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The influence of substrate type on macroinvertebrate assemblages within agricultural drainage ditches

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Abstract Artificial drainage ditches are common features in lowland agricultural catchments that support a wide range of ecosystem services at the landscape scale. Current paradigms in river management suggest activities that increase habitat heterogeneity and complexity resulting in more diverse floral and faunal assemblages; however, it is not known if the same principles apply to artificial drainage ditch systems. We examined the effects of four artificial substrates, representing increasing habitat complexity and heterogeneity (bricks, gravel, netting and vegetation), on macroinvertebrate community structure

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Environment Agency of England, Stepping Stone Walk, Winfrey Avenue, Spalding, Lincolnshire PE11 1DA, UK within artificial drainage ditches. Each substrate type supported a distinct macroinvertebrate community highlighting the importance of habitat heterogeneity in maintaining macroinvertebrate assemblages. Each substrate type also displayed differing degrees of community heterogeneity, with gravel communities being most variable and artificial vegetation being the least. In addition, several macroinvertebrate diversity metrics increased along the gradient of artificial substrate complexity, although these differences were not statistically significant. We conclude that habitat management practices that increase habitat complexity are likely to enhance macroinvertebrate community heterogeneity within artificial drainage channels regardless of previous management activities.

Keywords Artificial waterbody · Drainage and irrigation channel · Invertebrate · Species richness · Artificial substrates · Community composition

Introduction

Freshwater habitats are globally important reservoirs of biodiversity, supporting 140,000 known species and delivering a wide range of ecosystem services from the provision of water through nutrient cycling and storage (Brooks et al., 2016; IUCN, 2016; Reid et al., 2019). As a result, the management and conservation of freshwater systems has received increasing attention over the past two decades (Smith et al., 2014; Wohl et al., 2015), with many restoration activities focusing on mitigating some of the most deleterious anthropogenic impacts by increasing habitat diversity and landscape connectivity (Geist & Hawkins, 2016; Abell et al., 2019). Habitat heterogeneity is widely considered to regulate aquatic macroinvertebrate diversity (Sartori et al., 2015; Pilotto et al., 2016; Oertli & Parris, 2019) and is commonly incorporated into restoration activities with the goal of improving community resilience to environmental change (Giller et al., 2004; Penaluna et al., 2017).

Across the world, artificial waterbodies and anthropogenically constructed drainage networks cover large areas of lowland agricultural catchments, providing water resources for irrigation and mitigating flood risk (Blann et al., 2009; Verdonschot et al., 2011; Rogger et al., 2017). In the UK, the construction of artificial drainage networks over the past 300 years has resulted in a decline of natural fenland/wetland habitats (The South Lincolnshire Fenlands Partnership, 2019), leaving many aquatic species inhabiting a fraction of their historic range. As a result, artificial drainage channels may provide the only widely available habitat for aquatic taxa in intensively farmed lowland catchments (Langheinrich et al., 2004; Shaw et al., 2015; Hill et al., 2016). Given the widespread occurrence and recognised biodiversity value of drainage ditches, there are significant opportunities to manage and enhance habitat heterogeneity to support and, in many instances, improve biodiversity in agricultural catchments (Scherr & McNeely, 2008; Mantyka-Pringle et al., 2016). However, the role of habitat heterogeneity in influencing the faunal communities of drainage ditches within Europe remains poorly quantified due to limited biomonitoring of 'Artificial Waterbodies' (AWBs) under the EU Water Framework Directive (WFD) 2000/60/EC.

AWBs are defined for WFD purposes as waterbodies created by human activity which, in combination with Heavily Modified Waterbodies (HMWBs), comprise the majority of channels within poorly drained lowland agricultural catchments (Sherriff et al., 2015). Such waterbodies are commonly constructed to fulfil specific economic or societal purposes. Owing to their anthropogenic origin, and in many instances highly modified morphological and hydrological characteristics, AWBs are expected to obtain the standard of

"Good Ecological Potential" (GEP), rather than "Good Ecological Status", under the WFD (Borja & Elliott, 2007). This target reflects the physical and chemical heterogeneity of AWBs and the societal functions that they provide. AWBs may also be located in both urban and rural locations dictating that the definition of GEP is typically considered on a site-by-site basis (European Commission, 2003). As a result, many artificial drainage ditches within agricultural areas are not regularly monitored and remain largely unstudied (Hill et al., 2016). This lack of monitoring means there is limited knowledge regarding the effects of common management techniques on the aquatic communities that inhabit them and how such techniques may be adapted or better deployed to maintain both the societal purpose of the channel and promote physical and biological diversity within lowland agricultural catchments.

