Flood disturbance affects macroinvertebrate food chain length in an alluvial river floodplain

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Abstract:

- 1) Characterizing food-web responses to environmental factors could greatly improve our understanding of environment-biota relationships, and especially in floodplains where trophic interactions can be particularly important during phases of hydrological disconnection. The effects of floodplain hydrology and environmental attributes on structural aspects of biotic assemblages have been extensively studied, but responses at the functional level remain largely unknown.
- 2) Here, we characterized a central aspect of food-web architecture, the food chain length, as the maximum trophic position within 24 macroinvertebrate communities of parafluvial habitats in the Maggia river floodplain, in Switzerland. We investigated how the food chain length changed with different levels of habitat size, primary productivity and disturbance, the three factors potentially affecting food chain length in both theoretical and empirical studies.
- 3) We found that food chain length was shorter in frequently flooded habitats and immediately after a flood. We also showed that trophic omnivory, where predators fed at lower trophic levels after flooding, and in more frequently flooded habitats, may explain these changes.
- 4) These findings show that trophic omnivory may explain how predators resist disturbance and are maintained in highly dynamic landscapes. But more importantly, given that trophic omnivory may overall weaken trophic linkages and thus increase food-web stability, this suggests that it could be a key mechanism in sustaining biodiversity in river floodplains.

1 **Introduction**

2 Riverine floodplains harbour high biodiversity, and deliver key ecosystem services to humans
3 such as water cleansing and flood protection. Despite this, their ecological status is
4 deteriorating rapidly worldwide and action is needed to protect these valuable ecosystems
5 (Tockner and Stanford 2002, Tockner et al. 2010). In alluvial floodplains, floods create and
6 maintain high habitat heterogeneity, resulting in ecological niches that sustain high levels of
7 biodiversity (Arscott et al. 2002, Stanford et al. 2005, Datry et al. 2014). In fact, flood
8 disturbance is a primary driver of floodplain ecological-biogeochemical functioning. Floods
9 influence primary production by transferring nutrients from the main channel onto adjacent
10 floodplains (Tockner et al. 1999, Tockner et al. 2000, Ahearn et al. 2006), enable organism
11 dispersal among floodplain habitats (Paillex et al. 2007, Gallardo et al. 2008, Fernandes et al.
12 2014), and open new ecological niches for colonization by resetting communities to earlier
13 successional stages (Townsend and Scarsbrook 1997, Amoros and Bornette 2002, Thomaz et
14 al. 2007). Floods should therefore also affect fundamental properties of food webs, such as
15 food chain length (Post 2002). A number of studies have focused on understanding the
16 environmental controls on structural aspects of communities within alluvial floodplain
17 ecosystems (reviewed in Amoros and Bornette 2002, Opperman et al. 2010), and have guided
18 effective restoration efforts in many places. However, recent research shows that better
19 knowledge of how environmental drivers affect functional aspects of communities, such as
20 the food web, can improve our understanding of environment-biota relationships and assist
21 species conservation in heterogeneous landscapes such as alluvial floodplains (Bellmore et al.
22 2013).

23 Food webs are a major focus in ecological research. Food webs describe the feeding
24 links between species within a community and thus are important for understanding
25 biodiversity and ecosystem function response to environmental change (Thompson et al.
26 2012). Food chain length (FCL: maximum trophic position among all members of a food

web) is a key attribute of food webs and is known to influence species diversity, community structure and stability (reviewed in Sabo et al. 2009), nutrient cycling, and contaminant concentrations in top predators (Cabana and Rasmussen 1994, Kidd et al. 1998, Sabo et al. 2009). FCL is an emergent property of food webs that incorporates different key processes such as the number of trophic levels and degree of trophic omnivory (Post 2002). Further, food-web size largely results from a combination of basal resource diversity and FCL (Layman et al. 2007). In resource-poor ecosystems with a low diversity of basal resources, such as subalpine alluvial floodplains for example, FCL variation may well capture changes in food-web size and architecture and thus food-web dynamics in general (Leibold et al. 1996, Holt and Polis 1997, Ward et al. 2015).

Ecosystem size, productivity, and disturbance level are three main features affecting food chain lengths (Sabo et al. 2009, Takimoto et al. 2013). The productivity hypothesis states that because much energy is lost at each trophic transfer (trophic efficiency usually ranges between 2% and 50%, Post et al. 2002), food chains will tend to be shorter in resource-limited ecosystems (Pimm 1982, Schoener 1989). The ecosystem size hypothesis posits that because larger habitats tend to be more environmentally diverse, they can accommodate more species and have longer food chains (May 1973, Cohen and Newman 1991, Post et al. 2000). Finally, the disturbance or dynamic stability hypothesis argues that long food chains are more vulnerable to disturbance and take longer to reassemble when disturbed, thus ecosystems with higher disturbance levels will have shorter food chains (Pimm and Lawton 1977, Pimm and Kitching 1987, May 2001). Each of these hypotheses has been supported to various degrees in experimental and natural systems, with FCL often positively affected by ecosystem productivity and ecosystem size (reviewed in Takimoto et al. 2013). However, results still remain equivocal for the disturbance hypothesis. For instance, reviews by Post (2002) and Takimoto et al. (2013) found no evidence for an effect of disturbance on FCL, whilst Sabo et al. (2009) conducted a meta-analysis of determinants of FCL in freshwaters and found a

negative effect of disturbance. One explanation for such inconsistency among these latter studies could be that drivers of FCL may interact in a context-dependent manner (Post et al. 2002). For example, productivity levels can dampen the effect of disturbance in modelled food webs (Moore et al. 1993).

