The effects of water chemistry and lock-mediated connectivity on macroinvertebrate diversity and community structure in a canal in northern England

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ABSTRACT

Freshwater ecosystems are under threat from habitat loss, partly due to urban expansion. However, some elements of urban freshwaters are already integral parts of the urban landscape and so are more resilient to loss, representing opportunities for the enhancement of freshwater resources within cities. This study investigated the biodiversity value of the Leeds-Liverpool Canal in Leeds, UK, in relation to its landscape context. Specifically, we tested the hypotheses that (i) biodiversity value is lowest nearest to the urban core, and (ii) the pattern of canal locks structured ecological communities. Nutrients, metals and dissolved carbon all existed at relatively low concentrations, contrary to what is often seen in urban water bodies, although concentrations were higher in the urban core. This gradient of chemical stress was associated with a decline in macroinvertebrate diversity towards the city centre, which manifested as pollution-sensitive taxa being excluded from this area. Community structures were found to vary between groups of sampling sites separated by locks, suggesting that locks may act as barriers for aquatic invertebrates by restricting dispersal. The results in this study indicate that canals in urban areas can be high-quality habitats, despite the associated anthropogenic stressors, and locks may represent a unique model for researching relationships between connectivity and community structure.

Keywords: canal, macroinvertebrate, pollution, connectivity, biodiversity, community structure

Introduction

Anthropogenic activities are continuing to alter the environment, resulting in the loss of biodiversity and changes in the structure and functionality of natural ecosystems. Anthropogenic stressors include habitat loss, pollution, the introduction of invasive species and the over-exploitation of natural resources, among others (Sala *et al.* 2000). These changes are a substantial threat to the ecosystem services necessary for human society, such as food and water production, carbon storage, climate regulation and nutrient cycling (Hooper *et al.* 2005). Urbanisation is one of the primary causes of habitat loss and is a major threat to biodiversity as it impairs ecosystems more severely than conversion to other types of land use (McKinney 2006). Urbanisation leads to habitat fragmentation

(York *et al.* 2011), improves the fitness of invasive species (McKinney 2006) and impairs gene flow by restricting the dispersal of many species (Riley *et al.* 2005). Urbanisation also causes global habitat homogenisation to the extent that cities on different continents can support more similar biodiversity than a city and its surrounding countryside (McKinney 2006). The majority of people in developed countries live in cities and urban populations are growing in many developing countries (Cohen 2006). As the global human population continues to grow, urban areas are expected to expand to accommodate them (Seto *et al.* 2012). As a result, the total land area covered by urban environments globally is expected to increase by 85% by 2030 (Seto *et al.* 2012). With current rates of biodiversity loss and the expansion of urban areas, it is important to incorporate biodiversity into urban planning to create more sustainable cities, buffering the damage caused by inevitable urbanisation in the future (Kowarik 2011). In addition to reducing biodiversity loss, ecosystems in urban environments are beneficial for human health and well-being (Dallimer *et al.* 2012). Urban ecology has largely been overlooked in comparison to the study of 'natural' ecosystems. However, for the reasons described above, urban ecosystems have received more attention from ecologists in recent years (Kowarik 2011).

Freshwater ecosystems are among the many affected by urbanisation. Indeed, freshwater ecosystems are experiencing a greater rate of biodiversity loss than many of their terrestrial counterparts, due to freshwaters often exhibiting higher initial levels of biodiversity (Sala *et al.* 2000). Vermonden *et al.* (2009) showed that urban drainage systems can support comparable levels of biodiversity to rural drainage systems and natural watercourses, and that they can support IUCN Red List species. Despite the high levels of biodiversity that freshwater ecosystems can support (Lundberg *et al.* 2000; Finlay 2002; Dudgeon *et al.* 2006), they cover only 0.8% of the Earth's surface and contain 0.01% of the Earth's water (Dudgeon *et al.* 2006). This relatively scarce resource is estimated to be of enormous value in terms of ecosystem services, such as food production, drinking water, waste assimilation and recreation. In their estimation of the value of ecosystem services, Costanza *et al.* (1997) valued those associated with freshwater at US$6,579 x 10^9 per year, exceeding the estimated value of all others except marine ecosystems.

71 Biodiversity in urban freshwaters, in particular, is not well understood. Besides natural waterbodies
72 such as rivers and streams, artificial freshwaters are common in urban areas and are created for a
73 wide range of functions, including transport and flood management, as well as aesthetic and
74 recreational purposes (Hassall 2014). The potential that these waterbodies have for providing islands
75 of habitat in an urban setting and thus increasing biodiversity has long been overlooked and
76 potentially underestimated (Hill *et al.* 2017). For example, networks of urban ponds increase
77 biodiversity in urban areas by acting as 'stepping stones', thereby allowing species to move through
78 urban landscapes (Fortuna *et al.* 2006; Garden *et al.* 2010), and urban ponds can support high levels
79 of biodiversity, despite the increase in anthropogenic stressors (Brand *et al.* 2010). Previous studies
80 have shown that urban ponds contain significantly greater macroinvertebrate family diversity (15.1 ±
81 0.6 SE) families than non-urban ponds (13.6 ± 0.3), although species richness did not differ (Hill et al.
82 2018).

83

84 The ecology of canals is under-represented in the urban and freshwater ecology literature despite
85 their prevalence in urbanised landscapes. There are 3,500km of canals in the UK alone, representing
86 at least 7.4km^2 of freshwater (assuming an average width of 2.1m). While some research has focused
87 on the relationship between canals and the dispersal of invasive species (Pimentel 2005; Leuven *et*
88 *al.* 2009), few have investigated the ecological and physical parameters of canals, such as their
89 hydrology, biodiversity, community structures or ecosystem functions, such as nutrient cycling
90 (Vermonden *et al.* 2009). As a result, their value as urban habitats and as refuges for freshwater
91 organisms is unclear (Chester & Robson 2013). As part of the European Union Water Framework
92 Directive (WFD), European rivers are expected to meet targets of good ecological quality, and are
93 therefore monitored for relevant ecological variables (e.g. biodiversity and physio-chemical
94 parameters; European Environment Agency 2017). Canals are rarely included in the WFD and so little
95 of their ecological quality is known. Even with the WFD in place, many rivers do not meet the targets
96 (Haase *et al.* 2013). With the lack of environmental targets set for canals in the UK and elsewhere, it
97 is likely that their potential for providing a good-quality habitat is not being utilised effectively. Canals
98 have a contrasting morphology to natural waterbodies such as rivers and streams; canals are
99 generally straighter and often have vertical banks, resulting in reduced morphological complexity.
100 Canals also have a unique hydrology and connectivity due to the action of locks. By opening and

