



Eurasian Beaver (*Castor Fiber*) Reintroduction: A Nutrient Mitigation Solution for Lowland Chalk Streams?

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Abstract

Globally scarce and ecologically valuable, the lowland chalk streams of southern and eastern England experience extensive eutrophication pressures arising from intensive agriculture. Mitigation measures are required to restore natural chalk stream functioning and the reintroduction of the Eurasian beaver (*Castor fiber*) could provide a solution. Here, we investigated the impact upon chalk stream hydrochemistry of the reintroduction of beavers to a 6-ha enclosure on the headwaters of the River Glaven, Norfolk. Over a two-year period (March 2022 – May 2024), 190 river water samples were collected across control and impact sites displaying minor-to-major hydrological disturbance from beaver activity, with samples analysed for nitrate (NO₃), phosphate (PO₄), and dissolved organic carbon (DOC). Results revealed significant reductions in nutrient concentrations downstream of the beaver enclosure (NO₃ = -43%; PO₄ = -51%), as well as significantly lower concentrations relative to the agricultural control site (NO₃ = -64%; PO₄ = -86%). Conversely, DOC concentrations were significantly higher downstream of the enclosure (+94%) and compared to the control (+272%). Greater reductions in nitrate and phosphate during the summer (NO₃ = -47%; PO₄ = -61%) compared to winter (NO₃ = -37%; PO₄ = -38%) indicated biological assimilation within the beaver wetland as a likely causal mechanism, whilst lower dissolved oxygen concentrations within the beaver ponds indicated a role for denitrification in nitrate removal. Overall, these results demonstrate that beaver wetlands can significantly mitigate eutrophication risk in agriculturally impacted chalk streams and provides further evidence in support of their wider reintroduction to English catchments.

Keywords Beaver; Reintroduction · Water quality · River · Nitrogen · Phosphorus

Introduction

Lowland chalk streams are a globally rare and ecologically important groundwater-dependent ecosystem found almost exclusively in southern and eastern England (Berrie 1992; Mondon et al. 2021). Defined as a river deriving the majority (> 75%) of its flow from an underlying chalk aquifer composed of fine-grained white limestone, they are characterised by cool, alkaline, mineral-rich waters with low turbidity, a clean gravel bed, and stable discharge (Berrie 1992). These characteristics provide optimal growing conditions for a diverse range of calcareous aquatic plant specialists,

whilst supporting abundant populations of aquatic invertebrates and salmonid fish species, making chalk streams one of the most important wild fisheries in the UK (Westlake et al. 1972; Acornley 1999; Acornley and Sear 1999). However, groundwater-fed chalk streams are highly vulnerable to drought, sensitive to water pollution, and have historically been subjected to intensive anthropogenic modification for agricultural land drainage and groundwater abstraction, resulting in severe physical, chemical, and ecological degradation (Wood and Petts 1999; Neal et al. 2000; Cooper et al. 2020). Suffering in particular from eutrophication as a result of nitrogen and phosphorus enrichment derived from agricultural fertilisers and sewage effluent (Bowes et al. 2005; Jarvie et al. 2006; Lloyd et al. 2019), just 23% of England's chalk streams are classified as being in 'good' ecological status and 0% are achieving 'good' chemical status in adherence to the EU Water Framework Directive (2000/60/EC) (O'Neill and Hughes 2014; Cooper and Hiscock 2023). Chalk streams are a UK government priority

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habitat for restoration (Environment Agency 2021) and mitigation measures are therefore required to improve chalk stream status. The reintroduction of the Eurasian beaver (*Castor fiber*) is currently being proposed more broadly by catchment conservation groups as a potential river restoration solution (Auster et al. 2020, 2023).

Once widespread across Europe, the Eurasian beaver was eradicated from most of its former range between the tenth and twentieth centuries due to overexploitation for its fur, meat, and castoreum, as well as through wetland drainage and woodland clearance leading to widespread habitat loss (Collen and Gibson 2000; Halley et al. 2021). Both the Eurasian and North America (*Castor canadensis*) species of beaver are recognised keystone species and ecosystem engineers (Law et al. 2017), significantly impacting upon catchment hydrological and geomorphological functioning through the creation of semi-permeable woody dams in lotic systems and thereby creating new lentic environments within the river corridor (Morrison et al. 2015; Brazier et al. 2021). These changes in riparian morphology can benefit the surrounding biotic communities and drive changes in fluvial biogeochemical cycles that can impact upon the hydrochemistry and nutrient fluxes (Rosell et al. 2005; Larsen et al. 2021). By significantly slowing water flow through catchments, beaver wetlands provide opportunities for enhanced surface water storage and groundwater recharge that in turn can reduce downstream flood risk, improve localised drought resilience, and mitigate water scarcity at the sub-catchment scale (Westbrook et al. 2006; Majerova et al. 2015; Neumayer et al. 2020; Smith et al. 2020). Beaver wetlands have also been shown to impact upon pollutant mobilisation and lead to improved downstream water quality through processes including enhanced deposition of suspended sediment and particulate-bound phosphorus, increased nutrient assimilation by aquatic plant communities, and increased denitrification within anoxic wetland sediments reducing dissolved nitrate concentrations (Lazar et al. 2015; Puttock et al. 2017; Wegener et al. 2017). It is partly for these reasons that numerous beaver reintroduction programmes are currently underway across Europe as catchment managers seek to restore lost ecosystem services using nature-based solutions (Stringer and Gaywood 2016; Thompson et al. 2020; Wróbel 2020; Halley et al. 2021). However, the biogeochemical impacts of beaver wetlands are highly variable and not always beneficial, with various studies reporting increases in ammonia, phosphate, dissolved organic carbon and heavy metal concentrations downstream of beaver wetlands (e.g., Butler and Malanson 2005; Błędzki et al. 2011; Ecke et al. 2017; Larsen et al. 2021). With such wide variability in reported beaver impacts, there is concern that potentially detrimental reintroduction schemes may be taking place based on a misunderstanding of the current science, especially in the absence of any prior studies from

catchments with similar hydrogeological and ecological characteristics.

In this regard, whilst a range of hydrological, biogeochemical, and ecological impacts of beaver wetlands have been demonstrated in several upland and impermeable catchments in the United Kingdom (Gaywood 2017; Puttock et al. 2018, 2021), to date, limited research has been conducted on the impact of beaver reintroduction in the lowland, groundwater-dominated, agricultural chalk stream catchments of southern and eastern England. Therefore, in September 2021, a pair of Eurasian beaver were reintroduced to the headwaters of the agriculture-dominated chalk stream River Glaven catchment, Norfolk, UK. The aim of this research was to assess the efficacy of Eurasian beaver reintroduction as a nature-based solution for mitigating agricultural nutrient pollution in this priority chalk stream catchment. This was achieved through the following research objectives:

- i. To compare the hydrochemistry of two neighbouring sub-catchments of the River Glaven – one with beavers (impact) and one without (control) – across two hydrological years (March 2022 – May 2024).
- ii. To evaluate how the degree of hydrological disturbance (dam and wetland creation) affected the spatial variability in water quality across the impact site.
- iii. To statistically investigate the relationships between hydrochemical parameters to ascertain which biogeochemical processes were driving variability in water quality.

