Beaver effects on macroinvertebrate assemblages in two streams with contrasting morphology

C.T. Robinson, P. Schweizer, A. Larsen, C.J. Schubert, A.R. Siebers

Aquatic Ecology, Eawag, 8600 Dübendorf, Switzerland
Institute of Integrative Biology, ETH-Zürich, 8092 Zürich, Switzerland
Soil Geography and Landscape group, Wageningen University, Droevendaalsesteeg 3, 6708 PB Wageningen, The Netherlands
Surface Waters, Eawag, 6047 Kastanienbaum, Switzerland

HIGHLIGHTS

• This study compared macroinvertebrates at two beaver complexes with contrasting topography over an annual cycle.
• Both complexes showed strong seasonality in physico-chemistry, but retention of nutrients (N, P) was highest in summer.
• Complexes, although different, showed seasonality in macroinvertebrate assemblages. Lentic taxa were common in beaver ponds.
• Seasonal dietary shifts occurred in spring/summer among sites at both complexes (autochthony increasing downstream).
• We conclude that topography can influence beaver effects on fluvial systems and resident biota in agricultural landscapes.

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ABSTRACT

Beaver populations are increasing throughout Europe and especially in Switzerland. Beaver are major ecological engineers of fluvial systems, dramatically influencing river morphology, ecohydrology and, consequently, aquatic and terrestrial biota. This study compared macroinvertebrate assemblages and trophic structure at two beaver complexes with contrasting topography in Switzerland over an annual cycle. One complex (Marthalen) was in a low gradient open basin, whereas the other complex (Flaach) flowed through a higher gradient ravine-like basin. Both complexes were embedded in an overall agricultural landscape matrix. Water physico-chemistry differed between the two complexes with nitrogen, phosphorus, and DOC being higher at Marthalen than at Flaach. Both complexes showed strong seasonality in physico-chemistry, but retention of nutrients (N, P) was highest in summer and only at Marthalen. Both complexes also showed strong seasonality in macroinvertebrate assemblages, although assemblages differed substantially between complexes. At Marthalen, macroinvertebrate assemblages were predominantly lentic in character at ‘pool’ sites within the complex. At Flaach, lotic macroinvertebrate assemblages were common at most sites with some lentic taxa also being present. Dietary shifts based on carbon/nitrogen stable isotopes occurred in spring and summer among sites at both complexes (autochthonous resource use increasing over allochthonous resource use downstream), although being most...
1. Introduction

Beaver (Castor fiber) populations are increasing throughout Europe (Stocker, 1985), being especially evident in Switzerland over the last decade (Larsen et al., 2020). The fluvial landscape in which beaver are now colonizing has changed tremendously over hundreds of years because of human land-use changes (Butler, 2006; Persico and Meyer, 2013). Today, many of the aquatic habitats available for beaver are embedded in an agricultural-urban matrix with patches of managed woodlands. This close proximity to human-dominated spaces enhances the risk of conflict but also harbors the potential for creative ecosystem management of fluvial networks. Beaver are keystone species in terms of ecological engineering and beaver activities can be used to mitigate anthropogenic impacts of streams in human-dominated landscapes (Pollock et al., 2003; Burchsted et al., 2010).

Streams in agricultural landscapes are designed for drainage, typically channelized with minimal riparian coverage, essentially decoupling the hydrological connectivity with lateral areas and local groundwaters (Allan, 2004). Through the building of dams, beaver increase water tables, retain sediments and organic matter, and increase the hydrological connectivity of streams with adjacent lands (Westbrook et al., 2006; Hood and Larson, 2015; Wegener et al., 2017). Beaver activities also are known to increase the overall biodiversity and secondary production of aquatic macroinvertebrates (McDowell and Naiman, 1986; Wright et al., 2002; Wright, 2009). Although there is much knowledge on the ecology of beaver (Morgan, 1868; Naiman et al., 1988), the engineering effects and ecological responses in agricultural streams is poorly understood. Because of their relatively recent increase in population size, the question remains as to whether beaver have similar eco-hydrological effects in agricultural landscapes (e.g., Law et al., 2016), especially in terms of enhancing aquatic biodiversity, a common restoration goal.

