

# Temporal variability in lotic macroinvertebrate communities associated with invasive signal crayfish (*Pacifastacus leniusculus*) activity levels and substrate character

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**Abstract** Invasive signal crayfish (*Pacifastacus leniusculus*) are considered to be the most prevalent non-native crayfish species in Europe. Where large populations become established they have significant and long-term effects on benthic macroinvertebrate communities. However, much less is known about how community effects associated with crayfish invasion change in the short-term as a function of varying activity levels during the summer months. We examined the macroinvertebrate community composition of two lowland UK rivers, one which supported a well-established non-native crayfish population (invaded) and one in which crayfish had not been recorded (control). Colonisation cylinders were deployed which recorded community composition over a 126-day time period. Results indicate that once the activity period commences, invasive crayfish consistently altered macroinvertebrate community structure regardless of substrate character. Invaded communities displayed reduced beta-diversity compared to control sites. However, effects on the macroinvertebrate assemblage varied over the period

when crayfish were active probably reflecting the behavioural activity of crayfish (which intensifies with increasing water temperature and during the spawning season) and life histories of other macroinvertebrates. The results indicate that crayfish invasions modify macroinvertebrate community composition, but over shorter timescales, the effects vary associated with their activity levels.

**Keywords** Colonisation · Non-native · Life-history traits · Habitat template · Fine sedimentation

## Introduction

Across the globe invasive species are spreading rapidly and represent one of the most significant threats to biodiversity, economic development and human health (Simberloff et al. 2013; Early et al. 2016). Invasive crayfish species are considered to be some of the most extensively distributed aquatic invasive species worldwide and within Europe the signal crayfish (*Pacifastacus leniusculus*; Dana) is one of the most widespread and successful non-native crayfish species (Hudina et al. 2015). Crayfish are widely acknowledged to be keystone species and often dominate benthic biomass where they occur (Crandall and Buhay 2008). Their polytrophic feeding habits ensure that if they reach high population densities

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within invaded ecosystems, their effects are extensive and often resonate throughout the food web (Momot et al. 1978; Guan and Wiles 1998).

Despite an increasing number of studies investigating the ecological effects of invasive crayfish, much of the research has been conducted in lentic ecosystems (e.g. Nyström et al. 2001; Ercoli et al. 2015a, b, Ruokonen et al. 2016) and is typically focussed on understanding the overall effect at the ecosystem level; with only a limited number of studies undertaking repeated sampling of the same sites. Much less is known about the temporal variability of invader effects on lotic communities. To date, only a few studies have considered the long term effect of signal crayfish on freshwater macroinvertebrate communities (see Wilson et al. 2004; McCarthy et al. 2006; Ruokonen et al. 2016; Mathers et al. 2016) and none have considered intra-annual temporal dynamics at shorter time scales (i.e. multiple months) once an invasive population has become established (i.e. associated with key life history characteristics and crayfish activity levels). Understanding and quantifying the extent of invader effects will continue to be constrained until studies are conducted that span the appropriate spatial and temporal scales (McCarthy et al. 2006).

Community composition of lotic macroinvertebrate populations vary over space and time associated with physical properties such as flow, water quality and the availability of resources, but also demonstrate short term (seasonal) temporal shifts related to individual taxon life histories (Hynes 1972; Beche et al. 2006; Tonkin et al. 2017). Many taxa exhibit seasonal life cycles which are tied to optimal environmental conditions including temperature (Huryn and Wallace 2000), flow (Bunn and Arthington 2002) and food availability (Anderson and Cummins 1979; Murphy and Giller 2000), or to avoid competition via temporal niche separation (Grant and Mackay 1969; Bjelke et al. 2005). Crayfish also display variations in levels of activity, which generally increase with rising water temperatures (Johnson et al. 2014). These changes in macroinvertebrate taxon abundances and crayfish activity levels over time may affect the magnitude of crayfish effects within the invaded ecosystem, particularly if preferential prey items are depleted over the seasonal timeframe when crayfish are active.

The physical habitat template of the ecosystem in which biological invasions take place will most likely control the effect the invader has on the receiving ecosystem. A number of studies have documented highly variable effects of non-native taxa as a function of the physical characteristics of the ecosystem (Vilà et al. 2011; Klose and Cooper 2012). Heterogeneous habitats, which contain boulders and cobbles, macrophytes and interstitial habitat potentially provides refuges for prey items and may reduce the effects of predation compared to areas with low habitat complexity (Crooks 2002). Fine sediment loading can lead to the homogenisation of lotic ecosystems and a loss of habitat (Wood and Armitage 1997), but may also lead to reduced macroinvertebrate diversity through elevated drift or direct burial (Wood et al. 2005; Larson et al. 2010; Jones et al. 2012). Such alterations to resident macroinvertebrate assemblages (in particular species richness) associated with the habitat template may modify the interactions and effects of invasive crayfish on the wider macroinvertebrate community (Fitzgerald et al. 2016).

This study investigated the effect of invasive signal crayfish within a high resolution sampling timeframe. In contrast to other studies, which have examined the net effect of large established populations of crayfish on stream communities via spot sampling throughout the year, this study aimed to examine the temporal variability of crayfish effects (if any) throughout the main period of crayfish activity. We specifically sought to address the following research question—do crayfish effects on the wider macroinvertebrate community intensify as the activity season proceeds or are the effects on the macroinvertebrate community consistent regardless of crayfish activity? Crayfish are cold-blooded and therefore activity levels are strongly associated with water temperature. Consequently, crayfish activity is most pronounced during the summer months and has been reported to cease below 5 °C (Bubb et al. 2004; Johnson et al. 2014). Given the potential moderation of predator–prey interactions associated with the local physical habitat, the study also considers the role of substrate character, specifically fine sediment content, in influencing invasive crayfish community effects.

## Materials and methods

### Study sites

The study took place on two small lowland rivers in Rutland (UK); the River Gwash (52°38'N, 00°44' W) and the River Chater (52°37'N, 00°44'W). Historic routine sampling by the Environment Agency (1989–2015) and contemporary sampling during the study period by the author has not recorded any signal crayfish in the River Chater (control river), whilst density estimates in the Gwash (invaded river) during 2014–2015 indicated a mean catch per unit effort of 4.7 individuals per trap per night ( $n = 20$ ). Both of these rivers formed part of a long-term analysis in which the River Gwash demonstrated a significant divergence in assemblage composition following crayfish invasion (1996) compared to the River Chater (and other control rivers; Mathers et al. 2016). Community composition was historically comparable in both rivers and the divergence in communities associated with crayfish presence has persisted over time. Study sites were selected to be as broadly comparable in physical characteristics (channel size, water chemistry, altitude and geology) as possible and experienced similar hydroclimatological regimes given they were located 2.6 km apart (Fig. 1).