closing locks, sections of a canal alternate between a chain of standing, isolated waterbodies and a connected, running waterbody. Additionally, while the flow of water is generally downstream, adhesion on canal boats and the action of bow waves result in some upstream movement (Liddle & Scorgie 1980). The action of locks may facilitate the transport of nutrients, pollutants and organisms between sections of a canal and there is evidence that hydrological connectivity across canal networks drives changes in algal community structure (Kelly & Hassall 2018). Furthermore, when a lock opens, the increased turbidity of the water elevates the concentration of dissolved oxygen, which has the potential to increase productivity and ecosystem function (Boets *et al.* 2010). These features make canals unique habitats, which, due to a lack of previous research, have uncertain effects on canal biodiversity. Like other urban ecosystems, canals are often subject to higher levels of pollution when compared with rural freshwaters (Paul & Meyer 2001). While rural freshwaters can be polluted by agricultural run-off, canals are often polluted due to their proximity to roads and industrial sites, and from sewage outlets that feed into the water (Paul & Meyer 2001). However, due to the lack of research on canal ecology, the effects of pollution on biodiversity and community structure are unclear (Gessner *et al.* 2004).

Research into the biodiversity and biotic community structure of canals, as well as the effects of pollution and lock-generated connectivity, could contribute to a greater understanding of the value of canals as urban ecosystems and their ecological functionality. Improving understanding of the ecology of canals is imperative to improving management practices to ensure that canals are managed in a way that increases urban biodiversity without negative effects, such as transferring invasive species (Pimentel 2005) or the development of algal blooms (Vos & Roos 2005). Such improvements would contribute to alleviating the biodiversity loss associated with urban expansion and improving the quality of urban ecosystems for the benefit of human health and well-being. The aim of this study was to investigate the biodiversity value of canals in cities, focusing on the roles of water quality and lock-mediated connectivity. To do this, macroinvertebrate and water samples were collected from a 2km stretch of the Leeds-Liverpool Canal in northern England. Two hypotheses were tested: (1) macroinvertebrate diversity decreases with increasing nutrient and heavy-metal pollution through the exclusion of pollution-sensitive taxa at more polluted sites and (2) locks structure macroinvertebrate community assemblages by creating barriers between sites.

Methods

Fieldwork took place in Leeds, West Yorkshire, UK, on the Leeds-Liverpool Canal, which runs between Hull and Liverpool, connecting the North and Irish Seas. The canal sits within the 1,100km^2 catchment of the River Aire. This catchment has a population density of 1,000 people per km^2 concentrated in major conurbations of Leeds and Bradford in the lower catchment where our study is situated. The upper catchment is dominated by grassland and pastoral landscape with low population densities. Our site sits within the most highly urbanised area of the Aire catchment and so might represent one of the more impacted areas of freshwater in the region. A 2km stretch of the canal from Leeds city centre (53.793°N, -1.550°E) towards Armley (53.802°N, -1.576°E) (Fig. 1) was used in this study, in which 15 sites were selected. This stretch of canal is publicly accessible via a towpath that runs along its northern bank. The southern bank varies in accessibility. The canal has no strict dredging regime and is dredged on an ad-hoc basis. The section of canal used in this study has not been dredged since at least 2010 and high levels of silt on the canal bed have been reported, although no data regarding silt composition or concentrations are available. A stretch of canal that is designated as a site of special scientific interest (SSSI; sites allocated legal protection under UK legislation for their wildlife and/or geological interest, which are maintained to preserve or enhance their habitats or features; Natural England 2013) is located 750m west of the most westward site. All sites were at least 100m away from locks and each other. All fieldwork was conducted with permission from the Canal and River Trust and took place in June and July 2019.

Due to a lack of information regarding the water quality and pollution levels of the site, a wide range of potential pollutants, including nutrients, metals and dissolved carbon, were tested for: ammonia (NH_4), nitrite (NO_2), nitrate (NO_3), phosphate (PO_4), calcium (Ca), magnesium (Mg), sodium (Na), potassium (K), arsenic (As), aluminium (Al), lead (Pb), zinc (Zn), copper (Cu), cobalt (Co), manganese (Mn), chromium (Cr), cadmium (Cd), iron (Fe), dissolved organic carbon (OC) and dissolved inorganic carbon (IC). Two water samples were collected at each site between 24th June and 8th July 2019. A bucket, fixed to a rope, was lowered into the canal to collect a mixed water sample that included the lower and middle depths of the canal. The water was mixed and two water samples were then taken

160 from the bucket in 50ml sampling pots. Water samples were then filtered using 0.45µm nylon syringe
161 filters that had been washed using deionised water. All samples were filtered on the same day as
162 collection. For each water sample, 10ml of filtered water was pipetted into 15ml test tubes in
163 preparation for analysis for nutrients and metals. For samples to be analysed for metals, 15µl of
164 concentrated nitric acid (HNO_3; ARISTAR grade) was then pipetted into each sample to reduce the
165 loss of metals between filtration and analysis. For dissolved carbon analysis, 2ml glass auto-sampler
166 vials were filled with filtered water from each sample. Nutrients, dissolved carbon and metals were
167 analysed using an Auto Analyser (Skalar San++), Combustion Analyser (Analytik Jena Multi N/C
168 2100) and Inductively Coupled Plasma – Optical Emission Spectrophotometer (ICP-OES; Thermo
169 Scientific iCAP7600), respectively. Analyses were performed on individual tubes, rather than in
170 replicates.