The building of beaver dams along streams typically increases the area of lentic habitat, often modifying riparian areas into productive wetlands (Cunningham et al., 2006; Westbrook et al., 2011; Hood and Larson, 2015). The inclusion of wetlands along stream corridors alters the seasonal inputs and storage of organic matter (carbon) and other organic constituents (nutrients) in the aquatic realm (Catalan et al., 2017; Larsen et al., 2020). Along with changes in coarse habitat properties (juxtaposition of lentic and lotic habitats) that influence the distribution and abundance of macroinvertebrates (Margolis et al., 2001b, McCaffrey and Eby, 2016), alterations in organic resources should be reflected in the diets of secondary consumers. For instance, the proportion of terrestrial (allochthonous) and aquatic (autochthonous) carbon resources should differ along beaver complexes, being especially evident between flowing waters upstream and wetland areas associated with beaver ponds (Wohl, 2013). Primary production by aquatic plants is notably high in wetlands and this carbon source is likely transferred to streams below beaver complexes and incorporated into food webs (e.g., Bledzki et al., 2011; Wegener et al., 2017; Larsen et al., 2020). Although the functional feeding groups of macroinvertebrates have been linked to changes in habitat properties, e.g., high shredder abundance in pond areas (Law et al., 2016; Washko et al., 2020), essentially nothing is known on the carbon transfer of organic resources associated with beaver complexes.

The primary goal of the study was to compare the effects of beaver activity on macroinvertebrate assemblages and trophic structure in two streams embedded in an agricultural landscape. One stream (Marthalen) flowed through a relatively flat landscape while the other (Flaach) flowed in a more confined valley. First, we predicted the effects of beaver activity would be more pronounced in Marthalen because hydrological connectivity would be higher and water residence time longer than in the more confined stream. Pond development would be more extensive and wetland in character at Marthalen than at Flaach, thereby providing more habitat for lentic macroinvertebrates. Second, we predicted the trophic structure, i.e., consumer diets, to change along each complex in relation to shifts in aquatic versus terrestrial sources of organic matter. Lastly, we predicted both systems would display strong seasonality in consumer diets in line with seasonal changes in assemblage structure and organic matter inputs.

2. Study sites

The study took place at two beaver complexes in canton Zurich near Marthalen (47°36′N, 8°37′E) and Flaach (47°33′N, 8°36′E), Switzerland (Fig. 1). Beaver have been present in both systems since 2008, and both complexes had multiple dams. The beaver complex at Marthalen had a beaver lodge, whereas the beaver used the banks for housing at Flaach. The beaver complex at Marthalen was in a nationally-protected oak forest with the stream draining into the river Thur. Five sites were located at Marthalen, one in the stream above the beaver complex, 3 within the beaver complex, and one in the stream below the complex (Fig. 1). The three sites in the complex were located at the upper, middle and lower sections of the complex. The upper site was in a flooded oak forest (site Oak), the middle site was in an active pond area with a beaver lodge in the vicinity (site Pond), and the lower site was in a flooded pine forest (site Pine). The complex was considered swamp-like as the area had a low gradient (<1%) and the flooded areas were quite extensive (>30 m in width) relative to the Flaach complex (max width of 10 m). The beaver complex near Flaach was situated in an agricultural area with the stream (Langwiesenbach) draining into the river Rhein. Six sites were located along the Flaach complex, one in the stream above the complex, 4 within the complex (two in pond areas and two in stream sections between ponds), and one downstream of the complex. The Flaach complex flowed through a confined ravine-like system between agricultural fields that limited the lateral influence of the ponds. The overall gradient was steeper than Marthalen, averaging ca. 2%. The upper and lower stream sites in both systems had widths ranging from 1.6 to 3.5 m with water depths typically ~20 cm. The fluvial stretches used at both locations were ca. 0.7–1.0 km long between the upper and lower stream sites.

