

Research Article

Impact of invasive quagga mussel (*Dreissena rostriformis bugensis*, Bivalva: Dreissenidae) on the macroinvertebrate community structure of a UK river

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Abstract

The arrival of invasive quagga mussel (*Dreissena rostriformis bugensis*) to the UK necessitates rapid study to evaluate its impact on benthic community structure where colonisation has occurred. In the Wraysbury River (west London), impact on benthic invertebrate community structure by invasion of quagga mussel was measured by comparing a series of invaded and uninvaded study sites over an annual period of monthly sampling. It was apparent that despite quagga mussel consistently forming a large proportion of stream biomass in invaded sites, community taxon richness and composition did not vary significantly in comparison to uninvaded sites. Similarly, total community biomass and density when excluding quagga mussel was mostly homogeneous across the study reach, with the exception of one site with the highest quagga mussel biomass and density. If quagga mussel biomass and density increased over time to levels found at this site, more significant changes to native community structure might be expected. This study represents a first benchmark for understanding the progression and impacts of quagga mussel invasion in UK rivers and these results will be essential for comparison in evaluating future change and impacts.

Key words: Ponto-Caspian, Wraysbury River, community ordination, biomass, colonisation

Introduction

The structure of freshwater communities throughout the world is altered by the colonisation of non-native species (Strayer 2010; Błońska et al. 2015). While some alien taxa appear to cause little deleterious change to native communities, others are invasive and can cause significant reductions in native biodiversity and impact ecosystem processes (Parker et al. 1999; Francis and Chadwick 2012). In the United Kingdom and other European countries, various taxa-specific studies provide a range of evidence for such impacts (e.g. Alderman et al. 1990; Aldridge et al. 2004; Gherardi and Acquistapace 2007; Sousa et al. 2011). Further, invasive species are receiving increasing attention from both competent authorities and the public (Pfeiffer and Voeks 2008; Francis and Chadwick 2012). Rising awareness of the monetary cost associated with biotic invasions also drives concern (Elliott et al. 2005; Williams et al. 2010), expanding the need for study on high impact species.

Several freshwater invasives have recently been ranked for the UK by their potential to invade and diminish biodiversity (Roy et al. 2014). These include the bivalve mollusc *Dreissena rostriformis bugensis* (Andrusov, 1897), widely known as the “quagga mussel”. In September 2014, this species was confirmed for the first time in the UK in the Wraysbury River, a small tributary of the River Thames in west London (Aldridge et al. 2014).

A native of the Ponto-Caspian region, quagga mussel is a close relative of *Dreissena polymorpha* (Pallas, 1771), the “zebra mussel”. Dreissenid mussels rapidly colonise lentic systems (Karatayev et al. 2015), typically contributing a large proportion of total benthic invertebrate biomass (e.g. Dermott and Kerec 1997; Stewart and Haynes 1994; Burlakova et al. 2005). As physically robust (Czarnołęski et al. 2006; Kobak et al. 2010) and highly fecund (Mackie 1991; Closs et al. 2004), *Dreissena* spp. often form dense colonies of over 1000 individuals m⁻² on the benthic littoral (Mackie 1991; Ricciardi et al. 1997;

Strayer et al. 1999). Such environments have been very well studied: *Dreissena* spp. in lakes may act as efficient filter feeders (Hecky et al. 2004; Vanderploeg et al. 2010), removing plankton, bacteria and suspended silt from the water column. This shifts native taxa biomass from the pelagic to benthic zones (Stewart and Haynes 1994).

Quantitative observation of *Dreissena* spp. impacts in rivers is less frequent than in lakes. However, studies in various environments consistently suggest colonization may alter invertebrate habitat availability (Stewart and Haynes 1994; Botts et al. 1996; Kuhns and Berg 1999; Beekey et al. 2004); swamp the shells of native Unionid mussels (Nalepa 1994; Ricciardi et al. 1998; Sousa et al. 2011); and consume seston, thereby reducing phytoplankton abundance and limiting other filter feeding invertebrates and pelagic feeding species including certain fish (Jack and Thorp 2000; Fuentes 2003). Further, *Dreissena* spp. presence in interconnected rivers could facilitate the establishment of other Ponto-Caspian invaders that hold evolutionary traits adapted for cohabitation (Kobak et al. 2014; Gallardo and Aldridge 2015). Field-based evidence for such relationships are currently limited; however in laboratory experiments the Ponto-Caspian shrimp *Dikerogammarus villosus* (Sowinsky, 1894) utilised *Dreissena* spp. beds as refugia from predation more effectively than *Gammarus fossarum* (Koch, 1835), a western European counterpart (Kobak et al. 2014).

The potential for quagga mussel colonisation to cause such facilitative effects for either invasive or native species in rivers is uncertain. In lakes, *Dreissena* spp. beds are known to provide both complex habitat and refugia for other invertebrate species to flourish (Stewart et al. 1998; Bially and MacIsaac 2000; Ricciardi 2001; Burlakova et al. 2012). They have also been considered as a bioremediation tool for regulating algal blooms, improving water clarity and encouraging macrophyte settlement (Stybel et al. 2009; McLaughlan and Aldridge 2013). In many cases, *Dreissena* spp. colonies have been associated with marked increases in native invertebrate richness and biomass (Higgins and Vander Zanden 2010; Karatayev et al. 2015); however little comparative work has been done for lotic systems.

Uncertainty and limited study of *Dreissena* spp. colonisation impacts on community structure in rivers highlight the need for further observation. Within the UK, this is particularly pressing in the case of quagga mussel because it has been ranked as the most threatening potential invasive species to UK biodiversity (Roy et al. 2014). The colonisation of quagga mussel to the Wraysbury River (Aldridge et al. 2014) allows for a timely study to evaluate

invertebrate community structure in a newly colonised lotic system. The objective of our study was to assess the impact of quagga mussel on invertebrate community structure by comparing a series of localised invaded and uninvaded sites along the Wraysbury River.