This study serves as an empirical assessment on the potential for beaver reintroduction to mitigate agricultural nutrient pollution in chalk stream catchments, and in so doing can help to support policymakers' currently assessing the wider reintroduction of beavers in England.

Methods

Study Location

The River Glaven, Norfolk, UK, is a 17 km length, lowland (< 80 m above sea-level), groundwater-dominated chalk stream that drains a catchment area of 115 km² prior to discharging into the southern North Sea at Cley-next-the-Sea (52°57'26.1"N 1°02'36.9"E). Whilst the River Glaven is ungauged, it is hydrologically similar to the neighbouring River Stiffkey catchment (88 km²) which has a mean annual discharge of 0.597 m³ s⁻¹ and a baseflow index of 0.79 close to the tidal extent (NRFA 2024). The catchment bedrock is Cretaceous White Chalk which is overlain by complex superficial deposits of Pleistocene glacial tills and

glaciofluvial sands and gravels of widely varying thickness (Holt-Wilson 2014). Climatologically, the catchment experiences a temperate maritime climate, with a mean annual temperature of 10.7 °C and a mean annual precipitation total of 637 mm (1991–2020; Met Office 2024).

The River Glaven is a Biodiversity Action Plan Priority Habitat due to the diversity of its distinctive calcareous flora and fauna, with the wider catchment also supporting 171 species of conservation concern and eight Sites of Special Scientific Interest (SSSI) that cover 19% of the catchment (NBIS 2014). However, much of the river habitat is in unfavourable condition due to a combination of poor water quality and a degraded hydromorphology as a result of historic land drainage. Arable agriculture (wheat, barley, oilseed rape, sugar beet) is a major driver behind this degradation and dominates land use in the catchment (76%), with the rest of the catchment comprising woodland (14%), grassland (5%), rural settlements (4%) and heathland (1%).

This study focuses specifically upon a ~500 m stretch at the uppermost limit of the River Glaven at Baconsthorpe Wood (69–76 m above sea-level), where in September 2021

a pair of Eurasian beavers were introduced into a 6-ha enclosure within a homogenous poplar-dominated (*Populus* sp.) deciduous woodland (Fig. 1). At this location, the River Glaven upwells from the underlying chalk aquifer at the very top of the enclosure as a first-order headwater stream (< 1 m wide) surrounded by intensive arable farmland.

Experimental Design

During the first 12 months following reintroduction, the lower section of the woodland was transformed into a complex mosaic of channels and ponds due to the beavers' damming, canal digging, and tree felling activity. This activity notably increased from early 2023 onwards after the birth of two beaver kits in 2023 and a further two kits in 2024 and resulted in heightened activity within the mid-section of the enclosure. By summer 2024, a total of 13 dams had been constructed in a cascade through the site with the majority of these built along the line of the pre-existing stream channel. The dense tree canopy prohibited an aerial drone survey to accurately quantify the proportion of the site impacted by

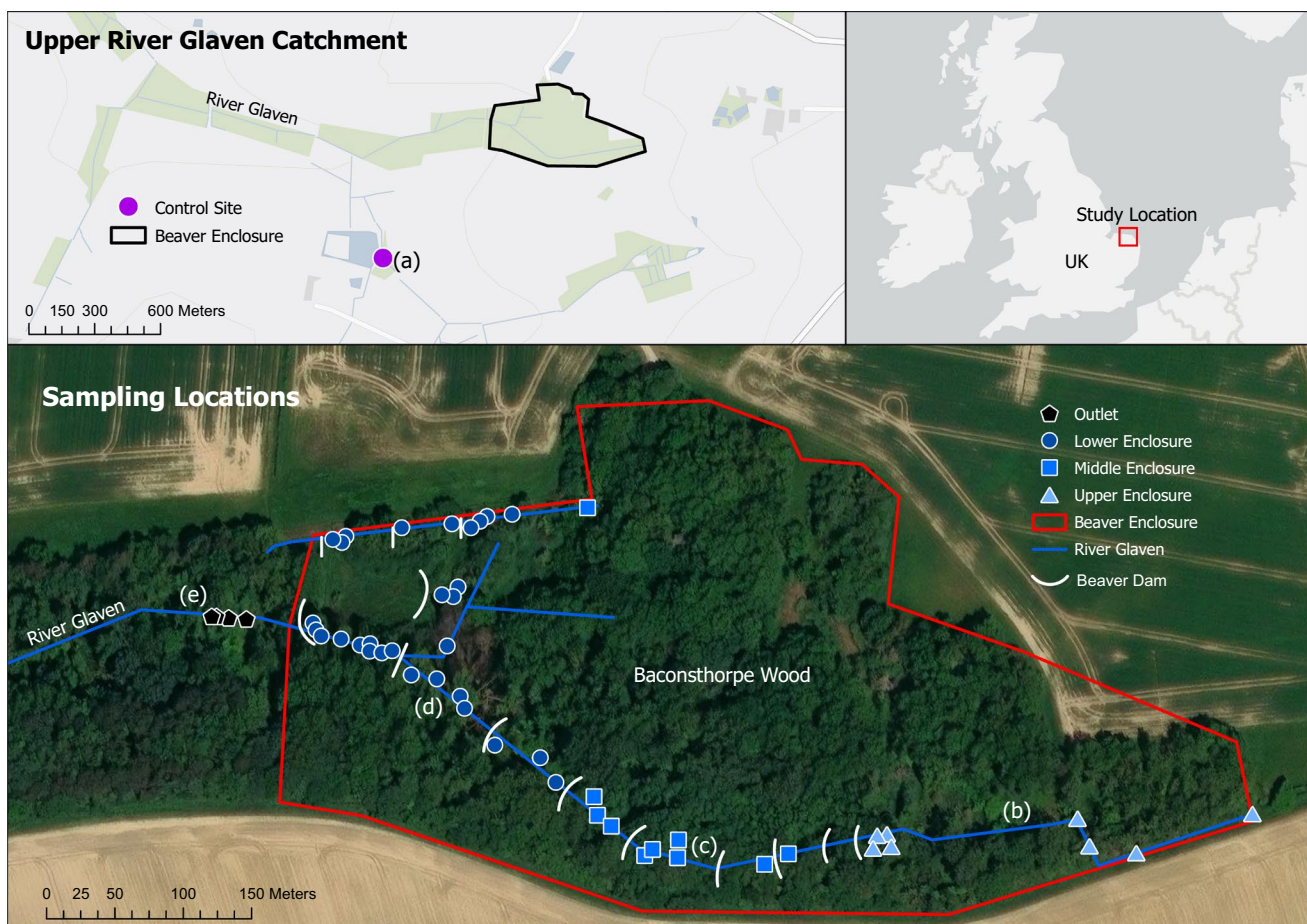


Fig. 1 Eurasian beaver reintroduction site on the chalk stream River Glaven, UK. Sampling locations classified according to the degree of hydrological disturbance by the beavers. Letters refer to Fig. 2 photograph locations

the beavers, but was estimated based on ground observations to be ~40% by summer 2024. To assess the impact of this activity upon the fluvial hydrochemistry, the study area was broadly classified into four categories based on the degree of visual hydrological disturbance (Fig. 2):

Minor disturbance (upper enclosure): no evidence of dam building; lotic dominated environment with unimpeded stream flow.