171

172 Invertebrate samples were taken via sweep sampling, using a pond net fixed to an extendable metal
173 pole. The net was used to disturb the canal bed before being moved in a figure-of-eight motion five
174 times. The contents of the net were then emptied into a plastic tray containing a small amount of
175 canal water. Any large pieces of vegetation were checked for invertebrates before being discarded.
176 The contents of the tray were then emptied into a 4l sampling pot and taken to the laboratory for
177 identification. Invertebrates were identified to family level (Dobson *et al*. 2012) and the number of
178 individuals of each family was recorded. The identified invertebrates were then stored in ethanol, so
179 that they could be reviewed later if required. All invertebrate samples were identified and preserved
180 on the same day as collection to reduce the likelihood of predation within the sample. All sampling
181 equipment was soaked in hot water for at least 30 minutes after use to ensure that successive
182 samples were not contaminated. Two samples were collected at each site. The first samples were
183 taken between 24th June and 10th July 2019 and the second samples were taken between 12th July
184 and 22nd July 2019. Sites were sampled in the same order both times so that the length of time
185 between sample collection was roughly consistent across all 15 sites.

186

187 Statistical analysis of the data was carried out in R v3.5.1 (R Core Team 2018). To test the effects of
188 water chemistry variables on macroinvertebrate diversity and community structure, water chemistry

189 variables were combined into principal components (PCs) and Shannon's Diversity Index (*H*;
190 Shannon 1948) was calculated for each macroinvertebrate sample using the "vegan" R package
191 (Oksanen *et al.* 2019). Shannon's Diversity Index was chosen over other indices because it accounts
192 for evenness of species, rather than being skewed by the presence of rare species, of which some
193 were found. Shannon's Diversity Index has also been commonly used in previous studies
194 investigating freshwater invertebrate diversity (Hirst *et al.* 2002; Moore & Palmer 2005), so the use of
195 this index allows for direct comparisons to be made with existing literature. Mean diversity was
196 calculated for each site and relationships between the first three PCs and macroinvertebrate diversity
197 were tested. A redundancy analysis (RDA) was then calculated using water chemistry PCs, sites and
198 taxa, and relationships between PCs and community structure were tested.

199

200 To test the effects of lock-mediated connectivity on community structure, sampling sites 2-7 were
201 grouped into "Lock A", 8-9 into "Lock B", 10-11 into "Lock C" and 12-15 into "Lock D" based on groups
202 of sites separated by locks (Fig. 1). An RDA was carried out using lock groups, sites and taxa, and
203 differences in community structure between lock groups was tested using a permutational ANOVA.

204

205 **Results**

206 Of the water chemistry variables tested, all were found to be present in the water samples except Cd,
207 Co and Cr. K and Mg were excluded from statistical analysis due to them showing little variation
208 between sites. Cu, Al, As and Pb were also excluded due to concentrations at or below the lower
209 detection limits of the instruments used (Cu≤0.004mg/L, Al≤0.03mg/L, As≤0.2mg/L, Pb≤0.1mg/L) and
210 showing little variation between sites. The mean concentrations of water chemistry variables at each
211 site are shown in Table S1.

212

213 Pearson correlation tests were used to test for collinearity between all chemical variables except Zn,
214 for which a Spearman's rank test was used. The correlation tests were carried out in a matrix, using
215 the "Hmisc" R package (Harrell *et al.* 2019). Chemical concentrations were scaled so that the varying
216 magnitudes did not cause the data to skew. A principal component analysis (PCA) was then used to

visualise the correlations between variables (Fig. 2A) and the resulting PCs were used to explain general patterns in the correlated water chemistry variables. PC1 has positive loadings (R>0.6) of NH_4, NO_2/NO_3, PO_4, ZN, and MN and negative loadings of Na. PC2 has positive loadings of NO_2, Ca, and inorganic C. Pearson correlations showed that there was a significant decline in PC1 across the sites (R=-0.812, P<0.001; Fig. 2B), but not in PC2 (R=-0.325, P=0.238) or PC3 (R=-0.041, P=0.886).

A total of 6636 macroinvertebrate specimens were collected across the 15 sampling sites, belonging to 19 orders and 35 families (Table S2). Site 1 was the least diverse (Shannon's diversity 0.490), while site 12 was the most diverse (2.044). There was a significant increase in diversity from sites 1 to 15 (R=0.575, P=0.025; Fig. 3). Correlation tests showed that there was a significant correlation between diversity and water chemistry PC1 (R=-0.575, P=0.025) but not between diversity and PC2 (R=-0.036, P=0.899) or PC3 (R=0.229, P=0.411).

Macroinvertebrate community data were transformed using Hellinger transformation in order to give low weight to instances where no or small numbers of animals were found. A redundancy analysis (RDA) was then calculated using water chemistry PCs, sites and taxa, and a subsequent ANOVA-like permutation test indicated that there were relationships between the first three PCs and community structure (PC1: $F_{1,11}$=2.465, P=0.030; PC2: $F_{1,11}$=3.203, P=0.013; PC3: $F_{1,11}$=2.358, P=0.036). Lumbriculidae was found to be marginally positively associated with PC1 (R=0.514, P=0.050) and Asellidae was found to be positively associated with PC2 (R=0.544, P=0.036).

An RDA was calculated using lock groups, sites and taxa, and a subsequent one-way ANOVA showed that there was a significant difference in community structure among lock groups ($F_{3,10}$=2.852, P=0.002; Fig. 4). One-way ANOVAs showed that there was a significant difference in Asellidae ($F_{3,10}$=9.415, P=0.003), Chydoridae ($F_{3,10}$=4.372, P=0.033) and Gammaridae ($F_{3,10}$=4.302, P=0.034) abundance between lock groups. Tukey post-hoc tests showed that the greatest differences were between groups A and D for Asellidae (P=0.002) and Chydoridae (P=0.021), and between groups A and C for Gammaridae (P=0.034).

Discussion

Both water chemistry and locks were found to have a significant association with macroinvertebrate community structure. Macroinvertebrate diversity significantly increased with increasing distance from the city centre – a pattern associated with lower concentrations of certain pollutants. Invertebrate communities also showed strong structuring by locks, which may indicate a role for lock-mediated connectivity in driving community organisation.

