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The effects of non-native signal crayfish (*Pacifastacus leniusculus*) on fine sediment and sediment-biomonitoring



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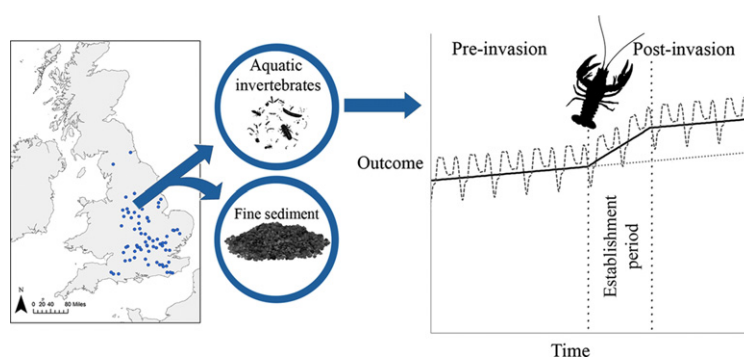
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HIGHLIGHTS

- The North American signal crayfish has invaded freshwaters throughout Europe.
- Signal crayfish may influence biomonitoring tools and/or fine sediment conditions.
- Long-term environmental data is analysed using Interrupted Time Series analysis.
- Small changes to biomonitoring tools and fine sediment followed crayfish invasions.
- Signal crayfish appear unlikely to lead to incorrect diagnoses of sediment pressure.

GRAPHICAL ABSTRACT



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ABSTRACT

The North American signal crayfish (*Pacifastacus leniusculus*) has invaded freshwater ecosystems across Europe. Recent studies suggest that predation of macroinvertebrates by signal crayfish can affect the performance of freshwater biomonitoring tools used to assess causes of ecological degradation. Given the reliance on biomonitoring globally, it is crucial that the potential influence of invasive species is better understood. Crayfish are also biogeomorphic agents, and therefore, the aim of this study was to investigate whether sediment-biomonitoring tool outputs changed following signal crayfish invasions, and whether these changes reflected post-invasion changes to deposited fine sediment, or changes to macroinvertebrate community compositions unrelated to fine sediment.

A quasi-experimental study design was employed, utilising interrupted time series analysis of long-term environmental monitoring data and a hierarchical modelling approach. The analysis of all sites ($n = 71$) displayed a small, but statistically significant increase between pre- and post-invasion index scores for the Proportion of Sediment-sensitive Invertebrates (PSI) index biomonitoring tool ($4.1, p < 0.001, 95\%CI: 2.1, 6.2$), which can range from 0 to 100, but no statistically significant difference was observed for the empirically-weighted PSI ($0.4, p = 0.742, 95\%CI: -2.1, 2.9$), or fine sediment ($-2.3, p = 0.227, 95\%CI: -6.0, 1.4$). Subgroup analyses demonstrated changes in biomonitoring tool scores ranging from four to 10 percentage points. Importantly, these subgroup analyses showed relatively small changes to fine sediment, two of which were statistically significant, but these did not coincide with the expected responses from biomonitoring tools. The results suggest that sediment-biomonitoring may be influenced by signal crayfish invasions, but the effects appear to be context

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dependent, and perhaps not the result of biogeomorphic activities of crayfish. The low magnitude changes to bio-monitoring scores are unlikely to result in an incorrect diagnosis of sediment pressure, particularly as these tools should be used alongside a suite of other pressure-specific indices.

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1. Introduction

Biological invasions of non-native species (herein invasive species) represent a significant threat to global biodiversity (Simberloff et al., 2013). Invasive species can exert strong pressures on the resident native biota of invaded habitats, both directly, through predation, competition or displacement, and indirectly by disrupting trophic dynamics (Lodge et al., 2012; Early et al., 2016), and altering the physical and chemical characteristics of the habitat (Johnson et al., 2011; Fei et al., 2014; Greenwood and Kuhn, 2014). With freshwater invasions expected to increase as a result of climate change and globalisation, invasive species have the potential to result in widespread ecological impacts; defined as measurable changes to the state of an ecosystem (Ricciardi et al., 2013; Kumschick et al., 2015).

In Europe, one widespread freshwater invasive species is the North American signal crayfish (*Pacifastacus leniusculus*). Signal crayfish are omnivorous, opportunistic feeders, consuming algae, detritus, macrophytes, benthic macroinvertebrates, fish and other crayfish (Harvey et al., 2011). Recent research has suggested that predation on macroinvertebrates by signal crayfish (McCarthy et al., 2006; Mathers et al., 2016a), can lead to changes to biomonitoring tool outputs (Mathers et al., 2016b). Given the reliance of regulatory agencies globally on biomonitoring tools to diagnose ecological degradation in freshwater ecosystems (Birk et al., 2012), it is crucial that the potential for invasive species to influence tool outputs is better understood (MacNeil et al., 2013).