Food chains length can vary with the addition or removal of a top predator (additivity mechanism) or intermediate consumer (insertion mechanism), or by varying levels of trophic omnivory of top predators (omnivory mechanism) feeding at higher or lower trophic levels (Vander Zanden et al. 1999, Post and Takimoto 2007, Ruhi et al. 2016). Warfe et al. (2013) suggested that analyzing these mechanisms in parallel to FCL dynamics provides a framework for better understanding processes linking environmental drivers, community composition and food chain length. The additivity mechanism has received much attention in ecological research (Post et al. 2000) partly because understanding how top predators are maintained has far-reaching consequences on community assembly (McPeck 1998, Chase et al. 2002, Chase et al. 2009), nutrient cycling (Schmitz et al. 2010), and carbon storage (Atwood et al. 2013, Atwood et al. 2015). Townsend et al. (1998) examined insertion mechanisms and found that insertion of feeding links increased FCL in more productive New Zealand streams. The effect of trophic omnivory on food chain length has received considerable attention in recent years and several studies found that it explained food chain shortening in streams with high disturbance levels (McHugh et al. 2010, Ruhi et al. 2016). Omnivory is ubiquitous in freshwaters (Thompson et al. 2007, Thompson et al. 2012) and both theory and observations indicate that it is especially prevalent in ecosystems with high levels of disturbance and intermediate resource availability (Fagan 1997, France 2012).

Alluvial river floodplains are ideal ecosystems for studying the effects of environmental heterogeneity on biota (Tockner et al. 2010). Floodplains are often described as dynamic habitat mosaics with differing levels of disturbance, productivity, sizes and local environmental conditions (Amoros and Bornette 2002, Stanford et al. 2005, Whited et al.

2007). In addition, examining food-web structure across floodplain habitats could bridge the gap between classic small-scale food-web studies and landscape ecology, thus providing a framework for understanding which food-web attributes are important for sustaining species within heterogeneous landscapes (Winemiller 2005, Bellmore et al. 2013). Further, trophic interactions can play a particularly important role in structuring communities in floodplains, especially during phases of hydrological disconnection (Townsend and Scarsbrook 1997, Fairchild et al. 2000, Chanut et al. 2019). Altogether, alluvial floodplains are particularly suitable for examining the effects of habitat productivity, size and disturbance regime on FCL, reinforcing the call for food-web studies in these systems.

In the present study, we examined how habitat size, productivity and disturbance regime affect FCL in aquatic parafluvial habitats of an alluvial floodplain. We explored mechanisms (species addition, insertion, trophic omnivory) most likely explaining changes in FCL along measured environmental gradients. In our study system, an alluvial floodplain chosen for its great diversity of parafluvial habitat size, productivity and disturbance regimes, flow regulation has altered the seasonality of the flow regime and the interval time of floods is now largely uncorrelated to their magnitude (Perona et al. 2009). Consequently, environmental conditions largely differ from those under a natural flow regime to which local species are adapted (Lytle et al. 2004), and floods likely act as disturbance to local communities as well as other properties of alluvial floodplains. We therefore hypothesized that flood disturbance would be the main force constraining FCL, with shorter food chains in frequently flooded habitats (H_1). We also expected that species richness and community composition would be altered (reset) immediately after a flood, causing FCL to be shorter (H_2).

Methods

Study area

The Maggia River is located in the south-eastern part of the Swiss Alps, flowing southward into Lake Maggiore (Figure 1). It has one of the few remaining near-natural floodplains in Switzerland, being a site of national importance (Kuhn and Amiet 1988). Its catchment covers 930 km² with elevations ranging from 200 to 3300 m a.s.l. Owing to the presence of two glaciers in the headwaters and snowfall precipitation in winter, the hydrological regime is classified as glacio-nival. The flow regime of the river was substantially modified following the construction of a complex hydropower scheme in the headwaters in 1953 (Pfamatter and Zanetta 2003, Molnar et al. 2008). The original high flows during snowmelt were replaced by essentially constant flows (minimum flow requirements ~ 1.5 m³/s) with occasional flood peaks and with no correlation between flood magnitude and return period (Molnar et al. 2008, Perona et al. 2009).