Material and methods

Study area

Quagga mussel was first found in the UK in the Wraysbury River by the UK Environment Agency (Aldridge et al. 2014). Situated near Staines-upon-Thames (western London), this stream is a shallow (< 0.5 m depth) and relatively short (c. 8.7 km) branch of the River Colne system, a tributary of the River Thames. The catchment is Devensian gravels and the river is dominated by a sandy gravel/pebble substrate. At the study reach the stream has a homogeneous width (approximately 4–5 m) and is predominantly characterised by laminar, glide flow. Land use is varied throughout the catchment and local features include an area of protected pastoral moorland, multiple navigational canals, patches of suburban housing and a section of the London orbital motorway. Seasonal records collected by the UK Environment Agency between January 2014 and December 2016 give mean nutrient concentrations for the Wraysbury River as total oxidised nitrogen 9.4 N mg L⁻¹, and orthophosphate 0.3 mg L⁻¹ (EA, pers. com. 2017).

A nearby reservoir (Wraysbury Reservoir) is of particular note. Quagga mussel in the Wraysbury River were found to be restricted downstream of a small, intermittent pumping facility servicing the reservoir (EA, pers. com. 2014). For this study, six approximately equidistant sites were selected downstream of the facility with two additional sites located upstream (Figure 1: sites 1–8) along a 1.8 km reach. The sampling reach in each case was characterised by laminar, glide flow. An initial pilot study in April 2015 confirmed distances between study sites and that each held similar physical characteristics including mean stream depth and wetted width (Table S3). Qualitative estimations of substrate typology suggested a homogenous mixture of sand, gravel and pebble throughout the study sites (Table S3). These parameters did not appear to meaningfully change throughout the annual study period.

Monthly invertebrate sample collection was undertaken at each study site between May 2015 and May 2016. The sampling reach at each site was 25m² of the wetted channel downstream of the stream entry point. Biological sampling and supporting physicochemical measurements were completed within the last 3 days of each month. Physicochemical measurements, taken

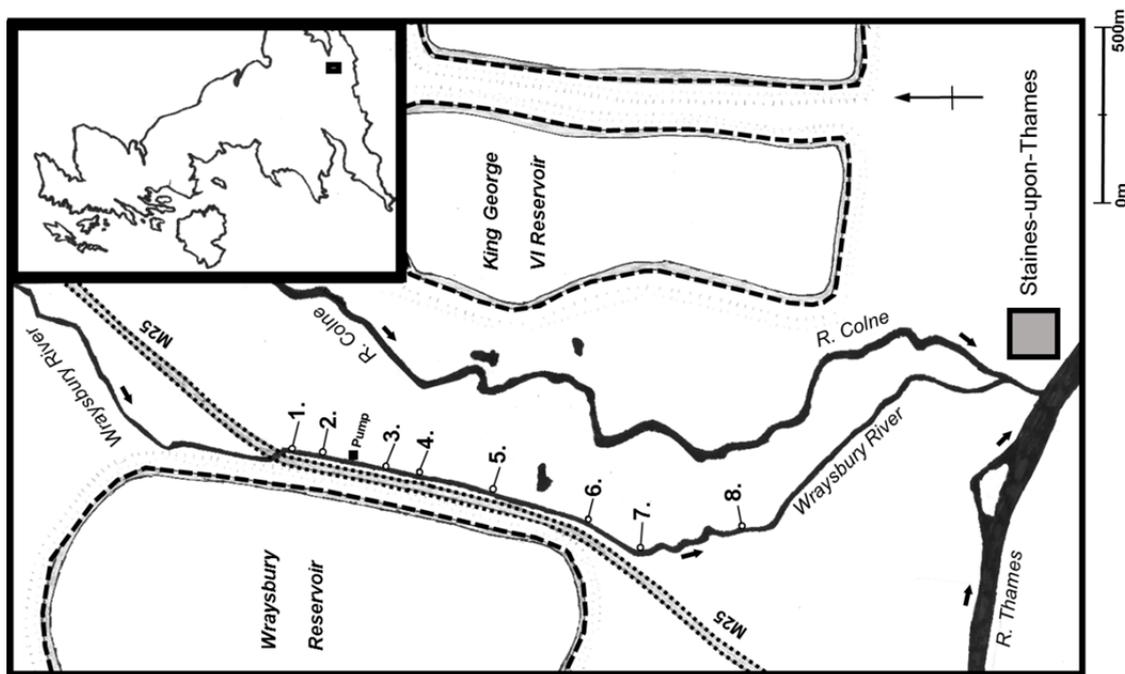


Figure 1. Location of the Wraysbury River study reach (~ Lat 51.45225; Long -0.520528) and associated study sites (marked 1–8). No quagga mussels were collected at sites 1 and 2 and these sites provide the uninvaded site group. The location of the pump facility between sites 2 and 3 is also marked. See Table S3 for coordinates of individual study sites.

to further characterise the Wraysbury River and confirm a reasonable similarity in conditions between the invaded and uninvaded sections of the river, included stream conductivity ($\mu\text{s cm}^{-1}$), dissolved oxygen (DO; mg L^{-1}), pH, alkalinity (mg L^{-1}), hardness (mg L^{-1} as CaCO_3), temperature ($^{\circ}\text{C}$) and flow rate (m s^{-1}). For stream conductivity, DO, pH, and temperature, data was collected on the same day as biological sampling with 5 spot samples per study site using a HACH™ HQ30d multi-probe and HI-9811-5N pH/EC/TDS/ $^{\circ}\text{C}$ portable meter. Alkalinity and hardness were measured with 3 0.5 L samples of stream water collected per site, then analysed in the laboratory within 24 hours of collection using a HACH™ digital titration kit. Stream flow rate (m s^{-1}) was measured on a quarterly/seasonal basis for each site using a propeller flow meter. Per site, 5 equidistant measurements at 0.6 depth were made throughout the channel width, half way between the top and bottom of the sampling reach.

