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Predation preference of signal crayfish (*Pacifastacus leniusculus*) on native and invasive bivalve species

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Abstract

Predatory, non-native fauna can influence biodiversity and trophic dynamics in invaded ecosystems. Signal crayfish (*Pacifastacus leniusculus*) are a highly successful invader, which have altered freshwater benthic communities, including bivalve populations. Bivalves are a keystone freshwater group in global decline, partly due to invasion by alien bivalve and crayfish species. However, little is known about the predatory impacts of invasive crayfish within co-occurring native and invasive bivalve populations. Mesocosm predation choice experiments considered relative signal crayfish predation rates between paired native (*Anodonta anatina* and *Unio tumidus*) and invasive (*Dreissena polymorpha*, *D. bugensis*, and *Corbicula fluminea*) bivalves, and between paired invasive bivalves. All bivalves were actively predated, but there was no consistent difference in the biomass of invasive versus native bivalves consumed. However, the effects of consumption were consistently different; 18.2% of invasive bivalves were lethally predated, with 100% of surviving individuals remaining undamaged, whereas 1.1% of native bivalves were lethally predated, but 100% of surviving individuals received nonlethal damage in the form of shell chipping, which could reduce long-term bivalve fitness in natural environments. In experiments considering paired invasive species, *D. polymorpha* was more resistant to predation when compared to other invasive taxa tested. The majority of field research considering aquatic invasions considers purely lethal predation effects inferred from invertebrate presence/absence. These experiments demonstrate the need to better understand both the processes and impacts of predation by invasive species, which may include substantial nonlethal effects on the fitness and life history of endangered taxa.

KEYWORDS

bivalve, invasive species, lethality, mussel, nonlethal effects, predation, signal crayfish

1 | INTRODUCTION

Predatory, non-native invasive fauna influence biodiversity and trophic dynamics in invaded ecosystems (Rayner, Hauber, Imber, Stamp, & Clout, 2007; Medina et al., 2011; David et al., 2017),

contributing to an estimated 58% of bird, mammal, and reptile extinctions worldwide (Doherty, Glen, Nimmo, Ritchie, & Dickman, 2016). Numerous studies have demonstrated deleterious impacts of non-native predation on native community structure, together with loss of endangered and/or endemic native species. Invasive species have

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particularly potent effects in freshwater environments (Sala et al., 2000), where they can establish more readily than in other environments due to frequent and widespread introductions (García-Berthou et al., 2005), and cause substantial disruption to the function of ecological communities (Gallardo & Aldridge, 2015; Guareschi, Laini, England, Barrett, & Wood, 2021; Havel, Kovalenko, Thomaz, Amalfitano, & Kats, 2015; Strayer, 2010).

Across European freshwaters, crustacea account for 53% of recorded invasive species (Karatayev, Burlakova, Padilla, Mastitsky, & Olenin, 2009), of which crayfish are some of the most successful (Kouba, Petrusek, & Kozák, 2014). Crayfish are particularly prolific invaders due to their broad diet, aggression, ability to live in diverse habitats, high reproductive capability, and behavioural plasticity (Weis, 2010). Crayfish are both keystone consumers and ecosystem engineers, which can exist at very high densities in invaded catchments (e.g., signal crayfish >100 crayfish m^{-2} ; Chadwick et al., 2021). As such, their introduction has led to deleterious ecological impacts via consumption and predation (Gherardi & Acquistapace, 2007; Jackson et al., 2014; Mathers et al., 2016; Mathers et al., 2020; Twardochleb, Olden, & Larson, 2013) and geomorphic impacts via burrowing (Harvey et al., 2011; Rice, Johnson, Mathers, Reeds, & Extence, 2016; Sanders, Rice, & Wood, 2021). In particular, signal crayfish (*Pacifastacus leniusculus*) have established in the United Kingdom (UK) since their introduction in the 1970s and are now present in at least 60% of river catchments throughout the UK (Holdich, James, Jackson, & Peay, 2014; Rogers & Watson, 2011). Signal crayfish have demonstrated potent predation impacts on cohabiting aquatic macroinvertebrates (Mathers et al., 2016; Mathers et al., 2020; Ruokonen, Karjalainen, & Hämäläinen, 2014), resulting in changes to community structure and function (Jackson et al., 2014; Mathers et al., 2016; Mathers et al., 2020; Nyström, Svensson, Lardner, Brönmark, & Granéli, 2001).