The alluvial floodplain used in this study was located in the middle of the valley; it is about 7-km long and nearly 2-km wide in some sections. Because of fairly low storage by the hydropower scheme and high lateral hillslope runoff during major rain events, larger flood peaks still occur but not lesser magnitude floods <10 m³/s. The combination of high flows and abundant bedload sediment (mean diameter of stones = 120 mm) maintains a heterogeneous floodplain mosaic. Within the floodplain, single-thread sections alternate with braided reaches where various types of parafluvial habitats occur: ponds, connected and disconnected side arms, and backwaters. For this study, we selected 24 permanently-wetted parafluvial habitats known to exhibit different flooding regimes (Chanut et al. 2019), including permanent ponds, disconnected side arms, and side arms connected at their downstream end to the main channel.

Determination of productivity levels, disturbance and habitat size

Surface biofilms (periphyton) were measured by randomly collecting 5 stones (cobble-size) within each habitat. Each stone was gently rinsed with distilled water in order to remove

particulate organic matter, the biofilm was then removed from each stone by scrubbing with a wire brush into a plastic container with 100 mL distilled water, and the scrubbed area measured (after Uehlinger 1991). For measurement of biofilm standing stocks, the biofilm suspension was filtered through a glass fiber filter (0.45 μm , Whatman GFF) and stored on ice in the dark. Each filter was dried at 60°C for 24h, weighed, then combusted at 450°C for 6h and reweighed to obtain AFDM (g/m^2). Particulate organic matter (POM) was collected at 3 locations within each habitat using a Hess sampler (250- μm mesh, 0.04 m^2 area) by disturbing the substrate to a depth of ~ 10 cm (Ruhi et al. 2016). The collected POM was preserved frozen at -25°C. Once in the laboratory, POM was thawed, a subsample then dried at 60°C for 24h, weighed, combusted at 450°C for 6h and reweighed for estimates of biomass as AFDM.

We measured habitat size as the wetted surface area of each habitat during low flow conditions, using GIS and a drone-captured high-resolution aerial image. Because water depth was rather shallow and homogeneous amongst habitats (mean = $0.73 \pm 0.2\text{m}$), these could not sustain a pelagic food web decoupled from benthic habitat; therefore, we used surface areas rather than volume as measure of habitat size.

We developed a 2D hydrodynamic model for the floodplain that enabled us to calculate two key hydrological metrics for each habitat: flood frequency over the two years preceding a sampling event and recent disturbance history represented by the number of days elapsed since the last flood. For a detailed description of the model and its accuracy, see Chanut et al. (2019). The model was constructed using Basement software (Faeh et al. 2010, developed at ETH Zurich: <http://www.basement.ethz.ch/>), which solves depth-averaged shallow-water Saint-Venant equations to calculate water depth, current velocity and bottom shear stress for each element within the modelling domain. Because of the spatial complexity of groundwater-surface water interactions in this alluvial floodplain that cannot be accurately simulated under the current state of system characterization, we only used the model to derive thresholds of discharge at which a given habitat becomes inundated with surface water as well

as local bottom shear stress. Our modelling approach consisted of running steady-state simulations for the range of flows corresponding to flood peaks that occurred between 13 March 2014 and the end of our study period on 28 October 2016. The duration of the modelling period (>2.5 y) was longer than the life cycle duration of present taxa; thus, it was deemed suitable to capture effects of hydrology on macroinvertebrates. For each discharge simulation, the model produced a simulated water depth for each cell of the modelling domain that was then overlapped with a map of our sampling sites to determine whether a particular habitat was flooded at a given discharge. We were then able to calculate a flood frequency for each habitat during the modelling period as well as the time elapsed since the last flood at each sampling campaign (February, August and October). During the modelling period, 45 floods occurred, with a minimum discharge of $10.1 \text{ m}^3/\text{s}$, maximum of $252 \text{ m}^3/\text{s}$, and average of $65.6 \text{ m}^3/\text{s}$ ($\text{SD} = 72.2$).

Food web sampling and sample processing

Samples were collected in February, August and October 2016. Of the initial 24 sites, we discarded sites where the collected invertebrate biomass did not allow accurate isotope measures (see below), retaining 17 sites from the February survey, 12 sites in August, and 20 sites in October. We tested whether the discarded sites significantly differed from the retained ones in terms of habitat variables and potential drivers of FCL and found no difference. The biofilm sampling procedure described above was repeated for 3 stone replicates per site for stable isotope analysis and the filters with biofilms were preserved frozen (-25°C). Potential allochthonous basal resources were collected at each site for isotope analysis: to ensure that most leaves and riparian plants available to macroinvertebrates were represented, a composite sample was hand-picked from 5 locations within each aquatic habitat and stored on ice before being preserved frozen (-25°C). For clarity, this composite sample of allochthonous plant material will be referred to as POM. For the analysis of community structure, benthic

macroinvertebrates were randomly collected ($n = 3$, at each site and date) using a Hess sampler (250 μm mesh, 0.04 m^2 area) and preserved in 70% ethanol. For food-web analysis, a semi-quantitative sample of benthic macroinvertebrates was collected (5 replicates at each site and date covering all microhabitats) using a kick-net (250- μm mesh) following standard methods described in Stark et al. (2001) and immediately stored on ice. Macroinvertebrates for food-web analysis were kept alive overnight in order to allow for the flushing of gut content (Siebers et al. 2019). Macroinvertebrate samples were then preserved frozen at -25°C until analysis. Visual surveys indicated that fish were extremely rare in the parafluvial habitats, consequently, we did not include fish in our trophic analysis.