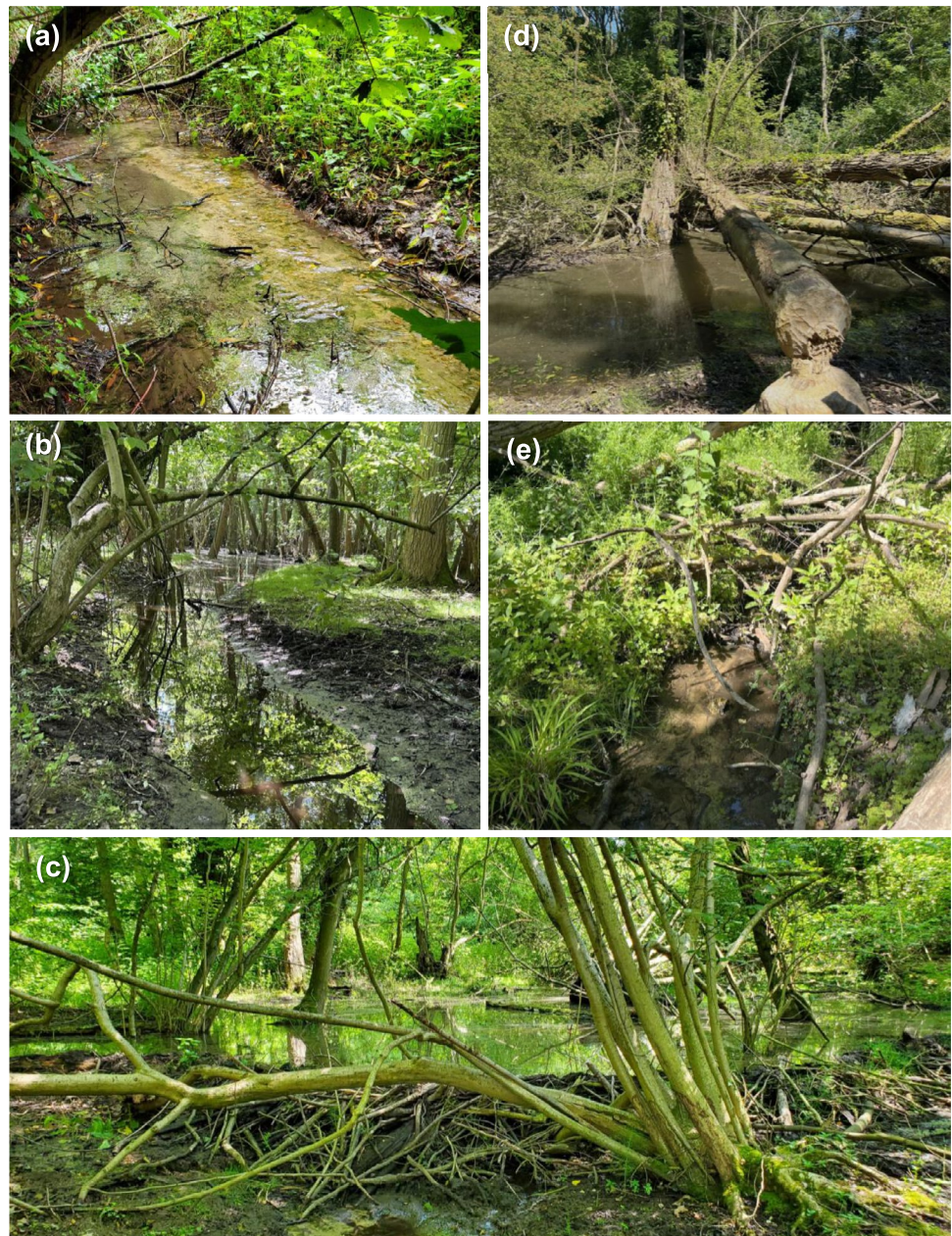
Moderate disturbance (middle enclosure): small to medium sized dams present with minor to moderate ponding evident; series of ponds separated by stretches of flowing and largely unimpeded stream channel.

Major disturbance (lower enclosure): large dams present with major ponding evident; lentic dominated environment with limited to no visible stream flow between dam structures.

Enclosure outlet: outside of the enclosure fence, receiving all water that passes through the enclosure and drains a catchment area of 0.35 km².

In addition, a neighbouring tributary 500 m south of the enclosure was selected as a **control site** without beavers and representative of a typical agricultural drainage channel in the Glaven catchment (Fig. 1). This control site was similarly a first order headwater stream (< 1.5 m

Fig. 2 River Glaven water sampling locations classified by the degree of hydrological disturbance. (a) control stream, no disturbance; (b) upper enclosure, minor disturbance; (c) middle enclosure, moderate disturbance; (d) lower enclosure, major disturbance; (e) enclosure outlet



wide) that drained a 0.94 km² catchment area encompassing the same soil types, bedrock, and superficial geology as the impact site, whilst also draining the same arable field (sugar beet in 2023, wheat in 2024) that separated the two locations.

Sample Collection

In total, 190 water samples were collected via manual grab sampling in 250 mL HDPE Nalgene bottles across the impact and control sites between March 2022 and May 2024 and subsequently returned on ice to the University of East Anglia for laboratory analysis. Samples were collected from both free flowing and ponded areas of the site. Due to the continual evolution of the site over the study period, sampling locations were not fixed between sampling rounds but rather varied in response to the disturbance conditions encountered at the time. Of these samples, 28 were representative of minor disturbance (upper enclosure), 34 of moderate disturbance (middle enclosure), 97 of major disturbance (lower enclosure), 16 from the enclosure outlet, and 15 from the control site (Fig. 1). Temporally, 105 samples were collected during the summer season (April – September) and 85 during the winter (October – March). In addition, *in-situ* measurements of dissolved oxygen (DO) and water temperature were recorded using a HANNA HI 9146 portable dissolved oxygen meter at each sampling location. Low stream discharge both into and out of the enclosure (the upper enclosure dried up completely during summer 2022) prohibited any continuous flow gauging and thus this study focused solely upon the hydrochemical impacts rather than the hydrology. However, a discharge record for the neighbouring, hydrologically similar, River Stiffkey is provided in the supplementary material (Figure SM1), with this revealing that mean summer discharge (0.073 m³ s⁻¹) was 21% of the mean winter discharge (0.341 m³ s⁻¹) during the period of data collection.