Benthic molluscan taxa, including native and invasive bivalves, are widely reported to be at a high risk of crayfish predation, which has been demonstrated in both field monitoring and laboratory experiments (e.g., Machida & Akiyama, 2013; Meira et al., 2019; Nyström et al., 2001; Sousa et al., 2019; Stenroth & Nyström, 2003; Zu Ermgassen & Aldridge, 2011). Where this occurs in natural environments, change to invertebrate community structure beyond that observed directly via crayfish predation may result. This is because bivalves can comprise over 50% of total benthic invertebrate biomass (Burlakova, Karatayev, & Padilla, 2005; Mills, Chadwick, & Francis, 2017) and are considered a keystone group for community function (Geist, 2010; Lopes-Lima et al., 2014; Lydeard et al., 2004). For example, complex shell interstices of mussel beds have been shown to facilitate increased macroinvertebrate density (Mills, Chadwick, & Francis, 2019; Ricciardi, Whoriskey, & Rasmussen, 1997; Sylvester, Boltovskoy, & Cataldo, 2007) by providing predation and flow refugia (Beekey, McCabe, & Marsden, 2004; Gutiérrez, Jones, Strayer, & Iribarne, 2003) alongside alteration of turbulent hydraulic flow structures near the bed (Constantinescu, Miyawaki, & Liao, 2013; Sansom, Bennett, Atkinson, & Vaughn, 2020). Live mussels may also filter significant proportions of planktonic biomass and

available nutrients from the water column (Rosa, Ward, & Shumway, 2018), depositing pseudofaeces that promote benthic periphyton growth (Cataldo et al., 2012; Ozersky, Barton, Hecky, & Guildford, 2013; Phelps, 1994), and provide new food sources for cohabiting benthos (Gutiérrez et al., 2003; van Broekhoven et al., 2015).

However, invasive bivalves can also have significant deleterious effects on native bivalves (Anastácio et al., 2019; Burlakova, Karatayev, & Padilla, 2000; Ferreira-Rodríguez, Sousa, & Pardo, 2018; Ricciardi, Neves, & Rasmussen, 1998; Sousa, Novais, Costa, & Strayer, 2014; Strayer & Malcom, 2007) and are potentially at lower predation risk from invasive crayfish than native mussel taxa due to factors such as shell thickness and reproductive capacity (Meira et al., 2019). For example, a greater shell thickness may provide a more robust defence against predation (Mascaro & Seed, 2001; Sun et al., 2017), and higher rates of fecundity may mean that the rate of animal reproduction may be able to keep up with or outpace the rate of population predation. This is important, because in natural environments, selective predation of native over invasive bivalves may accelerate establishment of invasive bivalve species by removing functional competitors. This could contribute to “invasional meltdown” mechanisms (sensu Simberloff & Von Holle, 1999; Simberloff, 2006), where the establishment of non-native species can develop niches to facilitate further invasions and system disruption. For example, the introduction of Ponto-Caspian zebra mussel (*Dreissena polymorpha*) has facilitated the further invasion of at least 14 species to the Great Lakes of North America by providing habitat complexity, food, and shelter (Ricciardi, 2001). This theory has been well evidenced in freshwater systems (e.g., Ricciardi, 2001), and it has been suggested that in the UK, where invasive crayfish, invasive bivalves, and native bivalves coexist, communities could be vulnerable to invasional meltdown (Gallardo & Aldridge, 2015). Therefore, specific understanding is needed concerning respective resilience of native and non-native bivalves to crayfish predation. A key factor to successful invasion is survival from predation pressure (deRivera, Ruiz, Hines, & Jivoff, 2005; Juliano, Lounibos, Nishimura, & Greene, 2010; Weis, 2011). Selective predation by signal crayfish upon invasive bivalves may also mediate deleterious impacts of invasive bivalves on native taxa.