### Colonisation cylinders

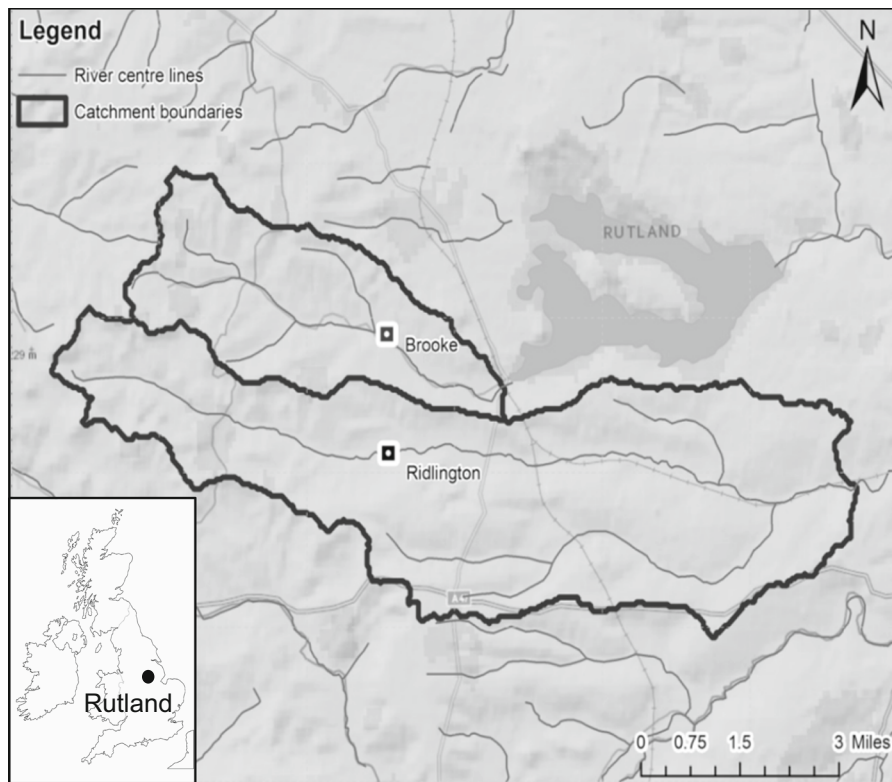
At both sites, colonisation cylinders were deployed which provided a constant record of the macroinvertebrate community. Each colonisation cylinder comprised a PVC cylinder (diameter 65 mm, height 200 mm) perforated with twelve horizontal holes (diameter 6 mm) to permit horizontal and vertical exchange of flow, macroinvertebrates, and fine sediment (Mathers and Wood 2016). All cylinders were filled with a prewashed gravel framework collected from each of the respective sample sites (truncated at 8 mm) that was enclosed in a net bag (7 mm aperture) within each cylinder.

A second cylinder treatment was deployed to allow investigation of how fine sedimentation of the substratum affects crayfish-macroinvertebrate interactions. In these cylinders, 250 g of fine sand (63–2000  $\mu\text{m}$ ) was added to the gravel framework. Preliminary tests indicated that this filled 100% of the

interstitial volume of the substrates. Signal crayfish have the potential to directly alter the input and output of fine sediment, which may have consequences for the in channel storage of fine sediments (Harvey et al. 2011). Crayfish burrowing activities may enhance the delivery of fine sediment (Faller et al. 2016) while the diurnal bioturbation of fine sediment associated with crayfish activity increases sediment fluxes out of the reach and winnows fines (Rice et al. 2016; Albertson and Daniels 2016). It is likely that the relative role of these contrasting processes varies depending on the spatial distribution of crayfish within a river reach and therefore the effect of crayfish on fine sediment loading may not be consistent. Consequently, the application of two sediment treatments in this study (i.e. no fine sediment and interstitial pore space filled with fines) enabled the potential effect of differing fine sediment loading and temporal variability of crayfish effects for the invaded ecosystem to be examined.

For the cylinders with enhanced fine sediment loading (hereafter referred to as clogged), a circular disk (64 mm diameter) was attached to the mesh bag which effectively sealed the base of the cylinder and reduced the loss of fine material vertically into the riverbed. Cylinders were inserted into the river bed by placing the PVC cylinders onto a steel pipe (35 mm diameter) that was then driven into the bed sediments by hand until a sufficient sized hole was formed. Cylinders were inserted flush with the sediment surface to a depth of 200 mm and left in situ for the entire sampling campaign. Every 14 days, the gravel netting bag was removed and replaced with fresh gravel, providing an ongoing record of the macroinvertebrate communities at this resolution. At the end of each 14-day sampling period, the net bag was carefully removed and placed directly into a sample bag. Empty cylinders were then replaced with the corresponding gravel bag treatment (clean or clogged). All invertebrate samples were preserved in the field in 10% formaldehyde and returned for the laboratory for processing and identification.

Colonisation cylinders were installed for 126 days providing nine 14-day sample sets (21st May–24th September 2015). At each riffle site (three sites at the invaded reach and two sites at the control; one until 2nd July 2015), four cylinders of each type (clean or clogged) were installed providing a total of 12 replicates in the invaded site and 8 (4 initially for 3 sample sets) at the control. In total, 213 and 112



**Fig. 1** Location of study sites on the River Chater (Ridlington, control) and River Gwash (Brooke, invaded), Rutland, UK

**Table 1** Summary of datasets collected for this study at the invaded (Gwash) and control (Chater) rivers during 2015

Sample set	Dates covered	Invaded		Control
		Colonisation cylinders	Crayfish trapping	Colonisation cylinders
1	21st May–4th June	n = 23	n = 1	n = 7
2	4th June–18th June	n = 24	n = 1	n = 7
3	18th June–2nd July	n = 24	n = 1	n = 8
4	2nd July–15th July	n = 24	n = 1	n = 16
5	15th July–30th July	n = 23	n = 2	n = 15
6	30th July–13th August	n = 24	n = 1	n = 14
7	13th August–27th August	n = 24	n = 2	n = 15
8	27th August–10th September	n = 23	n = 3	n = 15
9	10th September–24th September	n = 24	n = 3	n = 16

For each of the crayfish trapping replicates (n), a number of traps were set within the study reach (average of six per occasion)

substrate samples were examined from the invaded and control sites respectively (3 clean cylinders were not retrieved from both sites and 5 clogged cylinders

were lost at the control site; Table 1 provides a breakdown of sample dates and riffle replicates over time).