Sediment-specific indices (e.g. Proportion of Sediment-sensitive Invertebrates index; PSI, Extence et al., 2013, and Empirically-weighted Proportion of Sediment-sensitive Invertebrates index; E-PSI, Turley et al., 2016), which use macroinvertebrate community composition, have been developed to monitor fine sediment impacts. The PSI index has been shown to exhibit inflated scores following crayfish invasions (Mathers et al., 2016b). Higher PSI scores are normally indicative of lower fine sediment conditions, however, Mathers et al. (2016b) suggested that the post-invasion inflation of PSI scores were likely the result of selective predation by crayfish. Other research has shown decreased abundance of Gastropoda, Bivalvia and Hirudinea (preferential prey of crayfish; Crawford et al., 2006; Haddaway et al., 2012; Dorn, 2013), and a shift in community composition towards more mobile taxa that are able to avoid predation (Mathers et al., 2016a). These taxa generally score highly in the PSI index, resulting in a higher overall PSI score being recorded.

Crayfish are considered to be biogeomorphic agents, with the ability to rework substrate, increase suspended particulate matter, and alter stream sediment dynamics, primarily due to their burrowing in river banks (increasing erosion and bank collapse), construction of pits and mounds, their large size, aggressive nature, and general movement and foraging on the river bed (Harvey et al., 2011; Johnson et al., 2011; Rice et al., 2012; Albertson and Daniels, 2016). Therefore, whilst the effects on sediment-biomonitoring tool outputs may be the result of shifts in community composition from direct predation and/or the resulting changes to food web dynamics, they could also be partly the result of alterations to fine sediment conditions (i.e. resuspension of deposited fine sediment) caused by signal crayfish - a confounding factor that was not investigated by Mathers et al. (2016b).

The aim of this study was to utilise a quasi-experimental study design and interrupted time series (ITS) analysis to investigate whether inflation of sediment-biomonitoring tool (PSI and E-PSI) scores

occurred following signal crayfish invasions, and whether this was associated with changes to deposited fine sediment over time, or shifts in macroinvertebrate community composition resulting from other effects of crayfish invasion (direct or indirect). Interrupted time series analysis is able to estimate the effects of an intervention (e.g. invasion), taking account of pre-intervention long-term and seasonal trends, and autocorrelation, which are common in ecological applications (Friberg et al., 2009). The application of such techniques in epidemiology and clinical research is relatively common (Bernal et al., 2016; Gasparrini, 2016), however its use within invasion ecology is rare (e.g. Brown et al., 2011), likely due to the challenges of obtaining long term data for pre- and post-invasion periods. Time since invasion is an important consideration when studying the impact of invasive species on the receiving ecosystem and therefore, time series data are likely to provide important insights into these impacts (Strayer et al., 2006; Kumschick et al., 2015).

A further aim of this study was to investigate the influence of stream characteristics; habitat heterogeneity and percentage of coarse substrate, on invader impacts. A stream with high habitat heterogeneity/complexity is likely to provide a greater variety of habitat for benthic macroinvertebrate refugia, than those with homogeneous habitat, potentially resulting in increased community stability and resilience to predation (Brown and Lawson, 2010; Kovalenko et al., 2012). Substrate composition is a characteristic typically related to longitudinal gradients associated with channel gradient, stream power and flow (Church, 2002), and is thought to be an important driver of macroinvertebrate community composition (Minshall, 1984). Macroinvertebrate taxa have a variety of habitat preferences as a result of their biological traits (Extence et al., 2013), and as such, a stream with a high percentage of coarse substrate is likely to be inhabited by a different macroinvertebrate assemblage to one dominated by fine sediment. Signal crayfish invasions may impact these different assemblages to varying degrees, for example, due to the availability of preferential prey items.

This study was led by the following five hypotheses:

Hypothesis 1. The family-level PSI and E-PSI index scores are inflated after signal crayfish invasions.

Hypothesis 2. The percentage of fine sediment is lower at sites post-invasion compared with pre-invasion.

Hypothesis 3. The abundances of preferential crayfish prey taxa (e.g. Gastropoda and Hirudinea) are lower in the post-invasion periods.

Hypothesis 4. Changes to PSI and E-PSI index scores in post-invasion periods will be greatest at sites with low habitat heterogeneity.

Hypothesis 5. Changes to PSI and E-PSI index scores in post-invasion periods will be greatest at sites with low percentages of coarse substrate.

