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Eurasian beaver activity increases water storage, attenuates flow and mitigates diffuse pollution from intensively-managed grasslands

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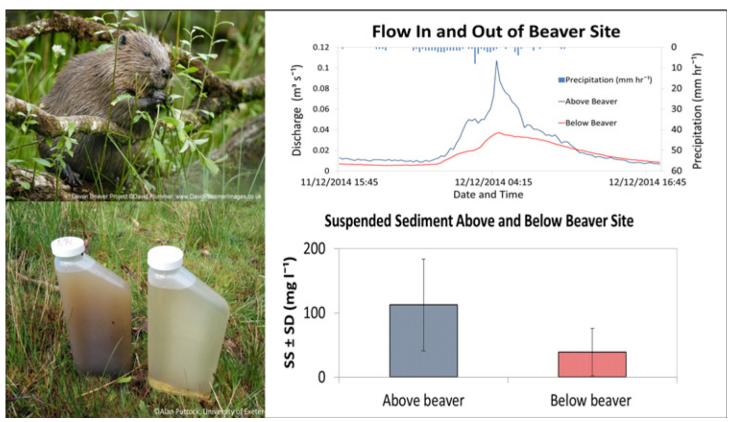
HIGHLIGHTS

- Beavers in wooded site, on first order tributary draining from agricultural land.
- Beaver activity has resulted in major changes to ecosystem structure at the site.
- Beaver activity increased water storage within site and attenuated flow.
- Reduced sediment, N and P, but more DOC in water leaving site.
- Important implications for nature based solutions to catchment management issues.

GRAPHICAL ABSTRACT



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ABSTRACT

Beavers are the archetypal keystone species, which can profoundly alter ecosystem structure and function through their ecosystem engineering activity, most notably the building of dams. This can have a major impact upon water resource management, flow regimes and water quality. Previous research has predominantly focused on the activities of North American beaver (*Castor canadensis*) located in very different environments, to the intensive lowland agricultural landscapes of the United Kingdom and elsewhere in Europe.

Two Eurasian beavers (*Castor fiber*) were introduced to a wooded site, situated on a first order tributary, draining from intensively managed grassland. The site was monitored to understand impacts upon water storage, flow regimes and water quality. Results indicated that beaver activity, primarily via the creation of 13 dams, has increased water storage within the site (holding ca. 1000 m^3 in beaver ponds) and beavers were likely to have had a significant flow attenuation impact, as determined from peak discharges (mean 30 ± 19% reduction), total discharges (mean 34 ± 9% reduction) and peak rainfall to peak discharge lag times (mean 29 ± 21% increase) during storm events. Event monitoring of water entering and leaving the site showed lower concentrations of suspended sediment, nitrogen and phosphate leaving the site (e.g. for suspended sediment; average entering site: 112 ± 72 mg l^{-1}, average leaving site: 39 ± 37 mg l^{-1}). Combined with attenuated flows, this resulted in lower diffuse pollutant loads in water downstream. Conversely, dissolved organic carbon concentrations and loads downstream were higher. These observed changes are argued to be directly attributable to beaver activity at the site which has created a diverse wetland environment, reducing downstream hydrological connectivity.

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Results have important implications for beaver reintroduction programs which may provide nature based solutions to the catchment-scale water resource management issues that are faced in agricultural landscapes.

1. Introduction

Beavers are widely referred to as ecosystem engineers (Hartman and Tornlov, 2006; Wright et al., 2002) as they modify river systems and surrounding riparian areas to create suitable habitat for themselves which subsequently benefits a wide range of other species. Beavers are also termed keystone species, having a disproportionately large impact upon fluvial ecosystems, relative to their abundance (McKinstry et al., 2001). The biggest hydrological impact of beavers results from their dam building ability and the consequent impoundment of large volumes of water in ponds (Butler and Malanson, 2005; Hood and Bayley, 2008). Dam and pond features can alter hydrological regimes, both locally and downstream (Burchsted and Daniels, 2014; Polvi and Wohl, 2012) whilst beavers also create bank side burrows, lodges, tunnels and canals to facilitate access to foraging areas (Gurnell, 1998). All of the aforementioned activities increase the structural heterogeneity of their environment (Rolauffs et al., 2001) having not only hydrological and geomorphological impacts, but creating a diverse range of habitats with significant (positive) biodiversity implications (Rosell et al., 2005).

Eurasian beavers (*Castor fiber*) were previously common across Europe including the UK. However, populations were greatly reduced by human activities, particularly over-hunting (Collen and Gibson, 2000), being effectively absent from the United Kingdom by the 16th Century (Conroy and Kitchener, 1996). Stimulated by the EC Habitats Directive, reintroduction programs have seen the re-establishment of Eurasian beaver colonies across northwest Europe (de Visscher et al., 2014), including Scotland (Jones and Campbell-Palmer, 2014). However, in England, there is currently only one known wild population, subject to a rigorous five year monitoring program (Natural England, 2015).

In addition to reported biodiversity benefits (Correll et al., 2000), it has been suggested that beavers could play a key role in the provision of environmental ecosystem services (EES) and as a nature based solution for the management of our river catchments (Brazier et al., 2016). Beaver dams can reduce channel flow velocity (Burchsted and Daniels, 2014) and attenuate storm event hydrographs (Nyssen et al., 2011) with positive impacts on flood risk alleviation (Collen and Gibson, 2000). During drier periods, increased water storage capacity (Hammerson, 1994) can help to maintain base flows, alleviating the risk of droughts downstream (Leidholt-Bruner et al., 1992). The altered flow regimes and water storage capacity also modify nutrient and chemical cycling in freshwater systems. Pond-dam complexes often act as sediment traps, storing fine sediments and nutrients which alter in-pond nutrient cycling (Klotz, 2007) supporting a positive effect on downstream water quality (Naiman et al., 1986).

Knowledge of how beavers impact on the environment and the role they may play in the provision of ecosystem services is vital to inform policy regarding both the reintroduction of *C. fiber* in the United Kingdom and the wider management of these animals in intensively-managed agricultural catchments worldwide (Burchsted and Daniels, 2014). However, much of the available research into the impacts of beavers focuses on the North American beaver (*C. Canadensis*) rather than the Eurasian beaver (*C. fiber*). Whilst there are behavioural similarities between the two species (Rosell et al., 2005), differences, particularly in the European landscape; with intensive agriculture and dense networks of infrastructure mean that their impacts cannot be presumed directly comparable with North American studies (Gurnell, 1998).

Therefore, to quantify the impacts of reintroducing the Eurasian beaver upon water storage, water quality and flow regimes this study addresses the following hypotheses:

H1. Beaver constructed features including dams, canals and burrows/lodges, significantly increase water storage within the landscape.

H2. Beaver dams significantly alter flow regimes resulting in attenuated storm flows.

H3. Beaver ponds act as sinks for diffuse pollutants, significantly improving water quality downstream.

2. Methods

2.1. Study site

Research was undertaken at the Devon Beaver Project controlled reintroduction site in Devon, South West England (DWT, 2013). The site is situated on a small first order stream in the headwaters of the River Tamar catchment, which is the only flow input to the site. Drainage ditches around the perimeter hydrologically isolate the site, ensuring that flow in can confidently be compared with flow out (also via one channel only). The site experiences a temperate climate with a mean annual temperature of 14 °C and mean annual rainfall of 918 mm (Met Office, 2015). In March 2011, a pair of Eurasian beavers was introduced to a 3 ha enclosure, dominated by mature willow and birch woodland, in addition to gorse scrub. Upstream, the site has a 20 ha contributing area dominated by grazed grassland. As illustrated in Fig. 1, beaver activity at the site has created a complex wetland environment, dominated by ponds, dams and an extensive canal network (DWT, 2013).

2.2. Experimental design, data collection and data analysis

2.2.1. Site structure and water storage

To quantify the spatial extent of surface water across this complex site, a combination of walkover, conventional ground-based surveys and unmanned aerial vehicle (UAV) surveys were undertaken. The walkover survey was undertaken prior to beaver reintroduction in 2010 as this was the best approach to survey the very densely vegetated site. The ground-based surveys utilised a Leica Total Station (TCR1205) to map the surface area of each pond and the average depth of each pond at the same time every year (March) from 2013, when seasonal reductions in vegetation cover allowed deployment of such hardware. Whilst being a highly complex site displaying a rapid and ongoing change, these data permitted an estimate of annual changes in both surface areas and pond volumes (area multiplied by mean of surveyed depth at 5–10 positons within the pond) to be made from 2013 to 2016. The UAV surveys were undertaken during the winters of 2014 and 2016 (See Puttock et al., 2015 for further details), to provide high-resolution ortho-mosaic images of the site (see Fig. 2). Winter flights were undertaken to minimise occlusion of the terrain and underlying pond structure by the deciduous vegetation canopy. Each pond (Fig. 2) was equipped with a dipwell at its deepest point to monitor water level from October 2014 onwards. Prior to these manual measurements of pond depths and bathymetry were made in parallel with annual total station surveys. Dipwells were instrumented with HOBO U20L pressure sensors (Onset, Bourne USA) with a 0–4 m range and 0.1% measurement accuracy (i.e. 4 mm measurement increments), recording data on a 15 min time step. Water level was calculated relative to atmospheric pressure recorded on site using HOBOware Pro 10.8 (Onset Bourne USA).

