decaying organic matter and depositing or eroding mineral material (D. B. Arscott personal observation). These processes create a mosaic of patches in time and space with differing trajectories of ecological succession (Amoros and others 1996; Ward and others 2002).

The hydrological regime of a catchment varies regionally because of river size and geographical variations in climate, geology, topography, and vegetation cover. Description of the hydrological regime includes magnitude, duration, frequency, timing, and predictability of flood events (Poff and Ward 1989; Puckridge and others 1998). Unfortunately, because of irregularities in the stage height time series and a limited rating curve (Campolo and

Table 2. Water Level, Discharge, Percent Surface Water in Active Floodplain, and Habitat-Specific Area Calculated from Each Mapping Date

Reach	Date	Water Level (cm)[a]	Discharge (m^3s^{-1})[a]	% Surface Water in Active FP	Two-way Connected (m^2/m)	One-way Connected (m^2/m)	Standing Water (m^2/m)
II							
	Aug. 1999	36	52.3	16	47.1	14.8	0.4
	Dec. 1999	21	31.3	11	12.7	11.7	0.1
	Aug. 2000	30	43.1	12	15.4	10.9	0.1
III							
	Aug. 1999	40	58.9	32	237.1	22.3	13.3
	Dec. 1999	40	58.9	27	191.4	31	11.8
	Aug. 2000	30	43.1	15	103.7	16.6	14.6
V							
	Aug. 1999	30	43.1	15	81	8.8	17.6
	Dec. 1999	30	43.1	16	107	6.2	17.2
	Aug. 2000	20	30.1	10	53.8	12.3	17.5
VI							
	Aug. 1999	35	50.7	17	125	0	13.6
	Dec. 1999	32	46.4	15	108.6	0	20.5
	Aug. 2000	20	30.1	12	84.1	0	17.7
Correlation with water level (r^2)				**0.67**	**0.47**	0.23	−0.41[b]
P value				**0.001**	**0.01**	0.11	0.06[b]

Pearson's product-moment correlations for each category versus water level are reported. Boldface values are significant.

[a] *Water level and discharge are from a station halfway along the river corridor corresponding to river-km 59.*

[b] *Standing water in reach II excluded.*

others 1999), precise measures of hydrological variability cannot be calculated for the Tagliamento; therefore, only qualitative observations on the general shape, timing, and predictability are reported herein. Flood probabilities in the Tagliamento are higher in autumn and spring and to some extent flood seasons are predictable (Figure 2b), although the prediction of a single flood event is difficult. Flood pulses are rare in winter and summer.

Within the Tagliamento catchment, an accurate flood forecast is possible only up to 5 h before flooding because of torrential rains and the short response time of the basin (Campolo and others 1999). From 1990 to 2001, high-magnitude flood events (more than 2.5 times the average flow) occurred more than three times a year. Flow pulses (that is, flooding below bank-full discharge) occurred with a much greater frequency, perhaps five to six times a year. Flow pulses in the Tagliamento also typically cause bed movement since bed sediment is unconsolidated and highly mobile. Duration of most hydrological events is very short in the Tagliamento, and inundation of the entire active floodplain, although fairly frequent (around three times a year), rarely lasts longer than 3 days (van der Nat and others 2002), in part owing to very high infiltration rates in some locations.

Morphodynamics

River change has been quantified at several spatial and temporal scales using various approaches, including historical maps (Warburton and others 1993), aerial photographs (Zah and others 2001), satellite images (Thorne and others 1993), and ground-based surveys using GPS (Brasington and others 2000). Gurnell and others (2000b), Petts and others (2000), and Arscott and others (2000) provide information on longitudinal patterns of river planform, sediment structure, and aquatic habitat structure along the Tagliamento River, and this study extends that information by incorporating a temporal dimension to geomorphology using dGPS field mapping surveys.