Benthic invertebrate survey

Each month between May 2015 and May 2016, five invertebrate samples were taken at each study site, in a random location within the 25m^2 sampling reach, using a Surber sampler ($0.33\text{ m} \times 0.33\text{ m}$ with a net-

mesh size of $250\ \mu\text{m}^{-1}$). Biological material and sediment was collected to an approximate depth of 2 cm into the river substrate. When captured, large pebbles were washed and removed and the remaining sample was collected in 0.5 L polyethene pots before preservation with Industrial Methylated Spirit (90%). In the laboratory, all individual specimens were removed from the sample, enumerated and identified under a high power ocular microscope. Identification was made to species level with the exception of *Simulium* spp., *Oligochaeta* spp., and the family Chironomidae which were identified to tribe. Specimens of Limnephilidae spp. and Hydropsychidae spp. were grouped at family level due to morphological ambiguity at their smallest size-ranges. All specimens were measured for length to the nearest 0.5 mm on their *a*-axis.

Data analysis

For this study, like previous quantitative studies of *Dreissena* spp. establishment (e.g. Stewart et al. 1998; Dermott and Kerec 1997; Bunnell et al. 2009), we analysed invertebrate community structure with emphasis on taxa biomass in addition to density. Biomass composition is generally considered a strong indicator of community structure (Saint-Germain et

al. 2007) and is frequently used when summarizing quantitative differences in freshwater invertebrate communities (e.g. Stone and Wallace 1998; Benke and Wallace 2003; Tessier et al. 2008). This approach is advantageous when individuals of different taxa range through several orders of magnitude in body mass, and may better provide a general picture of processes affecting community structure (*sensu* Saint-Germain et al. 2007). The use of biomass also permits assessment of the proportional, physical contribution of different taxa or taxonomic groups to the total benthos (e.g. Leeper and Taylor 1998; Bourassa and Cattaneo 2000; Howard and Cuffey 2006).

First, invertebrate richness and abundance was calculated for each sample. Estimates of total invertebrate biomass per site as dry mass g m^{-2} (herein referred to as biomass, DM g m^{-2}) were then obtained by summing individual biomass of all collected individuals. Biomass per individual was estimated from body size using previously published length-weight regressions (Smock 1980; Marchant and Hynes 1981; Huryn and Wallace 1987; Benke et al. 1999; Baumgärtner and Rothhaupt 2003; Stoffels et al. 2003; Edwards et al. 2009). Where conversion parameters were not available for a specific taxa, a published regression for members of the same genus was used in the first instance, or an averaged regression for the respective family or class (Table S1).

For each monthly dataset, a series of one-way ANOVAs were performed to assess the variability of mean taxa richness, invertebrate density (individuals m^{-2}) and total taxa biomass per site excluding quagga mussel. When a monthly dataset did not meet assumptions of normality (determined using Shapiro-Wilk), data were natural-log transformed prior to analysis. For mean quagga mussel biomass alone (within invaded sites 3–8 only), monthly datasets did not conform to parametric assumptions even following transformation so one way ANOVA on ranks were used. For all analyses where there was significant variation between site groups, post hoc pairwise comparisons were undertaken using a Tukey test.

Summaries of mean annual invertebrate density, Shannon-Weiner diversity (Magurran 1988; Krebs 1989), taxa richness and total community biomass (excluding quagga mussel) were also made for each site. Furthermore, the % contribution of different invertebrate feeding groups to mean annual biomass was also calculated for each site. Present taxa were assigned feeding groups according to previously published classifications (Mandaville 2002). Such analysis is a common approach when interrogating invertebrate assemblage data (e.g. Troelstrup and Hergenrader 1990; Walters and Post 2011; Cauvy-

Fraunié et al. 2016), providing further examination of community structure characteristics.

Community ordination analyses were used to further summarize the data set. Mean biomass values (g m^{-2}) per taxa for each site were analysed incorporating all monthly measurements. Data was $\text{Log}(X+1)$ transformed to moderate for the effects of rare or highly abundant taxa (Clarke and Green 1988; Legendre and Gallagher 2001) and all taxa accounting for less than 0.5% of total mean biomass per month were excluded to reduce distortion of assemblage differences. All analyses were completed using the statistical software package PRIMER-E v.6.1.13; Primer-E Ltd., 2009 (Clarke and Gorley 2006; Clarke 1993; Clarke and Warwick 2001).

Ordinations of community structure were performed using Non-Metric Multidimensional Scaling (NMDS) based on Bray-Curtis dissimilarities. This is a widely used approach for displaying invertebrate community structure data (e.g. Kobayashi and Kagaya 2004; Thomson et al. 2005; Ercoli et al. 2015) and was applied to display between-site differences in mean biomass composition as weighted by taxa present. All monthly data sets were incorporated into the analysis, with 12 data points per site averaged to show the mean annual placement of each site within the plot.

One-Way ANOSIM was then used to assess similarity in mean biomass composition between invaded and uninvaded site groups. Additionally, a similarity of percentages (SIMPER) analysis (Clarke and Warwick 2001) was used to determine the percentage contribution of different invertebrate taxa towards any dissimilarity in biomass composition between site groups. A second SIMPER analysis was then run to assess species contributors to similarity within site groups.