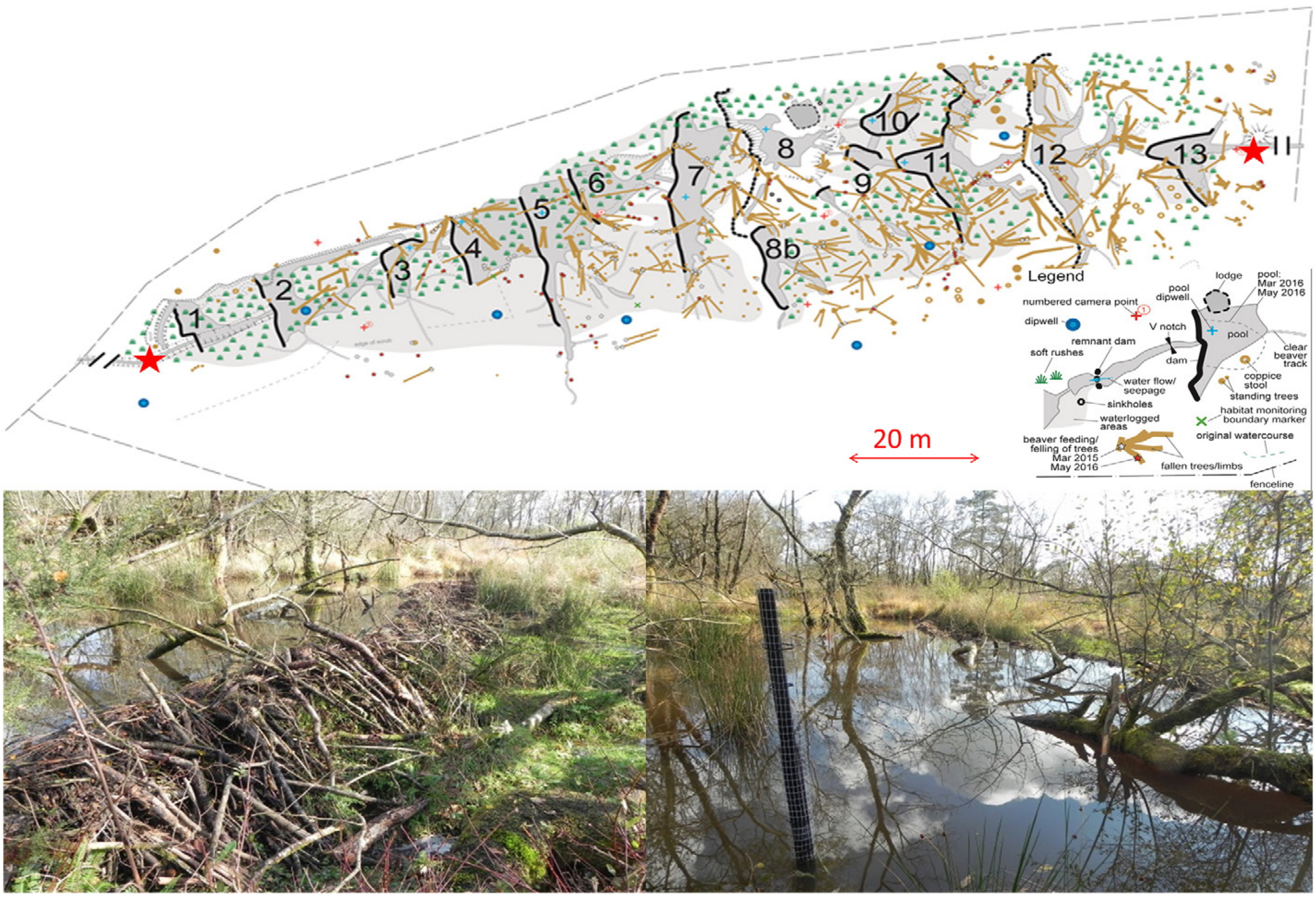

Fig. 1. Top: 2016 site schematic, reproduced with permission from SW Archaeology. Bottom: photos illustrating beaver created pond and dam structures. Bottom right pond illustrates a dipwell used to quantify change in water level over time. Images reproduced with permission from Devon Wildlife Trust. Red stars indicate location of Above Beaver (above pond 13) and Below Beaver (below pond 1) monitoring stations.

2.2.2. Flow

To understand the impact of beavers upon hydrological function (H1 and H2) flow in and out of the site was monitored to create a continuous record of discharge from October 2014 to January 2016. The Above Beaver (AB) and Below Beaver (BB) monitoring stations (Fig. 1) were equipped with a rated v-notch weir (60° angle) and stilling well. A depth to discharge relationship was calculated using the ISO (1980) and USBR (1197) recommended Kindsvater-Shen equation (Eq.1).

$$Q = 4.28\, C_e \tan\left(\frac{\theta}{2}\right)(H + k)^{5/2} \quad (1)$$

V-notch weir, depth to discharge calculation. Q = discharge ($L\ s^{-1}$); H = head on weir (cm); θ = angle in degrees; C_e and k are functions of θ (Kulin and Compton, 1975).

At each v-notch the stilling well was instrumented with an in-situ submersible pressure transducer (IMSL–GO100, Impress, United Kingdom). Rainfall was monitored using a tipping bucket rain gauge with 0.2 mm bucket size (RG1, Adcon Telemetry, Austria). All the above equipment connected to a 3G telemetry network (Adcon Telemetry, Austria), providing a live data feed of rainfall and water level/flow on a 15 min time step. Rainfall was recorded as a total for that 15 min time step whilst level was a mean value that could be converted to discharge (Eq. 1) to give an instantaneous discharge and multiplied by time (both for events and entire monitoring period) to calculate total discharge.

To characterise the flow regime at each site, event separation was undertaken on the rainfall and discharge data collected. This method was a modified version of that developed by Luscombe (2014) and as developed previously by Deasy et al. (2009); Glendell (2013). Briefly, the start of an event was identified as rainfall lasting longer than 15 min, with breaks <60 min. Baseflow was determined by discharge at the start of the event and the end point of the event was classified as the time at which baseflow returned to the pre-event level. The following event parameters were determined and are analysed herein: EP = Event Precipitation; Q_t = Total Event discharge; Q_p = maximum recorded event discharge; Q_{Lag} = time between peak rainfall and peak discharge. When considering the potential impacts of beaver activity upon storm flow and consequent flood risk downstream (H2), the largest events are of most interest. Therefore, the above hydrological analysis was repeated on a sub-set of the 20% largest events as determined by total event discharge entering the site.

2.2.3. Water quality

To determine water quality entering and leaving the site; an ISCO 3700 autosampler (Teledyne Isco, Lincoln, USA) was connected to each v-notch weir, allowing for flow-proportional sampling of water quality (each sample triggered by a 30 mm change in stage), with up to 24 samples during each storm hydrograph. A sampling campaign to determine the water quality of the catchment during rainstorm events was undertaken between 2014 and 2015, resulting in the collection of 226 water samples (across 11 events Above Beaver and 11 events

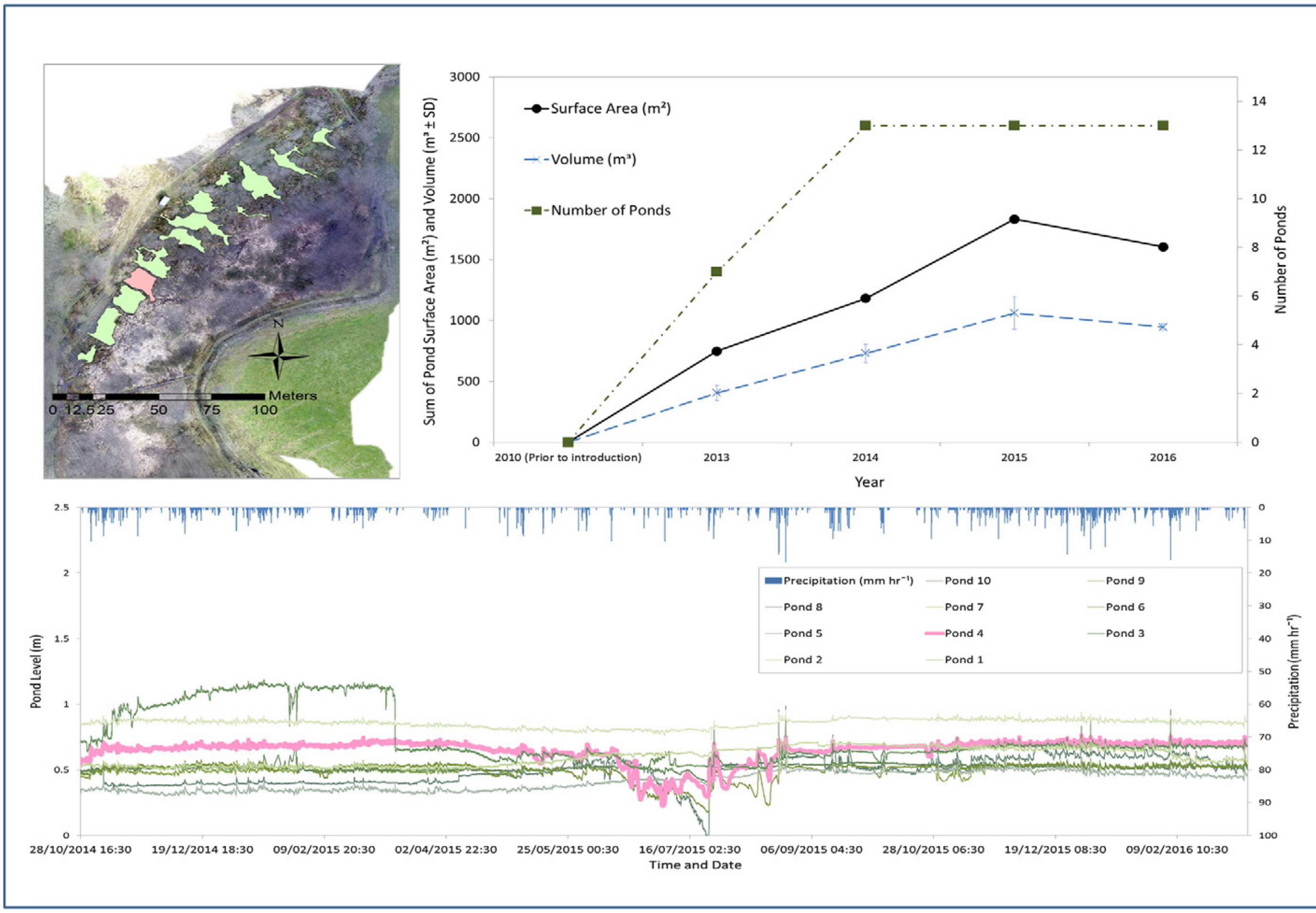

Fig. 2. Top left: UAV orthomosaic of site from 2016 with ponds digitised to illustrate surface water storage, pond coloured pink corresponds with Pond 4 level time series. Top right: graph illustrating change in (1) number of ponds since beaver introduction (green squares); (2) surface area of water in ponds (black circles) and (3) estimated volume of water storage (blue crosses). Bottom: Time series of level in ponds with Pond 4 highlighted and corresponding rainfall time series.

Below Beaver). Samples were retrieved within 24 h and transported back to the laboratory where they were stored in the dark at <4 °C prior to analysis.