Turnover of aquatic geomorphic types along the entire river corridor was high (Figure 4a) compared to most accounts of geomorphic change in river corridors (Warburton and others 1993; Brasington and others 2000; Zah and others 2001). Results indicated a propensity for aquatic areas in the headwater island-braided floodplain (reach II) to turn over more rapidly than those in lower floodplain reaches. However, this propensity can be influenced by local conditions and does not necessarily characterize all headwater floodplains. This was evident when we compared the aquatic habitat turnover in reach II (approximately

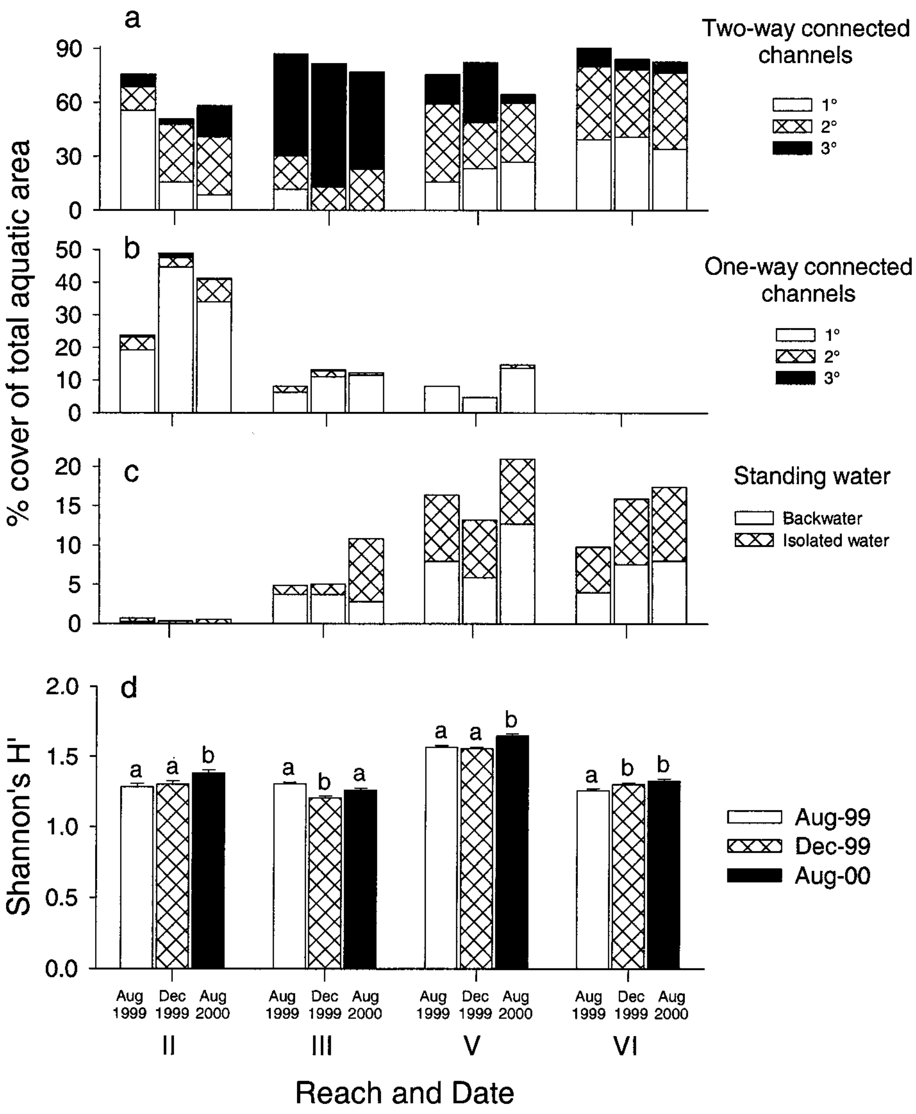

Figure 5. Percent cover of total aquatic area for each aquatic habitat type determined for reaches II, III, V, and VI for each map date (**a**–**c**). Two-way connected channels (**a**), one-way connected channels (**b**), and standing water (**c**) habitats are plotted separately. Designations 1°, 2°, and 3° correspond to primary, secondary, and tertiary channels (Bridge 1993). Panel (**d**) shows habitat diversity using Shannon's diversity (H′) calculated for habitats in reaches II, III, V, and VI in August 1999, December 1999, and August 2000. Letters indicate significant ($P < 0.05$) differences in habitat diversity between dates within a reach. Error bars are ±95% confidence intervals.