2. Methods

2.1. Site selection

The stream and river sites were selected from a database comprising all past macroinvertebrate samples collected by the Environment Agency of England. A systematic search of the entire database for "*Pacifastacus leniusculus*" returned all stream and river sites in England

where this species was recorded between the year 1990 and 2014. The mostly family-level taxonomic data created uncertainty whether records of the family Astacidae were referring to the native white-clawed crayfish (*Austropotamobius pallipes*), signal crayfish, or other invasive crayfish species. Therefore, to avoid misidentifying the timing of the first record of signal crayfish, those sites with “Astacidae” recorded prior to the first record of “*Pacifastacus leniusculus*” were removed from the dataset. There were no records of “*Austropotamobius pallipes*” in the outstanding data. For each of the remaining sites, the midpoint between the first record of “*Pacifastacus leniusculus*” and the previous sample, was designated as the date of invasion; sites with fewer than four pre-invasion and four post-invasion samples were subsequently removed from the dataset. Finally, for sites on the same watercourse, the site with >10 pre-invasion samples and the greatest number of post-invasion samples was retained, to ensure independence of sites. The 71 remaining sites (Fig. 1) had an average (mean) of 22 pre-invasion samples, collected over an average period of 14 years, and 10 post-invasion samples, collected over an average period of 6.5 years.

2.2. Sediment measurements

The substrate composition data within this study consisted of visual estimates of the percentage of the substrate composed of bedrock, boulders (≥ 256 mm), cobbles (64–256 mm), pebbles/gravel (2–64 mm), sand (≥ 0.06 and < 2.00 mm), and silt and clay (< 0.06 mm), recorded at the time of each macroinvertebrate sample. The size classes for sand, silt and clay were combined to form a substrate class referred to from this point forward as fine sediment. The visual estimate method used to collect these data is described in the Standardisation of River Classifications project protocol (EU-STAR, 2004). Briefly, it involves the operator carrying out a visual inspection over a given reach,

estimating the substrate composition and recording this as a percentage of the above classifications.

2.3. Macroinvertebrate sampling and calculation of sediment biomonitoring indices

The macroinvertebrate data used in this study were collected by the Environment Agency using the UK standard method; a standardised three-minute kick sample technique using a 900 μm mesh hand net, followed by a one-minute hand search. All in-stream habitats identified at the site were sampled in proportion to their occurrence (EU-STAR, 2004). Family-level taxonomic data were used to calculate two sediment-biomonitoring indices for each sample, the PSI index (Extence et al., 2013) and the E-PSI index (Turley et al., 2016).

The PSI index is a biomonitoring tool that is designed to identify the degree of sediment deposition in rivers and streams (Extence et al., 2013; Turley et al., 2014). The index uses macroinvertebrate sensitivity ratings, which were assigned following an extensive literature review, and utilising expert knowledge of biological and ecological traits. The E-PSI index was developed using these same broad sensitive and insensitive classifications, but employed empirical data to assign indicator weightings within them, to improve the sediment-specificity of the index (Turley et al., 2016). Both indices result in a score between 0 (high levels of fine sediment), and 100 (minimal fine sediment).

2.4. Statistical analysis

Interrupted time series analysis using segmented regression was employed to estimate the effects of crayfish invasions on biomonitoring tool outputs and fine sediment. A hierarchical modelling approach was applied to model differences in baseline levels and trends as random effects in R (R Development Core Team 2016). Linear mixed effect (*lme*) models (Pinheiro and Bates, 2000) and linear quantile mixed models (*lqmm*) (Geraci, 2014) were fitted to the time series data of E-PSI, PSI, and fine sediment, from all 71 sites. Both mixed effect models included fixed (invasion progress, time, and seasonal variation) and random effects (time and site). Time was a linear variable used to model the average trend (fixed effects) and site-specific (random effects) deviations from this trend.

An *a priori* definition of the type of impact (e.g. step change, slope change, combination) was necessary to avoid the potential for statistical artefacts to occur when testing numerous models (Bernal et al., 2016). Invasion impacts typically increase rapidly in the early stages of establishment, leveling-off in the long term (Strayer et al., 2006; Ricciardi et al., 2013). Predictions of establishment time for signal crayfish suggest that ~50% of invaded sites (at similar latitudes) are successfully established within 4 years (Sahlin et al., 2010). Therefore, the post-invasion periods in this study were modelled as gradual step changes, and a four-year establishment period was assumed following invasions (see Fig. 2). Although the impacts of some invasive species can take decades to become apparent (Strayer et al., 2006), this ecologically relevant modelling approach could provide an insight into the relatively short-term potential impacts following crayfish invasions.

The seasonal variations of PSI, E-PSI and fine sediment were modelled using harmonic functions of time (Hunsberger et al., 2002; Barone-Adesi et al., 2011). Invasion progress was coded between 0, prior to the invasion commencing (the midpoint between the first “invaded” sample and the previous sample), and 1, following the end of the 4-year “establishment period”, depending on the samples temporal position within the establishment period (e.g. a sample was coded as 0.5 if it occurred halfway through the establishment period).