Water quality samples were analysed for total oxidised nitrogen (TON), ortho-phosphate (PO_4), dissolved organic carbon (DOC) and pH within 48 h of sample collection (see Glendell (2013)) for relevant storage tests supporting such protocols). Total oxidised nitrogen and dissolved ortho-phosphate concentration were measured colourimetrically via a continuous flow auto-analyser 3 (Bran + Luebbe, Norderstedt, Germany) using Seal Analytical methods G-103-93 for PO_4 (SD 0.015 mg l^{-1}, detection limit 3 μg l^{-1}) and G-109-94 for TON (SD 0.007 mg l^{-1}, detection limit 6 μg l^{-1}). Following filtration, DOC concentration was analysed using a UV spectrometer with a 0–1000 mg l^{-1} range and detection limit (ProPS Trios Gmbh, Rastede, Germany) with a 10 or 20 mm path length at a spectral range of 190–360 nm (Grand-Clement et al., 2014). pH was measured relative to buffer solution standards of pH values 4 and 7 using an Accumet AB15/15 + pH meter (Fisher Scientific, UK) measured at a resolution of 0.01 pH. Total suspended sediment (SS) concentration was determined gravimetrically, by the mass of sediment per sample volume following evaporation. Following collection, each water sample was allowed to settle for 1 week. Without disturbing the sediment, most of the water sample was then decanted and measured. The remaining water and sediment was agitated, measured, poured into a pre-dried and weighed evaporating dish and placed in an oven (80 °C) until dried (Glendell, 2013). Instantaneous loads of relevant water quality variables were extrapolated for the event period sampled, using the Webb and Walling method (Clark et al., 2007; Glendell and Brazier, 2014; Walling and Webb, 1985) presented in Eq. (2).

$$F = K * Qr * \left(\sum_{i=1}^{n} Ci * Qi\right) / \left(\sum_{i=1}^{n} Qi\right) \quad (2)$$

where: F = is the total solute load for sampling period (g); K = time period over which the load occurred (seconds); Qr = mean discharge from a continuous record (m^3); Qi = instantaneous discharge ($m^3\ s^{-1}$); Ci = instantaneous concentration (mg l^{-1}); n = number of samples.

2.2.4. Statistical analysis

To determine if differences in water storage between survey years were significant (H1) a Mann-Kendall non-parametric test was used to determine whether there was significant ($p < 0.05$) change over time. Correlations between dipwell level and rainfall/season were tested using the non-parametric Spearman's rank correlation coefficient. For the event hydrological characteristics (H2) and measured water quality determinands (H3), exploratory analysis illustrated that data were not normally distributed and were therefore log transformed for normality. To establish whether observed variance between sites was statistically significant, an independent two-tailed heteroscedastic *t*-test was used. The tests assumed unequal variance between samples and was carried out at the 95, 99 and 99.9% confidence levels

($p < 0.05$, $p < 0.01$, $p < 0.001$). Correlations between water quality variables were undertaken on non-normalised data using the non-parametric Spearman's rank correlation. All tests were undertaken using SPSS v23 (SPSS Inc., IBM, USA). Unless otherwise mentioned, all errors are standard deviations.

3. Results

3.1. Site structure and water storage

To address H1, results of site surveys were analysed to determine the change in water storage within the site. In 2010, the walkover survey of this site measured no ponded surface water, reporting only a small first-order stream of ca. 183 m length and 93 m^2 surface area. A pair of beavers was introduced to the site in 2011; since when, a significant change in ecosystem structure, most notably a three-order of magnitude increase in ponded surface water storage, has been recorded (Fig. 2). The site has changed from a woodland site, with no permanent surface water storage, to a site dominated by 13 dam-pond structures, with dam lengths extending to 30 m (Fig. 1), covering a surface area of over 1500 m^2 (recorded maximum of 1832 m^2 in 2015 survey). Within the ponds, approximately 1000 m^3 of water is stored at any one time (maximum of 1062 ± 23 m^3 observed in March 2015).

Site surveys showed that beaver activity has continuously modified the site throughout the study period. Results presented in Fig. 2 show the number of ponds increased from 7, in 2013, to 13 in 2014 and have since remained stable. The corresponding surface area of water increased from 750 m^2 in 2013 to 1181 m^2 in 2014, followed by a further increase to 1832 m^2 in 2015, before showing a slight reduction to 1605 m^2 in 2016; showing a significant increase over the monitoring period ($p < 0.05$, N = 5). Estimated volumes of water stored in ponds, showed a significant upward trend overall ($p < 0.05$, N = 5). More specifically, water volume showed an upward trend between 2013 (405 ± 61.12 m^3) and 2014 (731 ± 72.25 m^3) and again an increase to 2015 (1062 ± 133 m^3), but a decrease between 2015 and 2016 (945.85 ± 26.97 m^3). Water storage in ponds, measured since 2014 via dipwell levels (Fig. 2) overall showed no significant inter-annual variability ($p > 0.05$, N = 47,887). However, there was intra-annual variability, which was partly driven by rainfall, varying seasonally. Dipwell levels showed a significant correlation with rainfall ($p < 0.01$, $R = 0.116$, N = 47,887), whilst mean levels were higher during the wet season of the hydrological year (1st October–1st April) compared to the dry season ($p < 0.001$, N = 47,887). Whilst not tested quantitatively, intra-annual variability was also observed to be related to beaver dam building or breaching activity, which could both enhance and draw-down water stored in individual ponds.

3.2. Flow

To understand the hydrological response to rainfall at the site and the impact of beaver activity (H2), rainfall and accompanying discharge data for the Above Beaver and Below Beaver monitoring stations, for the entire monitoring period, are presented in Fig. 3. Discharge at both monitoring sites showed a positive correlation with rainfall ($p < 0.01$, Above Beaver $R = 0.218$; Below Beaver $R = 0.181$, N = 59). The hydrological response to rainfall events varied in magnitude at the Above and Below Beaver monitoring stations. Relationships between Above Beaver and Below Beaver rainfall and flow data for a range of summary metrics (total event discharge, peak event discharge and peak rainfall to peak discharge lag time) are illustrated in Fig. 4. As can be seen from the example events in Fig. 3 and relationships for all events in Fig. 4 (peak observed event discharge (m^3 s^{-1}, $p < 0.001$ $R^2 = 0.81$); total storm event discharge (m^3, $p < 0.001$ $R^2 = 0.70$); peak rainfall to peak lag time (minutes, $p < 0.05$, $R^2 = 0.18$), the Below Beaver site shows a more attenuated response to rainfall events than the Above Beaver site, despite the distance between these monitoring locations being <200 m. When comparing population means across the events monitored, Below Beaver events were smaller, showing $34 \pm 9\%$ lower total event discharges during rainfall (AB = 1718 ± 1641 m^3; BB = 1137 ± 1059 m^3, $p < 0.05$, N = 59) and $30 \pm 19\%$ lower in terms of peak discharges (AB = 0.04 ±

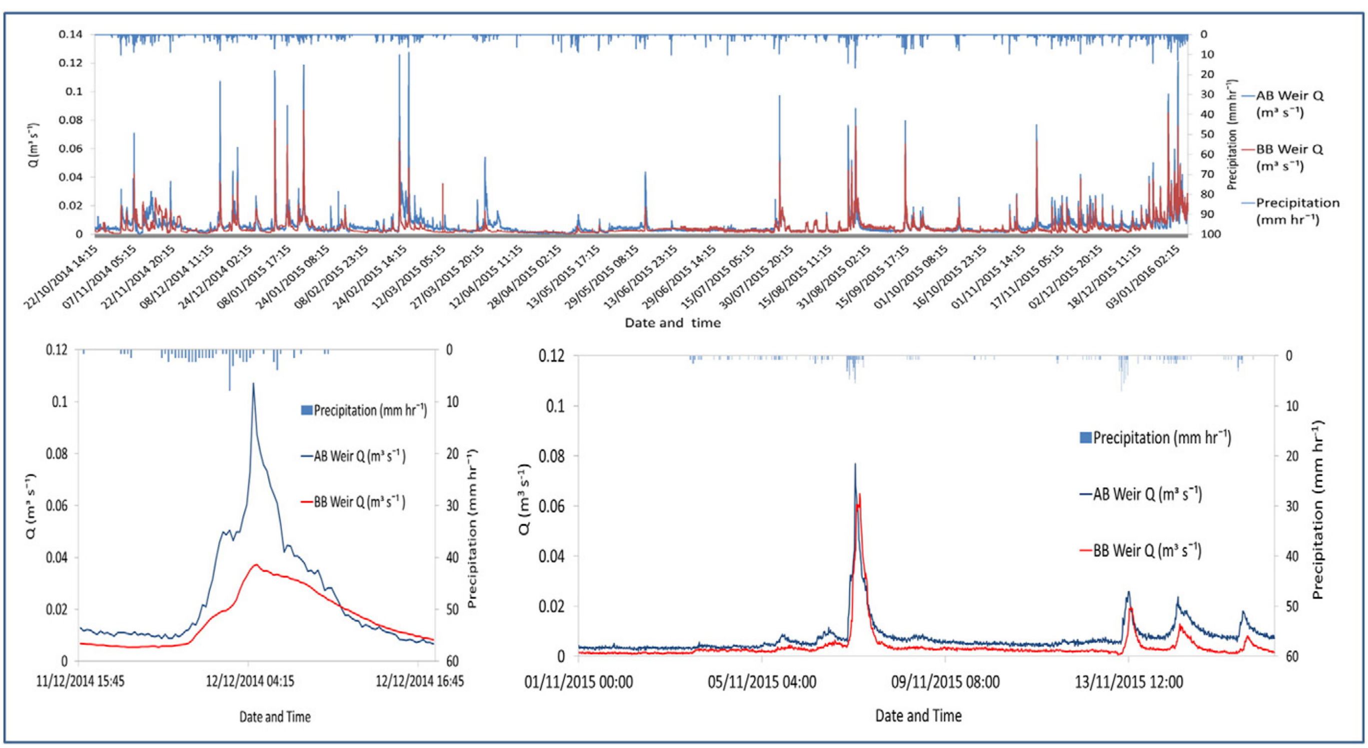

Fig. 3. Top: discharge (m^3 s^{-1}) and rainfall (mm h^{-1}) time series for monitoring period. Bottom left: zoom in on example storm event hydrograph from December 2014. Bottom right: zoom in on example hydrograph from November 2015. For all graphs, blue line is Above Beaver monitoring station (AB) and red line is Below Beaver (BB) monitoring station.