Overall, the stretch of canal that was used in this study exhibited low concentrations of pollutants for an urban waterbody (Smolders 2003; Santoro *et al.* 2009). We find a mean concentration of 0.051mg/L (range 0.019-0.101) for NH_4, 0.038 (0-0.077) for NO_3 and 0.022 (0.009-0.045) for PO_4. These concentrations are lower than those found in an urban river catchment in northern England (NH_4: 0.500 [0.400-0.600]; NO_3: 2.88 [0.900-4.300]; PO_4: 0.360 [0.100-0.600]) (Medupin 2019). Concentrations of NO_3 and PO_4 have also been shown increase with urbanisation (Rothwell *et al.* 2010). Most of the water chemistry variables were also low in comparison to a rural upland headwater (NH_4: 0.060 [<0.004-2.160]; NO_3: 2.000 [<0.500-6.000]) and a rural lowland catchment with intensive cattle farming (NH_4: 1.080 [0.020-13.800]; NO_3: 9.000 [<0.500-52.000]) (Jarvie *et al.* 2008), both in south west England. However, we did find a higher mean concentration of Ca (38.967mg/L [38.700-41.900]) than the aforementioned rural waterbodies (2.300 [0.9-11.6] and 24.900 [10.200-103.000], respectively), although the maximum Ca concentration found in the lowland catchment was higher than that of our study. Ca has been shown to vary considerably across catchments (0.002-6636.000mg/L), with less variability in NH_4 (0.100-30.000) and NO_3 (0.001-1.600) (Rothwell *et al.* 2010). The low concentrations of heavy-metals found in water samples, and the absence of some such as Cd and Pb, is particularly surprising given the well-documented association between these pollutants and run-off from industries in urban environments (Davis *et al.* 2001). This is especially true for this study site, as there is a lack of riparian vegetation at the site, which would be expected to coincide with higher concentrations of pollutants associated with road run-off and other typical urban pollution sources due to a lack of filtration and phytoremediation by riparian plants (Schlosser & Karr 1981; Valera *et al.* 2019). While the site is close to a stretch of canal designated as a SSSI,

suggesting the pollution levels may be low, the apparent high water quality shown in this study indicates that this is a high-quality habitat despite its location in the centre of a large city. That being said, there are still variations in the water chemistry variables found that correlate with the biological community of the Leeds-Liverpool Canal.

The results from this study show that canal habitats can contain comparable macroinvertebrate diversity to other, more natural habitat types. We find a mean family richness of 10.6 (range 4-20) which is similar to reports of agricultural UK ditch habitats (mean 9.0 [2-15] and 9.8 [1-18]), while being lower than agricultural ponds (16.3 [2-32] and 14.5 [3-27]), rivers (29.4 [16-36]), or streams (13.9 [3-31] and 12.5 [6-16]) (Davies et al. 2008), as well as lower than UK urban ponds (15.1 [2-46]) (Hill et al. 2018) and a nearby UK urban river (19.8 [13-23]) (Medupin 2020). Macroinvertebrate diversity significantly increased from sites 1-15, moving out from Leeds city centre. The results also show a significant decrease in diversity as PC1 increases, indicating a shift in water chemistry variables from higher concentrations of Na, NO_2 and IC towards higher concentrations of NH_4, Mn, PO_4, NO_3 and Zn. One contributing factor in this shift in water chemistry along the stretch of canal is possibly the sewage outlet approximately 90m east of site 1 (Fig. 1), as water chemistry variables associated with sewage, such as NH_4, NO_3 and PO_4 (Neal *et al.* 2005), are in higher concentrations closer to site 1. This may cause the exclusion of more pollution-sensitive taxa, such as Ephemeroptera and Coleoptera, close to the sewage outlet, and may explain the dominance of highly tolerant taxa, such as Lumbriculidae, at site 1 (Lumbriculidae accounted for 32% of the mean number of organisms found at site 1 across the two samples). Lumbriculidae are highly tolerant to pollution and are low-scoring on water quality measuring procedures such as the biological monitoring working party (BMWP; Paisley & Walley 2014). Santoro *et al.* (2009) found that, of the macroinvertebrates that they studied, Lumbriculidae was the only taxon to be resistant to polluted sites in their study of a heavily polluted river in Italy. They found that all organisms had large quantities of heavy-metals in their tissues, though this apparently did not affect the fitness of the Lumbriculidae. In our study, Ephemeroptera, Coleoptera and some Trichoptera were more abundant and diverse in sites furthest from the city centre. Buss *et al.* (2002) found that chironomids (Diptera), a pollution-tolerant taxon, increased in abundance with higher levels of pollution. While chironomids were found to be almost ubiquitous in this study (present at sites 2-15), they were absent from the site with seemingly the

304 worst water quality and were not found to associate significantly with water chemistry PCs. Similarly to
305 this study, Godfrey (1978) found that Asellidae were ubiquitous, likely due to their tolerance to
306 pollution. They also found that not all Trichoptera were affected by pollution. In this study,
307 Leptoceridae (Trichoptera) were found at all sites except site 1, despite them apparently being
308 pollution-sensitive indicators of good water quality, according to the BWMP (Paisley & Walley 2014). It
309 is unclear why this taxon would be so widespread when other Trichoptera, such as Odontoceridae
310 (found only at sites 12 and 13), appeared to be more restricted, but it is interesting that another study
311 found a similar inconsistency in the distribution of Trichoptera (Godfrey 1978). Hirst *et al.* (2002) found
312 that macroinvertebrate diversity decreased with increasing metal pollution. However, in contrast to our
313 study, they found that a rise in pollution increased evenness rather than excluding sensitive taxa. It is
314 clear that there is still a lack of consensus on the exact effects of water chemistry variations on
315 freshwater ecosystems, exacerbated by the fact that different studies test for different variables,
316 making comparisons problematic.