## Crayfish activity

Trapping was conducted on an intermittent basis throughout the sampling campaign as a surrogate for adult crayfish activity (see Table 1 for a breakdown of trapping occasions). Periodically ( $n = 15$ ), baited “trappy” traps ( $50 \times 20$  cm with an opening of 5 cm and mesh size 3 cm) were deployed at the invaded site at three locations throughout the reach (upstream, middle and downstream). This sampling strategy enabled a spatially representative record of activity levels as crayfish are known to move sporadically to new locations and therefore not reside at a single location (Bubb et al. 2002). On each occasion traps were set at a location during the afternoon and retrieved the following morning with a minimum of two traps per location. Catch Per Unit Estimates (CPUE) were calculated from the total number of adult individuals caught for each sampling set and presented as an abundance index. Trapping often leaves juvenile crayfish population’s uncharacterised (Holdich et al. 1999), however juvenile crayfish were regularly recorded in the colonisation cylinders. This provided a means of assessing the relative abundance of juvenile crayfish during the survey season. The number of juvenile crayfish recorded in the cylinders for each sample set was standardised to the number of individuals per  $m^2$  by dividing the total number of crayfish for each sample set by the total sample surface area of the cylinders ( $\text{ind}/m^2$ ).

## Laboratory procedures and statistical analysis

Within the laboratory, samples were processed for invertebrates by passing the cylinder samples through a series of sieves (4 mm, 2 mm and 250  $\mu\text{m}$ ). All macroinvertebrates were identified to the lowest taxonomic level possible, which was usually species or genus with the exception of Oligiochetea (order), Diptera families (including Ephydriidae, Ptychopteridae, Chironomidae, Psychodidae, Simuliidae, Ceratopogonidae and Stratiomyidae), Sphaeriidae and Zonitidae (family) and Ostracoda, Hydracarina and Collembola which were recorded as such.

To identify temporal changes in macroinvertebrate communities associated with crayfish activity and species life-cycles, non-metric multidimensional scaling (NMDS) centroid plots were employed over time for the invaded and control sites (sample sets 1–9).

Distances among centroid matrices were constructed by calculating the averages (e.g. the centroid—the centre-point of all replicates for each sample set in multi-dimensional space) using Bray–Curtis similarity coefficients (Anderson et al. 2008). Compositional differences in communities between the control and invaded sites were examined using non-metric multidimensional scaling (NMDS) plots using Bray–Curtis similarity coefficients for the overall data set and for each individual sample set. This approach enabled examination of whether community effects were temporally similar or whether they varied over time.

A One way ANOSIM (Analysis of Similarities) was used to examine differences in the communities amongst the control and invaded rivers for the overall data set and for each sample set (1–9). For each dataset, a random Monte Carlo permutations test was performed (999 random permutations). Both P and R ANOSIM values were examined, with R values  $>0.75$  indicating strong separation amongst groups,  $R = 0.75\text{--}0.25$  indicating separate groups with overlapping values and  $R < 0.25$  as barely distinguishable groups (Clarke and Gorley 2006). To examine if invaded or control communities were more or less heterogeneous than the other, homogeneity of multivariate dispersions (beta diversity) between aquatic macroinvertebrate assemblages based on Bray–Curtis distance matrices from the centroid were calculated using the PERMDISP function and compared using One-Way ANOVA (Anderson 2006; Anderson et al. 2006, 2008). Taxa contributing to the divergence of communities were identified through the application of the similarity percentage (SIMPER) with a number of these in addition to those that have been cited in previous literature associated with crayfish invasions, selected for further statistical analysis. All ordination analyses were performed in PRIMER Version 7.0.11 (PRIMER-E Ltd, Plymouth, UK).

Community abundance and taxa richness metrics were derived from the raw data, in addition to richness of Ephemeroptera, Plecoptera and Trichoptera (EPT) groups. To examine differences in macroinvertebrate metrics and individual taxon abundances associated with crayfish presence, generalised linear mixed effects models were developed (GLMMs). Models were fitted using the ‘lme4’ package in R version 3.2.2 using the ‘glmer’ function (R Development Core Team 2014). To examine differences associated with the volume of fine sediment, treatment was specified

as a fixed factor and riffle was nested within site as a random factor (columns within individual riffles and sites are less independent of each other). Models were fitted using a Poisson error distribution and log link structure.

## Results

### Community composition associated with crayfish presence and sediment treatment

A total of 69 taxa were recorded from the 169 colonisation cylinders; of these 57 were recorded in the invaded river (mean 6.62, range 1–14) and 54 in the control river (mean 7.06, range 2–16). In all, 17,734 individuals were recorded from the nine sampling sets (invaded river mean 55.02, range 14–168; control river mean 54.68, range 9–136). Communities at the invaded site were dominated by *Gammarus pulex* (56.69% of total abundance), Chironomidae larvae (14.10%) and *Potamopyrgus antipodarum* (9.92%). The most abundant taxa at the control site were *Gammarus pulex* (69.70% of total abundance), Oligochaeta (5.63%) and Chironomidae (4.66%).

Non-metric Multi-Dimensional Scaling (NMDS) ordination diagrams for the entire dataset and the nine individual sampling sets indicated distinct clusters of macroinvertebrate communities at the invaded and control river on all occasions (Fig. 2). The degree of separation between the groups remained consistent over time with all sample sets indicating highly significant differences for all pairwise comparisons (ANOSIM; eight of nine sets and global dataset  $p \leq 0.001$  and set 2  $p = 0.002$ ; Table 2).

When sediment treatment was considered, the crayfish invaded site had a different macroinvertebrate community composition compared to the control site. However, it was also evident that there were significant differences between sediment treatments which were distinct for both the control and invaded sites. Four distinct clusters were evident in the ordination plots as a function of the presence of crayfish and substrate treatment (Fig. 3; only one sampling period, set 4, is shown for conciseness, for all sampling periods see Figure S1), and in all instances these differences were statistically different (ANOSIM all  $p$  values  $< 0.003$ ; Table S1). Clean substrate