Table 3. Pearson's Product-Moment Correlations between Water Level and Percent of Aquatic Area of Each Habitat Type for All Reaches and with Reach II Excluded

	Two-way Connected			One-way Connected			Standing Water	
	1°	2°	3°	1°	2°	3°	BW	ISO
All reaches								
r^2	−0.01	**−0.34**	**0.38**	−0.08	0.01	−0.03	−0.15	−0.18
P value	0.79	**0.05**	**0.03**	0.38	0.75	0.57	0.22	0.17
Without reach II								
r^2	−0.16	−0.33	**0.47**	0.00	0.22	0.23	**−0.60**	**−0.70**
P value	0.28	0.10	**0.04**	0.96	0.21	0.20	**0.01**	**<0.01**

BW, backwaters; ISO, isolated water bodies. Boldface values are significant.

700 m a.s.l.) with a headwater floodplain (approximately 800 m a.s.l.) on the But River (a tributary of the Tagliamento) near the village of Timau (Figure 1).

Arscott and others (forthcoming) reported that aquatic habitat turnover was considerably lower (less than 30% change after an autumnal flood season) for this forested floodplain than it was in reach II (around 65%) and pointed out that it was similar in structure and turnover to reach VI. They concluded that local conditions—such as slope, sediment size, degree of forestation, and land-use activities—had considerable influence on degree of aquatic habitat change and resulting habitat characteristics.

The analysis of changes in floodplain planform (braiding and sinuosity) (Figure 4) and composition (landscape cover elements); (Figure 5 and Tables 2 and 3) indicated very little change in either of these attributes due to flooding, despite high turnover (Figure 4). In general, water-level differences between mapping dates explained some of the variation in habitat composition for all reaches under investigation (Table 2). In reach II, changes in primary and secondary braiding of two-way and one-way connected channels could be attributed to differing water levels. Intuitively, at a higher water level (reach II, August 1999), more channels were two-way connected; conversely, at lower water level (reach II, December 1999), more channels were one-way connected. Changes in geomorphic type composition were attributed primarily to differences in water level rather than to actual changes in the relative abundance of types. In addition, changes in diversity of geomorphic types were minor, did not manifest in a consistent manner among floodplains, and did not correlate with water level. These results all support our initial hypotheses that (a) aquatic habitat turnover following flooding was high, (b) composition of habitat types is stable over time, and (c) fluctuations in habitat composition and abundance are mainly caused by water-level changes rather than by actual changes in the relative abundance of types, over the time period investigated. Supplementary to the first hypothesis, the magnitude of flooding determined the extent of aquatic habitat turnover.

Three geomorphic aspects of the floodplains under investigation changed in the downstream direction. First, there was an increase in the presence of standing water, which was associated with decreasing slope and sediment size distribution on the floodplain (Arscott and others 2000). Second, aquatic habitat turnover decreased with decreasing elevation and slope. Third, the dominant type of channel movement, evident from visual inspection of maps (Figure 3), changed from avulsion processes (changes in channel direction) in reach II to cut-and-fill processes in reach VI. In reaches III, IV, and V, there was a mixture of both types of channel movement. Longitudinal patterns of total stream power (Gurnell and others 2000b) and vegetation within the active corridor (Gurnell and Petts 2002) are likely to be important factors that regulate channel movement along a river corridor.

Kollmann and others (1999) observed high rates of erosion of islands over periods as short as 5 years in the Tagliamento, corresponding with increases in the extent of vegetated islands on other parts of the floodplain. Their results suggested a high turnover of island vegetation but also supported a type of island development described as "cyclical succession." Glova and Duncan (1985), working on assessment of flow reduction effects on fish habitat in a large braided river in New Zealand, observed considerable lateral channel movement caused by single flood periods. However, they stated that "the river as a whole appears to be in a state of dynamic equilibrium, the net effect being that a habitat lost (or gained) within a given reach is replaced (or lost) elsewhere." Findings reported herein support these observations and lend credence to the applicability of the "shifting mosaic steady-state" model (Bormann and Likens 1979) to riverine corridors.