3. Methods

Sites were sampled in spring (April 2018), summer (July 2018) and winter (January 2019) to characterize the seasonality in physicochemistry and macroinvertebrate assemblages present at the different sites. At each site and date, a water sample was collected in a 0.5-liter plastic bottle (triple rinsed, no headspace) for water chemistry analysis in the laboratory. Water samples were analyzed for pH, alkalinity, nitrate, nitrite, total nitrogen, sulfate, ortho-phosphate, total phosphorous, dissolved organic carbon (DOC), total organic carbon (TOC), and total inorganic carbon (TIC) following methods detailed in Tockner et al. (1997). Spot measures of electrical conductivity (WTW LF330...
conductivity meter, Germany), turbidity (NTUs, Cosmos Ag, Switzerland), temperature and dissolved oxygen (Hach-Lange LD0101, Germany) were taken in the field on each sampling date using portable meters. Widths (n = 5 transects), depths (10/transect = 50) and mid-depth velocities (10/transect = 50) were recorded at each site as well.

Five stones were collected from the streambed to assess biofilm development at each site on each date. Stones were scrubbed with a metal brush and an aliquot of the slurry filtered through a glass fiber filter (Whatman GF/F), dried at 60 °C, weighed, combusted at 500 °C for 3 h, and reweighed for determination of ash-free dry mass of the biofilm. Macroinvertebrates were collected using a semi-quantitative sweep method with a standard kick-net (250-μm mesh). Kick-net samples were collected for a standardized time (3 min total) in the various habitats found at each site by disturbing the stream bottom and sweeping the area for macroinvertebrates. Samples for a site were composited and stored in 70% ethanol for later analysis in the laboratory. In the laboratory, large visible macroinvertebrates were initially handpicked from each sample for 30 min, then the sample was subdivided (usually into 6 subsamples) and a total of 300 or more invertebrates were handpicked from a subsample using a dissecting microscope at 10× magnification. Additional subsamples were handpicked until 300 or more individuals were collected. This technique allowed for determining the taxonomic richness at a site as well as taxa abundances. Macroinvertebrates were identified to at least family level using Tachet et al. (2010) and counted.

The benthic trophic structure at each site and date was determined using stable isotopes of carbon (δ13C) and nitrogen (δ15N). Here, separate sweep samples were used to collect macroinvertebrates at a site. Specific habitats also were searched by hand to collect macroinvertebrates (e.g., those attached to stone and wood substrates). Macroinvertebrates were sorted in the field and returned to the lab in falcon tubes (50 ml) alive for storage overnight at 4 °C to evacuate guts. Further, riparian beetles and spiders were collected for isotope analysis. The following day, macroinvertebrates were identified to family or genus (Tachet et al., 2010) and stored at −20 °C until analysis. Basal organic resources collected included wood, macroalgae, CPOM, FPOM, biofilm and riparian plants, and were stored at −20 °C until analysis.

Basal organic resources used for isotope analysis were dried at 60 °C, homogenized using a typical coffee grinder, carbonates removed by acidification with 10 ml 1 M HCL, samples redried at 60 °C, and then aliquots of 0.8–1.5 mg placed into tin capsules for isotope analysis. Individual 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., Manchester, U.K.) for measures of total C content, total N content, δ13C and δ15N. International isotopic reference materials for δ13C and δ15N were NBS 19, L-SVEC, IAEA-N-1 and IAEA-N-2. Analytical uncertainty was 0.2‰ for δ13C and 0.3‰ for δ15N.

3.1. Data analysis

Data from the physico-chemical samples were log(x + 1) transformed (except pH) and then analyzed using Principal Components Analysis (PCA). The PCA was used to illustrate seasonal changes within and between the two locations with sites acting as replicates. Nutrients (N, P) were examined for differences between upper and lower stream sites at each location with the expectation that both nutrients would be taken up within the beaver complexes and thus have lower values at downstream sites relative to upstream sites. As we were primarily interested in whether lentic taxa became prevalent within the beaver complexes, macroinvertebrates were analyzed at the family and order level using non-metric multidimensional scaling (nMDS) and Bray-Curtis dissimilarities with the Vegan package in R 3.4.2 (R Core Team, 2017). The nMDS grouping results (site and season) were then tested with PERMANOVA using the ‘adonis’ function in Vegan.