The macroinvertebrate samples collected for food-web analysis and community analysis were hand-picked and identified to the lowest possible taxonomic level using Tachet et al. (2010). 14 taxa were identified to the species level and 12 to the family level (Table S2, Supporting Information). Invertebrates were assigned as primary consumers or predators following Tachet et al. (2010). Organic matter samples (biofilm and POM from above) were thawed and rinsed with distilled water. Biofilms, POM and invertebrates were then freeze-dried for 24h in a Lyovac GT 2-E lyophilizer (STERIS GmbH, Hürth, Germany). Each invertebrate and organic matter sample was homogenized with a mortar and pestle and ca. 0.5-1.5mg of each placed into a tin cup. The number of invertebrate individuals required to reach the weight of 0.5-1.5mg varied, but a minimum of 3 individuals was always incorporated into the sample. All samples were combusted in a Vario PYRO Cube elemental analyzer (elementar Analysensysteme GmbH, Langenselbold, Germany) connected to an IsoPrime isotope ratio mass spectrometer (GV Instruments Ltd., Wythenshawe, UK) for measurement of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$. Reference materials for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were provided by Biogeochemical Laboratories, Indiana University (NBS 19, L-SVEC, IAEA-N-1 and IAEA-N-2). Analytical precision was 0.1‰ for $\delta^{13}\text{C}$ and 0.2 ‰ for $\delta^{15}\text{N}$. *Data analysis*

Isotopic niche indices – We computed the trophic position of each predator i in site j as:

209
$$TP_{ij} = \lambda + (\delta^{15}N_{ij} - \delta^{15}N_{base,j})/\Delta$$

210 Where $\delta^{15}N_{ij}$ is the $\delta^{15}N$ value for the predator i in site j , $\delta^{15}N_{base,j}$ is the lowest value
 211 for a consumer within site j (Table 1), λ is the trophic position of the primary consumer (i.e. 2)
 212 and Δ is the mean trophic enrichment factor of 2.2‰ (Post 2002, McCutchan et al. 2003). We
 213 chose to use the minimum consumer $\delta^{15}N$ value at each site as a basal reference for our
 214 calculations, because isotopic values of primary consumers average the values of basal
 215 resources, which varied considerably among sites and dates (Jardine et al. 2014). We
 216 estimated FCL within each habitat as the maximum trophic position (MTP) occupied by a
 217 predator (Post et al. 2000, Ruhi et al. 2016, Table 2).

218 *Isotope mixing model analyses* – We used stable isotope ($\delta^{13}C$ and $\delta^{15}N$) mixing models to
 219 estimate the proportional contributions of different basal resources to invertebrate food webs
 220 within each habitat. We first ensured that biofilm and POM were indeed well separated
 221 resources by comparing their average $\delta^{13}C$ values. Biofilm and POM samples had markedly
 222 different $\delta^{13}C$ values, with POM exhibiting lower and more stable values among sites, as
 223 expected for allochthonous sources from riparian trees (Table S2, Supporting Information).
 224 We tested whether consumer isotope values could be suitable for use with mixing models
 225 using the Monte Carlo simulation of the possible range of isotopic mixing models developed
 226 by Smith et al. (2013). A total of 1500 iterations were performed with sources corrected by
 227 ranges for trophic enrichment factors (TEF): for $\delta^{13}C$, 0.4 ± 0.3 , and for $\delta^{15}N$, 2.2 ± 0.3 (Post
 228 2002, McCutchan et al. 2003). Samples were excluded from further analysis when they fell
 229 outside the 95% confidence bounds indicating suitability for mixing model analysis (Smith et
 230 al. 2013, Philips et al. 2014). Next, we used the Bayesian mixing model SIAR (Parnell et al.
 231 2010) to produce probability distributions of the contributions of basal resources to consumer
 232 isotope values. As filamentous algae were rarely found, the model was restricted to two basal
 233 resources (terrestrial plant litter and periphyton). We did not include prior information on diet

proportions as there were only two sources in the mixing model (Fry 2013, Brett 2014). Models were run separately for each site and season (February, August, and October). Terrestrial plant and periphyton $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were set at averages and standard deviations for each season. Each model was set to run 500,000 times, with the first 50,000 iterations discarded. All models were created using the SIAR package in R 3.5.0 (R core team, 2018).