317

318 In other habitat types, it might have been tempting to suggest that other factors could have influenced
319 macroinvertebrate diversity or the variations in community structure. Heino (2000) found that physical
320 habitat variables such as size of waterbody, depth and vegetation cover accounted for more variation
321 in macroinvertebrate community structure than water chemistry variables. For example, crustaceans
322 were ubiquitous throughout the stretch of canal; isopods and amphipods were found at all sites and
323 water fleas were found at all sites except site 4. These taxa are less effective colonisers than semi-
324 aquatic taxa such as Diptera and may favour the stability of canals and potentially other man-made,
325 highly maintained habitats (Gasith & Resh 1999). However, much of the difficulty in making
326 comparisons between the findings of this study and others is that there is a lack of studies
327 investigating canal ecology, so comparisons can only be drawn from studies researching other types
328 of waterbody. The hydromorphological structure of canals is relatively uniform and so this variable is
329 unlikely to be a key factor. Some studies have found that the influence of water chemistry variables is
330 secondary to that of hydrological connectivity (Heino 2000; Gallardo *et al.* 2008), especially as
331 variations in water chemistry are often related to connectivity (Zimmer *et al.* 2000). It is, therefore,
332 difficult to say whether variations in water chemistry are truly driving differences in diversity and
333 community structure in this study, or whether all three variables are similarly influenced by

connectivity. However, again the aforementioned studies have investigated natural waterbodies with different connectivity mechanisms to canals. Connectivity within the canal network is present at a low level, with a steady but slow flow from summit to mouth and long retention times during periods of low lockage. Further research into the interactions between variations in water chemistry and the unique connectivity system of canals is needed. For example, do pollutants accumulate downstream as a result of the direction of flow? Do locks act as barriers, reducing the speed of movement of pollutants through canal systems? Where water quality is low due to point source pollution, how far from the source are the effects felt? Answering questions such as these would provide a greater understanding of how (or even *if*) pollutants are transported though canal networks.

Another potential factor that could contribute to the observed variations in diversity and community assemblage is the proximity of the tested sites to surrounding waterbodies. Ponds and ditches in the surrounding area could provide a source of taxa that can disperse to the canal. If this is the case, it may explain the increase in macroinvertebrate diversity from sites 1-15, as more built-up urban areas make it more difficult for invertebrates to disperse (Riley *et al.* 2005). As a result, sites further from the city centre may be more likely to be colonised by nearby habitats. For example, some studies have found that invertebrate diversity increases along an urban-rural gradient, with diversity and species richness in agricultural areas being double that of urban areas (Moore & Palmer 2005). However, the densely urbanised land surrounding the stretch of canal that was studied here lacks almost any surrounding water bodies within 1km of the canal apart from the River Aire which flows in parallel along the whole stretch.

Groups of sites separated by locks were found to have significantly different community structures. This would suggest that, despite the fact that lock gates open frequently, allowing water to flow between sections, locks act as barriers for aquatic organisms and limit dispersal, therefore creating differences in community structure. Taking the overall low concentrations of water chemistry variables in this particular stretch of the canal into account, the effects of connectivity could be considered to be more important than the effects of variations in water chemistry. In the RDA (Figure 4), the majority of taxa are aggregated in the centre of the plot, indicating a lack of variation in the abundance of these

363 taxa between lock groups. It is interesting that none of the outlying taxa away from the central cluster
364 are semi-aquatic, with the exception of Leptoceridae (Trichoptera). Many semi-aquatic taxa, such as
365 flying insects, are effective dispersers due to the adults' ability to fly between potential breeding sites
366 without having to rely as heavily on connectivity as fully aquatic taxa (Bilton *et al.* 2001). It may be
367 that, for this reason, locks are relatively ineffective as barriers to semi-aquatic taxa compared to
368 others such as the crustaceans Asellidae, Gammaridae and Chydoridae, although dispersal rates of
369 aquatic invertebrates that rely on vectors other than flight have not been well documented
370 (Vanschoenwinkel *et al.* 2008). However, it is difficult to confirm whether macroinvertebrate
371 assemblages are truly structured by locks or simply as a function of distance between sites and the
372 dispersal abilities of the taxa in question. Figure 4 shows that lock groups A-C are arranged in a
373 somewhat linear orientation, with group D removed from the trend. It may be that the differences in
374 community structure between groups A-C are due to the distances between them and the inability of
375 taxa to disperse over those distances, rather than because of a lack of connectivity. However, Figure
376 4 does not suggest a gradual trend through ordination space that might be indicative of isolation by
377 distance, but rather a clustering of sites within the lock groups. Interestingly, our data for canals
378 resemble findings from semi-natural systems of linked ponds: spatial structuring of community
379 structure at a larger scale with influence of local hydrogeochemical factors (Cottenie *et al.* 2001).
380 Future studies investigating the differing representation of semi-aquatic and fully aquatic taxa in
381 canals, over a larger spatial scale than this study, could allow for a better understanding of the effects
382 of locks on the dispersal of different taxa.

383

384 Other studies have shown that hydrological connectivity is a crucial factor in predicting
385 macroinvertebrate community structures (Gallardo *et al.* 2008) and this hydrological connectivity has
386 been shown to influence algal community structure in canals (Kelly & Hassall 2018). Taken together,
387 these findings suggest that canal lock systems could be analogous to other hydrological networks and
388 may provide an interesting testbed for ecological hypotheses about connectivity. For example, some
389 studies have investigated the effects of connectivity between rivers and floodplain wetlands, but,
390 unlike sections of canals, these systems are often connected for relatively short periods of time and
391 over a greater distance (Bornette *et al.* 2002; Sheldon *et al.* 2002). It is clear that more research into
392 the effects of connectivity on the biology of canals is needed.

Conclusion

This study presents evidence that canals can have high water quality and support a diverse range of macroinvertebrates, even in urban areas. With urban areas expected to continue to expand in the next decade (Seto *et al.* 2012), it is important that urban habitats such as canals are managed in a way that allows them to support as much biodiversity as possible, for the benefit of both wildlife and humans (Pimentel *et al.* 1997). Additionally, this study may be the first to attempt to evaluate the effects of locks on biodiversity and community structures. If locks are in fact the cause of the observed differences in macroinvertebrate community structure, as the results suggest, this study presents evidence that community assemblages in canals are structured in a way that is unique to this type of waterbody. Therefore, canals may represent not only potential ecosystems for increasing biodiversity in urban spaces, but also a unique model system for researching the effects of connectivity on biotic community structures.