This is of particular concern regarding interactions between native and invasive bivalves. Globally, native bivalves are in decline (Lopes-Lima et al., 2014; Lydeard et al., 2004) and are of high conservation importance in Europe (Lopes-Lima et al., 2017). A particular threat to native bivalves, and particular to Unionid freshwater mussels, is the establishment of invasive bivalves (Lopes-Lima et al., 2017). Five invasive bivalve species are currently established in European freshwater systems (*Corbicula fluminea*, *Corbicula fluminalis*, *Dreissena bugensis*, *Dreissena polymorpha*, and *Sinanodonta woodiana*), which frequently co-occur with native bivalves in river systems (e.g., Himson, Kinsey, Aldridge, Williams, & Zalasiewicz, 2020; Pecorelli, 2018; Sousa, Pilotto, & Aldridge, 2011).

Whilst many studies have considered interactions between crayfish and bivalves (e.g., Czarnoleski, Müller, Kierat, Gryczkowski, &

Chybowski, 2011; Naddafi, Eklöv, & Pettersson, 2007; Perry, Lodge, & Lamberti, 1997; Zu Ermgassen & Aldridge, 2011), only one study to our knowledge has considered the predation rates of crayfish on native and invasive bivalve species (Meira et al., 2019), where native bivalves (*Anodonta anatina*, *Potomida littoralis*, and *Unio delphinus*) were consumed, but invasive bivalves (*Corbicula fluminea*) were not. Further, no studies have compared the relative predation rates of crayfish between multiple invasive bivalve species.

Therefore, little is known about the potential consequences of the spread and introduction of invasive crayfish on co-occurring native and invasive bivalve populations, which may be an unknown, added pressure to the survival of endangered native bivalves. This study therefore aims to assess the relative proneness to predation of two native and three invasive bivalves to Great Britain under direct predation competition by signal crayfish through a series of ex-situ mesocosm experiments. It aims to address:

1. Do signal crayfish preferentially consume native over invasive bivalve taxa?
2. Which invasive and/or native bivalve taxa are least at risk from predation by signal crayfish?

2 | MATERIALS AND METHODS

Two ex-situ mesocosm experiments were designed to investigate feeding preferences of signal crayfish when presented with a choice of native or invasive bivalves. Bivalve taxa selected for study consisted of two native species: *Unio tumidus* (Unionidae) and *Anodonta anatina* (Unionidae), and three invasive species; zebra mussel (*Dreissena polymorpha*: Dreissenidae), quagga mussel (*Dreissena bugensis*: Dreissenidae), and Asian clam (*Corbicula fluminea*: Cyrenidae).

2.1 | Animal collection

Signal crayfish were collected from the River Bain (53.297, -0.132) in July 2019 using Swedish “trappy” traps and maintained at the Loughborough University River Science Laboratory. Crayfish were maintained in the laboratory under licence number E C ILFA 62 v2. For further details regarding project and trapping license detail, please contact the local Environment Agency area office in Spalding.

None of the tested bivalve species have been recorded at the collection site (Environment Agency, 2021; NBN Atlas, 2021). Crayfish were kept in two holding tanks (1.3 m × 0.7 m × 0.6 m), which were aerated, filtered, and filled to a depth of 0.2 m with 180 L of dechlorinated tap water. Holding tanks were kept at an ambient temperature (24°C), and had sufficient refuges (plastic pipes) for all crayfish to shelter. Crayfish were held in the laboratory for two weeks prior to being used in experiments. Crayfish were fed carrot sticks, but were starved for three days prior to the start of experimental runs to standardise predator hunger level (as in Meira et al., 2019). Crayfish were selected for the experiments that met the following criteria: large, adult

TABLE 1 Size range and mean size (length; mm) of bivalve taxa used in experiments

	Size range (length; mm)	Mean size (length; mm)
<i>A. anatina</i>	48–89	67.5
<i>C. fluminea</i>	10–36	21.1
<i>D. bugensis</i>	18–38	29.9
<i>D. polymorpha</i>	16–36	25.0
<i>U. tumidus</i>	45–89	68.6

crayfish (mean 52.7 mm carapace length; range 44–64 mm), not buried (carrying eggs); not in molt, retained both chelae (claws); antennae and all legs were all present and not damaged.

Bivalves (Table 1) were hand collected from large populations in the River Ant, Norfolk (52.751, 1.499; *A. anatina* and *D. polymorpha*), Hermitage Brook, Leicestershire (52.768, -1.191; *C. fluminea*), and the River Wraysbury, Surrey (51.452, -0.521; *U. tumidus* and *D. bugensis*). Bivalves species were kept in separate holding tanks (530 mm × 325 mm) filled to a depth of 150 mm with dechlorinated tap water. Holding tanks were aerated and kept at an ambient temperature. Bivalves were kept in captivity for no more than 72 hr prior to the start of experiments.