The trophic structure of macroinvertebrates was analyzed using stable isotope analysis. Initially, we tested whether consumer isotope values were suitable for use with stable isotope mixing models using the Monte Carlo simulation of the possible range of isotopic mixing models developed by Smith et al. (2013). A total of 1500 iterations were performed, with sources corrected by ranges for trophic enrichment factors (TEF): for δ13C, 0.4 ± 0.3, and for δ15N, 2.2 ± 0.3 (Post, 2002; McCutchan et al., 2003). Samples were excluded from further analysis when they fell outside the 95% confidence bounds indicating suitability for mixing model analysis (Smith et al., 2013; Philips et al., 2014). The Bayesian mixing model SIAR in R 3.4.2 (R Core Team, 2017) was used to examine probability distributions of dietary contributions of basal resources to primary and secondary consumers (Parnell et al., 2010). Aquatic producer (filamentous algae, biofilm) δ13C and δ15N values were not different from each other at either site (ANOVA; p = 0.37 to 0.58). Consequently, we pooled these resources into a single “aquatic OM” source (Philips et al., 2005). Terrestrial OM (wood, bark, leaves) δ13C and δ15N values did not vary across seasons.
(p = 0.19 to 0.99). Models were thus restricted to two basal resources (terrestrial OM and aquatic OM) and run using uninformative generalist priors (Fry, 2013; Brett, 2014). We ran separate models for each season within each river system. Aquatic OM δ13C and δ15N values were set at averages and standard deviations for each season within each river system. Terrestrial OM δ13C and δ15N values were set at averages and standard deviations for each river system across all seasons. We did not include additional prior information on diet proportions because sources in each mixing model were equal to the number of tracers (Fry, 2013; Brett, 2014). Trophic enrichment factors were set at 0.4 ±

4. Results

4.1. Physico-chemistry among sites and seasons

The principal components analysis of measured physico-chemical parameters clearly separated the two locations (Marthalen and Flaach) along axis-1 (Fig. 2). PCA axis-1 explained 39% of the variation in the data and was best determined by values of phosphorous (P), nitrogen (N) and total organic carbon (TOC) (factor loadings >0.70). The grouping of sites along PCA axis-1 indicated the stream at Marthalen had higher levels of P, N and TOC than the Flaach stream. PCA axis-2 explained 17% of the variation in the data and clearly distinguished the seasonality in physico-chemistry at both locations (Fig. 2). PCA axis-2 was best determined by values of temperature, electrical conductivity, and turbidity. Here, winter was more separated from spring and summer at both locations with lower values of temperature and turbidity, and higher electrical conductivity. Temperature and turbidity were higher, and conductivity lower, in spring than summer at Marthalen, whereas these values were opposite in Flaach for spring and summer (Fig. 2).

We evaluated the expectation of nitrate and phosphorous to be retained in the beaver complexes by comparing values at the upper and lower stream sites across seasons (Fig. 3). As the PCA results indicated, values of N and P, in particular, were higher in general at Marthalen than Flaach. Further, the retention of N and P clearly differed between locations and seasons. Retention of N and P was highest in summer at Marthalen with some retention evident in spring and no retention in winter. At Flaach, in contrast, some retention of N, but not P, was evident in summer with no retention of N or P observed in spring or winter (Fig. 3).

4.2. Macroinvertebrate assemblages among sites and seasons

Results of the nMDS analysis (stress = 0.22) clearly showed that macroinvertebrate assemblages differed among seasons at both locations along axis-1 (Fig. 4a, b). PERMANOVA indicated significant differences among seasons (PERMANOVA: p < 0.001, R2 = 0.21). Along axis-1, winter was situated on the left side of the plot, spring in the center, and summer on the right for both locations. Lotic taxa, e.g. baetids, elmids, simuliids, dominated the left side of the nMDS plot, whereas lentic taxa, e.g. pond snails, pond beetles, pond trichopterans, were more prevalent on the right side (Fig. 4b). At Marthalen, winter assemblages were clearly separated along axis-1 from spring and summer assemblages, whereas spring and summer assemblages overlapped in structure. In contrast, assemblages were clearly separated across all seasons at Flaach with no overlap in structure being observed. Axis-2 of the nMDS illustrated the variation among sites at each location in each season (Fig. 4a). Both locations showed similar and high range in values along axis-2 in all seasons, suggesting sites differed in assemblage structure within each season.