Moving forward, it is clear that more research on canal ecology is needed in order to put the results of this study into context and to assess the ecological quality of other canals. One issue in interpreting the results of this study is that the vast majority of studies investigating the effects of water chemistry and connectivity on biodiversity were researching natural waterbodies, making comparisons difficult. More research into this topic on other canals, particularly in more polluted areas and over larger spatial scales, would help to improve understanding of ecological patterns in canals. Results of such research would help to inform protection legislation and management decisions that could improve biodiversity in canals and the wider urban landscape. Currently, some canal management decisions are made purely with the needs of humans in mind, rather than biodiversity. For example, the stretch of canal used in this study is only dredged when sediment accumulation becomes an issue for boats, and lock gates are only opened for passing boats. If, for example, locks are consistently found to limit the dispersal of certain species, opening lock gates more regularly may help to promote dispersal. Alternatively, if locks are found to limit the dispersal of invasive species like *Dikerogammarus villosus,* locks may be a useful tool in slowing their spread. However, further research into specific management decisions such as this would be required to assess their effectiveness.

422

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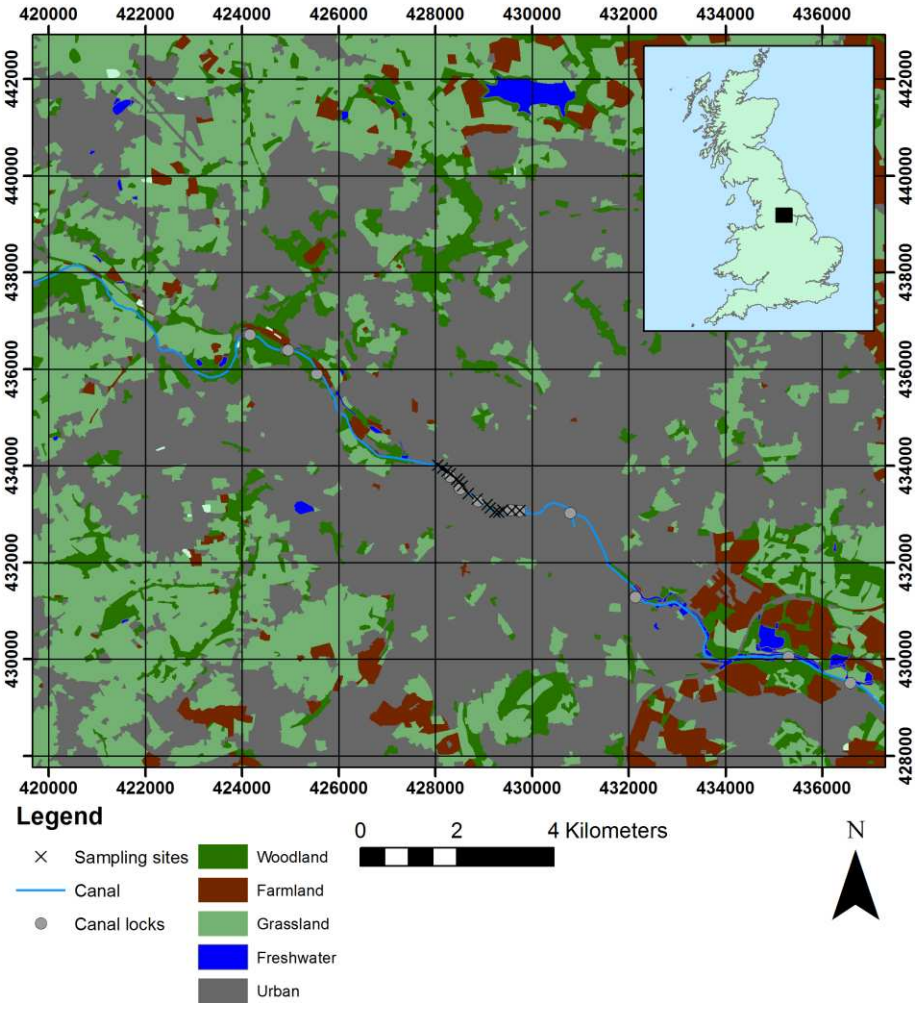
570

571 **Figures**



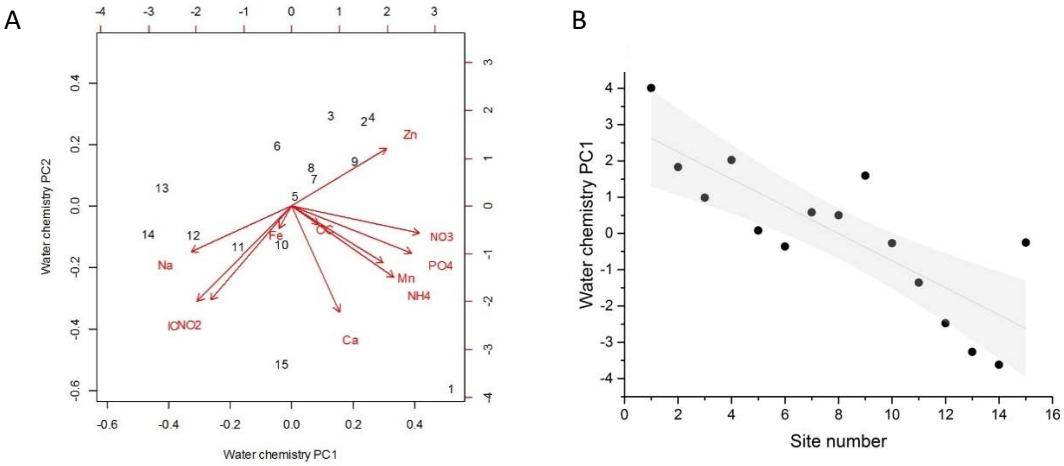
572

573 **Figure 1** Map showing the location of sampling sites and locks on the Leeds-Liverpool Canal,

574 England. Sites are numbered 1-15 from East to West. Locations of the sewage outlet and water

575 abstraction point were provided by the Canal and River Trust.