2.2 | Mesocosm experiments

Two mesocosm experiments were undertaken in the Loughborough University River Science Laboratory to address the research questions. In each case, polypropylene mesocosms (530 mm × 325 mm) without substrate were filled to a depth of 150 mm with dechlorinated tap water, aerated, and kept at an ambient temperature (24.1°C, ±1.9°C [SD]). Mesocosms were purposefully selected to be small and to exclude substrate to increase the chance of predator-prey encounters occurring (Houde & Petersen, 2009). Water quality measurements (O₂, temperature, and pH) were taken at regular intervals throughout the experiments, which were consistent throughout the experiments and between treatments (mean: 91% O₂; 24.1°C; 7.4 pH).

To test question 1, one signal crayfish was offered pairs of native and invasive bivalves to predate on. To test question 2, crayfish were offered pairs of invasive bivalves to predate on. Finally, paired experiments with no crayfish present were also run as control experiments to ensure crayfish actively predated the bivalves, as opposed to scavenging the remains of bivalves that had died from background causes during the experiment.

2.3 | Experimental procedure

For experiment 1, three specimens of either *A. anatina* or *U. tumidus* were placed equidistantly across the bottom surface in one of five replicate mesocosms. Then, a number of invasive bivalve specimens

(of a single species) were additionally placed in each mesocosm (Table 2). All bivalve specimens were assessed to be alive at the start of experiments; bivalves were considered dead if they were gaping, or if they offered no resistance to being teased apart with tweezers and did not reclose, as in Coughlan et al. (2020).

To ensure a similar potential encounter rate of crayfish with the tested taxa, the density of invasive bivalves per mesocosm chosen covered a total surface area of the respective mesocosm floor equivalent to that of the three *A. anatina* or *U. tumidus* specimens. For each mesocosm, this was accurately and precisely calculated using card tracings detailing the size of *A. anatina* or *U. tumidus* specimens used. Invasive bivalves were arranged in three groups on the mesocosm floor to provide spatial equivalence between the tested taxa (Figure 1). This pattern and spacing of bivalves was consistent across all experiments. Previous mesocosm experiments have measured mean maximum feeding rate of signal crayfish to be 0.90 g d⁻¹

TABLE 2 Bivalve pairings undertaken in the experimental runs. Numbers in brackets indicate the mean number of individuals used in each experimental treatment

	Bivalve 1	Bivalve 2
Experiment 1		
1	<i>D. bugensis</i> (14.4)	<i>U. tumidus</i> (3.0)
2	<i>D. polymorpha</i> (12.8)	<i>U. tumidus</i> (3.0)
3	<i>C. fluminea</i> (16.0)	<i>U. tumidus</i> (3.0)
4	<i>D. bugensis</i> (11.4)	<i>A. anatina</i> (3.0)
5	<i>D. polymorpha</i> (18.2)	<i>A. anatina</i> (3.0)
6	<i>C. fluminea</i> (16.2)	<i>A. anatina</i> (3.0)
Experiment 2		
1	<i>D. polymorpha</i> (15.6)	<i>D. bugensis</i> (14.8)
2	<i>C. fluminea</i> (14.8)	<i>D. bugensis</i> (14.4)
3	<i>C. fluminea</i> (13.0)	<i>D. polymorpha</i> (18.0)

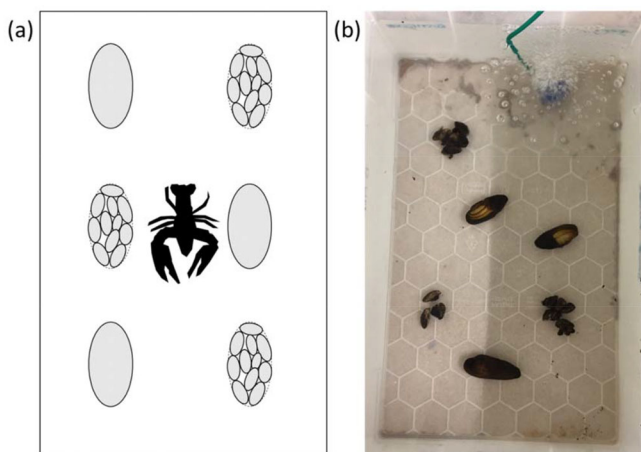


FIGURE 1 Placement of bivalves at the start of experiments, shown in (a) a schematic and (b) a photograph of an initial set up [Color figure can be viewed at wileyonlinelibrary.com]