Scatterplots of nMDS site scores within each complex and season clearly distinguished sites based on assemblage structure and were found significant using PERMANOVA (p < 0.001, R2 = 0.43) (Fig. 5). Sites at Marthalen grouped well in the nMDS scatterplot with the upper and lower stream sites typically separate from the more lentic sites in each season (Fig. 5a–c). The more lentic sites (oak, pond, pine) grouped together within each season, although still demonstrating some site differences in assemblage structure within a season. Further, specific sites showed differences among seasons, being especially evident at the pond and pine sites. Here, pine site shifted mostly along axis-1 among seasons, whereas pond site altered positions mostly along axis-2. In contrast, the oak site was typically on the right of the plot along axis-1 and central along axis-2. These results indicate that pond and pine sites were mostly lentic in assemblage structure, while oak had a mixture of lotic and lentic taxa present in most seasons (compare taxa in Fig. 4b).

The Flaach sites were mostly separated along axis-2 in spring and winter in the nMDS scatterplot (Fig. 5d–f), whereas assemblages in these seasons were a mix of lentic and lotic taxa along axis–1. Sites F1 and F4 (upper and lower stream sites) as well as site F5 and F6 (pool sites) were grouped together (F1 and F4 in the middle of the nMDS
plot, F5 and F6 in the upper section of the plot). The center of the nMDS plot was mostly lotic in assemblage structure, whereas the upper plot was mostly lentic in assemblage structure (see taxa distribution in Fig. 4b). Sites F2 and F3 (streams between pools) also mostly grouped together in spring and winter (Fig. 5d,f). These sites grouped with sites F1 and F4 in spring but not in winter where they showed a predominance of Valvatidae.

4.3. Consumer diet structure based on stable isotopes

We estimated the dietary proportions of allochthonous (terrestrial-based) or autochthonous (aquatic based) organic resources for macroinvertebrate consumers at the different sites at each complex across seasons. At Marthalen, there was a strong dietary shift to a predominantly autochthonous diet at sites lower (more downstream) in the complex in spring and summer, being particularly evident from sites Pond to the lower stream site (Fig. 6a–c). In these seasons, autochthonous resources contributed upwards of 80% to the diets of primary consumers. No dietary shift among sites was evident at Marthalen in winter where aquatic resources contributed on average ca. 60% to consumer diets at the different sites (Fig. 6c). To note here is that allochthonous resource use increased at the lower sites from <20% of the diets in spring and summer to ca. 40% in winter.

At Flach, autochthonous resources contributed a greater proportion to consumer diets in spring and summer (between 60 and 80% on average), whereas allochthonous resources played a greater role in winter, contributing on average ca. 60% to consumer diets (Fig. 6d–f). In spring, autochthonous contributions to consumer diets increased from the upper stream site (55%) to sites within the complex (ca. 70% or more), but decreased again to ca. 60% at the downstream site (Fig. 6d). Allochthonous resource use decreased through the complex at Flach in summer, from ca. 50% at the upper sites to ca. 30% at the lower stream site (Fig. 6e).

5. Discussion

This study compared the influence of beaver activity on macroinvertebrate assemblages in two contrasting fluvial systems. One system flowed through a relatively flat agricultural landscape (Marthalen), whereas the other system flowed through a ravine-like basin embedded in an agricultural landscape (Flach). We found the engineering effects of beaver to be more pronounced in the system flowing through the low gradient agricultural landscape (Marthalen) because the lateral connectivity and water residence was greater than in the higher-gradient ravine-like system (Flach) (Larsen et al., 2020). We further found macroinvertebrate assemblages to reflect this difference in engineering activity with lentic taxa being more prevalent in Marthalen than Flach. Lastly, we found consumer diets also to reflect the hydro-morphological differences between basins that affected allochthonous versus autochthonous resource pools, again being more evident at Marthalen than Flach.