Floodplain rivers and the dynamics that maintain them are becoming endangered components of the landscape because of river engineering efforts (Petts 1989; Ward and others 2002). The need to understand the processes that generate and maintain floodplains is a central focus for much of the current work in floodplain ecology and management (Hughes and Rood 2001). The importance of hydrology in structuring floodplains is well known. Sediment input, sorting processes, and sediment pulses along river corridors (*sensu* Schumm 1977) are also important mechanisms causing turnover and replacement of habitats. Sediment pulses can be visualized as a conveyor belt carrying sediment along a grinding machine that slowly transforms particles into smaller and smaller fractions. For a catchment in equilibrium with its sediment supply, the general sediment characteristics at a single location along such a conveyor belt remain relatively constant. Pulses of sediment transported through headwater floodplains may plug existing channels, causing channels to avulse into a new or a paleochannel (Leddy and others 1993; Richards and others 1993; Warburton and others 1993). This process (avulsion) was evident (Figure 3) in braided reaches II and III, where some side channels completely changed directions. In lower reaches (V and VI), channel movement occurred via cut-and-fill processes typical of meandering reaches. These observations illustrate how the mechanisms by which rivers migrate laterally change along the longitudinal dimension.

Dynamic Equilibrium in a Disturbed Environment

From a landscape perspective, at the scales of reaches (1–2 km) and corridors (170 km), habitats along the active floodplains of the Tagliamento are in a state of dynamic equilibrium (*sensu* Huston 1994). Bormann and Likens (1979) proposed the shifting mosaic steady-state model (a type of dynamic equilibrium) to explain how patches of forest oscillated among several stages of succession, thereby sustaining an equilibrium of patch types at the scale of the entire forest. We believe that the dynamics of the riverine habitat conform to the shifting mosaic steady-state model. For a discussion regarding the ecological relevance of the shifting mosaic steady-state model, refer to Turner and others (1993) and Huston (1994).

Huston (1979) initially described how, under nonequilibrium conditions, a dynamic balance between the rate of competitive displacement and the forces that prevent equilibrium could be established that would allow the continued coexistence of species that would otherwise be competitively excluded. This dynamic equilibrium of fluctuating population, community, and ecosystem properties results from an approximate balance among opposing local and regional processes (Huston 1994). At the habitat scale in our study (for example, main channels or backwaters), there is likely to be a dynamic balance between competitive interactions and disturbance forces that constrain such interactions, the balance of which changes depending on the time since the last disturbance (flood). When viewing a floodplain reach or the entire corridor, there is a mosaic that, at any single point in time, contains a diversity of habitat types collectively encompassing many seral stages (that is, communities at different points along their trajectory to competitive equilibrium). This is evident from vegetation patterns within the active corridor (Kollman and others 1999).

The recovery of communities after disturbance is best described as homeorhesis, which states that if perturbed, a system returns to its preperturbation trajectory or rate of change rather than an artificial "undisturbed" state (O'Neill and others 1986). The impact of disturbance on a community depends on many factors, including (but not limited to) magnitude, duration, frequency, and duration of the disturbance (Pickett and others 1989); and the resistance, resilience, or persistence of the species within the community (for example, Uehlinger 2000).