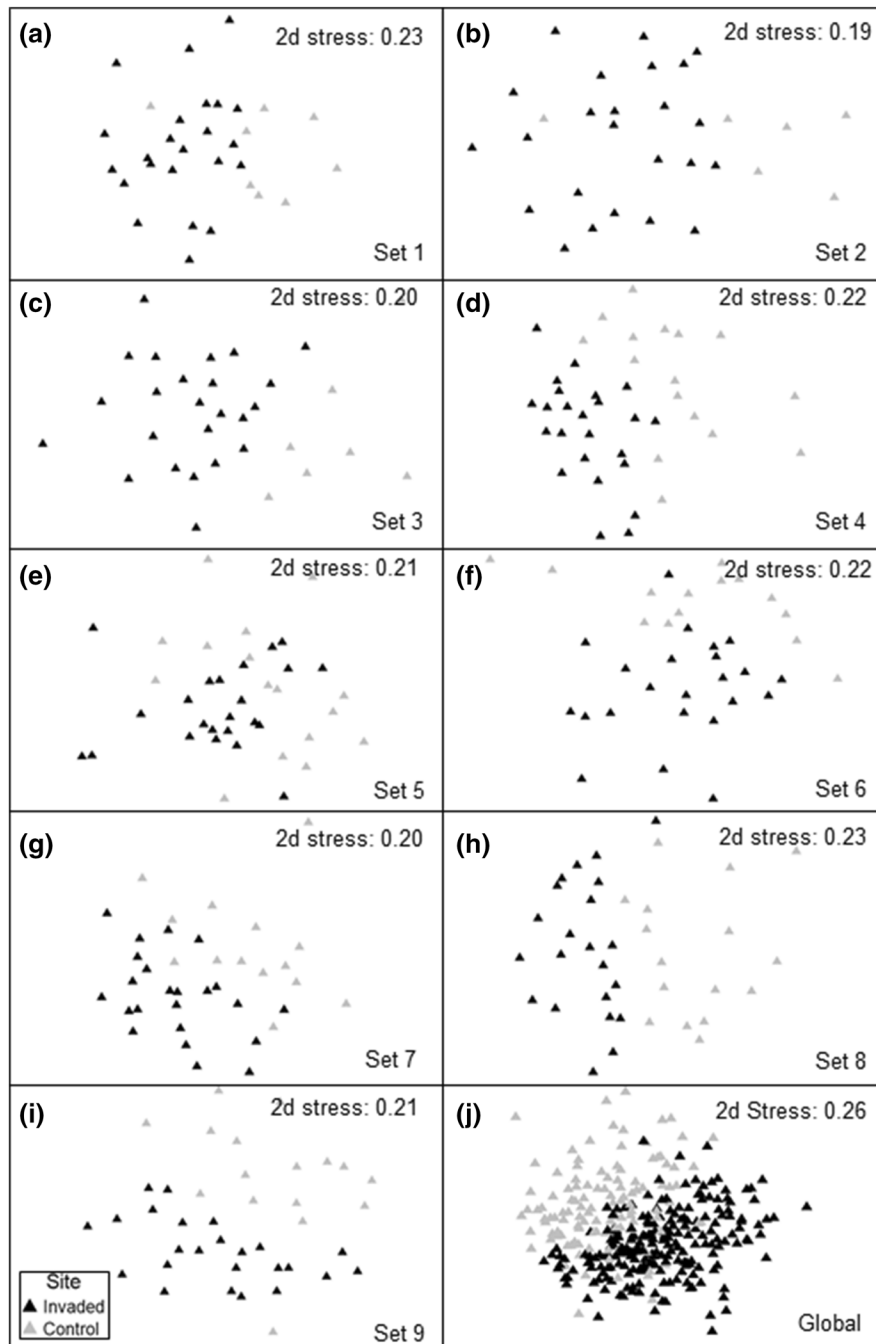
communities demonstrated the greatest separation between invaded and control communities with all pairwise comparisons being significant compared to 7 out of the 9 clogged sets (Table 2).

Both the invaded and control site demonstrated comparable trajectories of assemblage change over time (Fig. 4). However, the change in composition over time remained consistent at the control site, whilst Sets 4–8 at the invaded site cluster together followed by another shift in composition for Set 9. Multivariate dispersion indicated a shift in the heterogeneity of the communities over time. Invaded communities demonstrated similar beta diversity to the control site for the first three sample sets (average distance for invaded 29.30 and 29.04 for control communities), after which control communities displayed greater heterogeneity (sets 4–9; control site average distance 31.58) with invaded sites demonstrating a noticeable reduction in beta diversity (average distance 28.17). Only Set 4 of the pairwise distances was determined to be significantly different ( $T = 3.13$ ,  $p = 0.008$ ; Table 3). When the global dataset was considered, the control site was significantly more heterogeneous ( $T = 3.77$ ,  $p = 0.001$ ) than the invaded site (average distances 34.44 control and 31.21 invaded). The top ten taxa driving dissimilarity overall between control and invaded sites were Chironomidae (5.65% dissimilarity), Oligochaeta (5.11%), *P. antipodarum* (5.03%), *G. pulex* (4.26%), *Erpobdella octoculata* (3.81%), *Dicranota* sp. (2.81%), *Habrophlebia fusca* (2.79%), *Baetis* sp. (2.29%), *Elmis aenea* (adult; 2.01%) and Sphaeriidae (1.90%).

### Community metrics and individual taxon abundances associated with crayfish presence

Total community abundance did not vary significantly by site or time ( $p > 0.05$ ). Taxa richness varied significantly over time ( $Z_{10,320} = -3.64$ ,  $p < 0.001$ ) and displayed a significant site: time interaction ( $Z_{10,320} = 2.17$ ,  $p = 0.03$ ) with lower numbers of taxa on most sampling occasions at the invaded site (Fig. 5). EPT abundance and richness varied over time (both  $p < 0.001$ ) but not by site ( $p > 0.05$ ).

When individual taxon abundances were considered, the Hirudinea species, *E. octoculata*, displayed consistently lower abundances at the invaded site ( $Z_{10,320} = 2.03$ ,  $p = 0.043$ ; Fig. 6a). Mollusca

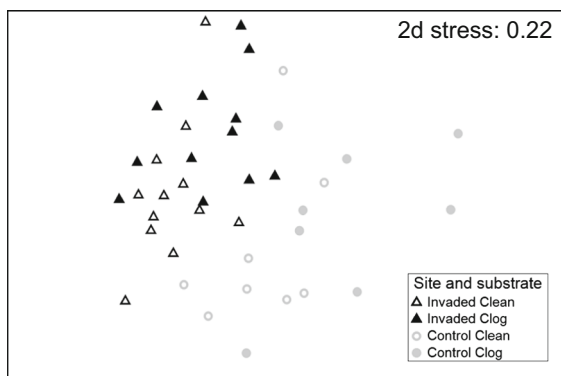


**Fig. 2** Non-metric multidimensional scaling (NMDS) of macroinvertebrate community data using the Bray–Curtis similarities coefficients for cylinder sets 1–9 (a–i; 21st May–24th September 2015) and global data set (j). *Black*