5.1. Beaver engineering effects on physico-chemistry

Both fluvial systems flowed through an overall agricultural landscape matrix with relatively high levels of nutrient (nitrogen, phosphorus) inputs. Measured values of nitrate were 4 mg/l or higher in both systems, whereas phosphorus was 4–6× higher in Marthalen than in Flach. Further, results showed that dissolved organic carbon also was greater at Marthalen than Flach. Nutrient and carbon resources differed between the systems but not among seasons within each system. Similar seasonal differences were found in each system in temperature, lowest in winter as would be expected, and electrical conductivity (highest in winter) and turbidity (lowest in winter). Seasonal changes in the latter two parameters likely reflected seasonal changes in flow in respect to seasonality in precipitation and lateral inputs from agricultural lands (Allan, 2004).

Through the engineering of beaver dams on streams, beaver increase water residence time, increase groundwater tables, and increase lateral hydrological connectivity (Naiman et al., 1988; Green and Westbrook, 2009; Larsen et al., 2020). In this context, we expected the beaver influence on ecohydrology to be greater at Marthalen than Flach as expressed in a higher retention of nitrogen and phosphorus at Marthalen. Water residence time should be greater at Marthalen because of the relatively flat landscape and enhanced lateral connectivity due to beaver dams and the various channels developed by beaver (Stocker, 1985). The confined, ravine character of the Flach complex minimized the lateral development of the fluvial network with dams, retaining waters within a primary channel built up with slow-flowing ponds behind beaver dams (Wegener et al., 2017; Puttock et al., 2018; Larsen et al., 2020). As expected, retention of nutrients was higher at Marthalen than Flach for both nitrate and phosphorous (see Fig. 3). However, this retention was evident only in the summer sample, with minor retention also occurring in spring at Marthalen. The lower phosphorus levels, concomitant with low water residence time, at Flach may have limited the nutrient retention capacity of that system. For instance, nitrate showed some retention in the summer sample at Flach, although levels were in a similar range as found at Marthalen. Margolis et al. (2001a) also noted strong seasonal differences in retention, being highest in summer. The greater potential water storage (lateral hydrological connectivity) at Marthalen than at Flach likely played a key
role in the contrasting retention of nutrients in each system (Johnston, 2001, Hood and Larson, 2015, Wegener et al. 2017, Larsen et al., 2020). Further efforts are warranted to fully quantify the retentive capacity of beaver complexes in a landscape context, especially in regards to seasonality. The results suggest that beavers through their engineering of dams can increase the retention of nutrients in agricultural landscapes, thus slowing the transport of nutrients downstream (Maret et al., 1987; Smith et al., 2020).

5.2. Beaver engineering effects on macroinvertebrate assemblages

Beavers are well-known ecological engineers (Ives, 1942; Naiman et al., 1988; Larsen et al., 2020), causing most streams to become more wetland in character. Consequently, alterations in fluvial habitat from strictly lotic to a mix of lotic and lentic ecotypes allows colonization by more lentic macroinvertebrates and those preferring slower waters in beaver modified fluvial systems (Law et al., 1987; Smith et al., 2020). The extent of habitat change reflects the hydrological alteration within the effected landscape, and thus the lentic habitat available for colonization by lentic macroinvertebrates. In a landscape context, beaver modified fluvial habitat in wide, flat landscapes such as at Marthalen will have more lentic habitats available than those in more confined valley landscapes such as at Flaach. Although both complexes were colonized by lentic macroinvertebrates, we found lentic taxa to be more prevalent at Marthalen than Flaach. More lentic taxa and at relatively high abundances included a variety of 'pond' snails (Physidae, Hydrobiidae, Planorbidae), numerous Odonata, the mayfly Serratella spp., Trichoptera, water beetles (Coleoptera) and Gerridae. Importantly, lentic taxa also occurred at Flaach, indicating beaver impoundments in confined valley landscapes also provide suitable habitat for lentic macroinvertebrates (see Washko et al., 2020). In both situations, the overall biodiversity of stream macroinvertebrates was greater in the presence of beaver complexes. Beavers increase the retention of nutrients in agricultural landscapes, thereby slowing the transport of nutrients downstream (Maret et al., 1987; Smith et al., 2020).