Flood dynamics along the Tagliamento do not change aquatic habitat composition; rather, they remove benthic communities and reconfigure the spatial environment, leaving the same types and similar numbers of habitats available for recolonization. Habitats along this floodplain river are in a continual cycle of recovery from the last disturbance. The brevity of this study may limit the conclusions that can be drawn; however, speculation about how a change in the flood regime may influence habitat dynamics is warranted. Lowering the flood frequency or lessening the magnitude of flooding (related to drought conditions) is likely to have a considerable impact on open gravel landforms within the active zone. Along the Piave River in northeast Italy, Surian (1999) noted a narrowing of the active corridor caused by a change in the hydrology of the system after irrigation was developed in the basin. Without the scouring forces of flood flows, woody vegetation rapidly colonized the active corridor, constraining the main channel and eventually filling in or plugging other floodplain water bodies. An increase in flood frequency or magnitude may cause the active corridor to expand (that is, creating a greater bare gravel surface area). In either case, the balance of the shifting mosaic steady state would be interrupted, and homeorhesis (*sensu* O'Neil and others 1986) would prevail once the changes to the hydrological regime stabilized.

CONCLUSIONS

Hydrology is one of the major factors influencing community structure in streams (Stanford and Ward 1983; Reice 1985), and its influence on pattern and process operates at all scales and hierarchies. It is therefore critical to develop a broad, multiscale, and multivariable approach that can help us to understand the influence of hydrology on geomorphic and ecological pattern and process in riverine landscapes. This study has illustrated the influence of the physical forces of flooding on aquatic geomorphic type composition, configuration, and turnover along the Tagliamento River. Flooding is undoubtedly the major factor responsible for spatial–temporal patterns in abiotic and biotic variables. Floods transport and distribute sediments, thus reshaping floodplains (Leopold and others 1964). Sediment distribution determines the grain and extent of subsurface flow paths, and these flow paths directly and indirectly influence the physical–chemical and thermal conditions of aquatic habitat (Wondzell and Swanson 1996; Malard and others 2001; Arscott and others 2001). Other research conducted along the Tagliamento relating biotic patterns to hydrology has included vegetation within the active zone (Kollman and others 1999; Gurnell and others 2001; Karrenberg and others 2002), amphibians (Klaus and others 2001), aquatic invertebrates (Arscott 2001), and periphyton (D. B. Arscott unpublished). Current and future research will focus on linking biological communities to landscape structure and dynamics. This emerging science should lead to an increased understanding and predictive power regarding factors influencing community structure and persistence along river corridors.

The results of this study indicated a surprisingly high rate of aquatic habitat turnover along the entire river corridor. Aquatic habitat turnover in floodplains along the Tagliamento corridor decreased along the longitudinal dimension. Composition and planform of the aquatic environment changed little in response to flooding, but composition was responsive to water-level fluctuations. Standing waters (backwaters and isolated water bodies) in floodplains increased in number and area along the longitudinal dimension. Previous research has focused on how lateral configurations of floodplains change along the longitudinal continuum of the Tagliamento. Future research needs to focus on the biological significance of standing waters to floodplain diversity and should attempt to represent aquatic habitat ontogeny (for example, successional trajectories) in models of the distribution of biotic communities.

ACKNOWLEDGMENTS

This project could not have been possible without logistics, field, and laboratory assistance from several people, including Y. Arscott, C. Claret, B. Keller, F. Moesslacher, C. Rust, C. and D. di Scandiuzzi, and A. Schmidt. A. Deana (Direzione Regionale dell'Ambiente), R. Furlan (D.R. della Pianificazione Territoriale, Regione Autonoma Friuli-Venezia Giulia, Trieste), and F. Baruffi (Autorita di Bacino dei Fiume Tagliamento) provided hydrological data and aerial photographs. This work was supported in part by a grant from the ETH-Forschungskommission (0-20572-98).

REFERENCES

Amoros C, Gilbert J, Greenwood MT. 1996. Interactions between units of the fluvial hydrosystem. In: Petts GE, Amoros C, editors. Fluvial hydrosystems. London: Chapman & Hall. p 184–210.

Arscott DB. 2001. Habitat heterogeneity and aquatic invertebrates along an Alpine floodplain river [dissertation]. Swiss Federal Institute for Environmental Science and Technology (ETH/EAWAG). 238 p.

Arscott DB, Keller B, Tockner K, Ward JV. Habitat structure and trichoptera diversity in two headwater floodplains, NE Italy. Int Rev Hydrobiol. Forthcoming.