Laboratory Analysis

On return to the laboratory, all samples were vacuum filtered through pre-weighed 0.7 µm filter papers to remove suspended solids, with filters then oven dried at 105 °C for 2 h and reweighed to determine the total suspended solid (TSS) concentration. On the resulting filtrate, nitrate (NO₃-N) concentrations were determined using a Lovibond MD 600 multiparameter photometer with a precision of 0.5 mg N L⁻¹ and detection range of 1–30 mg N L⁻¹. Phosphate (PO₄-P) concentrations were determined colorimetrically (molybdate) using a spectrophotometer (885 nm) with a precision of 3 µg L⁻¹. Non-purgeable dissolved organic carbon (DOC)

concentrations were determined using a Skalar Formacs CA15 TOC/TN analyser with precisions of 0.49 mg L⁻¹.

Data Analysis

All data processing and analysis was conducted in R Studio v4.4.0 (R Core Team 2024), with spatial mapping conducted in ArcPro 3.3.0. The significance of beaver impacts upon water quality were assessed statistically by comparing the data between the upper vs outlet (paired) and outlet vs control (unpaired) locations using the non-parametric Wilcoxon signed-rank and rank-sum tests, respectively. The relationships between individual parameters were assessed via a linear correlation matrix using the ‘*pairs*’ function. To identify whether there were distinct hydrochemical signatures for each of the disturbance regimes, a principal components analysis (PCA) was undertaken on the standardized hydrochemical data using the ‘*FactoMineR*’ package (Le et al. 2008). Missing data were imputed prior to running the PCA using the ‘*missMDA*’ package (Figure SM2), whilst an eigenvalue cut-off point of > 1 was used as the criterion for retaining principal components (Table SM1).

To provide broader context, the hydrochemical data were compared against the EU Water Framework Directive (2000/60/EC; WFD) environmental quality standards (EQS) for freshwater (Table 1). The EU WFD had the original aim to ensure that all waterbodies within member states achieve ‘good’ qualitative and quantitative status by 2015. However, by 2015 only 53% of waterbodies were meeting this target and many member states applied for extensions to the end of the second (2015 – 2021) and third (2021 – 2027) management cycles to achieve this goal (Cooper and Hiscock 2023). For WFD classification purposes, this tributary of the River Glaven was designated as a small (< 100 km² catchment), lowland (mean altitude < 200 m), calcareous river system.

Results & Discussion

Hydrochemical Signatures

The results of the PCA are displayed in Fig. 3 for the first two components which collectively explained 58.2% of the variance in the full dataset. The PCA biplot reveals the degree of differentiation in hydrochemistry between the different disturbance regimes, whilst the variable correlation plot displays the relationship between the six measured parameters. Positively correlated variables are grouped together, whilst negatively correlated variables are positioned on opposite sides of the plot origin. The distance between the variables and the origin (i.e. the length of the arrow) represents the factor loadings, with longer arrows

Table 1 EU Water Framework Directive environmental quality standards (EQS) applied to the River Glaven (WISE-Freshwater 2022)

Parameter	Units	Environmental Quality Standard (EQS)				
		Bad	Poor	Moderate	Good	High
Nitrate ¹	mg N L ⁻¹	> 11.3	11.3 – 5.6	5.6 – 3.6	3.6 – 0.8	< 0.8
Reactive phosphorus ²	mg P L ⁻¹	> 1.003	1.003 – 0.173	0.173 – 0.069	0.069 – 0.036	< 0.036
Dissolved oxygen ³	%	< 45	45 – 54	55 – 60	61 – 70	> 70
Water temperature ³	°C	> 30	30 – 28	28 – 23	23 – 20	< 20
TSS ⁴	mg L ⁻¹	-	> 25	-	< 25	-

¹The UK does not formally assign an EQS for riverine nitrate and thus the thresholds used here reflect typical values applied in other EU member states under the EU Nitrates Directive (91/676/EEC)

²UK Technical Advisory Group (UKTAG) Recommendations on Phosphorus Standards for Rivers (2013)

³The Water Framework Directive Standards and Classification Directions for England and Wales (2015)

⁴EU Freshwater Fish Directive (2006/44/EC)

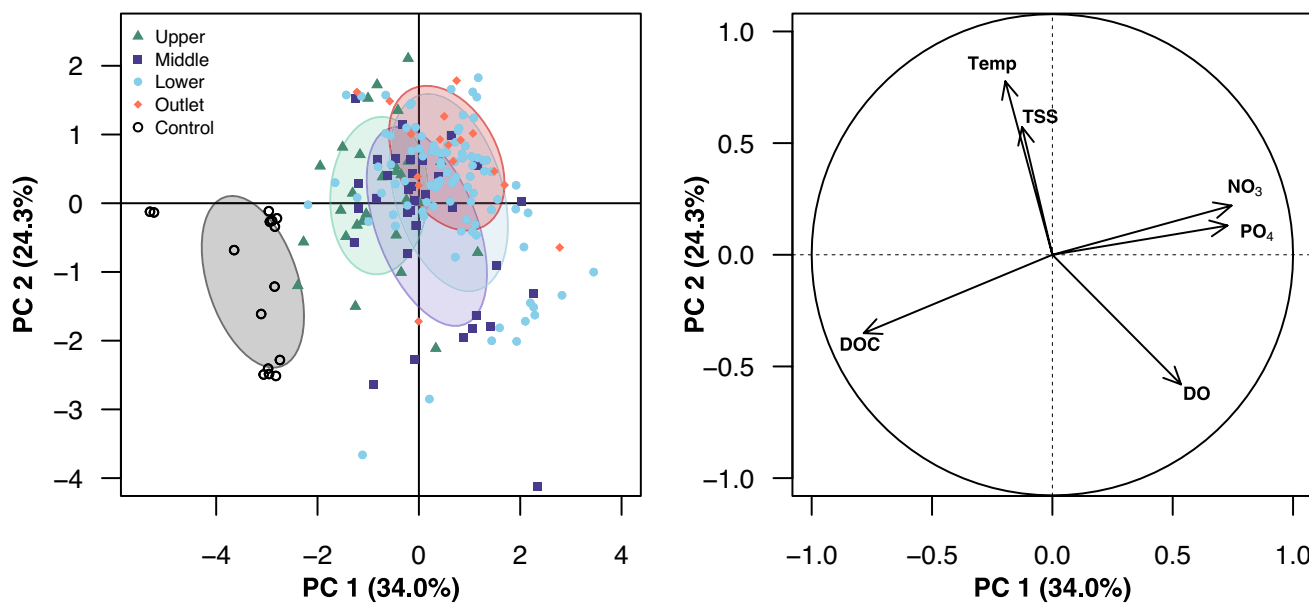


Fig. 3 Principal components analysis plots of the control and impact site hydrochemistry for the first two components. **(Left)** biplot of individual datapoints with data grouped by sampling location and

associated disturbance regime; shaded ellipsoids encompass 50% of the group range. **(Right)** variable correlation plot with arrow length proportional to the factor loading

indicating the variable yields greater discrimination between the disturbance classifications.