Statistical analysis

In order to test which of the three potential scenarios of environmental control on FCL control was supported more, and specifically test H_1 , we constructed a global generalized linear mixed effect model (GLMM) including all potential drivers of FCL: biofilm standing crop (g/m^2), particulate POM (g/m^2), habitat surface area (m^2), time since last flood (days), and flooding frequency (flood events/year). Because of the repeated-measures structure of our dataset, we used site ID as a random effect in all models to account for unmeasured site-specific effects and season as a fixed factor in each model to correct for seasonal effects. All GLMMs were constructed with the *lme4* R package (Douglas et al. 2015). We then used a backward model selection procedure based on the Akaike Information Criterion (AICc), where model terms are sequentially removed until the most parsimonious model with the lowest AICc is found. Then, to refine our test of the productivity effect on FCL, we tested whether the availability of a given type of organic matter (POM or biofilm) affected FCL when community-wide dietary proportions were primarily based on this given organic resource. For that, we first separated sites along the median values of community-wide diet proportions produced by the mixing models, at a 50% level cut-off; i.e., communities were primarily fueled either by biofilm or POM. We then tested whether the availability of each resource type (biofilm and POM) affected FCL in each category.

We then tested H₂ and the relative importance of each of the three potential mechanisms driving FCL: addition, insertion and trophic omnivory. For the insertion mechanism, we tested the relative effects of each of the potential FCL drivers on the composition (presence absence) and structure (abundances) of primary consumer assemblages (Ruhi et al. 2016). For this, we constructed a distance-based redundancy analysis model using the Jaccard distance for composition and the Bray-Curtis distance for structure, incorporating all potential drivers of FCL. We then conducted a similar backward model selection procedure as for the drivers of FCL with the fixed effect “season” being incorporated in all final models. The same procedure was repeated on the predator assemblages to test for addition mechanisms. We also tested the effect of taxa richness on FCL using a GLMM with site ID as a random effect and season as a fixed effect. We examined the omnivory mechanism by testing which of the potential drivers of FCL most affected the average trophic position of all predators at a site (Ruhi et al. 2016). Here, we used a similar GLMM and model selection procedure as for the FCL control with average trophic position of predators as the independent variable. Here, we report the marginal R² for all GLMMs.

RESULTS

Environmental drivers overview

Surface areas of parafluvial habitats ranged from 7.2 to 877.2 m² and productivity levels varied widely among habitats: POM ranged from 0.04 to 2.18 g/m² and biofilm standing crop from 0 to 14.2 g/m². Discharge threshold values for habitat inundation ranged from 10 to 250 m³/s (mean = 49 m³/s, median = 35 m³/s, SD = 58 m³/s). Flood frequency for the different parafluvial habitats ranged from 0.52 to 18.04 floods per year (Table S4, Supporting Information). Time elapsed since the last flood varied greatly among habitats at each date, owing to the wide range of inundation thresholds (Table S4, Supporting Information).

There was some level of covariation between some of these metrics, but none exceeded a Spearman Rank coefficient of 0.42 (Table S1, Supporting Information).

Community and Food web overview

A total of 26 invertebrate taxa were identified, of which 19 were primary consumers and 7 were predators (Table S2, Supporting Information). FCL ranged from 2.89 to 5.62 in February, from 2.37 to 4.29 in August and from 3.10 to 5.99 in October. The median values for the distribution of the proportion of diet composed of POM varied between 0.25 and 0.65 in February (median = 0.49), 0.20 and 0.57 in August (median = 0.44) and between 0.16 and 0.67 in October (median = 0.42) (Table S3, Supporting Information).

Environmental controls on food chain length

The final model retained for FCL ($AIC_c = 101.68$, $R^2 = 0.376$) included a positive linear relationship between FCL and time since last flood ($p = 0.047$, Figure 2a) and a negative relationship with flooding frequency ($p = 0.036$, Figure 2b). The other terms in the initial global model were not retained in the model selection because FCL was not correlated to habitat size (Figure 2c), biofilm standing crop (Figure 2d), or biomass of POM (Figure 2e). When we separated food webs based on their community-wide dietary proportions, FCL was not correlated to biofilm standing crop (Figure 2d) for food webs with a community-wide dietary proportion composed of >0.5 biofilm ($p = 0.09$). Similarly, FCL was not correlated to POM biomass for food webs with a community-wide dietary proportion composed of >0.5 POM ($p = 0.51$).

Potential mechanisms driving changes in FCL

The qualitative analysis of top predator identity suggested the identity of the predator occupying the top of the macroinvertebrate food chain did not depend on the disturbance

level. Some variation occurred, with for instance Dytiscidae being top predators only in rarely flooded habitats and Perla only in frequently flooded habitats, but this only concerned 2 sites and 1 site respectively (Figure S1, Supporting Information; Table 2). The composition (species occurrences) and structure (species abundances) of primary consumer and predator assemblages were not affected by any measured FCL drivers (Table 3). Similarly, FCL was not correlated to taxa richness ($p = 0.254$, Figure 3, Supporting Information). For the test of omnivory, the final model ($AICc = 293.98$, $R^2 = 0.315$) included positive relationships between the trophic position of predators and the time since last flood ($p = 0.004$, Figure S2b Supporting Information), POM ($p = 0.014$, Figure S2c Supporting Information) and a negative relationship with flooding frequency ($p = 0.003$, Figure S2a Supporting Information).