Model assumptions were checked and the residuals of the *lme* models showed some degree of heteroscedasticity. Despite this, they provide a useful indication of the magnitude of effects. The *lqmm* is less reliant on distributional assumptions, but in this study comes at the cost of precision, and therefore the *lqmm* results are only presented

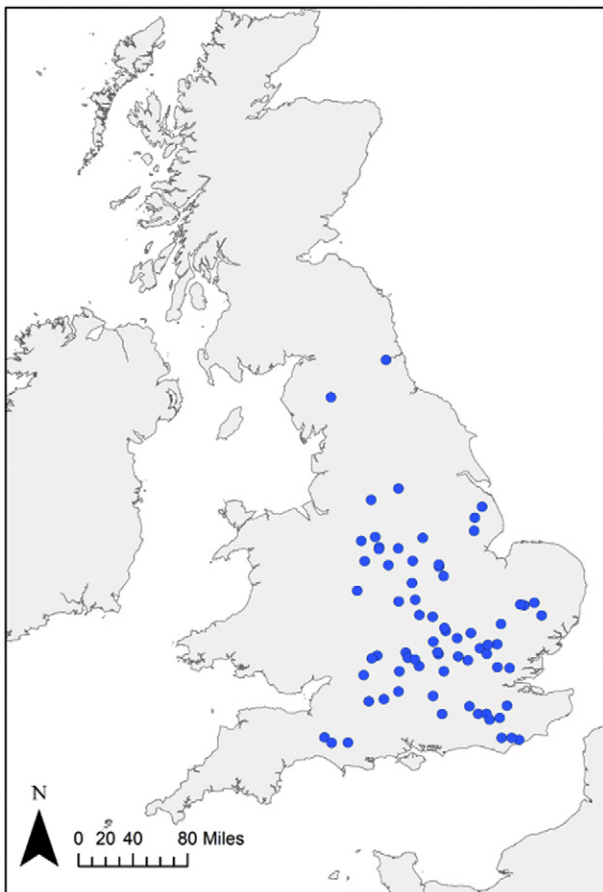


Fig. 1. Locations of the selected river sites throughout England.

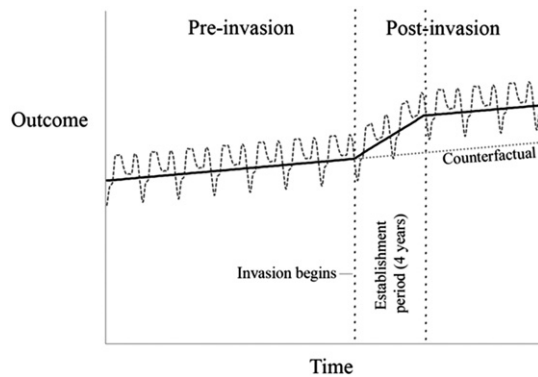


Fig. 2. Conceptual diagram of the gradual step change modelling approach used in this study. Solid line represents the regression line (site-specific). Dashed line represents the long term and seasonal variation (based on data from all study sites). Dotted vertical lines mark the beginning and end of the crayfish 'establishment' period.

in the supplementary material (Table S1), to allow comparison of the effect estimates. After controlling for seasonality there was little evidence of autocorrelation of residuals.

The multiple associations tested were based on specific *a priori* hypotheses, and in these circumstances it has been suggested that adjustments for family-wise error rates (e.g. Bonferroni-Holm corrections) can be overly conservative (Moran, 2003), and therefore in this study *p*-values were not adjusted.

2.5. Subgroup analyses

Subgroup analyses were conducted to investigate whether the effect of crayfish on biomonitoring tool scores and fine sediment conditions varied as a function of habitat characteristics. The dataset of 71 sites was split into three roughly equal groups based on (i) substrate/habitat heterogeneity, and (ii) percentage of coarse substrate.

2.5.1. Habitat heterogeneity

The 71 sites were ranked and divided into three subgroups according to their median substrate Shannon diversity (Heterogeneity Group 1–3; low to high). This was calculated using the Shannon diversity of each samples' substrate composition in the pre-invasion period. The Shannon Diversity Index (*H*) has been previously used as a measure of habitat heterogeneity in ecological and geomorphological research (Yarnell et al., 2006), and is calculated using the following formula:

$$H = -\sum (p_i \ln p_i)$$

where p_i is the proportion of the streambed categorised as substrate size class *i*.

2.5.2. Percentage of coarse substrate

The 71 sites were also ranked and divided into three subgroups based on the median of their pre-invasion estimates of coarse substrate (Substrate Group 1–3; low to high % coarse substrate), which ranged from 5%–100% (boulders, cobbles, pebbles and gravel).