The benthic substrates of many agricultural drainage ditches are dominated by relatively homogenous fine sediment deposits (Clarke, 2015; Sherriff et al., 2015). As a result, to maintain the conveyance capacity of drainage ditches, macrophyte management and dredging of deposited sediment take place at regular intervals (Whatley et al., 2014a; Hill et al., 2016). These activities can have significant effects on both the structure and function of the floral and faunal communities (Foster et al., 1989; Whatley et al., 2014b) which may have positive or negative effects (Teurlincx et al., 2018). The distribution and richness of macrophytes are reported to be the most significant controls upon macroinvertebrate assemblages (Painter, 1999; Langheinrich et al., 2004). In addition, structural heterogeneity within the macrophyte community (i.e. a range of submerged, floating and emergent macrophytes) has also been reported to be associated with increased faunal diversity at the reach scale (Rooke, 1984; Higler & Verdonschot, 1989; Whatley et al., 2014a). However, this increase has been attributed to the presence of a limited number of specialist macroinvertebrate species, with structural heterogeneity having limited effects when considered alongside adjacent riparian vegetation communities and water quality characteristics (Verdonschot et al., 2012). Despite these findings, the potential wider effects of habitat complexity (encompassing both mineral and macrophyte substrates) and its influences upon drainage ditch macroinvertebrates remain poorly quantified. This study, therefore, aimed to characterise

the role of habitat complexity in supporting heterogeneous benthic macroinvertebrate assemblages in two types of drainage ditches (main arterial and side channels) with contrasting management practices in the UK.

Materials and methods

Study sites

Deeping Fen (52.746827° N, 0.24762523° W) is a 120 km² area of low-lying land bounded by the River Welland and the River Glen, Lincolnshire, UK. An extensive network of drainage ditches and water pumping stations operate within the Welland and Deeping's Internal Drainage Board Area. A total of four ditches (50 m study reaches representative of the wider agricultural landscape) were sampled comprising two drainage ditch types: (i) main/large arterial drainage ditches (> 5 m wide) which are maintained with annual channel dredging and;(ii) side/small drainage ditches (narrower at c.3 m wide) which typically connect to main arterial channels at right angles at both ends and form the boundary of fields. All channels were straight, slow flowing and had steep vegetated banks that were maintained annually by cutting/mowing (side channels) or were subject to vegetation management of one bank on an annual basis (main arterial channel). Dredging and vegetation cutting occurred in the autumn prior to the study and as a result all channel margins were vegetated. Substrates within all channels were dominated by fine sediments with limited areas of coarser substrates (sand and fine gravel) being present. This substrate composition reflects the wider intensive arable landscape which is characterised by low channel slopes intersected with straight artificial drainage channels. Macrophyte growth was abundant on both riparian margins in the side channels where water depths varied between <40 cm and 1.5 m and patches of vegetation alternated with areas of open water. In the main arterial channels, macrophytes were also abundant in the narrow riparian fringe and within the channel. Floating and submerged macrophytes occurred throughout all the main arterial study reaches and water depth varied between < 40 cm and > 2 m. All main arterial ditches comprised a deeper central area (> 2 m depth) and a shallow marginal shelf (< 40 cm to 1.5 m) providing a comparable sampling environment to side ditches. Samples were collected on two occasions: May, when water levels were low, and June, when water levels were on average 1 m higher. These sampling periods thereby encompassed typical management practices within the ditches of increasing water levels during the summer to support crop irrigation and also provided temporal replication.

Experimental design and macroinvertebrate sampling

Four artificial substrates were deployed within the study to reflect an increasing gradient of habitat complexity, from simple minerogenic substrates to more complex artificial vegetation substrates. Each substrate provided a similar surface area for colonisation. The four substrates deployed were as follows: (1) building brick—a hard impervious surface (22 \times 10×7 cm), (2) rolled netting with 15 mm mesh—a highly porous substrate representing vegetation detritus (2 m long sections were rolled and folded into a $25 \text{ cm} \times 13 \text{ cm}$ dimension and were deployed in pairs), (3) gravel trays— $(8 \times 13 \times 6 \text{ cm filled with})$ homogenous 20 mm clasts and were deployed in pairs) and (4) artificial plants-made from bubble wrap to ensure buoyancy in the water column (two 30 \times 50 cm sections rolled and 20 cm cuts were made vertically every 2.5 cm to create individual fronds). Netting was secured in place with tent pegs and artificial plants were secured to a brick using cable ties. The resultant substrates represented two minerogenic and two artificial vegetation substrates of differing structural complexities (high and low).