Discussion

In this study, hydrological disturbance negatively affected food chain length (FCL) in parafluvial habitats of an alluvial floodplain. Trophic omnivory where predators fed at lower trophic levels after flooding, and in more frequently flooded habitats, may explain these changes in FCL. We showed that flooding had minor direct effects on community composition and structure as well as species richness, but still caused substantial changes in FCL, a key property of food webs, which thus influences structural and functional properties of ecosystems. These results consequently have potentially important implications for species conservation in alluvial floodplains.

FCL is affected by hydrological disturbance in an alluvial floodplain

Here we tested how ecosystem size, productivity, and disturbance regime affected FCL in an alluvial floodplain. We found that only the dynamic stability hypothesis was supported by the data. Specifically, food chains were shorter after a flood and in frequently

flooded habitats, supporting H₁. To date, variations in FCL in natural systems have most often been attributed to gradients of productivity or ecosystem size, but the effect of disturbance remains equivocal and little documented (but see McHugh et al. 2010, Sabo et al. 2010, Ruhi et al. 2016). McHugh et al. (2010) and Ruhi et al. (2016) quantified disturbance as a combination of geomorphological metrics and hydrological variability and found that stream reaches with high disturbance levels had shorter food chains. Sabo et al. (2010) found that increased hydrologic variability reduced FCL in 36 North American rivers. Here we show that flood disturbance is the main driver behind FCL changes in an alluvial floodplain system. Although the effect of disturbance on FCL remains uncertain both in terrestrial and freshwater systems (Post 2002, Takimoto et al. 2013), our results are significant not only for the understanding of floodplain functioning, but also for our understanding of the drivers of FCL in general.

Parafluvial habitats in floodplains share characteristics of both ponds and streams, and the positive effect of habitat size on FCL in these systems has been well documented (Takimoto et al. 2013). In contrast, we found no support for this hypothesis. This finding may potentially be due to the range of habitat sizes in the study floodplain which was too narrow to have an effect on FCL. Indeed, research suggests that longer food chains occur in larger lakes with more diverse habitats, because of compartmentalization (Post et al. 2000, Krause et al. 2003). Additionally, Tunney et al. (2012) showed that food chains were longer in pelagic food webs of larger lakes, whereas in smaller lakes with a higher proportion of benthic littoral habitat, food chains were shorter and omnivory prevailed. The shallow depth (<1m) and overall small size of parafluvial habitats in the Maggia floodplain could not sustain a pelagic food web decoupled from benthic and littoral habitats, which could explain why we found no effect of habitat size on FCL. Yet, we cannot exclude that FCL response to habitat size may have differed if fish had been included in our calculations of FCL. Indeed, the presence of fish would undoubtedly lengthen the food chain, but most importantly, given that we are primarily

interested in the macroinvertebrate food chain, we cannot entirely rule out that the effect of disturbance on FCL could be mediated by fish presence. For instance, more frequently disturbed habitats could have greater fish abundances, and their predation might explain the reduced FCL. Yet, despite the lack of fish data here, we argue that this is highly unlikely. First, we did not notice any fish presence or difference amongst habitats in this regard during the sampling. Second, we showed that there was no significant taxonomic turnover between habitats along the gradient of disturbance, this means that even if more disturbed habitats had more fish, these did not affect species occurrences. And finally, during a field experiment in this floodplain where fish were added to parafluvial habitats, no difference was found in macroinvertebrate community structure between ponds with and without fish (personal observation).

We found that the availability of resources did not affect FCL, even when we separated food webs according to respective community-wide dietary proportions. By doing so, we attempted to take into account that POM-fueled food chains may be more sensitive to changes in POM availability and similarly those fueled by biofilms. Post (2002) pointed out that the positive effect of resource availability on FCL remains uncertain in natural ecosystems and showed that resource availability affects FCL only at extremely low resource levels (between 1 and 100 g C m⁻² y⁻¹). Because all our study sites, even the most productive ones, were within this range, this may explain why we found no effect of resource availability on FCL here. Further, biofilm standing crops were slightly negatively affected by flooding frequency in our system, suggesting that some of effects of organic resources on FCL may have been confounded. Another potential explanation for the lack of relationship between productivity and FCL could be that biofilm and POM biomass did not accurately represent productivity levels. Other studies in freshwater used these metrics (Thompson and Townsend 2004, Warfe et al. 2013, Ruhi et al. 2017) and we argue that these were the most adequate to properly capture the gradient of productivity within the floodplain, compared to alternatives such as nutrient

content or primary invertebrate consumer biomass (McHugh et al. 2010). First, nutrient content is unlikely to accurately describe productivity in this floodplain, because rapid fluctuations in nutrient concentrations with inundation may not necessarily lead to higher resource availability (Amoros and Bornette 2002, Ahearn et al. 2006). In addition, several encountered invertebrate taxa (e.g. leuctra, tipulidae) are known to feed primarily on allochthonous leaf litter, thus for these, nutrient concentrations would not accurately describe available resources. Second, using the biomass of primary consumers as a proxy for productivity may also lead to equivocal results, given other factors such as environmental filtering or biotic interactions may greatly affect abundances of macroinvertebrates. Finally, we deliberately discarded phytoplankton as a measure of productivity in this system after having found no evidence of planktonic primary production in a previous field campaign. This lack of planktonic production was somewhat expected from the overall low nutrient contents and limited water residence time in these parafluvial habitats. Indeed, despite their apparent isolation, all habitats had a slow flow of water. In addition, given that macroinvertebrates here were primarily benthic, it is unlikely that phytoplankton would constitute a useable resource.