Results

A total of 81642 invertebrate individuals comprising 57 taxa were identified with a mean annual richness of 15 taxa throughout all sites. Quagga mussel was consistently found at sampling locations below the reservoir pump facility (Sites 3–8), where mean annual density was 54 individuals m^{-2} . While nearly all other taxa were native, several other invasive species were found at low abundance at some sites during the study period: *Crangonyx pseudogracilis* (Bousfield, 1958), *Potamopyrgus andirpodarum* (Gray, 1843) and *Dreissena polymorpha* (zebra mussel). Notably, no Ponto-Caspian shrimp of *Dikerogammarus* spp. were found in our survey. In terms of mean annual abundance, dominant native taxa across all study sites were *Gammarus pulex* (Linnaeus, 1758), *Ephemera danica* (Müller, 1764), *Elmis aenea* (Müller, 1806) and Orthocladiinae spp. (see: Table S1). Mean

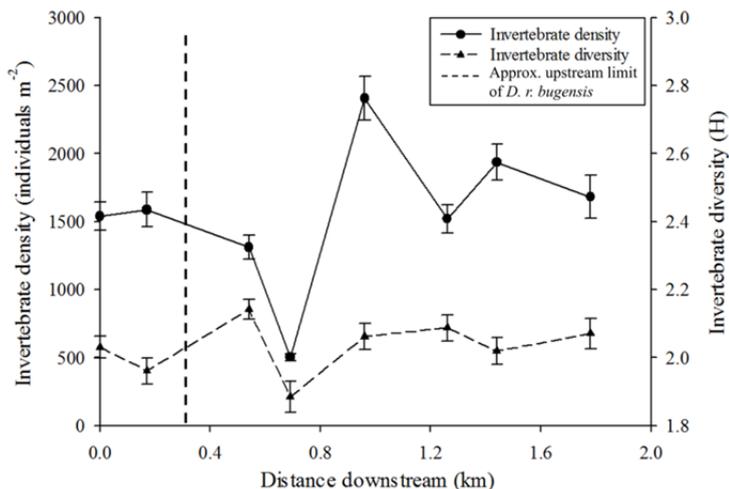


Figure 2. Mean annual total invertebrate density (individuals m⁻²) and Shannon-Weiner diversity (H') scores per site with downstream distance from Site 1. Error Bars denote standard error.

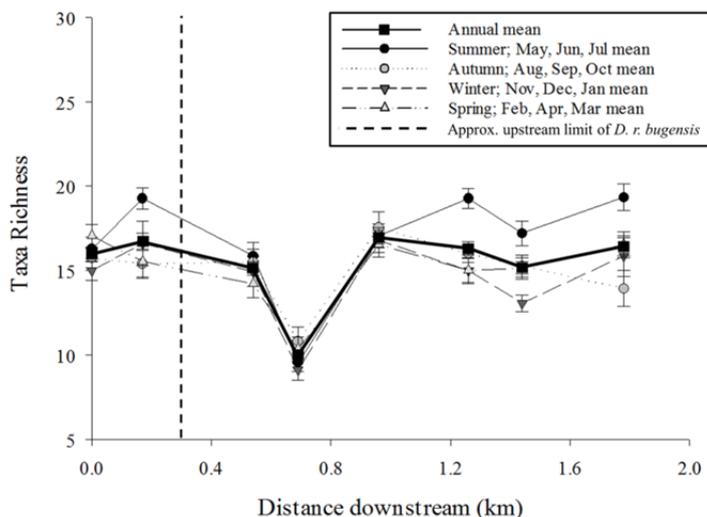


Figure 3. Mean annual and seasonal taxa richness with downstream distance from Site 1. Error bars denote standard error.

annual invertebrate density was consistent throughout the study reach, (range: 1300–2000 individuals m⁻² per site) with the exception of a low figure at site 4 (c. 500 ind. m⁻²) and high at site 5 (c. 2400 ind. m⁻²). Mean annual values for the Shannon-Weiner index of diversity were also similar throughout the study reach (range 2.0–2.2), but with a lower value at site 4 (1.8; Figure 2).

Supporting physicochemical measurements presented strong homogeneity of conditions between all sites throughout the study period. Stream water pH (7.8–8.5), temperature (8–21 °C), conductivity (512–811 μs cm⁻¹), dissolved oxygen (8–14 mg L⁻¹) and flow rate (0.25–0.3 m s⁻¹) varied as expected through the year, but were very similar among study sites for each month measured (Table S2). Comparatively, measures of stream hardness (260–486 mg L⁻¹ as

CaCO₃) and alkalinity (196–263 mg L⁻¹) varied more throughout the year; however the range of recorded mean values per site also remained small within each monthly survey (Table S2). Overall, these measurements suggested very similar physicochemical conditions across all study sites. Furthermore, values were as expected given the location, geology, seasonal climate and previous monitoring records from the UK Environment Agency (EA., 2016; pers. com). Invaded and uninvaded site groups were very similar and could theoretically support similar ecological communities.

Mean annual taxa richness (excluding quagga mussel) was consistent between both invaded and uninvaded site groups with an exception at site 4, where it was found to be lower than all other sites (Figure 3). This pattern was maintained when data was split into seasonal means, but with generally higher

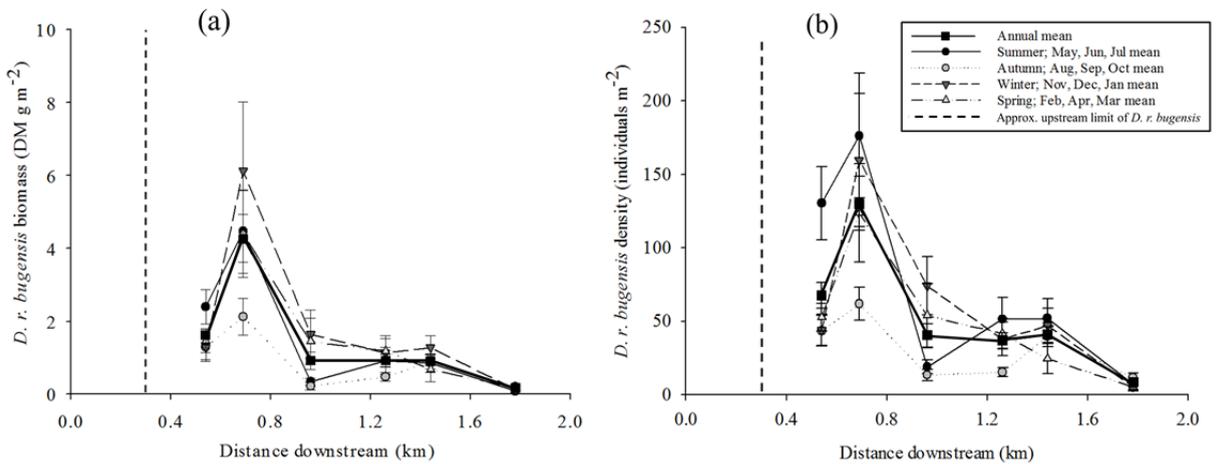


Figure 4. Graphs showing mean annual and seasonal (a) *D. r. bugensis* biomass (DM g m⁻²) and (b) *D. r. bugensis* density (individuals m⁻²), with downstream distance from Site 1. Error bars denote standard error.

richness found in the summer period (Figure 3). ANOVAs showed that mean taxa richness differed significantly between study sites in every month except April 2016. Tukey's tests showed differences were driven by lower richness at site 4 (Table S4).