576



577

Figure 2 A) Principal components analysis of water chemistry variables for the 15 sampling sites. Numbers represent sites, which are consecutive along the canal from east (closest to urban core) to west (furthest from urban core). B) PC1 represents a shift from higher concentrations of Na, NO_2 and inorganic carbon (IC) to higher concentrations of NH_4, Mn, PO_4, NO_3 and Zn, and was found to have a significant negative relationship with site. The trendline represents a significant correlation (R=-5.013, P<0.001) and the shaded area represents the 95% CI of the regression line. PC2 represents a shift from higher concentrations of Zn to higher concentrations of IC, NO_2 and Ca, and did not have a significant relationship with site (R=1.238, P=0.238).

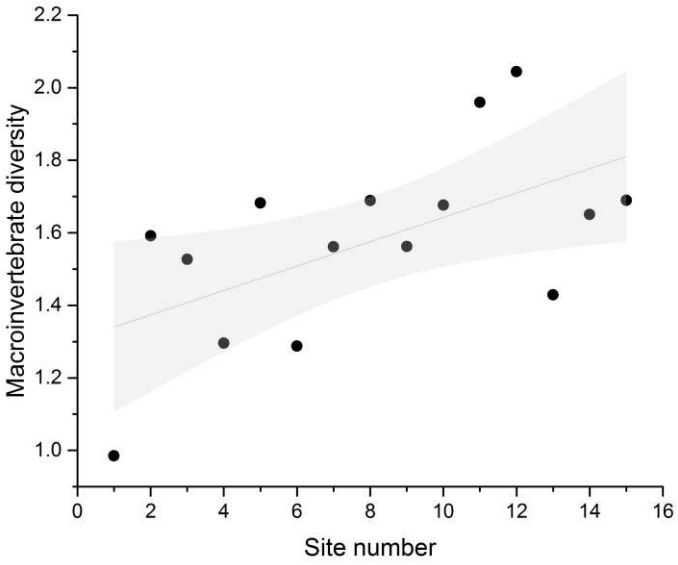
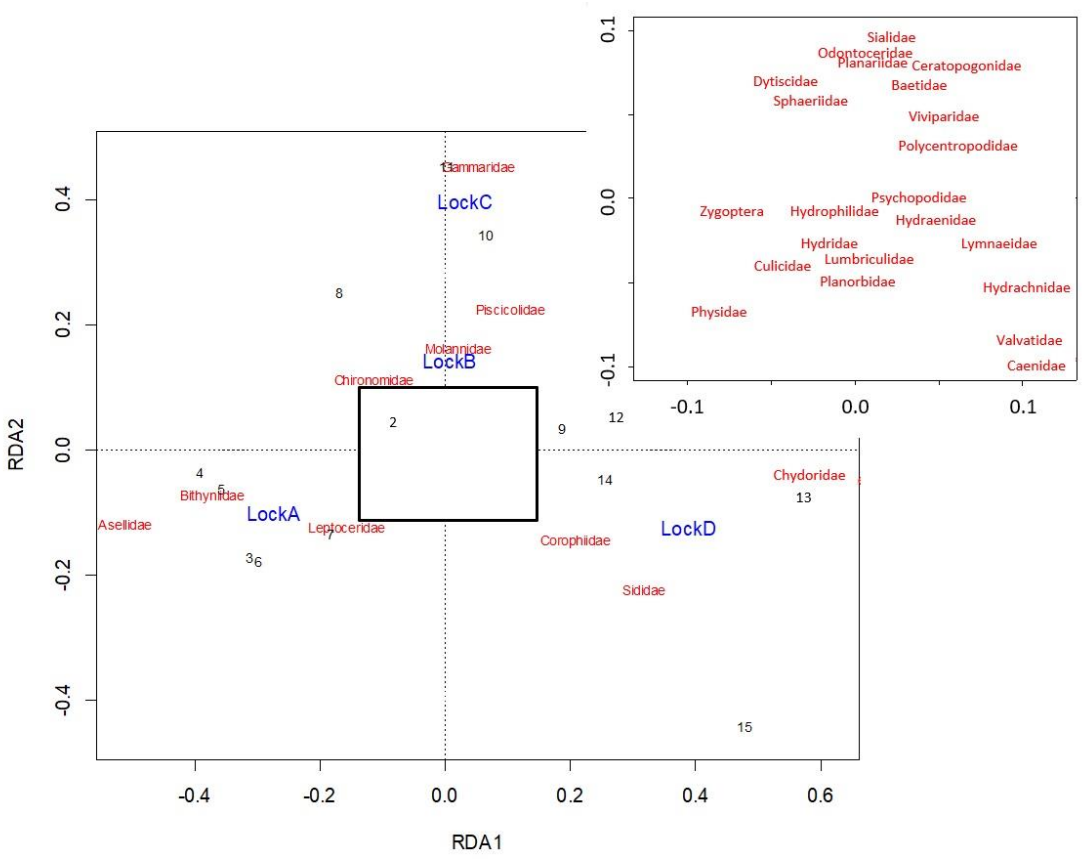


Figure 3 Shannon's Diversity Index significantly increased across sampling sites. The trendline represents a significant correlation (R=0.575, P=0.025) and the shaded area represents the 95% CI of the regression line.



591

592 **Figure 4** Redundancy analysis (RDA) showing the effects of lock groups (A, B, C, and D) on
593 macroinvertebrate community structure. Numbers represent sites, which are consecutive along the
594 canal from east to west. The central region indicated by the black square is expanded in the upper
595 right to show species more clearly.

596

597 **Appendix**

598 **Table S1** Mean concentration (mg/L) of water chemistry variables found in water samples from each
599 site. OC and IC refer to organic carbon and inorganic carbon, respectively.