Arscott DB, Tockner K, Ward JV. 2000. Aquatic habitat diversity along the corridor of an Alpine floodplain river (Fiume Tagliamento, Italy). Arch Hydrobiol 149:679–704.

Arscott DB, Tockner K, Ward JV. 2001. Thermal heterogeneity along a braided floodplain river in the Alps (Tagliamento River, N.E. Italy). Can J Fish Aquat Sci 58:2350–2373.

Benke AC, Chaubey I, Ward GM, Dunn EL. 2000. Flood pulse dynamics of an unregulated river floodplain in the southeastern U.S. coastal plain. Ecology 81:2730–2741.

Bormann FH, Likens GE. 1979. Pattern and process in a forested ecosystem. New York: Springer-Verlag.

Brasington J, Rumsby BT, Mcvey RA. 2000. Monitoring and modeling morphological change in a braided gravel-bed river using high resolution GPS-based survey. Earth Surface Proc Landforms 25:973–990.

Brinson MM. 1993. Changes in the functioning of wetlands along environmental gradients. Wetlands 13:65–74.

Bristow CS. 1987. Brahmaputra River: channel migration and deposition. In: Ethridge FG, Flores RM, Harvey MD, editors. Recent developments in fluvial sedimentology. Tulsa: Spec Publ Soc Econ Paleont Miner 39:63–74.

Campolo M, Andreussi P, Soldati A. 1999. River flood forecasting with a neural network model. Water Resour Res 35:1191–1197.

Claret C, Tockner K, Ward JV. 2002. Thermal heterogeneity of interstitial water in island-associated waterbodies of a dynamic flood plain. Verhand Int Verein Limnol. 28:345–351.

Dudgeon D. 1992. Patterns and processes in stream ecology: a synoptic review of Hong Kong running waters. Stuttgart: E. Schweiyerbart'sche Verlagsbuchhandlung. 147 p.

Fisher SG. 1987. Succession, scale, and hypothesis testing in streams. Can J Fish Aquat Sci 44:689.

Friend PF, Sinha R. 1993. Braiding and meandering parameters. In: Best JL, Bristow CS, editors. Braided rivers. London: Geological Society of London Spec Publ 75. p 105–111.

Glova GJ, Duncan MJ. 1985. Potential effects of reduced flows on fish habitats in a large braided river, New Zealand. Trans Am Fish Soc 114:165–181.

Grime JP. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am Nat 111:1169–1194.

Gurnell AM, Petts GE. 2002 Island-dominated landscapes of large floodplain rivers, a European perspective. Freshwater Biol 47:581–600.

Gurnell AM, Petts GE, Hannah DM, Smith BPG, Edwards PJ, Kollmann J, Ward JV, Tockner K. 2001. Riparian vegetation and island formation along the gravel-bed Fiume Tagliamento, Italy. Earth Surface Proc Landforms 26:31–62.

Gurnell AM, Petts GE, Hannah DM, Smith BPG, Edwards PJ, Kollmann J, Ward JV, Tockner K. 2000a. Wood storage within the active zone of a large European gravel-bed river. Geomorphology 34:55–72.

Gurnell AM, Petts GE, Harris N, Ward JV, Tockner K, Edwards PJ, Kollmann J. 2000b. Large wood retention in river channels: the case of the Fiume Tagliamento, Italy. Earth Surface Proc Landforms 25:255–275.

Hughes FMR, Rood SB. 2001. Floodplains. In: Warren A, French JR, editors. Habitat conservation: managing the physical environment. New York: Wiley. p 105–121.

Huston MA. 1994. Biological diversity: the coexistence of species on changing landscapes. Cambridge (England): Cambridge University Press. 679 p.

Huston MA. 1979. A general hypothesis of species diversity. Am Nat 113:81–101.

Junk WJ, Bayley PB, Sparks RE. 1989. The flood pulse concept in river floodplain systems. Proceedings of the International Large River Symposium. Can J Fish Aquat Sci 106:110–127.