(Rodríguez Valido et al., 2021), and so it was estimated that the number of native and invasive bivalves placed in each mesocosm (mean sum of biomass of all bivalves in each mesocosm = 131.2 g) were of excess predation mass to ensure that food availability was not a limiting factor. Finally, one signal crayfish was placed into the centre each mesocosm and allowed to move freely (Figure 1). The sex and carapace length of each crayfish was recorded prior to the experimental run. Carapace length did not differ between treatments ($F = 0.787$; $p = 0.617$). Experimental runs then lasted for 42 hr under natural light conditions, giving the crayfish two nights (whereon signal crayfish activity is highest; Harvey et al., 2014; Johnson, Rice, & Reid, 2014) to predate the bivalves. Experimental runs were visually observed during daylight hours so that the researchers could qualitatively observe crayfish hunting behaviour. Whilst signal crayfish are primarily crepuscular (Harvey et al., 2014), nocturnal observation was not possible due to laboratory opening hours and a lack of funding for video cameras. Both native taxa were individually tested with all three invasive taxa, providing six treatments, which were replicated five times, yielding 30 experimental runs (Table 2).

The second experiment compared the predation choice of signal crayfish when offered two species of invasive bivalves. This yielded three treatments (*D. bugensis* vs *D. polymorpha*, *D. bugensis* vs *C. fluminea*, and *D. polymorpha* vs *C. fluminea*), and 15 experimental runs. The card tracings from experiment 1 were used to calculate the abundance of bivalves to test, so that an equivalent bed surface area of bivalves were tested in all experimental runs.

2.4 | Recording measurements

The shell length of each bivalve, the number of bivalves, and the total wet weight biomass (accurate to 0.01 g) of all bivalves of each group were recorded at the start and end of each run, including any shell fragments remaining in the mesocosm at the end of each run. In addition, the number of animals killed (a clear breach of shell and at least partial consumption of body), and physically damaged but not killed (no shell breach) was also recorded. After the experiments concluded, bivalves were returned to aquaria containing dechlorinated tap water for 24 hr, after which mortality was assessed as above.

Predation impact was measured using five metrics: (1) the total biomass consumed (g), (2) the proportional biomass consumed compared to the biomass presented at the start of experiments (%), (3) the number of individual bivalves killed, (4) the proportion of individual bivalves killed (%), and (5) the percentage of surviving bivalves with physical nonlethal damage inflicted (%).

2.5 | Data analysis

The biomass of bivalves consumed were normally distributed (Shapiro-Wilk; $p > 0.05$), and so parametric tests (paired t-tests [t]) were undertaken to analyse differences in the biomass of bivalves consumed by crayfish in each treatment. The number of individual

bivalves killed and the percentage of surviving bivalves with nonlethal damage inflicted were not normally distributed (Shapiro–Wilk; $p < 0.05$) and could not be transformed due to the true presence of extreme values (e.g., where no bivalves were killed in an experimental run, and all bivalves were damaged by crayfish in an experimental run, respectively). Therefore, non-parametric tests (paired Wilcoxon signed-rank test [Z]) were undertaken to analyse differences in the number of individual bivalves killed and the percentage of surviving bivalves with nonlethal damage inflicted in each treatment. All data analyses were performed in SPSS Statistics V23 (IBM, 2015).

3 | RESULTS

Signal crayfish predated all mussel species in the experiments. No bivalve deaths were recorded in the paired experiments where

crayfish were not present, and so all damage and consumption of bivalves in the experimental runs were attributed to the predatory behaviour of crayfish. There was no relationship between crayfish size and the mass of bivalves consumed ($r = 0.097$, $n = 45$, $p = 0.527$). In addition, there was no significant difference in the mean mass of bivalves consumed between male (12.9 g, SD = 8.8 g, $n = 25$) and female (10.0 g, SD = 6.9 g, $n = 20$) crayfish ($t_{[43]} = -1.242$, $p = 0.221$).