Site	NH4	NO2	NO2+NO3	PO4	Ca	Na	Zn	Mn	Fe	OC	IC
1	0.101	0.003	0.08	0.043	40.7	12.894	0.007	0.043	0.050	0.81	34.74
2	0.047	0.001	0.05	0.020	38.7	12.346	0.007	0.035	0.009	1.90	32.49
3	0.021	0.001	0.04	0.022	39.0	12.473	0.007	0.032	0.038	1.29	32.91
4	0.061	0.003	0.06	0.031	37.8	12.689	0.013	0.027	0.055	0.71	32.70
5	0.050	0.002	0.05	0.024	39.5	13.905	0.006	0.015	0.067	1.55	33.49
6	0.045	0.002	0.04	0.024	38.2	14.078	0.006	0.023	0.099	1.03	32.92
7	0.058	0.002	0.06	0.023	38.7	13.398	0.007	0.021	0.042	1.58	34.02
8	0.061	0.002	0.04	0.023	38.7	13.331	0.008	0.024	0.053	1.06	33.67

9	0.071	0.002	0.04	0.024	39.2	12.736	0.013	0.024	0.023	1.14	33.69
10	0.061	0.002	0.04	0.018	39.6	14.353	0.008	0.025	0.069	1.67	34.83
11	0.034	0.005	0.04	0.015	39.6	13.987	0.009	0.024	0.017	1.62	35.26
12	0.036	0.004	0.04	0.010	38.9	14.109	0.001	0.020	0.072	1.65	35.25
13	0.036	0.004	0.02	0.016	38.0	13.950	0.000	0.021	0.011	0.00	35.90
14	0.020	0.005	0.01	0.013	38.9	13.701	0.000	0.023	0.060	0.63	36.06
15	0.073	0.006	0.04	0.029	39.4	13.608	0.000	0.032	0.057	1.93	35.24

Table S2 Abundance of macroinvertebrate families. ST refers to site number and SA refers to sample number (i.e. ST1SA1 is the first sample taken from site 1).

Haliplidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Baetidae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	2	0	1
Hydrachnida	0	1	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	1	0	2	0	2	0	10	0	33
Sididae	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7	0	25	300	20
Hydridae	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Phryganeida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Corophiidae	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	17	0	3	1	1	3	2
Hydrophilida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0

Hydraenidae	Planariidae	Polycentropo	Odontocerid	Sialidae	Viviparidae	Molannidae	Caenidae	Valvatidae	Lymnaeidae	Psychodidae	Chaoboridae
0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0
0	0	1	0	2	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0
0	0	0	0	1	0	0	0	4	0	0	0
0	0	0	0	0	0	0	0	0	0	0	0
0	0	1	0	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	0	0	0	0
1	0	0	0	0	0	0	0	4	1	0	0
0	3	0	0	0	0	0	0	0	0	0	0
0	0	2	0	0	0	0	0	0	2	0	0
0	0	2	0	0	0	0	0	0	0	0	0
0	1	0	0	0	0	0	0	0	0	0	0
0	0	0	1	1	1	4	0	0	0	0	0
0	0	0	0	2	0	0	0	0	0	0	0
0	0	0	0	1	1	0	6	3	0	0	0
0	0	0	0	0	1	0	2	0	0	0	0
0	0	0	0	0	0	0	2	1	2	1	0
0	0	2	0	0	0	1	0	1	1	0	0
0	0	0	0	0	0	0	0	2	0	0	2
10	0	4	0	1	0	0	0	2	2	0	1
0	0	9	0	0	0	0	3	3	6	0	0
0	1	0	0	0	1	0	0	1	2	0	0

Chydoridae	Gammaridae	Zygoptera	Leptoceridae	Bithyniidae	Planorbidae	Piscicolidae	Chironomida	Sphaeriidae	Ceratopogon	Physidae	Dysticidae
2	0	0	0	0	0	0	0	0	0	0	0
3	18	0	0	0	0	0	0	0	0	0	0
1	3	0	0	0	0	0	0	0	0	0	0
4	5	0	1	1	0	0	1	0	0	2	0
8	4	4	8	45	1	0	0	0	0	0	0
3	19	0	6	7	1	0	1	9	1	0	0
0	6	0	4	11	0	1	50	0	0	0	0
0	11	0	3	3	1	6	6	4	0	0	0
6	22	6	10	62	0	8	43	8	0	0	0
1	14	0	0	4	0	1	3	3	1	0	0
40	24	1	20	57	1	5	18	2	4	1	0
1	22	0	2	34	3	3	6	20	0	1	0
6	7	1	5	0	0	0	4	0	0	0	1
0	2	0	5	0	0	0	3	0	0	1	0
21	133	0	6	55	3	104	13	16	0	0	0
8	135	0	4	27	2	48	2	15	2	8	0
300	38	0	4	7	1	2	23	10	0	0	0
0	56	0	4	13	0	6	4	1	0	0	0
11	15	0	0	0	0	15	4	0	0	0	0
9	19	0	1	0	0	1	3	0	1	0	0
6	23	1	0	2	0	0	10	4	1	0	1
2	8	0	1	0	0	0	0	1	0	0	0
5	6	0	2	0	0	0	7	1	0	0	0
15	15	0	1	0	0	10	0	0	0	0	0
400	30	0	0	0	0	3	17	2	3	0	0
85	15	0	5	0	4	9	2	2	3	0	0
300	55	1	2	0	1	3	6	8	2	0	0
5	100	0	1	0	1	4	3	2	0	1	0
200	13	1	3	2	0	0	9	1	2	1	0
100	31	0	3	0	0	0	1	4	3	0	0

Family	Lumbriculida	Asellidae	Culicidae
ST1SA1	20	1	1
ST1SA2	0	15	0
ST2SA1	1	6	0
ST2SA2	1	11	0
ST3SA1	0	78	0
ST3SA2	0	38	1
ST4SA1	0	104	1
ST4SA2	7	90	0
ST5SA1	7	274	0
ST5SA2	7	12	0
ST6SA1	1	405	1
ST6SA2	0	174	0
ST7SA1	0	41	0
ST7SA2	0	17	0
ST8SA1	12	288	0
ST8SA2	1	152	0
ST9SA1	21	123	0
ST9SA2	7	55	0
ST10SA1	0	42	0
ST10SA2	0	9	0
ST11SA1	1	16	0
ST11SA2	0	4	0
ST12SA1	0	3	0
ST12SA2	0	23	0
ST13SA1	0	23	0
ST13SA2	7	15	0
ST14SA1	12	231	0
ST14SA2	25	91	0
ST15SA1	4	59	1
ST15SA2	1	69	0