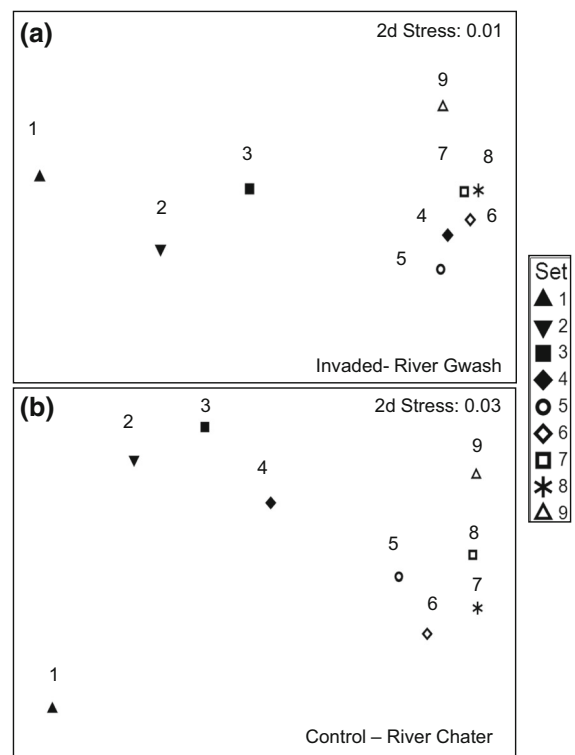
*triangles* = invaded (Gwash) and *grey triangles* = control (Chater). For a breakdown of sampling dates for the individual sample sets see Table 1

**Table 2** Summary of ANOSIM values over time by crayfish presence and sediment treatment

Set	Site differences		Clean versus clean		Clog versus clog	
	r value	p value	r value	p value	r value	p value
1	0.325	0.001	0.409	0.018	0.249	0.078
2	0.407	0.002	0.545	0.006	0.116	0.363
3	0.552	0.001	0.812	0.002	0.402	0.012
4	0.417	0.001	0.424	0.001	0.524	0.001
5	0.252	0.001	0.413	0.001	0.208	0.015
6	0.306	0.001	0.348	0.001	0.340	0.004
7	0.367	0.001	0.368	0.002	0.277	0.016
8	0.375	0.001	0.399	0.001	0.394	0.030
9	0.411	0.001	0.281	0.006	0.487	0.001
Global	0.342	0.001	0.306	0.001	0.306	0.001

**Fig. 3** Non-metric multidimensional scaling (NMDS) of macroinvertebrate community data using the Bray–Curtis similarities coefficients for cylinder sampling set 4 (2nd–15th July 2015) as a function of combined crayfish presence/absence and sediment treatment (clean or clogged). *Black open triangles* = invaded clean substrates; *black solid triangles* = invaded clog substrates; *grey open circles* = control clean substrates and; *grey solid triangles* = control clog substrates

responses varied, with *P. antipodarum* displaying greater abundances at the invaded site on a number of occasions (Site: time interaction  $Z_{10,320} = -2.35$ ,  $p = 0.019$ ; Fig. 6b) whilst Sphaeridae was recorded in greater numbers at the control site ( $Z_{10,320} = 3.427$ ,  $p < 0.001$ ) and varied over time ( $Z_{10,320} = 3.56$ ,  $p < 0.001$ ) and demonstrated a site: time interaction ( $Z_{10,320} = -3.16$ ,  $p = 0.002$ ). *Dicranota* sp. demonstrated significant differences in abundances associated with site ( $Z_{10,320} = -3.38$ ,  $p < 0.001$ ; Fig. 6c) and over time ( $Z_{10,320} = -13.61$ ,  $p < 0.001$ ). The coleopteran family Elmidae (comprising multiple species; *Limnius volckmari*, *Elmis aenea* and *Oulinus* sp.) were recorded in significantly greater

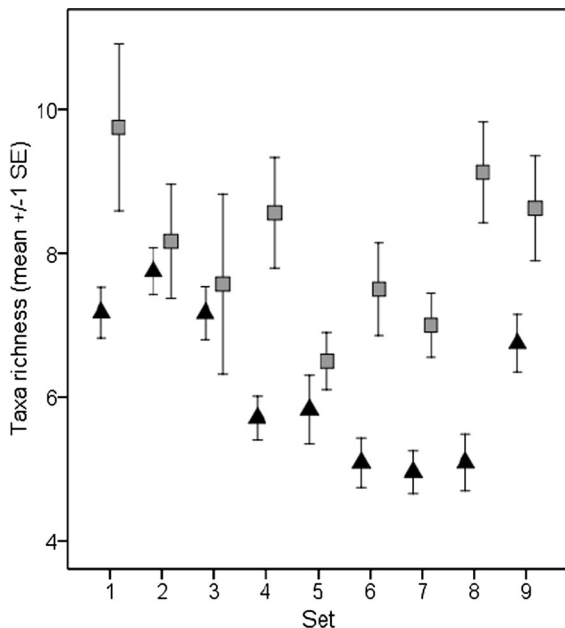
**Fig. 4** Non-metric multidimensional scaling (NMDS) temporal centroid ordinations of community data for cylinder sets 1–9 (21st May–24th September 2015) at: **a** River Gwash and; **b** River Chater. For a breakdown of sampling dates for the individual sample sets see Table 1

abundances at the control site in both larval ( $Z_{10,320} = 2.49$ ,  $p = 0.013$ ) and adult life stages ( $Z_{10,320} = 3.178$ ,  $p = 0.001$ ) with the effect consistent across the entire sampling period (Fig. 6d). Crayfish presence did not affect all taxa within the



**Table 3** Summary of PERMDISP analysis by crayfish presence. Significant results are emboldened

Set	Average distance		<i>p</i> value
	Invaded	Control	
1	28.18	27.53	0.852
2	30.23	29.69	0.856
3	29.61	29.90	0.956
4	26.04	32.02	<b>0.008</b>
5	27.62	31.62	0.224
6	28.08	29.74	0.561
7	28.31	31.66	0.223
8	27.36	30.78	0.129
9	31.60	33.67	0.438
Global	31.21	34.44	<b>0.001</b>

**Fig. 5** Mean ( $\pm 1$  SE) a) taxa richness over the nine sample sets (21st May–24th September 2015). *Black triangles* = invaded communities and *grey squares* = control communities. For a breakdown of sampling dates for the individual sample sets see Table 1

order of Ephemeroptera. The crawler *H. fusca* demonstrated significantly lower abundances on a number of sampling occasions at the invaded site with abundances being significantly lower during sampling set 3 (Site: time 3 interaction  $Z_{10,310} = 3.6$ ,  $p < 0.001$ ;

Fig. 6e), while the swimming taxa *Baetis* sp. demonstrated no significant difference between the invaded and control site but did vary in abundance over time ( $Z_{10,320} = -9.67$ ,  $p < 0.001$ ; Fig. 6f).

#### Signal crayfish activity

A total of 25 juvenile signal crayfish were recorded in the cylinders over the course of the sampling campaign. Individuals first appeared in the sampling record in Set 2 (early June), which also corresponded to the greatest abundance of individuals (12 ind = 150.5 ind/m<sup>2</sup>). Individuals were recorded in each set until sampling period 7 (late August), with a second peak being evident during set 5 (late July; 82 ind/m<sup>2</sup>; Fig. 7). There was no apparent preference displayed for clean or clogged substrates (22.3 and 24 ind/m<sup>2</sup> respectively).