**Fig. 5.** Results of the nMDS analysis using the relative abundances of macroinvertebrates collected at the different sites each season at the two beaver complexes (M = Marthalen: plots a–c; F = Flaach: plots d–f). Data represent the site differences in each season within each complex (stress = 0.22).
of beaver as most lentic taxa would likely not have been present or low in abundance otherwise.

The nMDS results clearly separated sites within each complex in respect to habitats being lentic or lotic, suggesting coarse-scale habitat properties dictate assemblage structure along beaver complexes. This result emphasizes the degree of habitat differentiation caused by beaver activities in fluvial networks that ultimately cause differences in biotic assemblages along the spatial dimension (Margolis et al., 2001b; Strzelec et al., 2018). The ecological engineering of beaver in fluvial networks creates a heterogeneous habitat matrix in the landscape (Burchsted et al., 2010; Hood and Larson, 2015), allowing biota adapted to diverse aquatic habitats to colonize and maintain populations. The effects of beaver ponds on fish distribution and abundance are well-documented (Schlosser and Kallemeyn, 2000; Collen and Gibson, 2001) as well as those of macroinvertebrates (Anderson and Rosemond, 2007; Law et al., 2016; Strzelec et al., 2018). Lentic waterbodies along beaver complexes typically show lower richness but greater productivity than adjacent lotic systems, but the overall effect is higher biodiversity and greater cross-system subsidy in beaver complexes (Anderson and Rosemond, 2007; McCaffery and Eby, 2016). An important finding in our study is that a similar biological response was found for streams embedded in an agricultural landscape (also see Law et al., 2016). Law et al. (2016) document an increase in gamma diversity due to the compositional shift in macroinvertebrates inhabiting beaver-modified habitats in agricultural streams. These findings suggest that beaver could be used as a management tool to improve the ecological condition of agriculturally impacted streams, for not only retaining organic matter (carbon) and nutrients (Klotz, 2010, Larsen

![Graph of data showing assimilation by macroinvertebrate consumers.](image-url)
et al. 2020), but also enhancing the overall biological potential or biodiversity of such systems (see Burchsted et al., 2010 for similar ideas for forested headwaters).

Strong seasonal effects were found in macroinvertebrate assemblages at all sites in both complexes. The greatest change was observed between summer and winter, with spring assemblages situated intermediate in the nMDS scatterplot. This result was to be expected as macroinvertebrate life histories are strongly seasonal with some taxa more common in summer and others being more common in winter (e.g. so-called winter stonies) (Hynes, 1970, Resh and Rosenberg, 1984, Merritt et al., 2019). Other taxa have generation times longer than a year, e.g. long-lived predacious coleopterans, and are present in both seasons but likely in different life stages (Lancaster and Downes, 2013; Merritt et al., 2019). Of note, was the presence of large invertebrate predators (odonates, coleopterans) in the more lentic sites and in high abundances, especially in summer. Importantly, the results suggest that the heterogeneous habitat matrix along beaver complexes complement the life cycles of numerous aquatic macroinvertebrates, thereby sustaining biodiversity over time.

5.3. Beaver effects on macroinvertebrate consumer diets

The proportion of aquatic carbon resources in the diets of consumers increased through each complex, being most evident in summer (also spring at Marthalen). Beaver complexes have strong impacts on the geomorphology of fluvial networks (Larsen et al., 2020) with beaver ponds acting as major deposit basins, retaining sediment and organic matter (Levine and Meyer, 2014, 2019). Beaver ponds also inundate adjacent terrestrial areas, often killing trees while increasing the production of primary producers and secondary consumers (McCaffery and Eby, 2016). Both streams above the complexes had adjacent riparian buffer areas next to agricultural fields that limited light to the streams during summer. The beaver ponds opened the overhead canopy, allowing light for primary producers. High primary production was quite evident at Marthalen with the ponds being filled with various aquatic macrophytes (also see Law et al., 2016), whereas ponds at Flach were mostly open with emergent macrophytes mostly growing along pond margins (authors, personal observation). In fact, dissolved oxygen levels at Marthalen reached 14 mg/l oxygen (ca. 120% saturation) in summer, showing the system to be super-saturated. In contrast, oxygen levels were at normal stream values (ca. 12 mg/l, 100% saturation) at Flach in summer, reflecting the lower residence time of water at Flach.