2.5.3. Shifts in community composition

Differences in the community composition between pre- and post-invasion periods were examined in *PRIMER 7* software via non-metric multidimensional scaling (NMDS) centroid plots and Bray-Curtis similarity coefficients. Analysis of similarity (ANOSIM; 999 permutations) was conducted to examine if the differences in communities were statistically different (R values: <0.25, barely distinguishable; 0.25–0.75, separated but overlapping; >0.75, well separated; Clarke and Gorley, 2001). To account for the variation in community composition over all

71 sites, ordination analyses were carried out on the subgroups. The similarity percentage function (SIMPER) was used to determine which taxa contributed most to the statistically significant differences between pre- and post-invasion community compositions. In order to use the available data, which was collected using a semi-quantitative technique, the raw abundance values were organised into ordinal classes (1 = ≤9, 2 = 10–32, 3 = 33–99, 4 = 100–332, 5 = 333–999, 6 = ≥1000).

3. Results

3.1. Sediment biomonitoring and fine sediment

The results demonstrate that the interrupted time series analysis of all sites combined, showed a small, but statistically significant increase between pre- and post-invasion PSI scores (4.1, $p < 0.001$, 95%CI: 2.1, 6.2), with no such evidence of differences for E-PSI (0.4, $p = 0.742$, 95%CI: -2.1, 2.9) or fine sediment (-2.3, $p = 0.227$, 95%CI -6.0, 1.4). Visualisations of the *lme* models are provided in the supplementary material (Fig. S1).

3.2. Habitat heterogeneity

Results from the analyses of sites grouped by their habitat heterogeneity highlight low magnitude changes to PSI scores. Statistically significant increases were evident in post-invasion periods for sites in Heterogeneity Group 2 (5.7, $p = 0.002$, 95%CI: 2.2, 9.3) and Heterogeneity Group 3 (7.4, $p < 0.001$, 95%CI: 4.0, 10.7).

E-PSI scores displayed low magnitude changes in post-invasion periods, with statistically significant changes in Heterogeneity Group 1 (-5.3, $p = 0.027$, 95%CI: -10.0, -0.6) and Heterogeneity Group 2 (4.9, $p = 0.026$, 95%CI: 0.6, 9.2).

A reduction in fine sediment was observed in post-invasion periods for sites in Heterogeneity Group 1 (-9.9, $p = 0.011$, 95%CI: -17.5, -2.2), but there was no evidence of changes to fine sediment in Heterogeneity Group 2 (0.0, $p = 0.987$, 95%CI: -5.9, 5.8) or Heterogeneity Group 3 (3.0, $p = 0.322$, 95%CI: -2.9, 8.9).

3.3. Coarse substrate

Analysis of the sites grouped by their percentage of coarse substrate demonstrated statistically significant increases in PSI scores post-invasion compared with pre-invasion, at sites with intermediate percentages of coarse substrate (Substrate Group 2: 10.1, $p < 0.001$, 95%CI: 6.8, 13.3). Other subgroups of sites showed no evidence of changes to PSI scores following crayfish invasions.

Low magnitude effect size estimates were shown for E-PSI scores, with statistically significant changes to post-invasion scores, in Substrate Group 2 (4.6, $p = 0.024$, 95%CI: 0.6, 8.6), and Substrate Group 3 (-4.2, $p = 0.034$, 95%CI: -8.0, -0.3).

The results from the analyses of fine sediment within the coarse substrate groups, displayed a statistically significant decrease in fine sediment (-10.9, $p = 0.011$, 95%CI: -19.3, -2.6) for sites with a low percentage of coarse substrate (Substrate Group 1). Other subgroups demonstrated no evidence of changes to fine sediment following crayfish invasions.

3.4. Shifts in community composition

Centroid NMDS ordination plots of all sites indicated some dissimilarities in macroinvertebrate community composition (ANOSIM $p < 0.001$) associated with crayfish invasion but with substantial overlapping (R value of 0.232). Subgroup analyses illustrated dissimilarities (with partial overlapping) between pre- and post-invasion communities, which coincided with those ITS subgroup analyses that were found to have statistically significant changes to their post-invasion PSI or E-PSI scores (Fig. 3e and f). The degree of separation between