Mean annual biomass throughout all sites was 2.10 g m⁻² including quagga mussel and 1.00 g m⁻² excluding quagga mussel. Among invaded sites, quagga mussel contributed 61% of mean annual biomass; however this proportion was distributed with high variation throughout the study reach. While closely reflecting measured trends in quagga mussel density (Figure 4b), upstream invaded sites presented higher quagga mussel biomass in comparison to those downstream (Figure 4a). Upstream sites 3 and 4 for example, exhibited higher mean annual values of 1.61 g m⁻² and 4.38 g m⁻², respectively. Furthermore, at site 4, quagga mussel alone contributed 90% of mean annual biomass composition. In contrast, the site placed farthest downstream (site 8) gave the lowest measures of quagga mussel biomass (annual mean: 0.15 g m⁻²), where it contributed to only 15% of mean annual biomass composition. When the data was split into seasonal means, similar trends were maintained, with both quagga mussel biomass and density higher in the winter and summer period while lower in Autumn (Figure 4a, b). ANOVAs showed that mean quagga mussel biomass differed significantly between invaded study sites for over half of the monthly measurements (Table S5). Tukey's tests showed this was primarily driven by high quagga mussel biomass at sites 3 and 4 with lower values at site 8 (Table S5).

When excluding quagga mussel, mean annual biomass of invertebrates varied less throughout the

study reach and closely reflected trends in invertebrate density (Figure 5a, b). Site 4 differed for both parameters, consistently presenting lower values in comparison to other sites. Similar trends of invertebrate biomass and density (excl. quagga mussel) were maintained for seasonal means but with higher values for both evident in the summer period; particularly at the most downstream sites (Figure 5a, b). ANOVAs on ranks presented significant differences between sites for mean invertebrate biomass in at least half the monthly measurements (Table S6), while for invertebrate density, ANOVAs showed differences in all monthly measurements (Table S7). Tukey's tests showed that in both cases this was largely driven by lower values at site 4 and in addition for density, higher values at site 5.

Analysis of mean annual invertebrate biomass by constituent feeding groups suggested that community structure at all sites was dominated by collector-gatherer taxa when excluding quagga mussel. With this analysis, collector-gatherers contributed between 60–80% of mean annual biomass at all sites (Figure 6a). In comparison, scrapers and predators consistently contributed only 0–10% throughout sites, while collector-filterers and shredders appeared to increase in importance with distance downstream. Collector-filterers (excluding quagga mussel) and scrapers rose from a 10–15% contribution to biomass at upstream sites (1–4) to between 15–25% at downstream sites (5–8).

When including quagga mussel, the contribution of collector-filterers to mean annual biomass increased significantly in invaded sites, replacing collector-gatherers as the dominant feeding group in all cases except the most downstream site (Figure 6b). This was

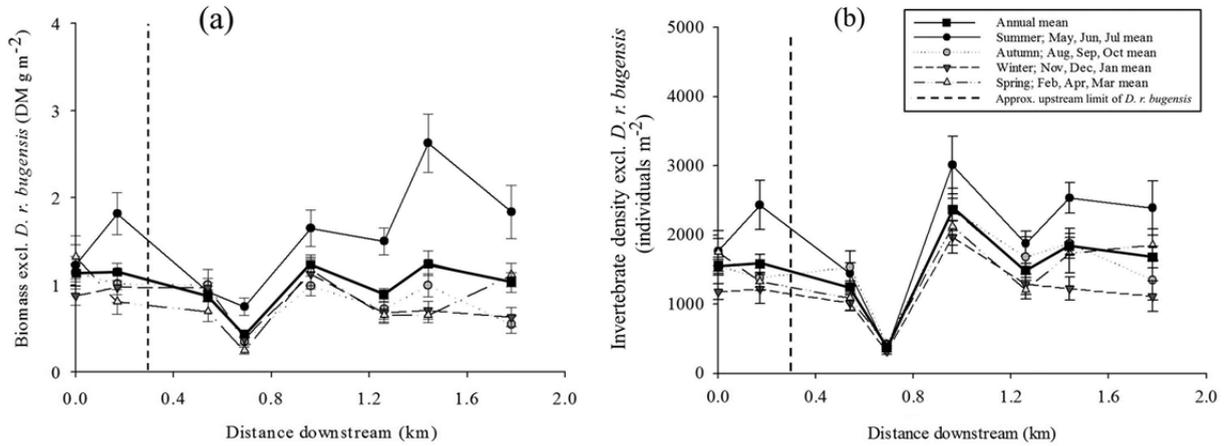


Figure 5. Graphs showing mean annual and seasonal (a) biomass of all taxa (excluding *D. r. bugensis*; DM g m⁻²) and (b) density of all taxa (excluding *D. r. bugensis*; individuals m⁻²), with downstream distance from Site 1. Error Bars denote standard error.