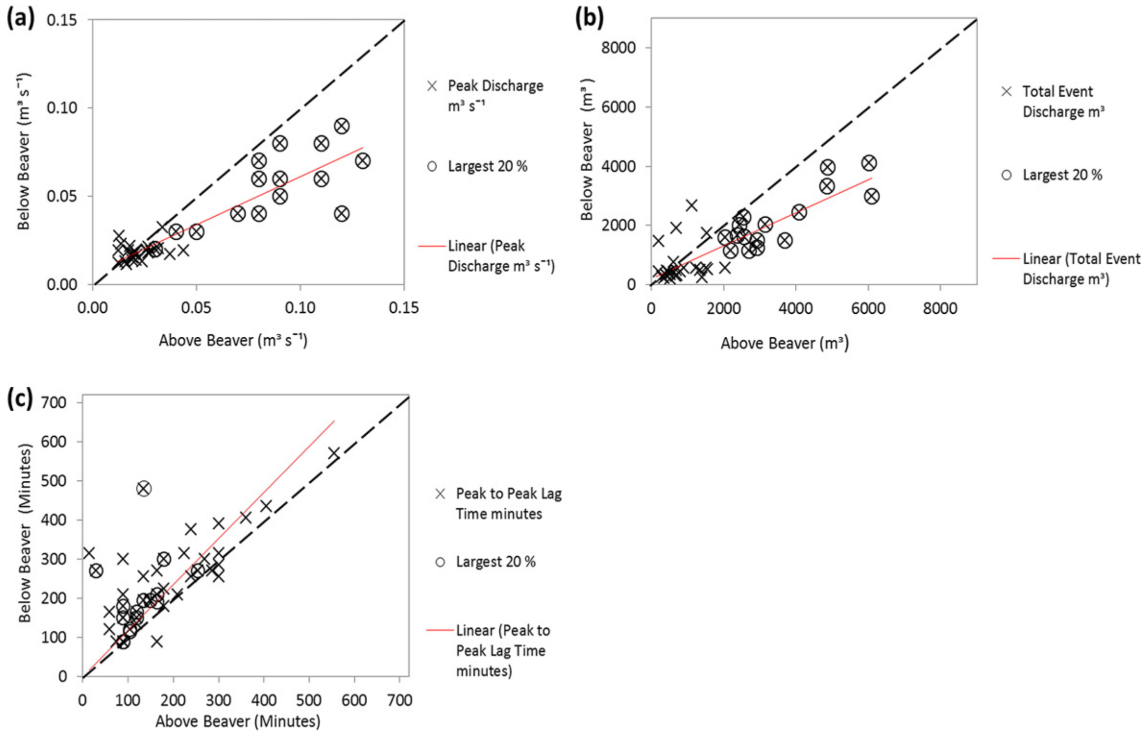

Fig. 4. For each rainfall event (N = 59) extracted from a continuous time-series of flow, relationships between hydrological response Above Beaver (x-axis) and Below Beaver (y-axis). Top left (a): peak observed event discharge ($m^3\ s^{-1}$, $p < 0.001$, $R^2 = 0.81$); Top right (b): total storm event discharge (m^3, $p < 0.001$, $R^2 = 0.70$); Bottom left: (c) peak rainfall to peak lag time (minutes, $p < 0.05$, $R^2 = 0\ 0.18$). For all graphs black dashed line through zero, represents a hypothetical 1:1 relationship between the two monitoring stations, whilst the solid red trend line represents the observed relationship. Black circles highlight results for the top 20% largest events (as determined by total storm discharge entering the site Above Beaver).

0.03 $m^3\ s^{-1}$; BB = 0.03 ± 0.02 $m^3\ s^{-1}$, $p < 0.001$, N = 59). Below Beaver, the hydrological response to rainfall was also more temporally attenuated with 29 ± 21% longer peak rainfall to peak flow lag times (AB = 127 ± 51 mins; BB = 198 ± 100 mins, $p < 0.001$, N = 59) and 32% longer average event durations (AB = 631 ± 335 mins; BB = 783 ± 326 mins, $p > 0.001$, N = 59). Based on a mass balance equation for the site, 22% more water entered the site Above Beaver (235,633 ± 24 m^3) over the monitoring period than left the site Below Beaver (183,617 ± 18 m^3).

Table 1 presents summary results for the top 20% of monitored storm events (N = 16) as classified by total event discharge entering the site, these are also highlighted in the overall dataset presented in Fig. 4 (in black circles). Whilst the top 20% of events contained higher peak and total discharges and shorter lag times compared to the entire dataset, the percentage differences observed were not significantly different ($p > 0.05$) to the complete dataset). During these largest events significant differences were still observed between the Above Beaver and Below Beaver sites. Flows were on average 37 ± 15% lower in terms of total event discharge (AB = 3472 ± 1333; BB = 2158 ± 962 m^3, $p < 0.001$, N = 16), 35 ± 14% lower in terms of peak discharge (AB = 0.08 ± 0.03; BB = 0.05 ± 0.02 $m^3\ s^{-1}$, $p < 0.001$, N = 16), and 28 ± 25% longer in terms of peak rainfall to peak flow lag times (AB = 127 ± 51; BB = 198 ± 100 mins, $p < 0.05$, N = 16) than the Above Beaver flows.

Table 1
Summary statistics for the largest 20% of events observed. ER = event rain; peak Q = peak discharge; total Q = total discharge. % difference is percentage difference between Above Beaver and Below Beaver with direction of change in brackets (±) for each metric.

Event		Above Beaver			Below Beaver			% difference		
Date	ER (mm)	Peak Q ($m^3\ s^{-1}$)	Total Q (m^3)	Lag time (min)	Peak Q ($m^3\ s^{-1}$)	Total Q (m^3)	Lag (min)	Peak Q ($m^3\ s^{-1}$)	Total Q (m^3)	Lag (min)
03/01/2016	37.8	0.09	6028.52	105	0.08	4110.78	115	11.11 (−)	31.81 (−)	8.70 (+)
22/02/2015	24.2	0.13	6094.1	120	0.07	2986.10	165	46.15 (−)	51.00 (−)	27.27 (+)
13/01/2015	33.2	0.12	4886.14	180	0.09	3968.06	300	25.00 (−)	18.79 (−)	40.00 (+)
01/01/2016	29.2	0.12	4859.59	135	0.04	3318.51	195	66.67 (−)	31.71 (−)	30.77 (+)
07/01/2015	30.8	0.09	4095.41	135	0.06	2455.51	480	33.33 (−)	40.04 (−)	71.88 (+)
25/08/2015	32.6	0.09	3696.48	90	0.05	1481.79	180	44.44 (−)	59.91 (−)	50.00 (+)
03/01/2015	23.8	0.11	3143.16	165	0.08	2024.49	210	27.27 (−)	35.59 (−)	21.43 (+)
29/03/2015	11.8	0.05	2933.54	255	0.02	1241.64	270	60.00 (−)	57.67 (−)	5.56 (+)
11/12/2014	24.0	0.11	2923.18	105	0.04	1492.61	120	63.64 (−)	48.94 (−)	12.50 (+)
19/11/2015	19.8	0.03	2705.2	150	0.02	1157.18	195	33.33 (−)	57.22 (−)	23.08 (+)
23/11/2015	18.4	0.04	2562.53	30	0.03	1626.15	270	25.00 (−)	36.54 (−)	88.89 (+)
29/11/2015	13.2	0.03	2431.96	120	0.02	2013.18	150	33.33 (−)	17.22 (−)	20.00 (+)
06/11/2014	23.0	0.07	2376.82	165	0.04	1656.27	190	42.86 (−)	30.32 (−)	13.16 (+)
22/08/2015	30.0	0.08	2200.77	90	0.04	1138.74	90	50.00 (−)	48.26 (−)	0.00 (+)
14/09/2015	27.2	0.08	2556.56	90	0.06	2267.29	90	25.00 (−)	11.31 (−)	0.00 (+)
07/11/2015	15.6	0.08	2050.29	90	0.07	1596.71	150	12.50 (−)	22.12 (−)	40.00 (+)
Mean	24.7	0.08	3471.52	126.56	0.05	2158.44	198.13	37.48 (−)	37.40 (−)	28.33 (+)
Standard dev	7.5	0.03	1332.82	50.78	0.02	962.34	97.59	16.92	15.36	25.10

3.3. Water quality

To address H3, measured concentrations for water quality determinands are summarised in Fig. 5 and detailed in Table 2. Analysis showed that; mean concentrations were higher and significantly different at the Above Beaver site, compared to the Below Beaver monitoring station for: SS (AB: 112.42 ± 71.47 mg l^{-1}, BB: 39.15 ± 36.88 mg l^{-1}, N = 226, $p < 0.001$); TON (AB: 3.35 ± 0.44 mg l^{-1}, BB: 2.19 ± 0.42 mg l^{-1}, N = 97, $p < 0.001$) and PO_4 (AB: 0.10 ± 0.08 mg l^{-1}, BB: 0.02 ± 0.01 mg l^{-1}, N = 123, $p < 0.001$). In contrast, DOC concentrations were significantly lower ($p < 0.001$, N = 226) at Above Beaver, compared to Below Beaver (AB: 5.11 ± 4.65 mg l^{-1}, BB: 11.87 ± 5.96 mg