Considering the very slow current velocities and the fact that both POM and biofilm were collected from the benthos, there was a risk for these two basal resources to be confounded. Specifically, biofilm could grow on the POM and fragments of POM could be deposited on the biofilm. But here the $\delta^{13}\text{C}$ values of these two sources were well separated (Table S2, Supporting Information), with $\delta^{13}\text{C}$ of POM averaging -29.5 ± 1.5 and with little variability between habitats as expected from allochthonous material, and $\delta^{13}\text{C}$ of periphyton more variable amongst habitats, likely as a result of different hydrologies (Finlay 2001). One limitation of our study though is that we only used AFDM to quantify biofilm standing stock. Here, a quantification of chlorophyll a concentration would refine the estimation of basal resource availability, by differentiating between living and dead algae which may contribute to invertebrate diet in different proportions.

In floodplain systems, Saigo et al. (2015) and Warfe et al. (2013) found little support for the three scenarios of environmental control examined in this study. These studies were completed in large river-floodplain systems where top predators were fish, and where long-lasting seasonal inundation periods enabled them to disperse between floodplain habitats, potentially dampening local controls on FCL (Saigo et al. 2015). In a sub-alpine alluvial floodplain like the Maggia system, floods are episodic, rarely lasting more than a day, and act as disturbances on aquatic ecosystems (Amoros and Bornette 2002, Opperman et al. 2010). This difference makes it difficult to directly compare our results with these two studies of FCL in floodplains, along with the fact that top predators in our ponds were invertebrates.

Trophic omnivory from predators drive changes in FCL

The changes in FCL along the disturbance gradient are likely the result of trophic omnivory from predators, an observation arising from two main lines of evidence.

First, we showed that the identity of the top predator did not vary markedly along the gradients of flooding frequency and time since last flood. This is an indication that shorter food chains in more disturbed habitats were not the result of differing feeding preferences by specific top predators. Although some taxa occupied the highest trophic position only in specific environments (e.g. Dytiscidae and low flooding frequency), this could not explain the observed pattern in FCL because most other taxa could occupy the highest trophic position in most environments. In addition, we found that the average trophic position across all predatory taxa was negatively affected by flooding frequency and positively affected by the time since last flood, similarly to FCL. This is a strong indication that the observed reduction in FCL with increasing disturbance levels would occur irrespective of the identity of the top predator.

Second, flooding frequency and time since last flood, the two drivers of changes in FCL, had no significant effect on the structure and composition of consumer and predator

assemblages. This suggests that changes in FCL were largely independent of taxonomic changes along disturbance gradients, and thus that neither insertion nor addition mechanisms were responsible for observed changes in FCL (Ruhi et al. 2016), thus rejecting H₂. This finding was further supported by the lack of correlation between taxa richness and FCL, showing that shorter food chains did not include significantly fewer species. Since FCL can only vary with insertion or deletion of species, or changes in trophic position of predators, this strongly suggests that trophic omnivory may be the mechanism driving changes in FCL in this floodplain. Although there was no significant species turnover and difference in the structure of predator and primary consumer assemblages (abundances) along the disturbance gradients, previous study in this system showed that the relative abundance of some taxa changed with disturbance levels (Chanut et al. 2019). Specifically, the authors showed that the proportion of Coleoptera and Diptera were higher in rarely flooded communities whereas the proportion of EPT taxa was higher in frequently flooded habitats.

Considering the absence of species turnover or changes in top predator identity along the disturbance gradient, the lack of relationship between taxa richness and FCL, the slight changes in species abundances along disturbance gradient, and the generalized decrease in trophic position of the predator assemblage, it seems likely that trophic omnivory from predators drove changes in FCL. Specifically, it is likely that predators were “forced” to feed lower down the food chain because prey availability in higher trophic levels was lower after flooding and in frequently flooded habitats. The effect of flooding frequency suggests that frequent flooding did not allow for rapid development of resources higher up the food chain, irrespective of the time since last flood. We cannot entirely rule out the potential effect of biofilm resource availability on trophic omnivory because it was weakly negatively correlated to flooding frequency and thus effects may be confounded.

McHugh et al. (2010) and Ruhi et al. (2016) also found that both fish and invertebrate predators fed at lower trophic levels when the level of hydrological disturbance increased in

streams. The fact that predator trophic position also increased with availability of POM, although it did not affect the structure or composition, of assemblages suggests that predators were able to feed at higher trophic levels in POM-rich habitats irrespective of their disturbance regime. However, this effect was not strong or consistent enough among predators to result in food chain lengthening in this study.