Karrenberg S, Edwards PJ, Kollmann J. 200 2. The life history of Salicaceae living in the active zone of floodplains. Freshwater Biol 47:733–749.

Klaus I, Baumgartner C, Tockner K. 2001. The dynamic riverine landscape along the Tagliamento (Italy, Friuli) as a habitat of a diverse amphibian community. Zeitschr Feldherpetol 8:1–10.

Kollmann J, Vieli M, Edwards PJ, Tockner K, Ward JV. 1999.

Interactions between vegetation development and island formation in the Alpine river Tagliamento. Appl Veget Sci 2:25–36.

Leddy JO, Ashworth PJ, Best JL. 1993. Mechanisms of anabranch avulsion within gravel-bed braided rivers: observations from a scaled physical model. In: Best JL, Bristow CS, editors. Braided rivers. London: Geological Society of London Spec Publ 75. p 119–127.

Leopold LB, Wolman MG, Miller JP. 1964. Fluvial processes in geomorphology. New York: Dover. 522 p.

Malard F, Mangin A, Uehlinger U, Ward JV. 2001. Thermal heterogeneity in the hyporheic zone of a glacial floodplain. Can J Fish Aquat Sci 58:1319–1335.

Michener WK, Haeuber RA. 1998. Flooding: natural and managed disturbances. BioScience 48:677–680.

Müller N. 1995. River dynamics and floodplain vegetation and their alteration due to human impact. Arch Hydrobiol Suppl 101:477–512.

Nakamura F, Swanson FJ, Wondzell SM. 2000. Disturbance regimes of stream and riparian systems—a disturbance–cascade perspective. Hydrolog Proc 14:2849–2860.

O'Neill RV, DeAngelis DL, Waide JB, Allen TFS. 1986. A hierarchical concept of ecosystems. Princeton (NJ): Princeton University Press. 154 p.

Petts G. 1989. Historical analysis of fluvial hydrosystems. In: Petts GE, Möller H, Roux AL, editors. Historical change of large alluvial rivers: western Europe. Chichester (England): J Wiley. p 1–18.

Petts GE, Gurnell AM, Gerrard AJ, Hannah DM, Hansford B, Morrissey I, Edwards PJ, Kollmann J, Ward JV, Tockner K, and others. 2000. Longitudinal variations in exposed riverine sediments: a context for the ecology of the Fiume Tagliamento, Italy. Aquat Conserv Mar Freshwater Ecosyst 10:249–266.

Pickett STA, Kolasa J, Armesto JJ, Collins SL. 1989. The ecological concept of disturbance and its expression at various hierarchical levels. Oikos 54:129–136.

Poff NL, Ward JV. 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. Can J Fish Aquat Sci 46:1805–1818.

Poff NL, Ward JV. 1990. Physical habitat template of lotic systems: recovery in the context of historical pattern of spatiotemporal heterogeneity. Environ Manage 14:629–645.

Poole GC, Berman CH. 2001. An ecological perspective on instream temperature: natural heat dynamics and mechanisms of human-caused thermal degradation. Environ Manage 27: 787–802.

Puckridge JT, Sheldon F, Walker KF, Boulton AJ. 1998. Flow variability and the ecology of large rivers. Mar Freshwater Res 49:55–72.

Reice SR. 1985. Experimental disturbance and the maintenance of species diversity in a stream community. Oecologia 67:90–97.

Richards K, Chandra S, Friend P. 1993. Avulsive channel systems: characteristics and examples. In: Best JL, Bristow CS, editors. Braided rivers. London: Geological Society of London Spec Publ 75. p 195–203.

Schumm SA. 1977. The fluvial system. New York: Wiley. 338 p.

Solow AR. 1993. A simple test for change in community structure. J Animal Ecol 62:191–193.

Sparks RE, Spink A. 1998. Disturbance, succession and ecosystem processes in rivers and estuaries: effects of extreme hydrologic events. Regulated Rivers Res Manage 14:155–159.