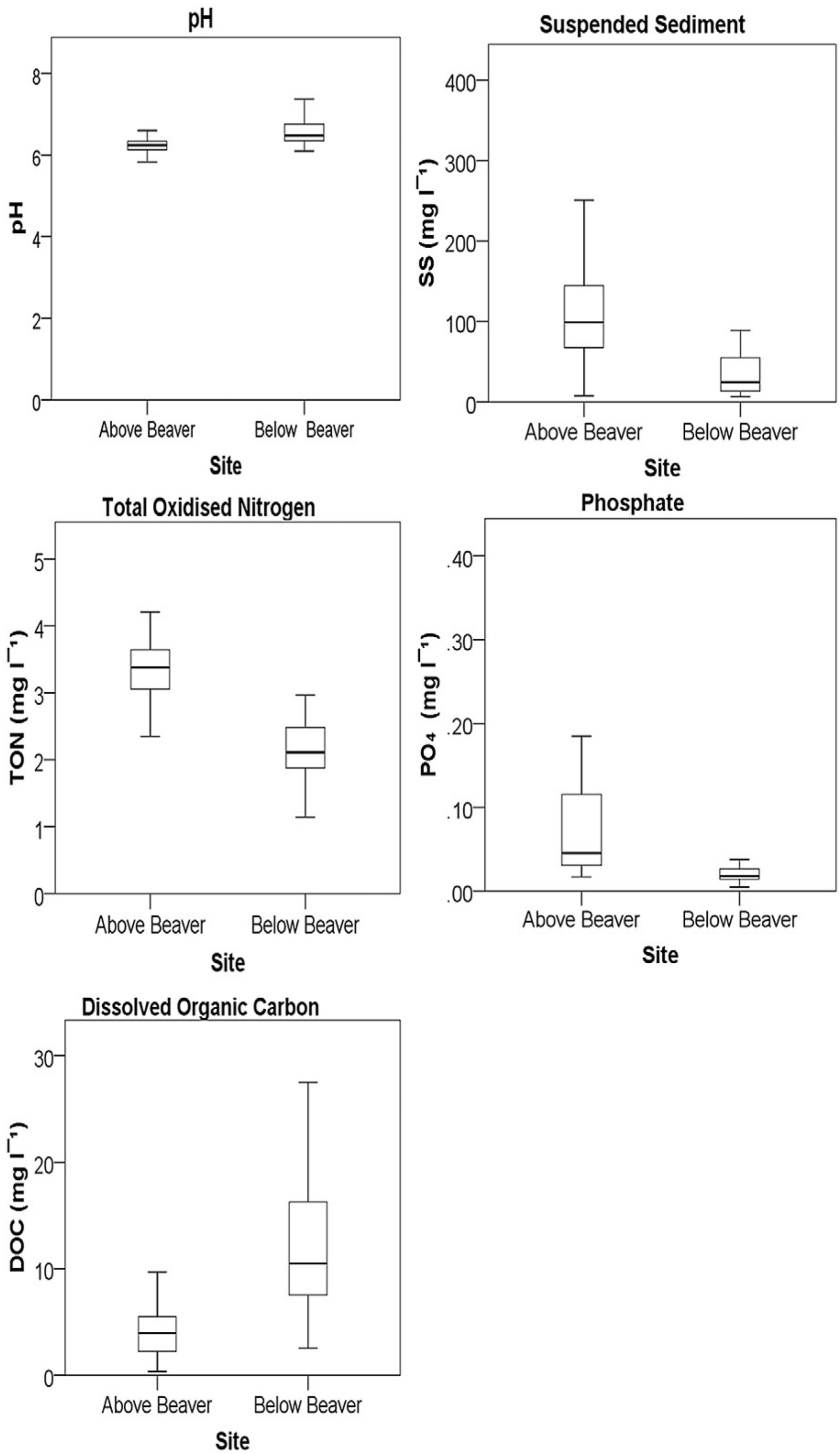

Fig. 5. Box and whisker plots summarising concentrations of measured water quality. Top left = pH ($p < 0.01$, N = 226); Top right = suspended sediment (mg l^{-1}, $p < 0.001$, N = 226); middle left = total oxidised nitrogen (mg l^{-1}, $p < 0.001$, N = 123); Bottom left = phosphate (mg l^{-1}, $p < 0.001$, N = 123) and bottom right = dissolved organic carbon (mg l^{-1}, $p < 0.001$, N = 123). Centre line on bar = median; upper limit of bar = upper quartile; lower limit on bar = lower quartile; whiskers = minimum and maximum values; circles and stars = data outliers.

Table 2
Water quality concentrations, instantaneous loads (calculated by multiplying concentration by discharge) and summary data for monitored water quality events: Above Beaver (AB), Below Beaver (BB). SS = suspended sediment, TON = total oxidised nitrogen, PO_4 = phosphate, DOC = dissolved organic carbon. NA = result not available to laboratory or sample collection issue. Sample Q = instantaneous discharge when sample was collected.

Event Start Date	Site	N	Sample Q (m3 s^{-1})	WQ concentrations (±SD)					WQ instantaneous loads (±SD)			
				pH	DOC (mg l^{-1})	TON (mg l^{-1})	$P0_4$ (mg l^{-1})	SS (mg l^{-1})	DOC (g min^{-1})	TON (g min^{-1})	P04 (g min^{-1})	SS (g min^{-1})
24/10/2014	Above Beaver	24	0.004 ± 0.001	6.23 ± 0.05	3.29 ± 1.27	NA	NA	158.38 ± 49.18	0.83 ± 0.38	NA	NA	38.24 ± 12.31
	Below Beaver	6	0.004 ± 0.001	6.32 ± 0.11	19.13 ± 1.32	NA	NA	57.44 ± 3.63	4.52 ± 1.10	NA	NA	13.48 ± 2.81
09/11/2014	Above Beaver	2	0.018 ± 0.000	6.31 ± 0.05	3.39 ± 0.37	NA	NA	129.26 ± 5.07	3.60 ± 0.40	NA	NA	137.35 ± 5.39
	Below Beaver	6	0.013 ± 0.009	6.45 ± 0.06	19.84 ± 2.10	NA	NA	57.57 ± 5.86	15.34 ± 10.88	NA	NA	42.28 ± 27.29
29/11/2014	Above Beaver	7	0.004 ± 0.002	6.22 ± 0.24	4.12 ± 1.67	NA	NA	144.50 ± 99.63	1.01 ± 0.73	NA	NA	28.03 ± 16.16
	Below Beaver	5	0.003 ± 0.001	6.38 ± 0.06	11.25 ± 0.58	NA	NA	19.31 ± 5.63	1.97 ± 0.76	NA	NA	3.39 ± 1.80
10/01/2015	Above Beaver	11	0.028 ± 0.025	6.21 ± 0.05	4.84 ± 1.10	NA	NA	129.70 ± 42.31	8.05 ± 6.61	NA	NA	189.88 ± 121.59
	Below Beaver	10	0.026 ± 0.021	6.29 ± 0.03	10.05 ± 0.33	NA	NA	42.94 ± 10.17	39.64 ± 12.15	NA	NA	179.77 ± 90.29
12/02/2015	Above Beaver	24	0.007 ± 0.003	6.15 ± 0.04	1.46 ± 0.91	NA	NA	99.09 ± 43.85	0.67 ± 0.47	NA	NA	42.21 ± 29.43
	Below Beaver	8	0.004 ± 0.001	6.21 ± 0.03	7.49 ± 0.22	NA	NA	41.00 ± 8.59	1.88 ± 0.66	NA	NA	10.78 ± 5.65
22/02/2015	Above Beaver	24	0.033 ± 0.028	6.32 ± 0.06	9.60 ± 5.31	3.20 ± 0.62	0.045 ± 0.02	58.06 ± 17.23	15.89 ± 7.32	3.31 ± 1.30	0.064 ± 0.051	111.07 ± 87.17
	Below Beaver	21	0.011 ± 0.011	6.81 ± 0.03	15.66 ± 1.01	1.33 ± 0.19	0.02 ± 0.01	34.17 ± 12.01	3.89 ± 0.01	0.33 ± 0.01	0.005 ± 0.000	8.48 ± 2.17
04/05/2015	Above Beaver	5	0.005 ± 0.001	6.07 ± 0.04	5.83 ± 0.68	3.50 ± 0.18	0.11 ± 0.02	170.23 ± 69.42	1.81 ± 0.51	1.07 ± 0.23	0.032 ± 0.009	50.47 ± 19.98
	Below Beaver	4	0.002 ± 0.001	6.68 ± 0.08	4.35 ± 0.99	1.96 ± 0.36	0.02 ± 0.01	12.38 ± 3.73	0.60 ± 0.41	0.23 ± 0.13	0.003 ± 0.003	1.42 ± 0.78
12/06/2015	Above Beaver	4	0.003 ± 0.001	6.45 ± 0.05	2.24 ± 1.27	3.48 ± 0.18	0.04 ± 0.00	84.50 ± 11.45	0.42 ± 0.21	0.68 ± 0.11	0.008 ± 0.001	16.63 ± 3.64
	Below Beaver	2	0.004 ± 0.000	6.32 ± 0.09	27.19 ± 0.31	1.81 ± 0.18	0.03 ± 0.00	27.77 ± 3.57	6.42 ± 0.32	0.43 ± 0.06	0.008 ± 0.001	6.58 ± 1.06
03/12/2015	Above Beaver	9	0.011 ± 0.006	5.99 ± 0.28	3.41 ± 0.62	3.47 ± 0.17	0.039 ± 0.02	83.90 ± 21.92	2.32 ± 1.46	2.30 ± 1.26	0.027 ± 0.020	59.80 ± 40.56
	Below Beaver	4	0.005 ± 0.001	6.55 ± 0.01	10.78 ± 0.03	2.01 ± 0.07	0.02 ± 0.00	13.43 ± 2.60	3.26 ± 0.59	0.61 ± 0.13	0.006 ± 0.001	4.13 ± 1.53
11/12/2015	Above Beaver	6	0.010 ± 0.002	6.38 ± 0.06	1.55 ± 0.31	4.01 ± 0.15	0.93 ± 0.01	71.18 ± 10.85	0.93 ± 0.29	2.38 ± 0.41	0.026 ± 0.006	41.99 ± 8.09
	Below Beaver	7	0.005 ± 0.003	6.51 ± 0.22	15.53 ± 1.04	2.18 ± 0.27	0.018 ± 0.00	12.71 ± 2.23	4.94 ± 2.81	0.68 ± 0.35	0.006 ± 0.004	4.32 ± 3.31
01/01/2016	Above Beaver	17	0.025 ± 0.017	6.16 ± 0.08	4.36 ± 2.58	2.97 ± 0.35	0.03 ± 0.02	45.91 ± 33.14	5.62 ± 4.13	3.91 ± 2.51	0.055 ± 0.075	83.42 ± 110.05
	Below Beaver	20	0.024 ± 0.011	7.01 ± 0.18	9.72 ± 1.38	2.57 ± 0.24	0.02 ± 0.01	18.64 ± 5.82	13.82 ± 6.83	3.68 ± 1.81	0.034 ± 0.025	26.26 ± 15.19
Mean	Above Beaver	133	0.013 ± 0.010	6.25 ± 0.20	5.11 ± 4.65	3.35 ± 0.44	0.10 ± 0.08	112.42 ± 71.47	3.41 ± 5.77	2.74 ± 1.99	0.03 ± 0.04	54.38 ± 74.38
	Below Beaver	93	0.009 ± 0.007	6.56 ± 0.29	11.87 ± 5.96	2.19 ± 0.42	0.02 ± 0.01	39.15 ± 36.88	7.02 ± 10.08	1.57 ± 1.94	0.02 ± 0.02	20.47 ± 42.26