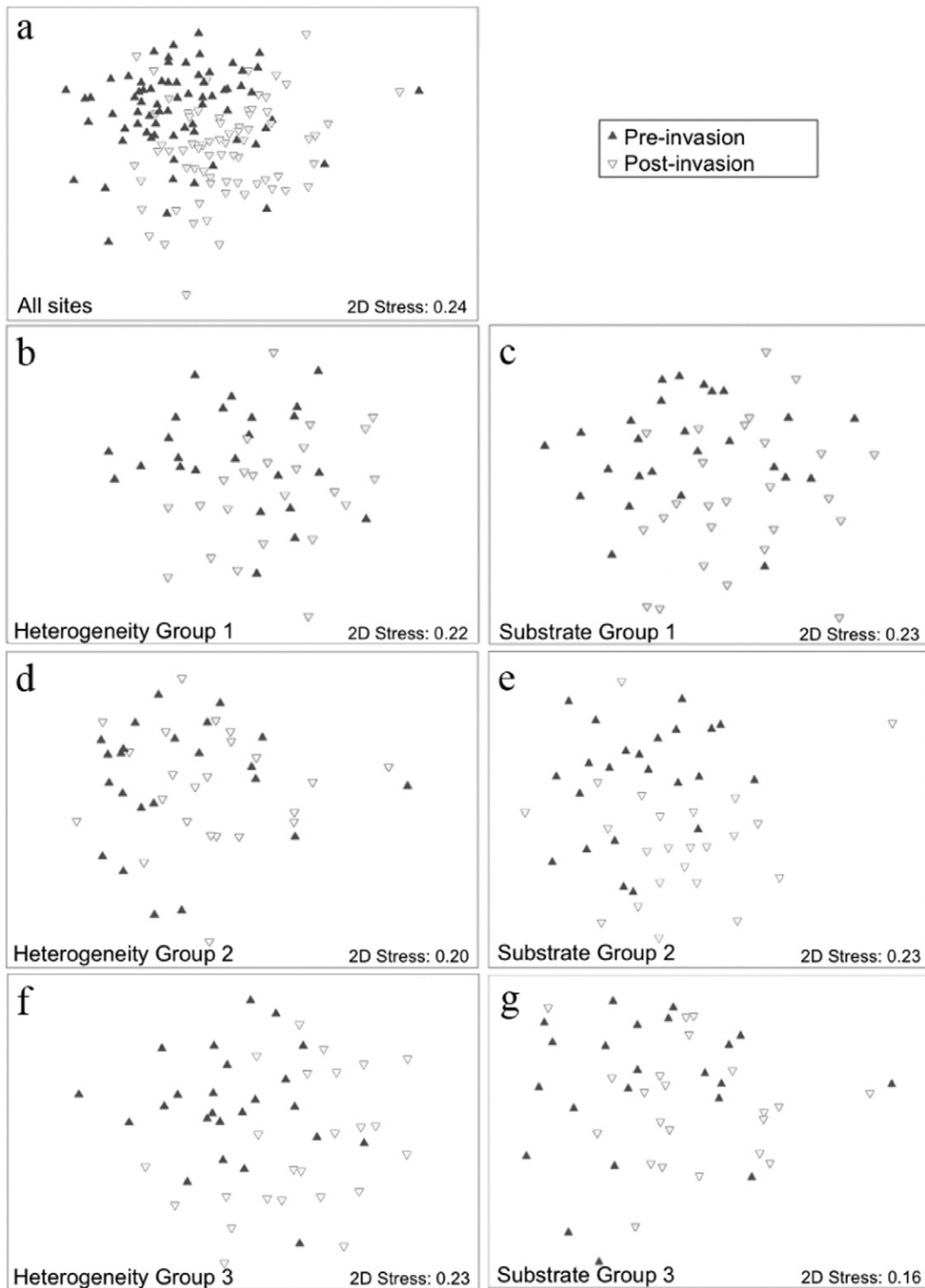


Fig. 3. a–g Non-metric dimensional scaling centroid plots of benthic macroinvertebrate community composition for all sites, and sites split into subgroups based on their (i) habitat heterogeneity and (ii) percentage of coarse substrate (both groups: 1–3 represents low–high).

pre- and post-invasion community compositions within subgroups indicated a statistically significant separation for Heterogeneity Group 3 (ANOSIM: $R = 0.333$, $p < 0.001$), and Substrate Group 2 (ANOSIM: $R = 0.329$, $p < 0.001$). Although the ITS analyses highlighted differences in post-invasion index scores in Heterogeneity Group 1 and Heterogeneity Group 2, ANOSIM indicated that whilst there were statistically significant differences in community compositions there was substantial overlapping ($R = 0.226$, $p < 0.001$ and $R = 0.152$, $p = 0.02$,

respectively). A summary of all ANOSIM values is presented in the supplementary material (Table S2).

SIMPER identified that nine of the 10 taxa most responsible for driving the differences in the subgroups pre- and post-invasion community compositions, were identical, with consistent increases in abundance of Hydrobiidae, Gammaridae, Oligochaeta, Baetidae, Chironomidae, Simuliidae and decreases in Sphaeriidae, Asellidae, and Hydropsychidae (Table S2).