For PC1 (34.0% of the total variance), the PCA biplot revealed a clearly distinct hydrochemical signature for the control site compared to the impact locations. The variable loadings (also see Figure SM3) revealed this differentiation was driven strongly by significantly higher concentrations of nitrate, phosphate, and DOC at the control site, despite the carbon and nutrient variables themselves being negatively correlated. In contrast, the hydrochemical composition of the four impact site locations displayed a much higher degree of overlap, although higher DOC and lower phosphate and nitrate did provide some degree of differentiation between the upper and outlet locations. For PC2 (24.3% of the total variance), the negatively correlated variables of dissolved

oxygen and water temperature proved to be the strongest discriminators, with lower dissolved oxygen within the middle enclosure and higher water temperatures at the control site driving this differentiation.

Given that the control site hydrochemistry had a distinct composition from the upper enclosure implies that a significant amount of the differentiation in water quality observed between the control and impact locations was driven by differences in the broader environmental setting rather than the beavers themselves. This is most likely due to the impact site having greater riparian woodland buffering making it less susceptible to receiving agricultural runoff from the neighbouring arable fields, whilst also increasing the potential for nutrient uptake by riparian trees and increasing leaf litter input leading to elevated organic matter concentrations.

Therefore, the assessment of the beaver impacts upon the hydrochemistry are most robust when comparing upper vs outlet locations, rather than the outlet vs control. Nevertheless, the control site serves as a good example of a typical chalk stream impacted by agricultural activity that is widespread across southern and eastern England.

Nitrogen

Substantial reductions in dissolved inorganic nitrogen concentrations were recorded across the beaver enclosure, with mean nitrate concentrations significantly ($p=0.012$) reduced by 43% between the upper (4.66 mg N L^{-1}) and outlet (2.68 mg N L^{-1}) monitoring locations (Fig. 4; Table 2). Spatially, this reduction was consistent along the 500 m stream reach, with mean concentrations reducing by 0.75, 0.88 and 0.35 mg N L^{-1} between the upper-middle, middle-lower, and lower-outlet locations, respectively. Mean nitrate concentrations at the enclosure outlet were also 64% lower than the neighbouring agricultural control site (7.49 mg N L^{-1}). In terms of the WFD classification, 75% of samples at the outlet were classified as 'good' or 'high' status for nitrate, compared with 44% in the upper enclosure and just 7% at the control site.

This pattern of reduced nitrate concentrations is broadly consistent with other studies which report reductions in dissolved inorganic nitrogen across beaver impacted fluvial systems (Ecke et al. 2017). Denitrification and biological assimilation are widely cited as the dominant nitrate removal mechanisms in beaver wetlands (Devito and Dillon 1993; Lazar et al. 2015; Saunders and Kalff 2001), and the results generated here are supportive of this. Mean nitrate removal between the upper and outlet sites was greater in summer (47%) than winter (37%), indicating increased biological assimilation of dissolved nitrogen during the growing season by phytoplankton, periphyton, macrophytes, microorganisms and floodplain trees. Similarly, higher mean water temperatures (summer = $14.8 \text{ }^\circ\text{C}$, winter = $11.0 \text{ }^\circ\text{C}$) and lower dissolved oxygen concentrations (summer = 56.2%, winter = 61.0%) during the summer months (Fig. 5) would have provided conditions more conducive to bacterially mediated denitrification, with nitrate concentrations displaying a positive correlation ($r=0.30$), albeit rather weak, with dissolved oxygen concentrations (Fig. 6; Table SM2). The lower dissolved oxygen concentrations within the beaver ponds were likely driven by a combination of higher water temperatures reducing oxygen solubility, reduced turbulence from a reduction in flow velocity, and increased aerobic decomposition of organic matter (Larsen et al. 2021).

Some studies have reported increases in nitrate concentration downstream of beaver wetlands as organic matter, mineralised to ammonium under low oxygen conditions within the wetlands, is oxidised to nitrate further downstream once

oxygen concentrations increase (Błędzki et al. 2011; Larsen et al. 2021). Whilst no evidence of ammonium oxidation was found in our study immediately downstream of the enclosure at the outlet site, further investigation at a greater distance downstream, coupled with the generation of ammonium data across the entire site, will be required to meaningfully assess this.

Phosphorus

As with nitrate, significant ($p=0.003$) phosphate reductions were observed across the beaver enclosure, with mean concentrations reducing by 51% between the upper ($0.041 \text{ mg P L}^{-1}$) and outlet ($0.020 \text{ mg P L}^{-1}$) monitoring locations (Fig. 4; Table 2). Spatially, mean phosphate concentrations decreased by 0.008 and $0.016 \text{ mg P L}^{-1}$ between the upper-middle and middle-lower locations, respectively, with a small increase of $0.003 \text{ mg P L}^{-1}$ observed between the lower and outlet sites. Mean phosphate concentrations at the enclosure outlet were also 86% lower than at the agricultural control site ($0.147 \text{ mg P L}^{-1}$), with phosphate concentrations more broadly being significantly ($p<0.001$) lower across the entire impact site. In terms of WFD classification, 100% of samples at the outlet were classified as 'good' or 'high' status for phosphate, compared with 63% in the upper enclosure and 0% at the control site.

Previous studies have generally reported a mixed picture regarding beaver impacts upon phosphorus concentrations due to competing biogeochemical processes occurring within different components of the wetland system (Ecke et al. 2017; Larsen et al. 2021). Here, mean phosphate removal across the beaver enclosure was greatest during the summer (−61%) compared to the winter (−38%), indicating a potentially dominant role for biological assimilation in the removal of dissolved phosphorus from the water column during the growing season, coupled with release via decomposition of organic matter during the winter (Withers and Jarvie 2006; Reddy and DeLaune 2008).

Dissolved phosphate can also adsorb onto the surfaces of metal oxyhydroxides in suspended sediments and subsequently be deposited within wetland bed sediments (Cooper et al. 2015), reducing the amount of dissolved phosphate available to be exported from the impact site. Here, however, whilst total suspended solid concentrations were significantly ($p=0.010$) higher in the beaver enclosure (16.0 mg L^{-1}) compared to the control (7.6 mg L^{-1}) (Fig. 5; Table 2), there was no significant correlation found between TSS and phosphate concentrations (Fig. 6). Other studies have conversely reported that dissolved phosphate concentrations can increase under the lower oxygen conditions commonly found in beaver wetlands due to phosphate release from the surfaces of metal oxides which dissolve under anoxic conditions and release adsorbed phosphorus (Klotz 1998).