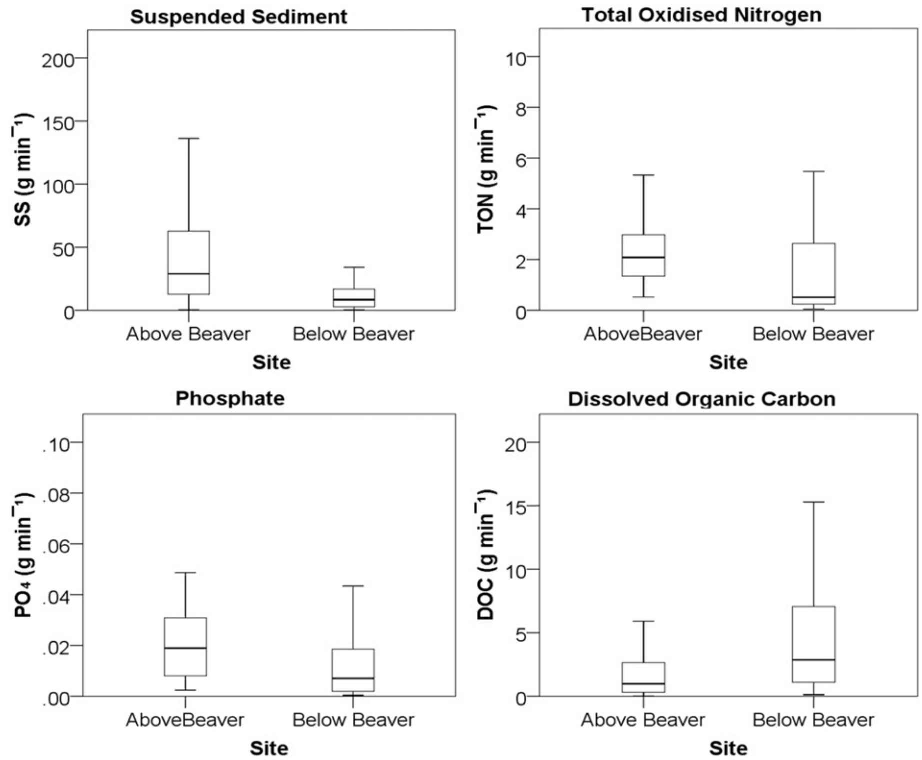

Fig. 6. Box and whisker plots summarising measured water quality instantaneous loads. Top left = suspended sediment (g min^{-1} $p < 0.001$, N = 226); top right = total oxidised nitrogen (g min^{-1} $p < 0.01$, N = 123); bottom right = phosphate (g min^{-1} $p < 0.05$, N = 123); bottom left = dissolved organic carbon (g min^{-1} $p < 0.001$, N = 226). Centre line on bar = median; upper limit of bar = upper quartile; lower limit on bar = lower quartile; whiskers = minimum and maximum values; circles and stars = data outliers.

l^{-1}). The pH of water samples at Above Beaver was slightly more acidic than at Below Beaver (AB: 6.25 ± 0.20, BB: 6.56 ± 0.29) and this difference was consistent enough across the sampling period to be statistically significant ($p < 0.01$, N = 226).

For each sample, concentrations of water quality determinands concentrations were multiplied with discharge at the time of collection to calculate instantaneous loads (Table 2). As summarised in Fig. 6 instantaneous loads were significantly higher at Above Beaver than at Below Beaver for; SS ($p < 0.001$, N = 226); TON ($p < 0.01$, N = 123); PO_4 ($p < 0.05$, N = 123). However, DOC instantaneous loads were observed to be significantly higher at Below Beaver ($p < 0.001$, N = 226). Fig. 7, presents scatter plots of the relationship between discharge and instantaneous nutrient loads. Whilst discharge and instantaneous load are auto correlated and therefore cannot be statistically analysed compared, Fig. 7 illustrates that the linear best fit lines between instantaneous loads and discharge (with the exception of DOC) were steeper at Above Beaver than Below Beaver, indicating that for a given discharge, loads are greater entering the site than leaving. Chemical water quality parameters also showed significant correlations with suspended sediment concentrations ($p < 0.01$) with total oxidised nitrogen (R = 0.628, N = 123) and phosphate (R = 0.811, N = 123) concentrations showing a positive correlation and dissolved organic carbon concentrations showing a negative correlation ($R = -0.278$, N = 226).

Total yields were also calculated for monitored events, to determine the difference between the total amounts of each water quality determinand entering at Above Beaver versus that leaving at Below Beaver. Summary results from each event are presented in Table 3. Calculated event yields all demonstrated that more SS ($p < 0.01$, N = 11), TON ($p < 0.05$, N = 6) and PO_4 ($p < 0.05$, N = 6) entered the site than left following rainfall events. DOC yields were more complex, overall showing a greater mean yield leaving Below Beaver. However, this difference was not significant ($p > 0.05$, N = 11). Whilst most events showed much more DOC leaving the site than entering, the opposite was true for a limited number (3 as shown in Table 3.), so whilst concentrations of DOC were higher below beaver ($p < 0.001$) the total amount and rate of water leaving the site during an event was lower.

4. Discussion

4.1. Site structure and water storage

Beavers engineer ecosystems to create an environment which provides security from predators, alongside easy access to and transportation of food/building materials (Zav'yalov et al., 2010). As beavers are more mobile and confident in water than they are on land (Kitchener, 2001), they have a preference for habitats with large areas of deep, slow flowing water (Collen and Gibson, 2000). Therefore, beavers will not always dam and their construction activity is typically restricted to lower order streams (Naiman et al., 1986), where water depths may not be sufficient for beaver movement and security. When dam building does occur, it increases the area of lentic habitats in systems that are typically dominated by lotic habitats (Hering et al., 2001). The increase in ponded areas above dams can also result in the creation of a stepped profile channel rather than the previous continuous gradient (Giriat et al., 2016). Whilst the structural changes will reduce downstream connectivity, they conversely increase lateral connectivity, forcing water sideways into neighbouring riparian land, inundating floodplains and creating diverse wetland environments (Macfarlane et al., 2015).

Prior to beaver introduction at the study site, a small, first order tributary with a width of ca 0.5 m was surveyed. As illustrated in Figs. 1 and 2, beaver activity has completely transformed the structure of the site, most notably through the construction of thirteen dams, blocking the movement of water, pushing it out laterally and creating ponds behind them. Results presented in Section 3.1. showed a significant increase in both the surface area and volume of water stored within the site that can be unequivocally linked to beaver activity. Therefore, H1; that

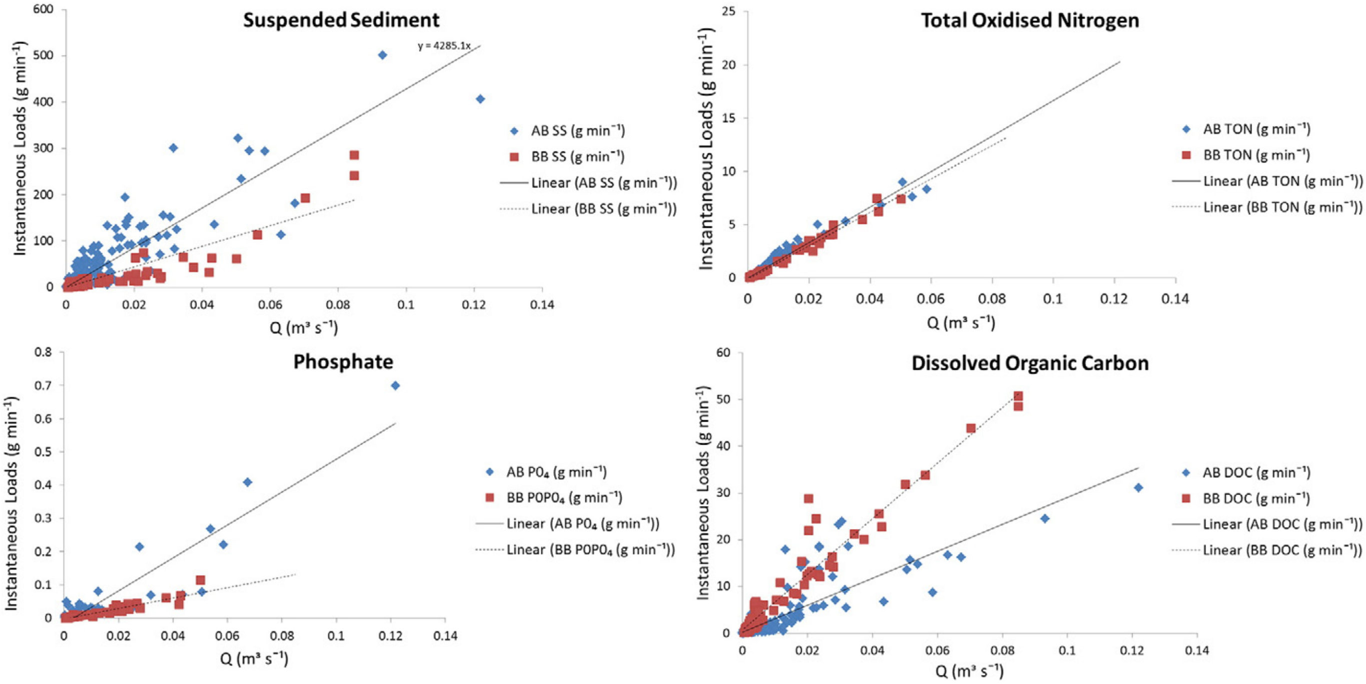

Fig. 7. Lines of best fit between instantaneous loads of measured water quality determinands and discharge ($m^3 s^{-1}$) at the time of sampling to demonstrate the different gradients at Above Beaver, compared to Below Beaver. Autocorrelation between discharge (Q) and load means that results are not statistically significant; however, they do illustrate the differing relationships observed at the Above Beaver and Below Beaver monitoring sites. Top left = suspended sediment (g min^{-1}, N = 226); top right = total oxidised nitrogen (g min^{-1}, N = 123); bottom right = total phosphate (g min^{-1}, N = 123); bottom left = dissolved organic carbon (g min^{-1}, N = 226). For all graphs: blue diamond's = Above Beaver and red squares = Below Beaver. Solid line = linear line of best fit for Above Beaver and dotted line = linear line of best fit for Below Beaver.

beaver activity significantly increases water storage within the landscape, can be accepted with confidence.