The proportional use of aquatic carbon resources was higher than terrestrial carbon resources at all sites in both complexes in spring. Here, samples were collected before leaf out, thus all sites were open to sunlight allowing development of primary producers. Indeed, aquatic resources contributed over 60% of consumer diets in spring, even reaching over 80% at more downstream sites at Marthalen. The substantial increase of aquatic resource use at the lower sites at Marthalen in spring was likely linked to the consumption of decaying aquatic plants that died during winter or algae. The increase in aquatic resource use from upstream to downstream at Marthalen was evident in both spring and summer, but consumption dynamics probably differed between seasons; e.g., differential consumption of dead versus living plants. This latter aspect needs additional research to confirm and quantify. The increased hydrological connectivity along with longer water residence times in beaver complexes enhances the biological activity of carbon resources in the environment (Larsen et al., 2020), especially in wetland habitats associated with beaver complexes such as those at Marthalen.

In winter, the proportional use of aquatic and terrestrial carbon resources was essentially the same at around 40–60% and with no clear downstream trends. Further, terrestrial carbon resource use was greater at most sites at both complexes in winter than in spring or summer. The increase in terrestrial carbon use in winter was likely related to greater inputs of terrestrial organic matter in the form of dead leaves from upstream sources as both streams had developed riparian areas. Leaves are a major source of carbon to temperate forested streams during autumn leaf fall (Vannote et al., 1980). Another explanation may be the shift in macroinvertebrate assemblage structure at both complexes. In winter, assemblages were dominated by trichopterans and asellids, both are known feeders (shredders) of coarse particulate organic matter such as leaves (Merritt et al., 2019). The shift in consumer diets across seasons and sites likely represents both the changes in resources available concomitant with changes in assemblage structure related to life history dynamics. For instance, diets of consumers at the upstream sites at both complexes were similar across seasons, whereas major seasonal shifts in diets occurred at sites within each complex. Thus, the results suggest that beaver complexes can enhance both the spatial and temporal habitat heterogeneity in fluvial networks (see Larsen et al., 2020), with consequent effects on aquatic biodiversity.

6. Summary

Beaver populations are increasing globally, often entering fluvial networks currently impacted by extensive human development. This study examined the influence of beaver complexes in two contrasting streams flowing through an agricultural landscape. The results indicate that beaver positively influenced the biodiversity of both systems by increasing the spatial and temporal heterogeneity of aquatic habitats in the landscape. The relative degree of influence in each system was related to coarse-scale landscape structure that dictated the water residence time and potential lateral connectivity. Marthalen flowed through a more flat terrain than the Flach system, which flowed through a confined valley. The lateral hydrological connectivity was greater and water resident time slower at Marthalen than at Flach with consequent effects on geochemistry. The Marthalen complex also differed in biodiversity from that of Flach due to its greater terrestrial area, although lentic taxa colonized both systems. Lastly, beaver activity altered the proportions of aquatic versus terrestrial carbon resources in macroinvertebrate consumer diets, most likely through changes in aquatic habitat structure. The results of this study suggest that beaver can be used to improve streams in agricultural landscapes, but the expectations of improvement must be placed in a landscape context.

CRediT authorship contribution statement

C.T. Robinson: Methodology, Investigation, Writing - original draft. P. Schweizer: Methodology, Investigation, Writing - original draft. A. Larsen: Writing - original draft. C. Schubert: Writing - original draft. A.R. Siebers: Methodology, Investigation, Writing - original draft.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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