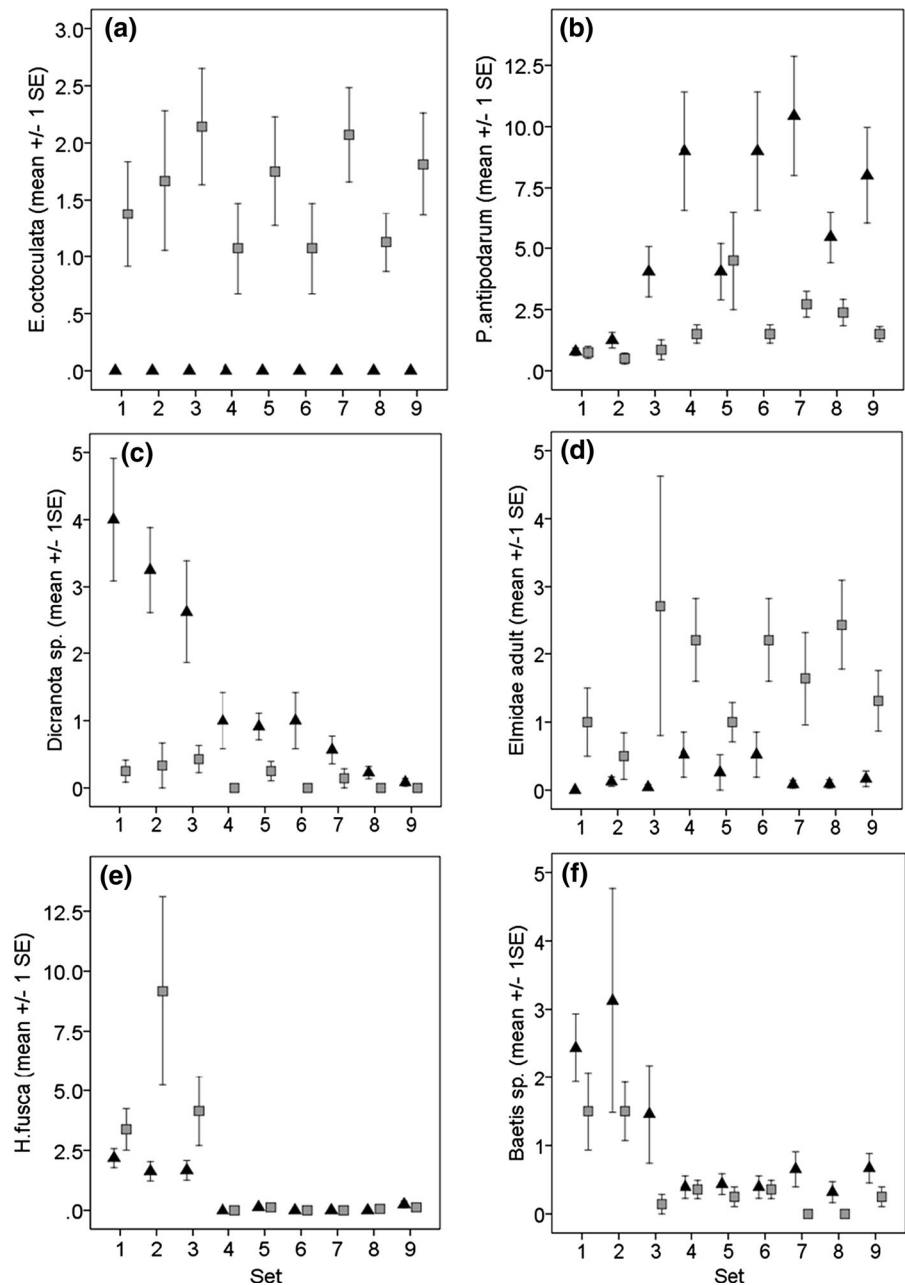
Trapping of the adult component of the population indicated temporal differences in the number of individuals trapped (average 3.9 adults, range 0–5.55 CPUE; Fig. 8). No crayfish were trapped during Set 1 and were recorded in low abundances during Set 3. Set 2 recorded large CPUE numbers similar to those recorded during Sets 4–9 and corresponded to the first occurrence of juvenile crayfish (young-of-year) in the cylinders.

#### Discussion

Crayfish effects for macroinvertebrate communities—temporal evolution during the summer months

The results from this study demonstrate that invasive signal crayfish have significant and persistent effects on the wider lotic macroinvertebrate community regardless of their activity levels. NMDS ordination analysis indicated distinct differences in the communities at invaded and control sites throughout the sampling period (21st May–24th September) and for each of the nine individual 14-day sampling sets. All pairwise comparisons were determined to be highly significant (all  $p < 0.002$ ) demonstrating the strong and persistent modifications to macroinvertebrate assemblages once invaded (Wilson et al. 2004; McCarthy et al. 2006). Crayfish also had a significant effect on beta diversity, with control communities

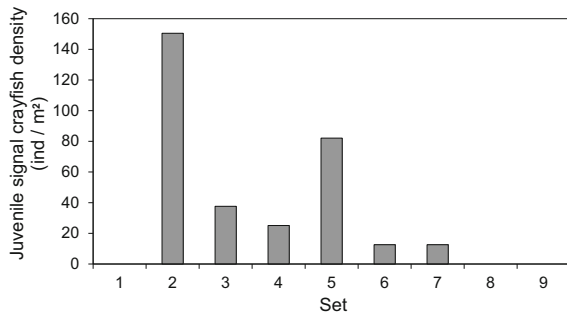
**Fig. 6** Mean abundances ( $\pm 1$  SE) of **a** *Erpobdella octoculata*; **b** *Potamopyrgus antipodarum*; **c** *Dicranota* sp.; **d** Elmidae adult; **e** *Habrophlebia fusca* and; **f** *Baetis* sp. over the nine sample sets. *Black triangles* = invaded communities and *grey squares* = control communities. For a breakdown of sampling dates for the individual sample sets see Table 1



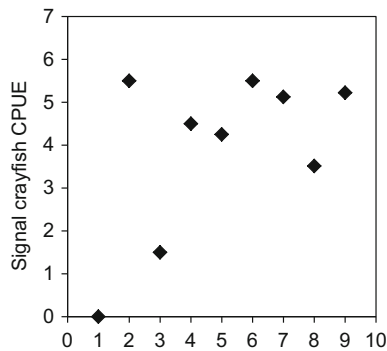
demonstrating a greater degree of community heterogeneity compared to those at the invaded site. When the temporal community effects and activity of crayfish were considered, both invaded and control communities demonstrated similar temporal trajectories of change reflecting natural variability in macroinvertebrate assemblages as a function of taxon life histories (Johnson et al. 2012). However, invertebrate communities at the invaded crayfish site demonstrated

some variations most likely reflecting modifications in crayfish activity levels over the sampling period.