All substrate treatments were randomly allocated to patches of open water within each channel to avoid any confounding factors associated with macrophytes. Four replicates (units) per substrate type per site were installed and left in situ for 6 weeks (4 sites \times 4 substrates \times 4 replicates \times 2 occasions = 128 sample units in total). Each substrate treatment covered a similar area within the channel facilitating comparison between sampling units. To avoid loss of invertebrates during collection, each substrate was placed directly into a net (1 mm mesh size) immediately downstream prior to transfer into a sample bag. Following retrieval of all substrate treatments, a 30-s sweep sample was collected covering an area comparable to that covered by a substrate treatment (approximately 0.5 m²) and encompassing both open water and macrophytes with a standard pond net (1 mm mesh size). This provided an indication of the differences between artificial substrate samples and the in situ substrates within the channels and served as a reference point for the potential pool of taxa able to colonise the artificial substrates. During the first sample visit (May), two sweep samples were collected from main ditches to encompass ecological variability associated with management practices: one close to and encompassing the uncut bank and one from the cut bank. During the second visit, one sweep sample was collected from each site (both main and side ditches). A total of 115 sample units were retrieved from the 2 time periods (consisting of 30 brick, 26 netting, 29 gravel and 30 artificial plant sample units with 2 bricks, 6 netting, 3 gravel and 2 artificial plant sample units being lost/ unable to be retrieved) with an additional 10 sweep samples being collected. All samples were preserved in the field in 4% formaldehyde. Within the laboratory, samples were rinsed through a sieve, processed and identified to species level wherever possible, with the exception of Hydrachnidiae and Oligochaeta which were recorded as such and Diptera, which where was recorded to family level (except Chironomidae which were divided into two groups-predatory Tanypodinae and other Chironomidae larvae).

Statistical analysis

Differences in macroinvertebrate community composition were examined via non-metric multi-dimensional scaling (NMDS) centroid plots with samples visualised by substrate type (with sweep samples included for visual comparison), channel type (main or side) and sample visit (time). Centroid matrices were derived by calculating the averages for each substrate type for each site (e.g. the centroid-the centre point of all replicates for each sampling method for each site for each occasion in multi-dimensional space) using Bray–Curtis similarity coefficients on log(x + 1)transformed data (Anderson et al., 2008). Differences in macroinvertebrate community composition were statistically explored as a function of the interactive explanatory factors of substrate type (excluding sweep samples), sample visit and channel type via a permutational multivariate analysis of variance (PERMA-NOVA) using the adonis function in vegan (Oksanen et al., 2016). To examine where significant differences occurred in relation to substrate type, pairwise comparisons of differences were performed using the pairwise.adonis function with Bonferroni corrections applied to account for multiple comparisons (Arbizu, 2019). To examine the heterogeneity of macroinvertebrate compositions as a function of the substrate type, channel type and sample visit, homogeneity of multivariate dispersions were calculated based on Bray-Curtis distances using the betadisper function and pairwise comparisons for substrate type (excluding sweep samples) were conducted using the permutest.betadisper function in vegan. Homogeneity and PERMANOVA tests were run on the original dataset (all 115 artificial substrate samples) to characterise community variability. To identify dominant taxa within macroinvertebrate assemblages for each substrate type (including sweep samples), sample visit and channel type, the similarity percentage (SIMPER) was applied using the simper function in vegan. Indicator taxa were identified for each substrate type (excluding sweep samples) using the multipatt function within the indicspecies package (De Cáceres & Jansen, 2016). An indicator value of > 0.25 was accepted as being ecologically relevant (Dufrêne & Legendre, 1997) and all significant indicators with a fidelity value of < 0.25 were removed to exclude rare taxa (De Cáceres, et al., 2012).