Spink A, Sparks RE, Oorschot MV, Verhoeven TJA. 1998. Nutrient dynamics of large river floodplains. Regulated Rivers Res Manage 14:203–216.

Stanford JA, Ward JV. 1983. Insect species diversity as a function of environmental variability and disturbance in stream systems. In: Barnes JR, Minshall GW, editors. Stream ecology. New York: Plenum., p 265–278.

Statzner B, Higler B. 1986. Stream hydraulics as a major determinant of benthic invertebrate zonation patterns. Freshwater Biol 16:127–139.

Surian N. 1999. Channel changes due to river regulation: the case of the Piave River, Italy. Earth Surface Proc Landforms 24:1125–1151.

Swanson FJ, Johnson SL, Gregory SV, Acker SA. 1998. Flood disturbance in a forested mountain landscape. BioScience 48:681–689.

Thorne CR, Russel APG, Alam MK. 1993. Planform pattern and channel evolution of the Brahmaputra River, Bangladesh. In: Best JL, Bristow CS, editors. Braided rivers. London: Geological Society of London Spec Publ 75. p 257–276.

Tockner K, Malard F, Ward JV. 2000. An extension of the flood pulse concept. Hydrol Proc 14:2861–2883.

Tockner K, Ward JV, Arscott DB, Edwards PJ, Kollmann J, Gurnell AM, Petts GE, Maiolini B. The Tagliamento River: a model ecosystem for alpine gravel-bed rivers In: Plachter H, Reich M, editors. Ecology and conservation of gravel bed rivers and alluvial floodplains in the Alps. Berlin: Springer, Forthcoming.

Townsend CR. 1989. The patch dynamics concept of stream community ecology. J North Am Benthol Soc 8:36–50.

Townsend CR, Scarsbrook MR, Dolédec S. 1997. The intermediate disturbance hypothesis, refugia, and biodiversity in streams. Limnol Oceanog 42:938–949.

Turner MG, Romme WH, Gardner RH, O'Neill RV, Kratz TK. 1993. A revised concept of landscape equilibrium: disturbance and stability on scaled landscapes. Landscape Ecol 8:213–227.

Uehlinger U. 2000. Resistance and resilience of ecosystem metabolism in a flood-prone river system. Freshwater Biol 45:319–332.

van der Nat D, Schmidt AP, Tockner K, Edwards PJ, Ward JV. 2002. Inundation dynamics in braided floodplains (Tagliamento River, northeast Italy). Ecosystems 5:636–647.

Warburton J, Davies TRH, Mandl MG. 1993. A meso-scale field investigation of channel change and floodplain characteristics in an upland braided gravel-bed river, New Zealand. In: Best JL, Bristow CS, editors. Braided rivers. London: Geological Society of London Spec Publ 75. p 241–255.

Ward JV. 1989. The four-dimensional nature of lotic ecosystems. J North Am Benthol Soc 8:2–8.

Ward JV, Tockner K, Arscott DB, Claret C. 200 2. Riverine landscape diversity. Freshwater Biol 47:517–540.

Ward JV, Tockner K, Edwards PJ, Kollmann J, Bretschko G, Gurnell AM, Petts GE, Rossaro B. 1999. A reference river system for the Alps: the 'Fiume Tagliamento.' Regulated Rivers Res Manage 15:63–75.

Welcomme RL. 1979. Fisheries ecology of floodplain rivers. London: Longman. 317 p.

White PS, Pickett STA. 1985. Natural disturbance and patch dynamics: an introduction. In: Pickett STA, White PS, editors. The ecology of natural disturbance and patch dynamics. New York: Academic Press. p 3–13.

Wondzell SM, Swanson FJ. 1996. Seasonal and storm dynamics of the hyporheic zone of a 4th order mountain stream. I: hydrologic processes. J North Am Benthol Soc 15:3–19.

Zah R, Niederöst M, Rinderspacher H, Uehlinger U, Ward JV. 2001. Long-term dynamics of the channel network in a proglacial floodplain (Val Roseg, Switzerland). Arctic Antarctic Alpine Res. 33:440–446.