During the first three sets of samples (late May–early July) both rivers demonstrated similar temporal changes and there was therefore some evidence to suggest that community effects were less marked following prolonged periods of lower water temperatures (i.e. over winter and early spring). Both invaded and control sites also displayed similar community



**Fig. 7** Density of juvenile signal crayfish recorded during individual sampling sets (21st May–24th September 2015) via the colonisation cylinders at the invaded site (Gwash). For a breakdown of sampling dates for the individual sample sets see Table 1



**Fig. 8** Adult signal crayfish catch per unit effort (CPUE) for each sample set at the invaded site (Gwash). For a breakdown of sampling dates for the individual sample sets see Table 1

heterogeneity during the early surveys (set 1–3) when adult crayfish activity was low (as determined by CPUE; although set 2 probably coincided with the release of young-of-year). However, Set 4 (early July) represents a discrete period during which the community trajectory differed markedly between control and invaded sites. At the invaded site, communities' clustered together during Sets 4–8 (early July–Mid September), whilst at the control site, the assemblage continued to demonstrate greater variability over time. This period coincides with increased adult crayfish activity associated with elevated water temperatures (average temperature of 14.7 °C compared to 13.7 °C in the preceding months; Fig. 9; Bubb et al. 2006). CPUE abundances increase considerably during Set 4 and remained consistently high throughout the remainder of the sampling campaign. Consequently, it is likely that despite crayfish having significant and

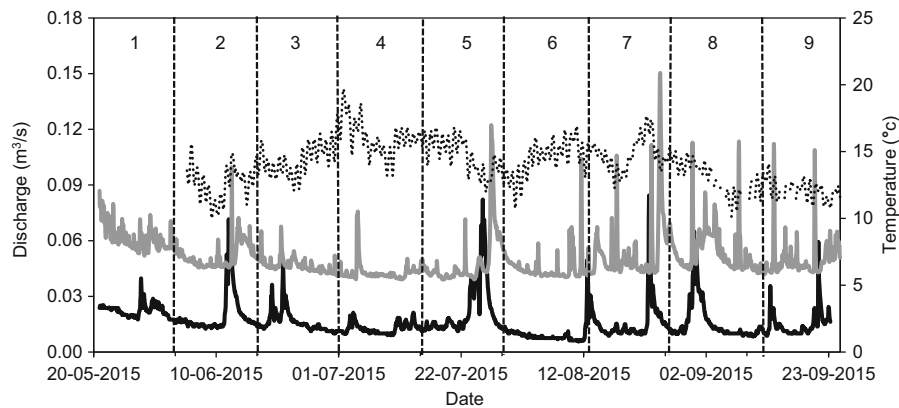
ongoing effects for the wider macroinvertebrate community, there were small scale differences over time. Notably, the only sample set to demonstrate significant differences in beta diversity between invaded and control rivers was Set 4, coinciding with the period when crayfish activity intensified.

From mid to late September (Set 9) there was a second shift in temporal community composition, potentially reflecting changes in crayfish behaviour, with this time period coinciding with the start of the mating season (Lewis 2002). The high temporal resolution dataset utilised in this study potentially enables the key stages in crayfish activity and their lifecycle to be identified. This study was conducted in a river which supported a well-established and abundant crayfish population (>20 years) and thus the overwhelming effect of crayfish presence is such that community composition has been modified (sensu Mathers et al. 2016). The life cycle/history characteristics of crayfish populations (increased activity in late spring and during mating) may have even more marked effects on invertebrate populations in rivers where the invasion is more recent or abundances are low as a result of preferential prey taxa (e.g. Hirudinea and Gastropoda) still being present at relatively high abundances.

#### The role of substrate character and crayfish presence on macroinvertebrate communities

When sediment treatment was considered, community effects of invasive crayfish presence were most pronounced within the clean substrates (evidenced in the ANOSIM values), but were still evident within the clogged substrates. Clean substrates are widely acknowledged to support a greater diversity of macroinvertebrates (Richards and Bacon 1994; Wood and Armitage 1999; Growns et al. 2016) and are therefore more likely to demonstrate a more marked effect of sustained crayfish predation associated with their initial higher taxa richness. In marked contrast, homogenous substrates (i.e. fine sediment dominated environments), which are typically species poor, may experience less significant effects following crayfish invasion as a function of the lower initial taxa richness.

Within boreal lakes, Ruokonen et al. (2014) documented habitat specific effects of signal crayfish for resident macroinvertebrate taxa. It is likely that the effects of crayfish invasion will vary dependent on



**Fig. 9** River discharge (hourly average  $\text{m}^3 \text{s}^{-1}$ ) for the River Gwash (black) and River Chater (grey) Rutland, UK during the sampling campaign from gauging stations (Manton  $52^\circ 38' \text{N}$ ,  $00^\circ 42' \text{W}$  and Fosters Bridge,  $52^\circ 36' \text{N}$ ,  $00^\circ 30' \text{W}$ ). Dotted black represents water temperature recorded on the River Gwash (hourly averaged). The river Chater temperature is a parallel

series and is therefore not presented. Dashed lines indicate the 2 week sampling periods (21st June–24th September 2015). Temperature data is not available until 4th July due to equipment failure. For a breakdown of sampling dates for the individual sample sets see Table 1

local habitat conditions which act as a physical template for resident taxa. Consequently, the effects of invasive species should be evaluated across a range of relevant habitats and spatial scales in order to enable the extent of invader effects to be quantified. Nevertheless, the results from this study indicate that when substrate conditions are considered, the effects of invasive crayfish were stronger and more consistent than the differences in communities associated with the volume of fine sediment present. That is, macroinvertebrate communities demonstrate a consistent and highly significant difference in composition as a function of the established invasive crayfish populations regardless of the substrate conditions.

#### Taxa–crayfish interactions

Crayfish presence did not significantly affect total macroinvertebrate abundance within this study. The effect of crayfish presence on invertebrate densities is highly variable with some studies indicating a reduction (Nyström 1999; Crawford et al. 2006) whilst others have reported no differences (Lagrange et al. 2014; Ercoli et al. 2015a). The inconsistent results suggest that any effect on total community abundances is weak and probably a function of original community composition, and highly dependent on individual species responses. Within this study, taxa richness was significantly lower at the invaded site compared to the control site. This effect remained consistent

throughout the sampling period, but was not as marked during sets 2 and 3, a factor reflected in the site: time interaction. Reduced taxa richness has also been documented in a number of other studies following signal crayfish invasion (e.g. Crawford et al. 2006; Ruokonen et al. 2014; Ercoli et al. 2015a, b).