Four macroinvertebrate community, indices were calculated from the data: mean community abundance, mean taxa richness, Shannon–Wiener diversity and Berger-Parker dominance. The latter metric was derived from Species Diversity and Richness IV (Seaby & Henderson, 2006) and the former using the diversity function in vegan. Statistical differences were tested by fitting linear mixed effects models using the function 'lme' in the package 'nlme' (Bates et al., 2015; Pinheiro et al., 2020). The interaction of substrate type (excluding sweep samples) and channel type was specified as fixed factors and ditch was nested within sample visit as a random factor (to account for the fact that samples within individual channels and sample visits are less independent from each other). Post hoc pairwise comparisons of substrate type were performed using least-square means and P values were adjusted for multiple comparisons via Tukey tests within the Ismeans package (Lenth, 2016). Community abundances were log(x + 1)transformed prior to statistical testing to comply with underlying assumptions. Ordination plots were

prepared in PRIMER Version 7.0.11 (PRIMER-E Ltd., Plymouth, UK; Clarke & Gorley, 2015) and all statistical analyses were performed in R version 3.6.0 (R Core Team, 2017).

Results

A total of 87 taxa were recorded from all samples, with the largest numbers of taxa recorded in the orders of Coleoptera (29), Gastropoda (16) and Hemiptera (8). SIMPER indicated that assemblages were dominated by 5 taxa: 2 crustacean, Gammarus pulex (Linnaeus, 1758) and Asellus aquaticus (Linnaeus, 1758), 2 Chironomidae (Tanypodinae and all other Chironomidae) and 1 Gastropoda, Bithynia tentaculata (Linnaeus, 1758); see Tables S1, S3, S3). In total, 11 taxa (mean ± 1 SE 9.13 ± 1.23) were recorded from the brick substrates, 37 (mean 15.5 ± 1.28) from the gravels, 53 (mean 16.25 ± 2.12) within the netting and 44 (mean 17.5 \pm 1.15) on the artificial plants. In addition, 66 taxa (mean 22.3 \pm 2.78) were recorded from the sweep samples. No taxa were unique to the bricks, 1 to gravels (Gastropoda), 7 to netting (2 Diptera, 3 Coleoptera, 1 Gastropoda and 1 Odonata) and 2 to artificial plants (1 Diptera and 1 Gastropoda). 18 taxa were unique to sweep samples (1 Diptera, 13 Coleoptera, 2 Hemiptera, 1 Gastropoda and 1 Odonata).

Macroinvertebrate community composition was significantly different among substrate types, with this factor also accounting for the greatest amount of variation in community composition (indicated by the highest F and R^2 values; Fig. 1a; Table 1). The individual substrates and sweep samples formed relatively distinct clusters in ordination space (Fig. 1a) with pairwise PERMANOVA's indicating that all substrate types statistically differed from each other (all adj. P = 0.006). Macroinvertebrate community composition also differed statistically as a function of channel type (main or side channel; Fig. 1b), sample visit (Fig. S1) and the interactions of substrate type: sample visit and channel type: sample visit (Table 1). There were no differences in community composition associated with the interaction of substrate type and channel type or the interaction of all three factors (Table 1). A total of 13 indicator taxa were identified: 2 for gravel substrates (*Sialis lutaria* and Sphaeriidae) and 11 for plant substrates (Tanypodinae, Oligochaeta,

G. pulex, *A. aquaticus*, *B. tentaculata*, *Athripsodes aterrimus* (Stephens, 1836), 3 species from the family Planorbidae and 2 *Polycelis* species), with no indicator taxa identified for brick or netting substrates (see Table 2).

Heterogeneity in macroinvertebrate communities differed among substrate types ($F_{4,175} = 6.094$, P < 0.001), being greatest in the gravel substrates (mean distance = 0.441), followed by the bricks (mean distance = 0.421), netting (mean distance = 0.394) and last the artificial plants (mean distance = 0.271). All substrate pairwise comparisons of multivariate dispersion were significantly different (all P < 0.001). Communities from side ditches (mean distance = 0.465) were significantly more heterogeneous than those in the main channel (mean distance = 0.381, $F_{1,178}$ = 13.217, P < 0.001). There were no differences in multivariate dispersion associated with sample visit (P > 0.05). Sweep samples had a mean distance of 0.366, but were not directly compared to the other substrates due to reduced replication and are only presented for comparative purposes.

Community abundance and taxa richness varied between substrate type (both P < 0.001), but demonstrated no differences as a function of channel type (main or side ditch). Community abundance demonstrated a significant interaction between substrate type and channel type (Table 3). Community abundance and taxa richness increased with greater substrate complexity, with artificial plants supporting the greatest numbers of individuals and taxa and brick substrates the fewest (Fig. 2a, b). Abundances recorded on artificial plants and brick substrates were statistically different to all other substrate types, and taxa richness of brick substrates was statistically different to all other substrates (see Table S4 for pairwise significance levels). Shannon-Wiener diversity and Berger-Parker dominance demonstrated no statistical differences for any of the factors tested (Table 3; Fig. 2c, d). For community abundances, taxa richness and Shannon-Wiener diversity, sweep samples visually supported the greatest values comparative to all substrate types, while there was no visual differences apparent between substrates for Berger-Parker dominance (Fig. 2).