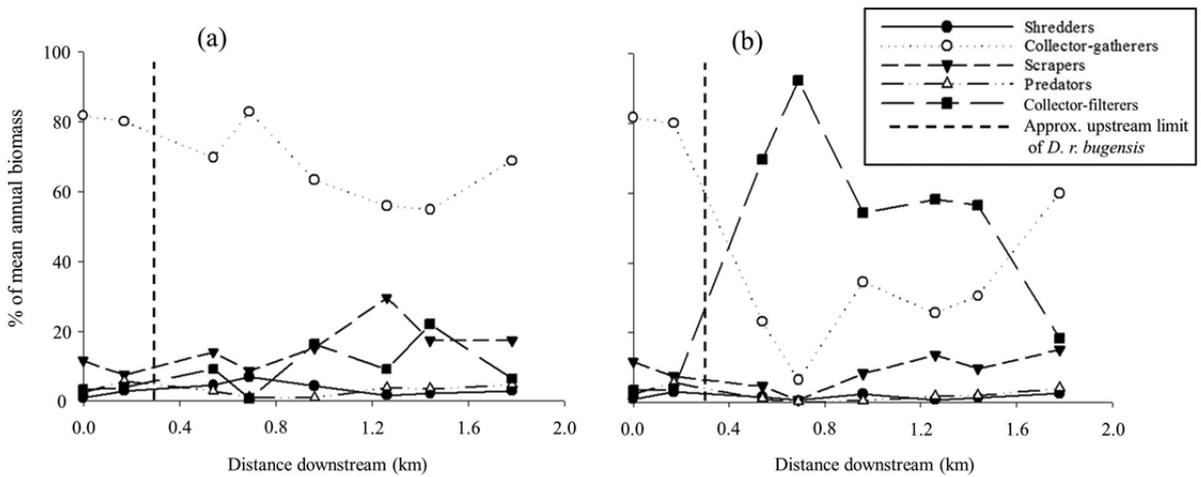


Figure 6. Graphs showing the percentage of mean annual biomass apportioned to functional feeding groups present with downstream distance from site 1 (a) excluding *D. r. bugensis* and (b) including *D. r. bugensis* (as collector-filterers).

particularly acute at the site of highest quagga mussel density (Site 4), where the contribution of collector-filterers to biomass increased from 1% to 92%. In contrast, site 8 held the lowest quagga mussel density and community structure here remained dominated by collector-gatherers. This most downstream site resembled proportional feeding group structures at the upstream, uninvaded sites (1–2).

According to the ANOSIM, moderate differences in community structure were detected between invaded and uninvaded sites based on their biomass composition throughout all monthly data sets ($R = 0.417$). A segregation of site groups was detected with the NMDS using the mean annual plot

coordinates for each site (Figure 7). Moderately invaded sites (3, 5–7) were strongly grouped near site 8, where the lowest quagga mussel density was found. The heavily invaded site 4 and uninvaded sites (1–2) each occupied distinct spaces on opposite sides of the plot with the site farthest downstream (8) placed closest to the uninvaded sites (1–2). The positioning of invertebrate taxa, including *D. r. bugensis*, was less clearly patterned. The majority of taxa clustered near the centre of the ordination plot with rarely occurring taxa (e.g. *R. peregra* (Müller, 1774) and *E. octoculata* (Linnaeus, 1758)) placed as relative outliers. The latter is an expected artefact of the technique (Clarke and Green 1988).

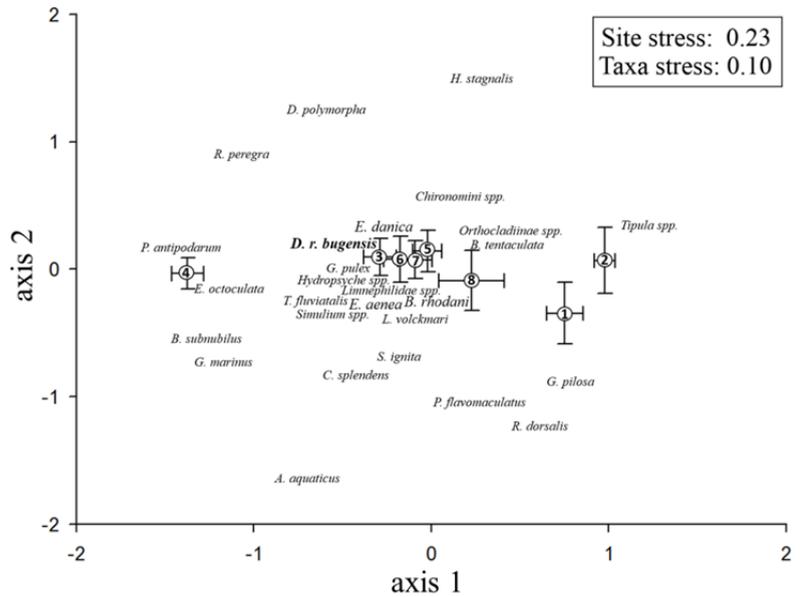


Figure 7. Non-metric Multi-dimensional Scaling (NMDS) ordinations of Bray-Curtis similarities in mean annual biomass composition both between sites and taxa. Error bars denote standard error.

Table 1. Results of a SIMPER analysis to determine the contribution of important taxa to mean dissimilarity of biomass (DM g m⁻²) between uninvaded and invaded sites, based on all months (top 12 taxa only).

Test Groups	Mean Dissimilarity (%)	Taxa	Dissimilarity (%)	Cumulative Dissimilarity (%)
Uninvaded v. Invaded Sites (1–8)	33.23	<i>D. r. bugensis</i>	28.6	28.60
		<i>Hydropsyche</i> spp.	7.18	35.78
		<i>T. fluviatilis</i>	6.52	42.3
		<i>B. rhodani</i>	6.09	48.39
		<i>L. volckmari</i>	6.05	54.44
		Limnephilidae spp.	5.79	60.23
		<i>Simulium</i> spp.	5.67	65.9
		<i>G. pullex</i>	4.70	70.6
		<i>C. splendens</i>	4.52	75.12
		<i>E. aenea</i>	4.36	79.48
		<i>E. danica</i>	3.68	83.16
		<i>B. tentaculata</i>	3.21	86.37

Table 2. Results of a SIMPER analysis to determine the contribution of important species to mean similarity of biomass (DM g m⁻²) within uninvaded and invaded site groups, based on all months (*D. r. bugensis* and top 5 other taxa only).