4. Discussion

4.1. Fine sediment

Despite crayfish being considered biogeomorphic agents, the results of this study provide limited evidence of changes to deposited fine sediment conditions following crayfish invasions. Nevertheless, in agreement with recent research focused on rusty crayfish (*Orconectes rusticus*), which observed reduced accumulation of fine sediment in invaded streams (Albertson and Daniels, 2016); two of the subgroup analyses demonstrated statistically significant, low magnitude declines in fine sediment (approximately 10 percentage points). Declines in deposited fine sediment may be the result of crayfish activity (e.g. foraging, general movement) on the streambed mobilising deposited fine sediment (Harvey et al., 2014; Albertson and Daniels, 2016; Cooper et al., 2016; Rice et al., 2016). The lack of a consistent effect on fine sediment in the analysis of all sites, and across subgroup analyses, suggests that the influence of signal crayfish on fine sediment may be context dependent, perhaps confounded by site-specific characteristics such as local bank biophysical properties (Faller et al., 2016) affecting fine sediment inputs associated with burrowing in river banks (Harvey et al., 2014). Other factors, such as site-specific changes to flow dynamics and catchment land use over time, may also be confounding the time series analysis of substrate composition (Allan, 2004; Dewson et al., 2007).

4.2. Biomonitoring tools outputs

Results from this study suggest that signal crayfish invasions may influence the scores from sediment-biomonitoring tools. In agreement with previous work (Mathers et al., 2016b), the PSI index was marginally inflated in post-invasion periods in the overall analysis, as well as in a number of subgroup analyses. The E-PSI index is slightly less affected, showing no inflation in the overall analysis, and changes of lower magnitude (compared to PSI) in the subgroup analyses. Importantly, the relatively low magnitude changes to both biomonitoring tool scores did not coincide with the expected alterations to fine sediment conditions. This suggests that changes to scores in post-invasion periods may not be the result of genuine geomorphic effects of crayfish. Instead, the changes to community composition (indicated by biomonitoring tool scores) may be the result of consumptive and/or non-consumptive effects of crayfish predation (Sih et al., 2010; Dorn, 2013), and/or indirect effects, such as altering predator-prey dynamics of native fauna or modifying other aspects of the habitat (Byers et al., 2010). Similarly to the fine sediment analyses, the lack of a consistent change to biomonitoring tool scores across all sites and subgroups, suggests that site-specific characteristics (abiotic and/or biotic) may influence the degree to which biomonitoring tools are affected by signal crayfish. Nevertheless, the effect estimates for both indices were relatively small (maximum of 10.1 index points) and are unlikely to result in an incorrect diagnosis of sediment pressure (or lack of).

The disparity between post-invasion PSI and E-PSI scores may be the result of the different methods of index development and calculation. The development of the family-level E-PSI index also involved the removal of a number of “sensitive” families from its calculation, due to their indifference to reach scale estimates of fine sediment (Turley et al., 2016).

4.3. Habitat heterogeneity

The subgroup of sites with more homogeneous substrate was predicted to be the most probable to exhibit differences between pre- and post-invasion biomonitoring outputs as a result of crayfish predation. These sites are likely to afford the least resilience to crayfish predation, providing fewer refugia (Brown and Lawson, 2010), and are likely inhabited by a community of fewer species (Tews et al., 2004). In partial agreement with this prediction, the subgroup had a small, but

statistically significant decrease in post-invasion E-PSI scores, and analysis of community composition indicated dissimilarities between pre- and post-invasion periods. However, the effect estimate and confidence interval with a lower limit of almost zero, suggests that the magnitude of the effect on E-PSI is low.

The PSI index exhibited inflated scores of low magnitude in the post-invasion period at sites with moderate and high habitat heterogeneity, but not at those with low heterogeneity. Heterogeneous substrate is often associated with zones of high velocity and well oxygenated water, areas that are typically inhabited by a high proportion of rheophilic and relatively fast-moving taxa (Dunbar et al., 2010), many of which are rated as highly sensitive to fine sediment. The inflated post-invasion scores and observed shifts in community composition at these sites may be the result of the crayfish having difficulties capturing fast-moving taxa, and instead selectively preying on slower moving taxa (many of which are rated as tolerant of fine sediment) resulting in a higher PSI score. A number of other studies have also suggested that more mobile taxa dominate in areas where crayfish are abundant (Nyström et al., 1999; Usio and Townsend, 2004).

4.4. Coarse substrate

Longitudinal gradients in rivers and streams, and the associated transition from coarse substrate to fine sediment are important influencing factors of macroinvertebrate community composition (Minshall, 1984). Sites in this study with an intermediate percentage of coarse substrate appear to be the most affected by crayfish invasions, in terms of their PSI scores, E-PSI scores and community composition. This effect may be the result of similar processes to those hypothesised for the observed changes to PSI scores at sites with high habitat heterogeneity. The sites in this subgroup (Substrate Group 2) have relatively equal proportions of coarse substrate and fine sediment, and as a result, sediment-sensitive and sediment-tolerant taxa are likely to be well represented in the macroinvertebrate community. Selective crayfish predation on slower moving, sediment-tolerant taxa would therefore result in inflated index scores.