3.1 | Predation selectivity of native and invasive bivalve taxa

Across all experimental runs where both native and invasive bivalves were presented to crayfish, a greater proportion of invasive bivalves were killed than native bivalves (18.2 and 1.1%, respectively).

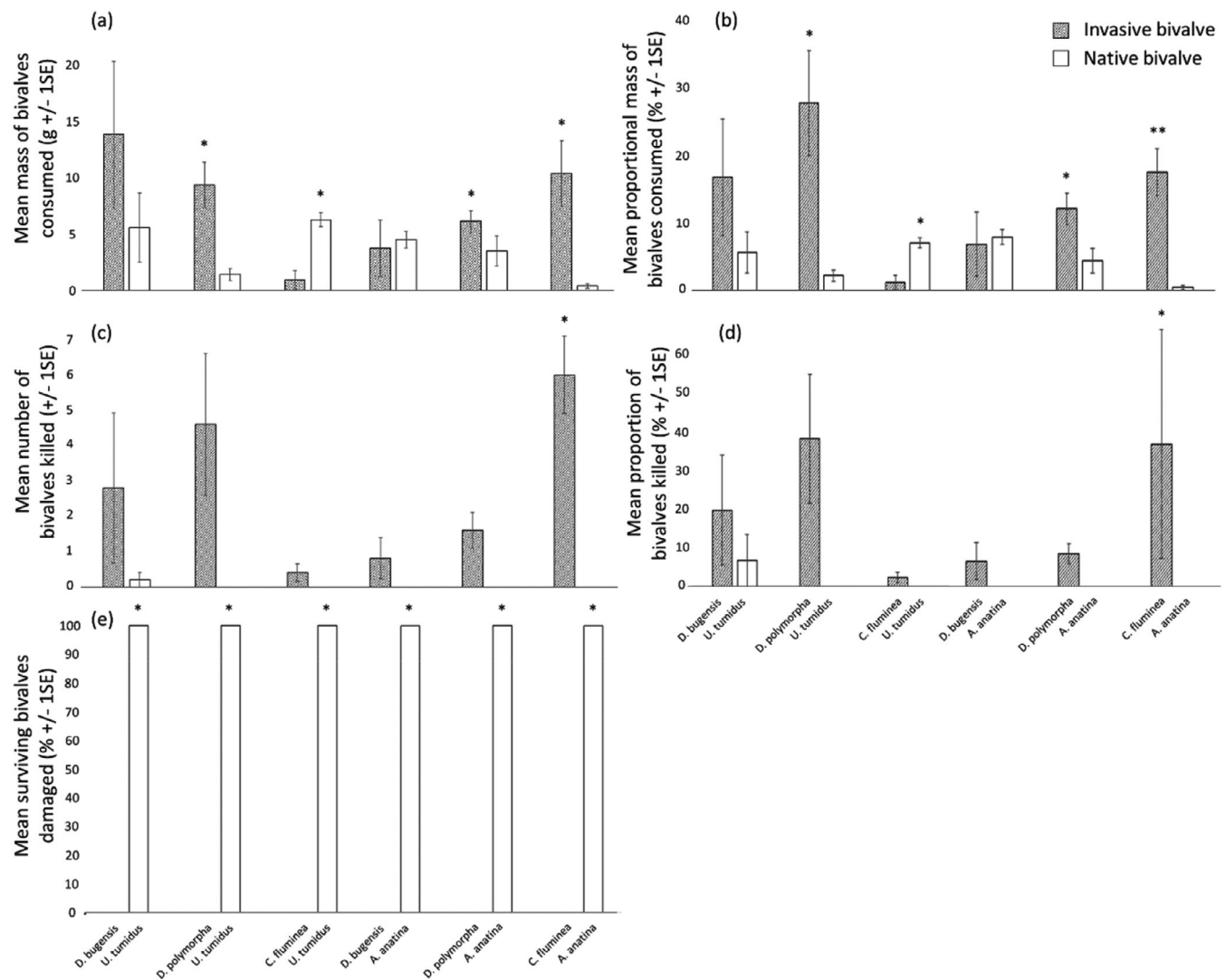


FIGURE 2 Crayfish predation of native and invasive bivalves, considering (a) biomass of bivalves consumed, (b) proportional biomass of bivalves consumed, (c) number of bivalves killed, (d) proportional number of bivalves killed, and (e) number of bivalves damaged by signal crayfish during experimental runs, of invasive species paired with *Unio tumidus* and *Anodonta anatina*. Significant differences are denoted by asterisks (* $p < 0.05$; ** $p < 0.01$)

However, a greater number of surviving native bivalves had nonlethal shell damage compared to invasive bivalves (100 and 0%, respectively).