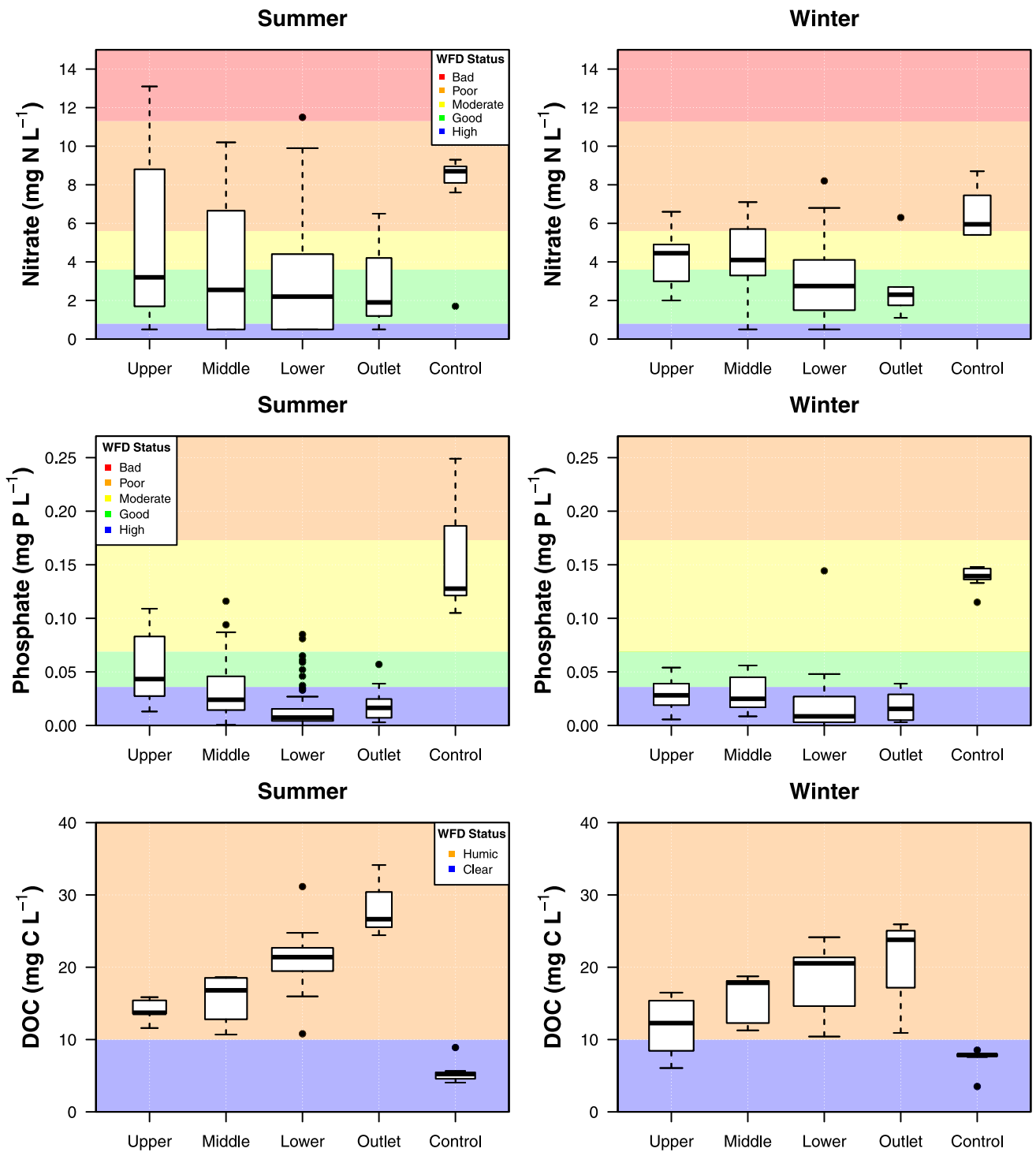


Fig. 4 Seasonal nitrate, phosphate, and dissolved organic carbon concentrations recorded in water samples collected across the control and impact sites between March 2022 and May 2024. The solid central line is the median, the boxes the interquartile range, the circles the

outliers, and the whiskers 1.5× the interquartile range or the maximum/minimum value if the latter is smaller. Box width is proportional to sample size

Yet here we found there to be a weak positive correlation ($r=0.29$) between dissolved oxygen and phosphate concentrations (Fig. 6), implying these abiotic processes were

potentially a less dominant control on phosphate concentrations than biotic assimilation. Nevertheless, further research at this site into the full suite of phosphorus phases (organic,

Table 2 Mean water quality parameters by monitoring location across the control and impact sites. Δ^{impact} refers to the percentage change between the upper and outlet monitoring locations within the impact site. Δ^{control} refers to the percentage difference between the control and outlet locations. See Fig. 1 for the position of the monitoring locations

Parameter	Units	Monitoring Location						
		Upper (n=28)	Middle (n=34)	Lower (n=97)	Outlet (n=16)	Δ^{impact} (%)	Control (n=15)	Δ^{control} (%)
NO ₃ -N	mg N/L	4.66	3.91	3.03	2.68	-42.5	7.49	-64.2
PO ₄ -P	mg P/L	0.041	0.033	0.017	0.020	-51.2	0.147	-86.4
DOC	mg/L	12.5	15.8	19.8	24.2	+93.6	6.5	+272.3
TSS	mg/L	19.0	17.8	14.4	17.6	-7.4	7.6	+131.6
DO	%	70.6	48.5	55.5	74.5	+3.9	64.3	+10.2
Temperature	°C	11.5	13.4	13.1	12.7		14.9	

particulate, dissolved, and total P) would be required to confirm the dominant biogeochemical processes.

Organic Carbon

In contrast to the nutrients, dissolved organic carbon concentrations significantly ($p=0.003$) increased across the beaver enclosure, with mean concentrations increasing by 94% between the upper (12.5 mg L⁻¹) and outlet (24.2 mg L⁻¹) locations (Fig. 4; Table 2). Spatially, mean DOC concentrations consistently increased by 3.3, 4.0, and 4.6 mg L⁻¹ between the upper-middle, middle-lower, and lower-outlet sites, respectively. Mean DOC concentrations were also 272% higher at the enclosure outlet compared to the control site (6.5 mg L⁻¹), with 100% of samples collected from across the impact site classified as 'humic' status compared with 100% classified as 'clear' status at the control.

These results are consistent with previous studies which have similarly shown that the elevated ecosystem productivity and enhanced residence times within beaver wetlands results in increased autochthonous carbon production and cycling that in turn leads to higher DOC concentrations downstream (Nummi et al. 2018; Larsen et al. 2021). Whilst typically lignin-rich and therefore more recalcitrant (Reddy and DeLaune 2008), large volumes of decaying woody biomass within the beaver ponds, dams and canals nevertheless provide an abundant supply of carbon which far exceeds the amount available at both the non-wooded agricultural control and upstream sites (Thompson et al. 2016). Additionally, the enlarged hyporheic zone caused by damming and flooding of the valley floor can increase the hyporheic zone exchange of carbon and mobilisation of existing organic matter stored within the floodplain soils (Nummi et al. 2018; Wang et al. 2018).