Fig. 1 Non-metric multi-dimensional scaling (NMDS) centroid plots of macroinvertebrate community data by **a** substrate type and **b** channel type (main or side) within agricultural

Discussion

We found that different artificial substrates supported distinct assemblages within drainage ditches that reflected varying levels of habitat complexity. However, the absence of significant differences in Shannon–Wiener diversity and Berger–Parker dominance

drainage ditches in Deeping Fen (Lincolnshire, UK). Note that sweep samples are included for comparative purposes only

between the artificial substrates examined highlights a similar number of relatively ubiquitous taxa that inhabited the different substrates within the ditches (as also evident in SIMPER results). Despite this, substrate type (a surrogate for increasing habitat structural complexity) was responsible for the greatest proportion of variance recorded in community

Table 1 Summary of PERMANOVA testing the	Factor	F	R^2	Р		
effect of substrate type	Substrate type	18.31	8.96	0.001		
(excluding sweep samples), ditch type, sampling occasion and the interaction of these factors	Sampling visit	6.75	3.30	0.001		
	Channel type	10.28	5.03	0.001		
	Substrate type \times channel type	1.48	0.73	0.142		
	Substrate type \times sample visit	2.41	1.18	0.016		
	Channel type \times sample visit	1.96	0.96	0.041		
Significant results are emboldened ($P < 0.05$)	Substrate type \times channel type \times sample visit	1.11	0.54	0.375		
Table 2 Summary of indicator taxa by substrate type	Taxa	Indicator	P value			
	Graval					
	Siglis lutaria (Linneeus, 1758)	0.502		0.002		
No indicator taxa were	Sphaeriidae	0.351		0.002		
	Artificial plant					
	Tanynodinae	0 774		0.001		
	Gammarus puley (Linnaeus, 1758)	0.672		0.001		
	Asellus aquaticus (Linnaeus, 1758)	0.604		0.001		
	Rithynia tentaculata (Linnaeus, 1758)	0.559		0.001		
	Polycelis tenuis Iima 1884	0.559		0.002		
	Polycelis nigra (O E Müller 1773)	0.536		0.001		
	Athrinsodes aterrimus (Stephens, 1836)	0.323		0.001		
	Planorbarius corneus (Linnaeus, 1758)	0.449		0.033		
netting substrates	Planorhis planorhis (Linnaeus, 1758)	0.395		0.035		
Bold values indicate	Oligochaeta	0.374		0.028		
significant results are emboldened ($P < 0.05$)	Bathyomphalus contortus (Linnaeus, 1758)	0.371		0.036		

 Table 3 Summary of univariate linear mixed effects model testing the effect of substrate type, channel type and the interaction of these factors

Response	Substrate type		Channel type		Substrate type \times channel type		$R^{2}m$ (%)	$R^{2}C(\%)$
	F	Р	F	Р	F	Р		
Abundance	46.12	< 0.001	0.67	0.500	3.67	0.032	62.23	88.00
Taxa richness	8.61	< 0.001	1.00	0.423	2.17	0.128	42.70	63.22
Shannon-Wiener diversity	1.90	0.166	0.01	0.946	1.32	0.299	22.70	27.19
Berger-Parker dominance	1.26	0.317	0.16	0.729	0.84	0.489	11.07	50.92

Significant results are emboldened (P < 0.05)

composition, suggesting that the principle of managing artificial drainage ditches through habitat characteristics may help support community heterogeneity and taxa richness. Although spatial and temporal variability was important in structuring community composition (as evident by community composition differing between sample visits and channel type), we found that each artificial substrate type supported distinct assemblages. Our results support the hypothesis of Verdonschot et al. (2012) who highlighted that ditch habitats are comprised of a 'core' of common species that occur widely, with a limited number of





Fig. 2 Mean (\pm 1 SE) **a** abundance, **b** taxa richness, **c** Berger–Parker dominance and **d** Shannon–Wiener diversity by substrate type within agricultural drainage ditches in Deeping Fen (Lincolnshire, UK). Substrates indicated by the same letter are statistically similar (all statistical differences reported P < 0.05;

see Table S4 for pairwise comparisons for abundance and taxa richness). Note that sweep samples were not included in the statistical comparisons due to differences in sampling approach and reduced replication and are included here for comparison only

taxa that may be unique to individual substrates/ habitats. Therefore, management strategies seeking to increase community heterogeneity by encouraging non-core species should consider undertaking management operations to increase habitat heterogeneity at the ditch scale (e.g. reflecting the "wider system" approach as proposed by Buisson et al., 2008).