4.5. Community composition

Invasive crayfish have been shown to alter native macroinvertebrate communities, reducing diversity and biomass, particularly of gastropods and bivalves (Klocker and Strayer, 2004; Crawford et al., 2006; Dorn, 2013). The consistent declines in Sphaeriidae (bivalve) abundance in post-invasion periods compared with pre-invasion periods in this study, agree with this previous research. The sedentary nature of this taxon is likely to result in a poor ability to evade predation, making them easy prey items. In contrast, a number of taxa (i.e. Hydrobiidae, Gammaridae, Oligochaeta, Baetidae, Chironomidae, and Simuliidae) were consistently identified as having a greater abundance in post-invasion periods. These taxa are likely to have biological traits that allow them to persist in the presence of crayfish (e.g. high mobility, high fecundity, multivoltine), and/or have innate or inducible defence mechanisms. For example, *Gammarus pulex* (Gammaridae) have been shown to increase locomotion, vertical migration and drift in the presence of predators (Haddaway et al., 2014).

4.6. Fine sediment quantification

Deposited fine sediment is a challenging environmental characteristic to quantify. It is unclear which sediment quantification technique is the most biologically relevant (Sutherland et al., 2012), or at which spatial or temporal scale sediment should be quantified to detect modifications arising from crayfish activity (Harvey et al., 2011). The visual estimate technique used in this study is a reach scale estimate that is likely to have biological relevance as it relates to niche availability (Turley et al., 2017). The technique is intended as a rapid assessment

approach, but has been criticised for its subjectivity and the associated operator error that can result in a low precision (Wang et al., 1996). In this study it was anticipated that the standardised training provided to the operators responsible for carrying out the visual estimate would have reduced the subjectivity and optimised the precision of the technique (Roper and Scarnecchia, 1995).

4.7. Limitations

In addition to the challenges concerning the quantification of fine sediment conditions, there are other noteworthy limitations of this study. The modelling approach and structure may have resulted in an over- or under-estimation of differences between pre- and post-invasion periods. Nevertheless, it was necessary to define an *a priori* model, and the model utilised in this study was based on invasion ecology theory and available knowledge of signal crayfish invasion dynamics (Sahlin et al., 2010; Ricciardi et al., 2013). In addition, the objective approach to identifying the date of invasion may have resulted in an underestimation of the differences between pre- and post-invasion periods. Due to the challenges of detecting crayfish at low densities (Peay, 2003), it is possible that the sites were invaded prior to the first detection, however, at low densities their impacts are likely to be less significant. Lastly, although the *lme* model residuals showed some signs of heteroscedasticity, which may have influenced estimates of statistical significance, the effect estimates are of greater interest, and were broadly similar to the *lqmm* results (which have less distributional assumptions) presented in Table S1.

4.8. Reliability of biomonitoring in the presence of invasive species

With current water legislation placing a strong emphasis on the use of biomonitoring (Birk et al., 2012), and aquatic biological invasions expected to increase in the future (Early et al., 2016), an understanding of the influences of invasive species on native biodiversity and their effect on the performance of biomonitoring tools is crucial. The context dependency shown in this study highlights the need for investigation of the potential for site-specific effects caused by invasive species (Klose and Cooper, 2012). Invader impacts are likely to be species-specific, impacting receiving communities and biomonitoring schemes to varying degrees. Knowledge of the invaders biological traits and ecological preferences (in their native range) may help focus research efforts on those species most likely to be impacting on biodiversity and biomonitoring (Pyšek et al., 2012). Additionally, investigation of the effects of other pressures on invader impacts and establishment rate/success (Didham et al., 2007; Diez et al., 2012) is important for determining the reliability of biomonitoring tools in invaded ecosystems.

In order for the impacts of invasions to be realised, data need to be available for both pre- and post-invasion periods at a suitable resolution to capture the natural community variation, and sampling variation of the outcome variable of interest, and ideally for a length of time that exceeds the successful establishment of the invasive species. However, studies of this temporal scale are often considered prohibitively expensive. The use of regulatory agency data that spans wide geographic areas, and which is often collected over multiple years, represents a coarse, but comparatively rapid and low-cost approach that can help to inform the protection and management of freshwater ecosystems (Dafforn et al., 2016).

5. Conclusion

The results of this study highlight the potential context dependency and variability of invader impacts, with the effect of crayfish invasions on biomonitoring tool outputs and community composition appearing to vary between sites. It is recommended that pressure-specific biomonitoring approaches be utilised in conjunction with the full range of biomonitoring tools available to the user, to assist with evaluating

the most probable causes of ecological degradation in rivers and streams.

Further research is needed to disentangle the multitude of possible factors, such as the presence of multiple pressures (e.g. channel modification, water quality and climate change) and extreme events (e.g. droughts and floods), which may facilitate more severe impacts on biodiversity following invasions. Conversely, it is also important to identify the characteristics and mitigation measures that can increase ecosystem resilience to invasions. Understanding the mechanisms by which invasion impacts are facilitated or mitigated is also crucial for the management and protection of aquatic ecosystems.

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