Omnivory is ubiquitous in freshwaters, and in highly disturbed environments because consumers can shift their diet when resource availability varies (Fagan 1997, in Wootton 2017). Empirical studies have shown that intermediate levels of trophic omnivory increase food-web stability (Denno and Fagan 2003, Thompson et al. 2012), and may therefore be “selected for” in highly disturbed environments. Because feeding at lower trophic levels often entails feeding on lower-quality resources (France 2012), it is likely that predators only shift their diet under necessity. This necessity may arise when environmental constraints shift the biomass distribution in the food chain towards a top-heavy distribution, when predators first recolonize after a flood for instance (Ward et al. 2017). If predators cannot disperse in search of higher-quality resources (Warfe et al. 2013), omnivory may act as a stabilizing force because predators must resort to feeding lower down the food chain. This shift in feeding releases primary consumers higher up the food chain from strong predation (Diehl 2003, Diehl and Feissel 2001). In contrast, stronger trophic interactions may result in the loss of consumers when strong predation adds to environmental constraints (Wootton 2017).

Moderate levels of omnivory can act as a stabilizing force on communities (Emmerson and Yearsley 2004, Gellner and McCann 2012, Ward et al. 2017). Therefore, understanding conditions in which the stabilizing effect of omnivory arises is key to understanding the response of food webs and communities to environmental change (Kratina et al. 2012, Wootton 2017). It is well documented that restoring variable flow regimes results in higher biodiversity in floodplains (Amoros and Bornette 2002, Opperman et al. 2010) because it maintains a dynamic habitat mosaic. We suggest that because predators feed on different

resources depending on the disturbance regime, maintaining the spatial heterogeneity in disturbance within a floodplain can result in overall weaker trophic interactions between predators and consumers. This, in effect, could increase the stability of the food web at the floodplain scale (Bellmore et al. 2015). Additionally, by shifting their diets, omnivorous predators may enable depleted consumer populations to better recover from environmental disturbance, resulting in the same stabilizing effect in time (Singer and Bernays 2003, Abrams and Fung 2010, Wootton 2017). We suggest that with spatially heterogeneous disturbance such as flooding, trophic omnivory causes the strength of trophic interactions between predators and consumers to vary among habitats, acting as spatial insurance (Loreau et al. 2003) where local populations of consumers are rescued from local extirpation by dispersal from other habitats where predatory pressure is diminished. Overall, maintaining the spatial mosaic of disturbance levels in floodplains thus should result in greater gamma diversity. We suggest that examining trophic omnivory in floodplains and its effect as a stabilizing force both within habitats at the community level and also at the landscape scale would be useful towards conserving these complex, threatened ecosystems.

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Conflicts of interest

The authors declare no conflict of interest.

Data availability statement

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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778

779 Table 1. List of primary consumer taxa that occupy the lowest trophic position at least once,
780 and proportions of habitats where they occupy the lowest trophic position.
781
782

Taxa	Frequency
Tanytarsini	2.0 %
Corixidae	57.1 %
Elmidae	6.1 %
Ephemerella	2.0 %
Habrolepoides	2.0 %
Haliplidae	6.1 %
Ecdyonurus	2.0 %
Hydropsyche	2.0 %
Hydroptilidae	6.1 %
Leuctra	2.0 %
Tipulidae	12.2 %

Table 2. List of predatory taxa (according to Tachet 2010) and proportions of habitats where they occupy the maximum trophic position.

Taxa	Frequency
Atherix	16.3 %
Chloroperla	10.2 %
Dytiscidae	4.1 %
Isoperla	10.2%
Hexatomini	34.7 %
Perla	2.0 %
Rhyaccophila SS	6.1 %
Tanypodinae	16.3%

Table 3. Results of the backward model selection performed on the distance-based redundancy analysis model testing the effect of putative FCL drivers on the similarity of predator and consumer assemblages (based on Jaccard's distance).

<i>Response</i>	<i>Driver</i>	<i>AICc</i>	<i>F</i>	<i>p</i>	<i>Proportion of variation explained</i>
<i>Predators</i>	Habitat size	183.11	1.074	0.35	0.174
	POM	183.28	0.913	0.41	
	Biofilm	183.88	0.356	0.89	
	Time since last flood	184.02	0.226	0.97	
	Flooding frequency	184.09	0.154	0.98	
<i>Consumers</i>	Time since last flood	238.41	1.576	0.06	0.219
	Biofilm	238.43	1.559	0.08	
	Flooding frequency	238.5	1.485	0.11	
	POM	238.59	1.404	0.13	
	Habitat size	238.83	1.177	0.35	

List of Figures

Figure 1. Map of Switzerland showing the location of the Maggia River floodplain and the parafluvial habitats sampled (24 habitats).

Figure 2. Plots showing the effects of the time since last flood (a), flooding frequency (b) habitat size (c), biofilm standing crop (d) and particulate organic matter (POM) (e) on food chain length (FCL). Plots (a) and (b) also show the significant linear relationships calculated with generalized linear mixed models (GLMMs).

Figure 3. GLMM plot showing the effect of taxa richness on food chain length (FCL).

Figure 1.

Figure 2.

Figure 3.