Test Group	Mean Similarity (%)	Taxa	Similarity (%)	Cumulative Similarity (%)
Uninvaded Sites (1-2)	76.46	<i>G. pullex</i>	24.15	24.15
		<i>E. danica</i>	21.81	45.97
		<i>E. aenea</i>	10.09	56.06
		<i>L. volckmari</i>	10.05	66.11
		<i>Hydropsyche</i> spp.	6.78	72.89
Invaded Sites (3-8)	75.80	<i>D. r. bugensis</i>	19.12	19.12
		<i>G. pullex</i>	15.83	34.95
		<i>E. danica</i>	15.46	50.41
		<i>L. volckmari</i>	9.69	60.10
		<i>Hydropsyche</i> spp.	6.75	66.85
		<i>E. aenea</i>	6.27	73.12

The SIMPER analysis showed 33% dissimilarity in mean biomass composition between uninvaded and invaded site groups, based on a mean of all monthly data sets (Table 1). Quagga mussel biomass contributed the most to this value (29% dissimilarity) with the

caseless caddis *Hydropsyche* spp. (Curtis, 1834) and mollusc *Theodoxus fluviatilis* (Linnaeus, 1758) also prominent (both driving 7% dissimilarity). The SIMPER analysis also presented high within-group similarity of uninvaded and invaded sites at 76% and

75%, respectively (Table 2). For both categories, the same five native taxa contributed most to within group similarity when excluding quagga mussel. These were *Gammarus pulex*, (24% uninvaded sites; 16% invaded sites), *Ephemera danica*, (22% uninvaded sites; 15% invaded sites), *Elmis aenea*, (10% uninvaded sites; 6% invaded sites), *Limnius volckmari*, Panzer, 1793 (10% uninvaded sites; 10% invaded sites), and *Hydropsyche* spp. (7% uninvaded sites; 7% invaded sites). Quagga mussel also contributed strongly towards defining the invaded site group (19%).

Discussion

Quagga mussel was consistently found in the Wraybury River downstream of the reservoir pump facility situated between invaded and uninvaded site groups. The highest estimate of mean annual biomass for the species at any one site (4.4 g m⁻²; site 4) was markedly lower than comparable mean figures from the Great Lakes Michigan (28.6 g m⁻²; Nalepa et al. 2009), Erie (24.7 g m⁻²; Patterson et al. 2005), and Ontario (86.9 g m⁻²; Wilson et al. 2006). Within invaded reaches the proportion of invertebrate biomass associated only with quagga mussel (annual mean: 61%) was lower than comparable values reported for sites at Great Lakes Erie (91%; Dermott and Kerec 1997), Ontario (98%; Birkett et al. 2015) and a series of smaller waterbodies within Eastern Europe (all > 93%; Burlakova et al. 2005). It is possible that our lower results reflect natural differences in the habitability of lotic and lentic systems for quagga mussel. For example, increased variation in planktonic food quality (Schneider et al. 1998), veliger larvae survival (Stoeckel et al. 1997) and ultra-violet light exposure at shallow stream depths (Aldridge et al. 2014) may limit *Dreissena* spp. success in riverine systems.

When excluding quagga mussel, mean invertebrate richness, biomass and density were significantly different between sites for at least half of monthly measurements; though patterns were largely driven by lower values at only one site (4). With similar indications apparent for Shannon-Weiner diversity (H'), such results were unexpected because relatively widespread impacts of *Dreissena* spp. invasions on benthic community structure have been reported from other studies (e.g. Stewart and Haynes 1994; Karatayev et al. 1997; Ricciardi et al. 1997; Karatayev 2002; Higgins and Vander Zanden 2010). Records from the Great Lakes region in particular show marked increases in taxa richness and biomass in response to *Dreissena* spp. colonisation (Burlakova et al. 2012; Karatayev et al. 2015). In such cases *Dreissena* spp. beds may facilitate other taxa by

physically enhancing habitat heterogeneity and providing an additional food source with their pseudofaeces (Botts et al. 1996; Burlakova et al. 2012). Significantly, our results did not provide convincing evidence for comparable processes in the Wraybury River. This was despite a clear segregation of uninvaded and invaded sites shown in the NMDS plot (Figure 7).

Expected differences in the biomass and density of certain taxa groups were not found. Prominent resident natives such as *Gammarus pulex* maintained consistent biomass and density throughout the study reach, with the exception of lower values at the site of highest quagga mussel density (Site 4; Table S1). This was in contrast to comparable taxa previously being shown to respond positively to *Dreissena* spp. colonisation (e.g. Stewart and Haynes 1994; Ricciardi et al. 1997; Dermott et al. 1998; Stewart et al. 1998). Additionally, other collector-filterers were thought to be among the most vulnerable to *Dreissena* spp. invasions due to direct trophic competition (Karatayev et al. 1997; Strayer et al. 1999). Despite this, the major collector-filterer present (caseless caddis *Hydropsyche* spp.) was found at higher densities within invaded sites (Table S1). Indeed, when excluding quagga mussel, the proportion of mean annual biomass represented by collector-filterers increased downstream (Figure 6a). While such trends are consistent with predictions of the River Continuum Concept (Vannote et al. 1980), the homogenous and localised nature of the study reach would likely preclude such effects normally found at a much larger catchment-scale.

The "within group" SIMPER analysis also provided limited evidence for expected differences between uninvaded and invaded sites. With the exclusion of quagga mussel the same five taxa contributed most towards the mean biomass composition of both invaded and uninvaded site groups when incorporating all monthly data sets (Table 2; *Gammarus pulex*, *Ephemera danica*, *Elmis aenea*, *Limnius volckmari* and collector-filterer *Hydropsyche* spp.). Again this contrasts with the lentic literature, where shifts in dominant faunal groups have been observed after colonisation (e.g. Stewart and Haynes 1994; Burlakova et al. 2005; Nalepa et al. 2009). It is possible that compared to the large, deep, lentic systems of these studies, the low quagga mussel densities recorded in Wraybury River are insufficient to produce comparable faunal shifts. In particular, the complex mussel beds expected to provide habitat space and refugia for other invertebrate species (Stewart et al. 1998; Bially and MacIsaac 2000; Ricciardi 2001; Burlakova et al. 2012) are likely to be absent or comparatively underdeveloped at lower densities.