We recorded increased variability of macroinvertebrate communities in minerogenic substrates relative to artificial vegetative substrates, likely reflecting a more varied habitat provision caused by the periodic

only filling of gravel interstices with fine sediments. The volume of fine sediment present within benthic habitats is known to be a strong control upon macroinvertebrate taxa (Wood & Armitage, 1997; Jones et al., 2012; Mathers & Wood, 2016), especially in anthropogenic systems such as AWBs and HMWBs that have been be subject to artificial widening and deepening via dredging (Whatley et al., 2014b; Shaw et al., 2015). In contrast, the artificial macrophyte

substrates (netting and artificial plants) represented a

more complex substrate that extended into the water

column. These substrates provided a more stable habitat (temporally and spatially), mostly free from the effects of sediment deposition, resulting in a more homogenous community. Our results provide further evidence as to the importance of diverse physical habitat provision in increasing levels of community heterogeneity (Verdonschot et al., 2016; Hasselquist et al., 2018).

More complex substrates (netting and artificial plants) typically supported greater taxa richness and abundance of individuals than minerogenic substrates (gravel and brick), providing evidence that structural complexity is important in driving artificial drainage ditch macroinvertebrate assemblages. These differences probably reflect increasing structural complexity of substrates, with artificial vegetation providing a greater number of feeding opportunities relative to the fine-grained monogenic substrates. Specifically macrophytes may (1) act as a direct food source or enable colonisation by epiphytic algae (Paice et al., 2017; Wolters et al., 2018a); (2) provide a more stable substrate (not prone to burial; Brookes, 1986; Cotton et al., 2006); (3) provide opportunities for filtering taxa to gain access to and protection from areas of high flow velocity within the channel (Phiri et al., 2011; Wolters et al., 2018b) and (4) provide a higher density of prey for predatory taxa than is available in benthic habitats (Khudhair et al., 2019). These feeding mode differences are reflected in our findings, with artificial macrophyte fronds being characterised by G. pulex, A. aquaticus and several algal grazing gastropods, whereas minerogenic substrates were characterised by burrowing taxa such as S. lutaria (Linnaeus, 1758) and Sphaeriidae.

Differences in community composition were also present as a function of channel type (side or main channel). It is likely that differences in management practices and, therefore, subsequent habitat provision drove these differences. Main arterial drainage ditches are managed via dredging and annual bank cutting of alternate banks, whereas side drainage ditches receive vegetation cutting of both banks annually. Although marginal cutting may represent a short-term homogenisation of habitat structure and complexity, this effectively resets successional trajectories and may promote increased diversity within floral and faunal communities (Teurlincx et al., 2018). The annual alternation of cutting vegetation on one bank (so that one bank is always left uncut) in main arterial drainage ditches is an activity which increases heterogeneity at the ditch scale (Buisson et al., 2008). However, we found that side drainage ditches supported more heterogeneous communities and this finding was consistent with previous research undertaken at the same study sites (Hill et al., 2016). This increased community heterogeneity may be associated with a range of habitat successional stages being present as a function of time since vegetation was last managed. In contrast, main arterial ditches always have one vegetated bank present. Despite these differences in natural community heterogeneity, no significant interactions were observed between substrate and channel type in relation to community composition. This suggests that colonisation of the artificial substrates appears to have occurred in a similar manner in both channel types regardless of differences in local management (both banks being managed on smaller side channels or only one bank being cut on main channels). As such, the implementation of management practices that increase habitat heterogeneity in drainage ditches is likely to provide benefits irrespective of historic management practices.

Conclusion

Despite anthropogenic pressures on drainage ditches (associated with their societal functioning for flood protection and irrigation), they have been shown to support diverse macroinvertebrate communities (Williams et al., 2004; Davies et al., 2008; Hill et al., 2016). Our results demonstrate that management practices that increase habitat complexity may contribute to local increases in community heterogeneity. At present, many management practices within drainage ditches involve vegetation cutting and dredging. We suggest that by differing the extent and frequency of vegetation cutting and dredging it may be possible to promote patch-scale habitat heterogeneity and complexity resulting in enhanced macroinvertebrate community heterogeneity.

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