When individual species were considered, the most widely cited taxa affected by crayfish invasion were the class of Hirudinea (leeches), which typically demonstrate significant reductions in abundance (Stenroth and Nyström 2003; Crawford et al. 2006). The unprotected soft bodies and relative slow mobility of these taxa make them ideal prey items for crayfish (Stenroth and Nyström 2003). Results from this study provide further evidence to support this finding, with only 11 individuals in this class being recorded at the invaded site during the entire sampling period (control site = 205 individuals). Moreover, one Hirudinea species, *Helobdella stagnalis* was unique to the control site. *E. octoculata*, the most abundant taxon in this class, occurred at low abundances throughout the sampling period with no temporal variation in numbers evident.

Another group of taxa which are typically associated with reductions in density, biomass and richness following invasive crayfish population establishment are Mollusca (Weber and Lodge 1990; Lodge and Hill 1994; Dorn 2013). Similar to Hirudinea, their reduced rate of mobility makes them susceptible to predation.

However, the effects recorded varied depending on the species considered, which most likely reflects varying life history characteristics and the ability to adapt behaviours that reduces the threat of predation. A number of species have been documented as demonstrating reduced reproductive rates whilst enhancing their growth rates (Hoverman et al. 2005), whilst others display avoidance behaviour by migrating to the waterline for several hours in the presence of crayfish (Alexander and Covich 1991a, b; Turner et al. 1999).

The latter strategy of avoidance has been recorded for *P. antipodarum* under experimental conditions (Haddaway et al. 2014) and may explain the ability of this species to maintain populations that are even greater than those at the control site within this study. This non-native taxon is tolerant of fine sediment and typically burrows into fine sediment deposits (Holmuzki and Biggs 2000; Suren 2005), a factor which may also facilitate predation evasion. In contrast, bivalves from the family Sphaeriidae were recorded in greater numbers at the control site, although there was a significant site: time interaction with the effect not being consistent over time.

Nyström (1999) suggested that benthic sediment dwelling taxa may dominate crayfish communities. Within this study, in addition to *P. antipodarum*, both Chironomidae and *Dicranota* sp., which have a high affinity for fine sediment deposits, were recorded in greater abundances at the invaded site (Fitter and Manuel 1986). *Dicranota* sp. had high initial abundances at the start of the study, when crayfish activity was minimal, but then displayed a marked reduction in numbers during the remaining sampling events. This taxon has a soft unprotected body similar to Hirudinea and may therefore still be susceptible to predation indicating the importance of considering temporal dynamics associated with faunal life cycles in biological invasion studies.

Within this study, the abundance of the coleopteran family Elmidae was also reduced at the invaded site for both larval and adult life stages. Despite being relatively mobile, the semivoltine life cycle (taking more than 1 year to complete its life cycle) of this taxa makes them more susceptible to disturbances (Elliott 2008) and may therefore make them more vulnerable to predation than other mobile taxa. Gut analysis led Guan and Wiles (1998) to conclude that Coleoptera made up a large component of lotic signal crayfish

diets and a number of field studies in lentic environments have suggested that the presence of Elmidae may indicate an absence of crayfish (Bjurström et al. 2010; Ruokonen et al. 2014, 2016).

Taxa in the order of Ephemeroptera have also attracted considerable attention when examining crayfish effects on macroinvertebrate communities with highly variable responses being documented (Mathers et al. 2016). Reductions in abundances (McCarthy et al. 2006) through to no change or enhanced abundances have been reported (Keller and Ruman 1998; Usio and Townsend 2004). In this study, contrasting effects were recorded for the swimming mayfly larvae *Baetis* sp. and the crawling taxon *H. fusca*. These differences most likely reflect the mode of locomotion with swimmers (*Baetis*) demonstrating enhanced mobility and are therefore able to evade predation more readily by swimming out of the way. In contrast crawlers (*H. fusca*) display slower locomotion (Peckarsky 1996), typically inhabiting pools and margin areas (Elliott et al. 1988), which may make them more vulnerable to predation by larger crayfish, which also favour pools (Clark et al. 2013).

#### Application of colonisation cylinders in the monitoring of juvenile crayfish populations

This study used colonisation cylinders to obtain a quantitative record of benthic macroinvertebrate communities over the 126 day study period. Initial deployment of the cylinders occurred before the main period of crayfish activity (late May) when water temperatures were low (average 12.78 °C) and therefore provided an opportunity to assess the ability of the method to quantitatively monitor juvenile crayfish abundances, which are notoriously difficult to sample (Moorhouse and Macdonald 2011). Results suggest that colonisation cylinders may be an appropriate technique to determine abundances of juvenile crayfish throughout the sampling period, with peak densities occurring during late June in this study but further testing is required to assess the wider transferability of such an approach. Egg hatching of signal crayfish occurs between late March and the end of July dependent on water temperatures, and it is likely that this peak in numbers reflects the time when eggs were released in this population. The densities recorded during this time frame were 150.5 ind/m<sup>2</sup> and reflects

the high fecundity of this species which make them successful invaders (Kouba et al. 2015).

Densities remained high (37–25 ind/m<sup>2</sup>) during the following 4 weeks, with a second peak in juvenile abundances in Set 5 (mid July; 82 ind/m<sup>2</sup>). Abundances declined over the next 4 weeks, with no juveniles recorded in the cylinders during the final two sample sets (September). This decline and absence at the end of the study may reflect intra-specific predation of adults upon juveniles (Guan and Wiles 1998) but could also reflect the rapid growth rates of signal crayfish and therefore larger body sizes at this stage inhibiting access to the subsurface substrates. The high number of juvenile crayfish recorded in this study indicates that interstitial habitats are a refuge for juvenile crayfish and an absence of such habitat (i.e. a lack of hyporheic zone within urbanised rivers) may limit the reproductive successes of crayfish populations through reduced survivorship.

#### Wider applicability of the study

The results of this study suggest that in addition to the major changes recorded in previous studies; changes to the macroinvertebrate community are dynamic reflecting short term temporal patterns. These are probably a function of key environmental controls (water temperate) and life history characteristics (of the invader and resident taxa) such as the timing of reproduction. Although in this study, changes over time were relatively modest, most likely associated with the well-established and abundant crayfish population which had significantly modified the resident communities prior to the current study, the variability recorded at newly invaded or sparsely populated communities may be more marked. The effect of crayfish presence within this river was so strong that changes in the community were evident regardless of substrate conditions and the effect of sedimentation and crayfish therefore resulted in distinct macroinvertebrate communities within each river.

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