The relatively homogenous assemblage of native invertebrates between invaded and uninvaded sites

suggests that for the Wraysbury River, the clustering of sites presented in the NMDS plot (Figure 7) was driven by the biomass of quagga mussel alone. This is strongly supported by the “between group” SIMPER analysis (Table 1) which presented quagga mussel as a large contributor (~ 29%) towards mean dissimilarity among site groups. However, it is important to reassert that at site 4, where the highest quagga mussel biomass and density was found, there was a significant reduction in mean invertebrate richness, biomass and density for over half the monthly measurements when excluding quagga mussel. While again contrary to expectations of general community facilitation derived from the lentic literature, it suggests that such densities of quagga mussel (site 4 annual mean: 130 individuals m⁻²) can cause loss of taxa in river ecosystems. Considering the fauna of the Wraysbury River, it is possible that such densities of mussel may form a barrier to surficial bed substrate preferred by locally dominant taxa such as the burrowing mayfly *Ephemera danica* and riffle beetles of family Elmidae. In time, these taxa could be replaced with a shift to different faunal groups at site 4, better reflecting trends described in lentic literature. Further monitoring would be required to observe possible shifts in invertebrate community structure, and caution should be taken to ensure that no unconsidered physicochemical differences confound findings between sites.

This study represents a first benchmark for understanding the progression and impacts of quagga mussel invasions in UK Rivers. Additional research might address why quagga mussel biomass found at the upstream invaded sites (3 and 4) was relatively high. This may be due to unconsidered factors of habitat suitability or the average settling distance of quagga mussel veligers from the reservoir pump facility. Indeed, the upstream proximity of well-established adult colonies to source veliger larvae is considered important for *Dreissena* spp. distribution in the North American Great Lakes region (Horvath and Lamberti 1999; Stoeckel et al. 1997) and river Don and Volga basins of Russia (Zhulidov et al. 2005). For the Wraysbury River, a source colony could be represented by the reservoir pump between sites 2 and 3.

The comparatively low quagga mussel biomass downstream of sites 3 and 4 (Figure 4) may alternatively be due to self-limitation effects of the species. It has been thought that upstream colonies of *Dreissena* spp. could limit seston availability for collector-filterers further downstream (Strayer et al. 1996; Fuentes 2003). Such a role would potentially cause quagga mussel to self-regulate their own population and that of other collector-filterers in the

Wraysbury River. It should be noted however, that our results presented a strong community of native collector-filterer taxa downstream of sites with the highest quagga mussel density. Further study might be undertaken to determine whether the dominant native collector-filterer in Wraysbury River (*Hydropsyche* spp.) may favour different sized planktonic food to that consumed by quagga mussel. Invertebrate feeding groups as described in this study are only categorised by the food acquisition method, not by the properties of food eaten (*sensu* Cummins and Klug 1979).

Conclusions

It is clear from this study that quagga mussel is well established in the Wraysbury River. Throughout an annual period of monthly sampling it was consistently found in sites downstream of a reservoir pump facility and in some cases comprised a significant proportion of total benthic biomass. In general however, quagga mussel biomass (both in amount and as a proportion of total benthic biomass) was not as high as that seen from studies in lentic systems.

Ordination analysis of mean biomass composition per site (when incorporating all monthly data sets) presented a segregation of uninvaded and invaded sites on the Wraysbury River. Despite this, the composition of fauna when excluding quagga mussel was found to be relatively homogeneous throughout. SIMPER analysis confirmed that the largest differences in community structure between invaded and uninvaded site groups was simply due to the presence of quagga mussel itself. Furthermore, changes to particular taxa in invaded sites were not identified as expected. When excluding quagga mussel, supposedly vulnerable collector-filterers were found to increase in importance within downstream invaded sites and the same five taxa contributed most to biomass composition within invaded and uninvaded site groups.

One site of high mussel density proved exceptional however, where quagga mussel formed a particularly large proportion of benthic biomass (site 4). Converse to expectations from lentic literature; mean invertebrate richness, biomass and density (all when excluding quagga mussel) was consistently lower here than at other sites. While caution should be taken to account for unconsidered confounding factors; it is possible that if quagga mussel were to increase to similar densities throughout the entire river, more significant changes to native community structure might be expected in future.

Excluding quagga mussel, invertebrate community structure in Wraysbury River appears conserved at

present. However, that this study is limited as it lacks pre-invasion data and it is also difficult to accurately ascertain the length of time since initial colonisation. The success and impact-magnitude of *Dreissena* spp. invasions are likely to vary temporally (Strayer and Malcom 2006; Karatayev et al. 2015) and there is need for regular, long term sampling of stream macroinvertebrates and other taxonomic groups to provide a clearer picture of post-establishment shifts in community structure. Using this study as a base line, progress in these areas would contribute towards knowledge of ecological impacts following *Dreissena* spp. invasions in rivers.

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Supplementary material

The following supplementary material is available for this article:

Table S1. Taxa list with mean annual abundance per site and total mean annual biomass cross all sites.

Table S2. Table of physicochemical data for stream dissolved oxygen, pH, alkalinity, hardness, temperature, and flow rate.

Table S3. Physical characteristics of study sites from an initial pilot study in April 2015.

Table S4. Mean monthly taxa richness per site (excluding *D. r. bugensis*).

Table S5. Mean monthly *D. r. bugensis* biomass per site.

Table S6. Mean monthly biomass per site of all taxa when excluding *D. r. bugensis*.

Table S7. Mean monthly invertebrate density per site when excluding *D. r. bugensis*.

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