Temporally, the increase in DOC leaving the enclosure was greatest during the summer (+102%) compared to the winter (+79%), matching the findings of other studies which have also reported a strong seasonality to DOC fluxes and linked this to elevated autochthonous carbon production in wetlands during the summer months (Larsen et al. 2021). This is also supported by the relatively strong

negative correlations found here between DOC and phosphate ($r=-0.50$) and DOC and nitrate ($r=-0.56$) (Fig. 6), indicating the biological assimilation of dissolved nutrient fractions into plant and algal biomass and the resulting increase in organic carbon production. Conversely, no relationship was found here between DOC concentrations and either dissolved oxygen, water temperature, or total suspended solids (Fig. 6).

Suspended Solids, Dissolved Oxygen & Water Temperature

Mean total suspended solids concentrations were 7% lower at the outlet (17.6 mg L⁻¹) compared to the upper (19.0 mg L⁻¹) monitoring location, however this reduction across the beaver enclosure was not significant and was less than reported elsewhere (Puttock et al. 2017) (Fig. 5). This reflects that, in contrast to previous studies undertaken on rivers with lower baseflow indices exposed to a greater amount of sediment-laden surface runoff, the river water in this study was almost exclusively upwelled chalk groundwater and thus contained comparatively little suspended sediment (and likely by extension, particulate phosphorus) upon entering the enclosure. Nevertheless, mean TSS concentrations were significantly ($p=0.028$) higher by 132% at the outlet compared to the control site (7.6 mg L⁻¹), aligning with some previous studies which have reported elevated TSS concentrations within beaver wetlands due to beaver activity entraining deposited bed sediments that accumulate behind dam structures (Ecke et al. 2017). TSS concentrations across the entire site were also significantly higher during the summer (20.2 mg L⁻¹) compared to winter (9.3 mg L⁻¹), reflecting the lower water levels during the summer months that lead to a concentration of any resuspended particulate material. In terms of the WFD classification, 85% of samples taken across the beaver enclosure had 'good' status, compared with 93% for the control site.

Dissolved oxygen concentrations were found to be highly variable between disturbance regimes, with mean concentrations being lowest in the deeper more heavily ponded middle (48.5%) and lower (55.5%) sites and highest in the shallower

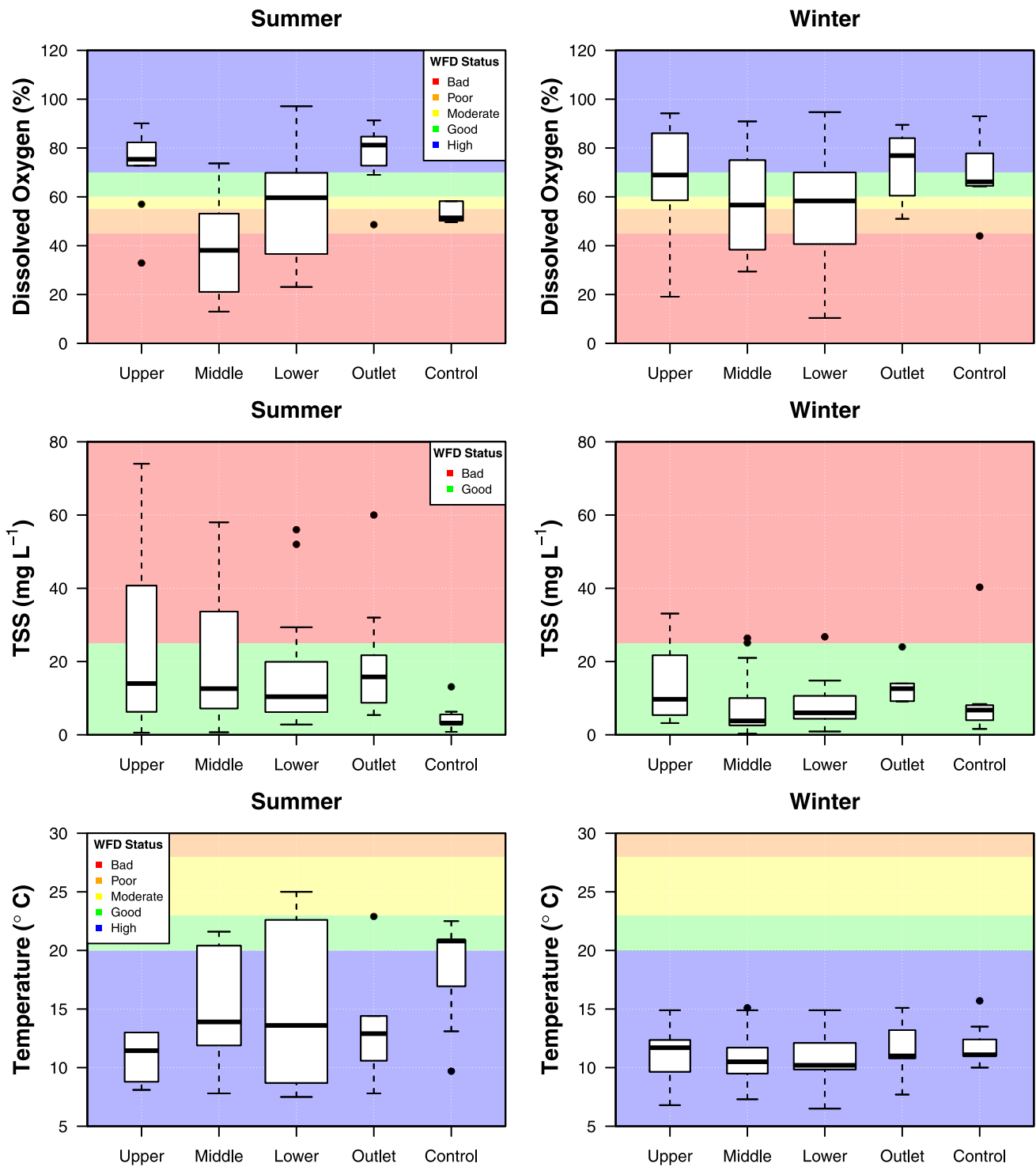


Fig. 5 Seasonal dissolved oxygen and total suspended solids concentrations, and water temperature recorded in water samples collected across the control and impact sites between March 2022 and May 2024. The solid central line is the median, the boxes the interquartile

range, the circles the outliers, and the whiskers 1.5×the interquartile range or the maximum/minimum value if the latter is smaller. Box width is proportional to sample size

more free-flowing upper (70.6%) and outlet (74.5%) locations where dissolved oxygen could more readily equilibrate with the atmosphere (Fig. 5; Table 2). Indeed, 61% of

samples in the middle and lower enclosure failed to achieve ‘good’ WFD status, compared to just 27% of the upper and outlet samples. These observations align with previous