Results, from this study reinforce the view that in small channels, beavers engineer freshwater systems and neighbouring riparian zones to create more suitable conditions (Collen and Gibson, 2000) and that beavers can alter their landscape rapidly over short periods of time. Beavers continually maintain the dam structures of inhabited beaver ponds. Stimulated by the sound of running water (Campbell-Palmer et al., 2015), they will fill gaps and carry out repairs when and where required, often every night, whilst also expanding into new resource gathering areas. Combined with fluctuating water levels driven by rainfall (or lack of rainfall), water storage within beaver impacted environments will be highly variable, but is clearly enhanced when compared with the pre-Beaver landscape.

4.2. Flow

This study quantified flow entering and leaving the beaver impacted site between October 2014 and January 2016. Results from above and below the beaver impacted site during storm events indicated that beaver activity had an attenuating impact upon flow, leading to: longer peak rainfall to peak discharge lag times, lower peak discharge and lower total event discharges. Results also showed more water in total entering the site than leaving, indicating that (1) water storage within the site is significant and (2) that the lateral redistribution and storage of water within the site led to significant infiltration, transmission and evapotranspiration losses (though these were not measured). Thus, these findings, at the headwater catchment scale, support previous findings from work at reach (Green and Westbrook, 2009; Nyssen et al.,

Table 3
Total yield of water quality determinands for monitored water quality events: Above Beaver (AB), Below Beaver (BB) and % difference between AB and BB in addition to direction of change between AB and BB in brackets (+/−). SS = suspended sediment, TON = total oxidised nitrogen, PO_4 = phosphate, DOC = dissolved organic carbon. NA = result not available to laboratory or sample collection issue.

Event N	Event start date	SS (kg)			TON (kg)			P (kg)			DOC (kg)		
		AB	BB	%	AB	BB	%	AB	BB	% less	AB	BB	%
7	24/10/2014	223.74	68.38	69 (−)	NA	NA	NA	NA	NA	NA	4.84	28.42	83 (+)
8	09/11/2014	27.51	9.04	67 (−)	NA	NA	NA	NA	NA	NA	0.72	3.31	78 (+)
9	29/11/2014	67.08	8.02	88 (−)	NA	NA	NA	NA	NA	NA	0.07	0.17	57 (+)
10	10/01/2015	295.93	146.70	50 (−)	NA	NA	NA	NA	NA	NA	13.80	32.53	58 (+)
11	12/02/2015	67.49	13.46	80 (−)	NA	NA	NA	NA	NA	NA	0.66	2.31	72 (+)
12	22/02/2015	352.03	88.70	75 (−)	3.08	2.79	9 (−)	0.33	0.06	83 (−)	50.37	42.79	15 (−)
13	04/05/2015	188.66	5.79	97 (−)	7.57	2.46	67 (−)	0.14	0.01	92 (−)	7.57	2.46	67 (−)
14	12/06/2015	36.19	8.71	76 (−)	1.49	0.57	62 (−)	0.02	0.01	41 (−)	0.87	8.50	90 (+)
15	03/12/2015	93.72	1.42	98 (−)	3.61	0.21	94 (−)	0.04	0.00	95 (−)	3.63	1.13	69 (−)
16	11/12/2015	48.80	4.99	90 (−)	2.76	0.78	72 (−)	0.03	0.01	78 (−)	1.08	5.71	81 (+)
17	01/01/2016	263.82	82.14	69 (−)	12.35	10.62	14 (−)	0.17	0.10	41 (−)	17.77	39.48	55 (+)
	Mean	151.36	39.76	78 (−)	5.14	2.91	53 (−)	0.12	0.03	72 (−)	9.22	15.16	38 (+)

2011) and larger catchment scales (Burns and McDonnell, 1998). Based upon results presented herein (Section 3.2), H2: that beaver dams significantly alter flow regimes resulting in attenuated flow is supported. Related work by colleagues emphasises the value of baseline data (Luscombe et al., 2016) in assessing the impact of landscape restoration techniques upon hydrology and the unavoidable lack of pre-beaver baseline in this study must be acknowledged as a limitation, which should be addressed in future studies. The flow attenuating response of beaver activity, observed both in this study and previous research (Green and Westbrook, 2009; Gurnell, 1998; Pollock et al., 2007), indicates that water is being trapped or at least slowed as it moves through beaver impacted sites. In a previous study, Green and Westbrook (2009) found that the removal of a sequence of beaver dams resulted in an 81% increase in flow velocity. The slow movement of water in beaver impacted sites is attributed to two main causes (1) increased water storage and (2) stream discontinuity and reduced longitudinal hydrological connectivity. Firstly, the increase in storage provided by beaver ponds and associated wetlands (Grygoruk and Nowak, 2014; Gurnell, 1998; Woo and Waddington, 1990) increases water retention times and reduces the velocity of the water. This in turn can increase the duration of the rising limb of the flood hydrograph which, in turn, can reduce the peak discharge of floods (Burns and McDonnell, 1998; Green and Westbrook, 2009; Nyssen et al., 2011). Finally, water stored in the site is released slowly as the leaky dams are drawn-down following rainfall, resulting in elevated baseflows from the site relative to flows into the site.

Water levels in ponds varied significantly as a result of meteorological conditions. Consequently, seasonal variations in water storage were observed as demonstrated by Majerova et al. (2015). It may be therefore expected that the attenuating impact of flow due to storage will be less during wet periods. However, results showed that the flow attenuation impact of the beaver site persisted through the winter months, when pond levels were higher. 14 of the 16 largest events were during the wettest part of the hydrological year and showed no significant reduction in flow attenuation when compared with all flow events (Figs. 3 and 4). That beaver activity still attenuates flow during large events, is supported elsewhere by Nyssen et al. (2011) who conducted one of the few in-channel hydrological studies of Eurasian beaver (*C. fiber*); finding that flow attenuation was greatest during larger events. The connectivity of landscapes is increasingly recognised as being a key control over their hydrological function (Bracken and Croke, 2007; Puttock et al., 2013). It is argued that the observed discontinuity or reduced downstream hydrological connectivity resulting from beaver dam building activity (also shown by Butler and Malanson, 2005), is a key reason for the flow attenuation impact observed herein, which persists even for larger events during the wetter, winter months.

It is important to acknowledge that beaver dam building activity is not a uniform activity and depends on the existing habitat, building material availability and channel characteristics (Collen and Gibson, 2000). Woo and Waddington (1990) identified multiple ways in which dam structure will influence flow pathways and that stream flow can overtop or funnel through gaps in the dams, leak from the bottom of the dams or seep through the entire structure. Whilst some of these pathways (through flow and underflow) were attributed to abandoned dams, visual observations made during this study found that all of these flow pathways can occur together. Whilst, the impact of dam structure upon connectivity and therefore, flow velocity will differ (Hering et al., 2001; Woo and Waddington, 1990), all dams will increase channel roughness and therefore, deliver a flow attenuation effect. In addition to dam structural variations, it is important to observe that the 13 dam and pond structures at the study site were not acting in isolation, but that the differences in hydrological function observed at Above Beaver and Below Beaver was rather a cumulative effect of the overall site structure. Previous studies also discuss the importance of the number of dams in a reach, with beaver dams having the greatest impact on hydrology when they occur in a series (Beedle, 1991; Gurnell, 1998). Sequences of debris dams in 3rd order, Northern Indiana streams were found to increase the retention time of water by a factor of 1.5–1.7 (Ehrman and Lamberti, 1992). Ponds located in series provide both greater storage and greater roughness, resulting in a greater reduction in flow velocities as shown by Green and Westbrook (2009). In another study, pond sequences have been shown to reduce the peak flows of 2-year return floods by 14% whereas individual dams reduced flood peaks of similar events by only 5.3% (Beedle, 1991).

Results presented herein provide strong evidence for the role that beaver dams or similar engineered woody-debris dams (Thomas and Nisbet, 2012), can play a role in flood-defence focused catchment management strategies. There is growing policy support for such 'working with nature' strategies in the UK (Environment Agency, 2014), whilst applied research in the USA has shown how beaver damming activity could be encouraged in locations that suffer from flooding (Pollock et al., 2014). Whilst it appears that such strategies would best be implemented in headwater, low-order tributaries, or in areas where traditional flood defences such as walls cannot be constructed (Wilkinson et al., 2010), further mechanistic understanding of how beaver damming should be encouraged and how many beaver dams would be required to achieve desired results, at different scales, is required (Pollock et al., 2014). Furthermore, as highlighted by Wilkinson et al. (2010) nature based solutions to flooding may potentially provide additional benefits such as water quality improvements. Catchment management strategies should therefore consider these multiple benefits, afforded by soft engineering approaches, alongside the traditional hard engineering flood defence approach (Wilkinson et al., 2014).

4.3. Water quality

4.3.1. Sediment dynamics

The hydrological changes in water storage and flow are likely to have implications for the chemical composition of water leaving the site (Naiman et al., 1986), in addition to stores and downstream fluxes of sediment and associated nutrients (Butler and Malanson, 1994; Lizarralde et al., 1996). Storm event monitoring of water quality at the study site showed lower concentrations and loads of suspended sediment leaving the site in contrast to sediment concentrations/loads entering the site. It is therefore suggested that beaver dams and ponds can exert a significant influence over channel sediment budgets, akin to the dam and woody debris that once played a vital role in the evolution of river networks and floodplains, through the storage of sediment and creation of riparian wetland and woodland. With the intensification of agriculture and the decline of beaver across Europe, in addition to geomorphological alterations such as damming and channelisation (Petts and Gurnell, 2005; Sear et al., 1995) the sediment storage capacity of rivers has declined. Many of these rivers are now experiencing significant rates of incision (Hering et al., 2001). Sedimentation has been reported in many studies of beaver dam morphology. In lower order streams, debris dams have been shown to account for up to 87% of sediment storage (Hering et al., 2001). Sediments, transported from upstream, are deposited in beaver ponds due to the sudden decrease in velocity associated with the decrease in stream power (Butler and Malanson, 1994). An additional benefit is that downstream of beaver dams, channel beds may be less impacted by sediment which has positive implications for the spawning of salmonids and the overall ecological status of the freshwater (Kemp et al., 2012).