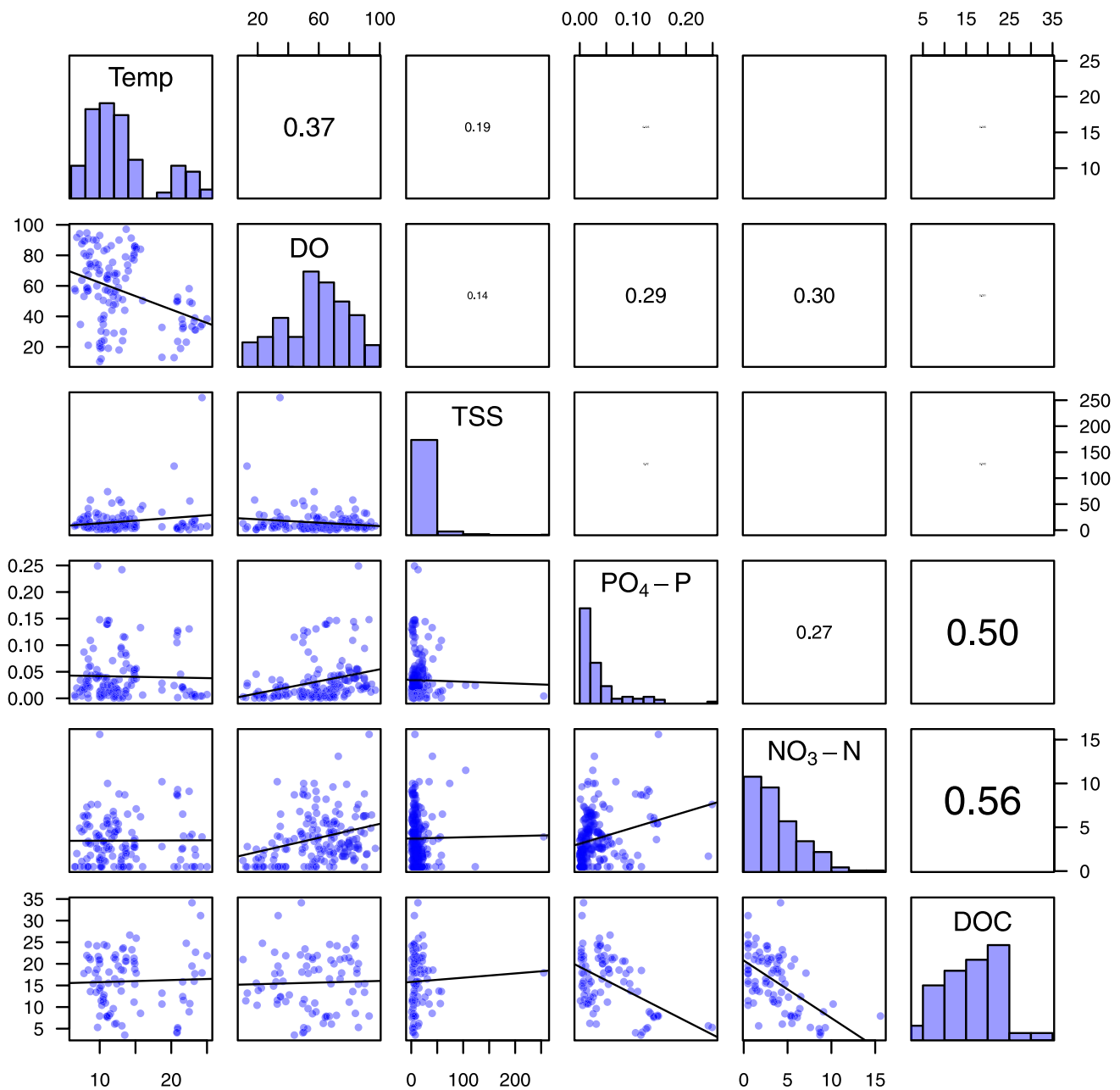


Fig. 6 Correlation panel plot of water samples collected across all sites over the full monitoring period (2022–2024). Units are in mg/L for TSS, PO₄-P, NO₃-N and DOC, % for DO, and °C for water temperature. The upper right panel displays Pearson's correlation coefficients

with text size proportional to correlation strength. The bottom left panel displayed the linear regression. Central histograms display the parameter distribution. Linear regression equations and significance values are displayed in Table SM2

studies that similarly report the development of anaerobic conditions behind beaver dams that may lead to localised deleterious impacts upon aquatic fauna, particularly sensitive fish species (Kemp et al. 2012). Aerobic decomposition of organic matter accumulated within the ponded sections, coupled with higher water temperatures and a raised water table, would all have played a part in reducing dissolved oxygen concentrations in the heavily impacted sections of the site (Larsen et al. 2021). Indeed, dissolved oxygen and

water temperature displayed a moderate ($r = -0.37$) negative correlation (Fig. 5) and mean oxygen concentrations were marginally higher during the cooler winter (61.0%) compared to warmer summer (56.2%) season.

Mean water temperatures were ~ 2 °C higher in the ponded middle (13.4 °C) and lower (13.1 °C) sections compared to the lotic upper enclosure (11.5 °C) with this temperature contrast being much more pronounced during the summer (Fig. 5), as observed in previous studies (Kemp et al. 2012).

This is likely to have been driven by the larger surface area of the ponds in sites of open canopy allowing for increased solar heating (Weber et al. 2017), with mean water temperatures also elevated at the more open (low tree cover) control site during the summer (18.3 °C). During the winter, all sites displayed comparable water temperatures.

Conclusions

With the reintroduction of the Eurasian beaver being proposed as a potential solution for restoring vulnerable chalk stream habitats in England, the research presented here has sought to provide greater insight into the capacity of beaver wetlands to mitigate eutrophication risk in agricultural chalk stream catchments. The main conclusions of the research are as follows:

1. Nitrate concentrations were significantly reduced downstream of the beaver wetland by 42.5% compared to upstream and by 64.2% compared to the control site, with biological assimilation and denitrification likely to be the main removal mechanisms.
2. Phosphate concentrations were significantly reduced downstream of the beaver wetland by 51.2% compared to upstream and by 86.4% compared to the control site, with biological assimilation likely the main removal mechanism.
3. Conversely, dissolved organic carbon concentrations significantly increased downstream of the beaver wetland by 93.6% compared to upstream and by 272.3% compared to the control site, likely driven by increased autochthonous carbon production and decomposition of woody biomass within the wetland.

Overall, these results demonstrate the reestablishment of beaver wetlands could mitigate eutrophication risk and in so doing support the EU Water Framework Directive goal of achieving ‘good’ physicochemical status in chalk stream catchments. However, further research is required into all dissolved, particulate, and gaseous phases of nitrogen, phosphorus and carbon to improve mechanistic understanding of the dominant biogeochemical processes driving these nutrient changes, and to assess whether the nutrient reductions reported here are likely to be maintained longer term.

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Data Availability The datasets generated during this study are available from the corresponding author on reasonable request.

Declarations

Competing Interests The authors have no relevant financial or non-financial interests to disclose.

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