The cumulative impact of beaver dams also seems noteworthy in terms of sediment-related water quality. Qualitative observations made at the site demonstrate that the majority of sediment is being trapped in the first few upstream ponds. Over time, sediment may continue to accumulate until each pond fills completely and sediments are colonised by plants forming beaver meadows (Polvi and Wohl, 2012) or the dam collapses (Butler and Malanson, 2005). The rate of sediment accumulation and the long term fate of these deposits will depend on the availability and composition of deposited sediment, the flow regime and the maintenance of the dam structures (Butler and Malanson, 2005; de Visscher et al., 2014).

It has also been argued that beavers can contribute to downstream sediment budgets; through the excavation of canal networks and bank burrows (de Visscher et al., 2014; Lamsodis and Ulevičius, 2012), in addition to the release of sediment following dam outburst floods (Curran and Cannatelli, 2014; Levine and Meyer, 2014). That enhanced fluxes resulting from beaver building activity were not observed herein, suggests that the structure and density of the dams was enough to mitigate the sediment fluxes observed from the intensively managed grasslands upstream over the monitoring period. Such landscapes have previously been shown to export significant amounts of sediment during high-energy storm events (Bilotta et al., 2010; Granger et al., 2010; Peukert et al., 2014), demonstrating the potential role that beaver dams could play in combatting diffuse pollution from agriculture. As with flow, a pre-beaver baseline would be desirable. However, based on the presented differences Above Beaver and Below Beaver it is argued that for suspended sediment, H3 – that Beaver ponds act as sinks for diffuse pollutants significantly improving water quality downstream can be accepted, with significant implications for addressing some of the problems attributed to loss of sediment from intensively farmed landscapes (Brazier et al., 2007).

4.3.2. Chemical water quality

Beaver activity can influence water chemistry and therefore downstream water quality via both abiotic and biotic processes (Cirmo and Driscoll, 1996; Johnston et al., 1995). It is believed that two key mechanisms affected the difference in water quality observed in the system reported herein: (1) flow was slowed resulting in the physical deposition of sediment and associated nutrients (2) the site increased in wetness altering the biogeochemical cycling of nutrients. Previous studies have found that when beaver dams inhibit the transport of fine sediments, this results in the storage of large volumes of organic and inorganic compounds within beaver ponds (Rosell et al., 2005), including nitrogen, phosphorus and particulate bound carbon (Lizarralde et al., 1996; Naiman et al., 1994). This structural change increases the volume of anoxic sediments and provides organic material to aid microbial respiration. Sediments and their associated nutrients are temporarily immobilised in pond sediments and taken up by aquatic plants, periphyton and phytoplankton. Increases in plant available nitrogen, phosphorus, carbon and increased light availability (due to canopy reduction) favour the growth of instream and riparian vegetation, thus further immobilising nutrients within plant biomass (Rosell et al., 2005).

Results presented in Section 3.3. showed TON and PO_4 to be significantly lower leaving the site, both in terms of concentrations and loads, indicating that beaver activity at the site created conditions for the removal of nitrogen and phosphorus entering the site. Correll et al. (2000) found that prior to dam construction, TON concentrations were significantly correlated with river discharge but after dam construction, no significant relationship was observed, although there was a correlation between discharge and nitrate. Similarly, Maret et al. (1987) identified reductions in Total Kjeldahl Nitrogen (TKN) downstream of beaver dams during high flows. It has also been shown that beaver ponds are particularly effective at nitrate retention (Devito et al., 1989). It is suggested therefore, that in agriculturally dominated catchments, particularly those located in Nitrate Vulnerable Zones, beaver ponds are potentially effective tools to manage N-related diffuse pollution problems from intensive agriculture upstream (Lazar et al., 2015).

Results suggest that beaver ponds can also act as sinks for phosphorus associated with sediments. Interestingly, Maret et al. (1987) identified that suspended sediment was the primary source of phosphorus found leaving a beaver pond; therefore, during conditions when more sediment is retained behind the dam than is released, total phosphorus retention is likely to increase. In a study of a beaver impacted and non-beaver impacted catchment, Dillon et al. (1991), found total phosphorus export was higher in the non-impacted catchment suggesting that phosphorus was being stored somewhere within the catchment – most probably in the beaver ponds. Lizarralde et al. (1996) also reported that whilst phosphorus concentrations were significantly higher in riffle sediments, due to extensive wetland creation, total storage was highest in Patagonian beaver ponds. Whilst results here demonstrated a steeper relationship between discharge and phosphate loads in water entering the site, when compared to water leaving the site, previous studies have focused primarily on the relationship between discharge and phosphorus concentrations and yields leaving ponds, with inconclusive results. Devito et al. (1989) reported a strong positive correlation between phosphorus loads and stream discharge. However, Maret et al. (1987) report a negative correlation between phosphorus concentrations and discharge and (Correll et al., 2000) report no correlation between nutrient flushing and stream discharge following dam construction. Climatic and seasonal changes (Devito and Dillon, 1993; Klotz, 2007) and organic matter availability (Klotz, 2007, 2013) have been shown to affect in-pond phosphorus-dynamics. However, with regard to downstream impact, the key consensus, that is supported by the correlation between suspended sediment and phosphate concentrations observed herein is that beaver ponds are most effective at retaining phosphorus associated with high sediment loads (Devito et al., 1989; Maret et al., 1987).

In contrast to the trends observed for nitrogen and phosphate, which correlated with suspended sediment, concentrations and loads of DOC increase on leaving the site, meaning that H3 (beaver activity significantly improves water quality), cannot be accepted for all three macronutrients. The increase in DOC concentrations observed were perhaps to be expected. The increase in sediment and nutrient storage discussed above, in-addition to the overall increase in wetland extent created an environment rich in organic matter, as previously shown by Vecherskiy et al. (2011). Similarly, Law et al. (2016), using colour as a proxy for DOC, observed increased concentrations below a series of beaver dams. Such ecosystems contrast starkly with the carbon depleted, intensively managed agricultural landscape upstream, a landscape that prevails across much of the western UK (Bilotta et al., 2010; Glendell and Brazier, 2014; Peukert et al., 2014, 2016) for examples. Therefore, the dams may trap sediment-bound particulate carbon meaning that ponds may act as net stores of carbon (Correll et al., 2000; Lizarralde et al., 1996; Naiman et al., 1986). However, as a consequence of this overall increase in carbon availability, significant exports of DOC have been observed either downstream (Correll et al., 2000; Naiman et al., 1994) or in comparison with non-beaver impacted catchments (Błędzki et al., 2011). Several authors have speculated that the cause of this DOC release relates to: (i) incomplete decomposition processes making DOC more available for loss (Cirmo and Driscoll, 1996); (ii) enhanced production during primary productivity; (iii) a product of enhanced microbial respiration (Correll et al., 2000) (iv) retention of particulate organic carbon and litter entering the site and subsequent decomposition (Law et al., 2016).As in other organic matter rich environments, DOC release may be expected to vary seasonally due to altering decomposition and production rates (Grand-Clement et al., 2014; Margolis et al., 2001). This also applies to pH which has been shown to be a first order control on DOC production and transport elsewhere (Clark et al., 2007; Grand-Clement et al., 2014). However, another study (Cirmo and Driscoll, 1996) found that a beaver impacted catchment contained higher levels of DOC both before and after $CaCO^3$ treatment when compared with a non-impacted catchment, suggesting that pH plays a limited role in the production of DOC.

This study showed pH to be marginally (but significantly $p < 0.05$) more alkaline in water leaving the site, which is in agreement with other studies showing higher pH levels in beaver ponds and immediately downstream (Cirmo and Driscoll, 1993, 1996; Margolis et al., 2001). However, whether this change in pH was of a large enough magnitude (mean 6.25 ± 0.20 Above Beaver and 6.56 ± 0.29 Below Beaver) to alter within site nutrient cycling is unclear.

Our study demonstrates that concentrations of DOC were significantly higher downstream, but overall losses of DOC were more variable due to the impact of lower, attenuated flows at Below Beaver. Whether losses of DOC from beaver impacted areas are a problem or simply a side effect of a landscape which otherwise acts as an increased carbon store (Johnston, 2014; Wohl, 2013), needs further investigation, in conjunction with an understanding of the impact of beavers upon gaseous carbon fluxes (Klotz, 2013; Wohl, 2013). Much of the existing research focuses on the potential for flushing from beaver ponds and impacts upon in-pond and downstream dynamics with inconclusive results (Correll et al., 2000; Devito et al., 1989; Maret et al., 1987). There is far less research on the potential for beaver ponds to trap or mitigate diffuse pollution from upstream, in agriculturally dominated catchments such as the site studied here, where sediment and associated nutrient losses have been identified as a key problem (Peukert et al., 2014).

5. Conclusion

The results presented within this study represent a significant contribution to our understanding of how Eurasian beaver can impact upon ecosystem structure, with major implications for environmental function, management and the provision of environmental ecosystem services. Specifically in the wooded site, upon a first-order tributary, beaver activity was shown to create a diverse wetland environment, dominated by a sequence of 13 pond and dam structures. The decreased downstream connectivity resulting from this change in ecosystem structure is highly likely to be responsible for the observed attenuating impact upon flood flows across a range of storm event sizes. Furthermore, for a range of key water quality determinands including; suspended sediment, total oxidised nitrogen and phosphate, both concentrations and loads were shown to be significantly lower downstream of the beaver impacted site.

The hydrological impacts of beaver activity are likely to be highly scale and site specific, depending on a range of factors including channel characteristics, food availability and population pressure. Therefore, further research across a range of temporal and spatial scales is required. However, given the widespread reintroduction of Eurasian beaver across Europe, in conjunction with the requirement for improved catchment and land management strategies, this research forms a solid base, from which to develop an understanding of how beavers may form a 'nature based solution' to the land management, water resource and flooding problems faced by society.

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