The mean total of invasive bivalve biomass (g) consumed was greater than for native bivalves in four of the six treatments (Figure 2a). Within treatments, this difference was significant in three cases (*D. polymorpha* vs. *U. tumidus*, mean = 9.35 and 1.41 g respectively; $t_{(4)} = 3.509$, $p = 0.025$; *D. polymorpha* vs. *A. anatina*, mean = 6.4 and 3.5 g, respectively; $t_{(4)} = 3.829$, $p = 0.019$; *C. fluminea* vs. *A. anatina*, mean = 10.38 and 0.38 g, respectively; $t_{(4)} = 3.375$, $p = 0.028$). In addition, a significantly greater mean native bivalve biomass was consumed in one treatment (*C. fluminea* vs. *U. tumidus*, mean = 0.90 and 6.26 g, respectively; $t_{(4)} = -4.523$, $p = 0.011$). These same pairwise differences were also observed considering the proportional biomass of each species consumed (Figure 2b).

Across all treatments, a greater number of invasive bivalve individuals were killed when compared to native bivalves (Figure 2c), but this was significant in only one of the six treatments (*C. fluminea* vs. *A. anatina*, mean = 6.0 and 0.0, median = 5.0 and 0.0; $Z = -2.032$, $p = 0.042$). This was also true of the proportion of individual bivalves killed (*C. fluminea* vs. *A. anatina*, mean = 36.9 and 0.0%, median = 31.3 and 0.0%; $Z = -2.032$, $p = 0.042$; Figure 2d). Across all treatments, crayfish killed only a single native bivalve individual (*U. tumidus*, in *D. bugensis* treatment).

Whilst a greater number of invasive individuals were killed over the full 2 hr, a greater proportion of native individuals were damaged (Figure 2e). This was largely in the form of shell chipping (Figure 3), which was observed on all native bivalves, but only on invasive bivalves that had also been successfully killed where the shell was subsequently breached; no surviving invasive bivalves had evidence of shell chipping present. Across all treatments that paired invasive and native bivalves, a significantly greater proportion of *U. tumidus* and *A. anatina* individuals (100% in all cases) were visibly damaged by signal crayfish when compared to *D. bugensis*, *D. polymorpha*, and

C. fluminea (0% in all cases; $Z = -2.236$, $p = 0.025$ in all cases; Figure 2e).

3.2 | Comparative predation of invasive bivalves

Across the three treatments which paired invasive bivalve taxa, a significantly lesser biomass of *D. polymorpha* was consumed than both *C. fluminea* (mean = 0.81 and 6.44 g; $t_{(4)} = 2.060$, $p = 0.047$) and *D. bugensis* (mean = 3.36 and 14.65 g; $t_{(4)} = -3.150$, $p = 0.010$; Figure 4a). These same pairwise differences were also observed considering the proportional biomass of each species consumed (Figure 4b). Fewer *D. polymorpha* individuals were also killed in treatments against *C. fluminea* (mean = 0.4 and 4.2) and *D. bugensis* (mean = 1.0 and 4.4), but these were not significant ($Z = -1.826$, $p = 0.068$; and $Z = -1.826$, $p = 0.068$, respectively). However, considering the proportion of individuals killed, the same directional differences were observed, but a significantly lower proportion of *D. polymorpha* individuals were killed than *D. bugensis* (mean = 6.1 and 30.2%, median = 0.0 and 25.0%; $Z = -2.023$, $p = 0.043$; Figure 4d). No surviving bivalves sustained clear physical damage.

There was no significant difference in the biomass of *C. fluminea* and *D. bugensis* consumed (mean = 4.28 and 9.07 g; $t_{(4)} = 1.517$, $p = 0.090$), or the number of *C. fluminea* and *D. bugensis* killed (mean = 5.2 and 1.8, median = 5 and 2; $Z = -1.633$, $p = 0.102$). This was also observed considering the proportional biomass of each species consumed.

4 | DISCUSSION

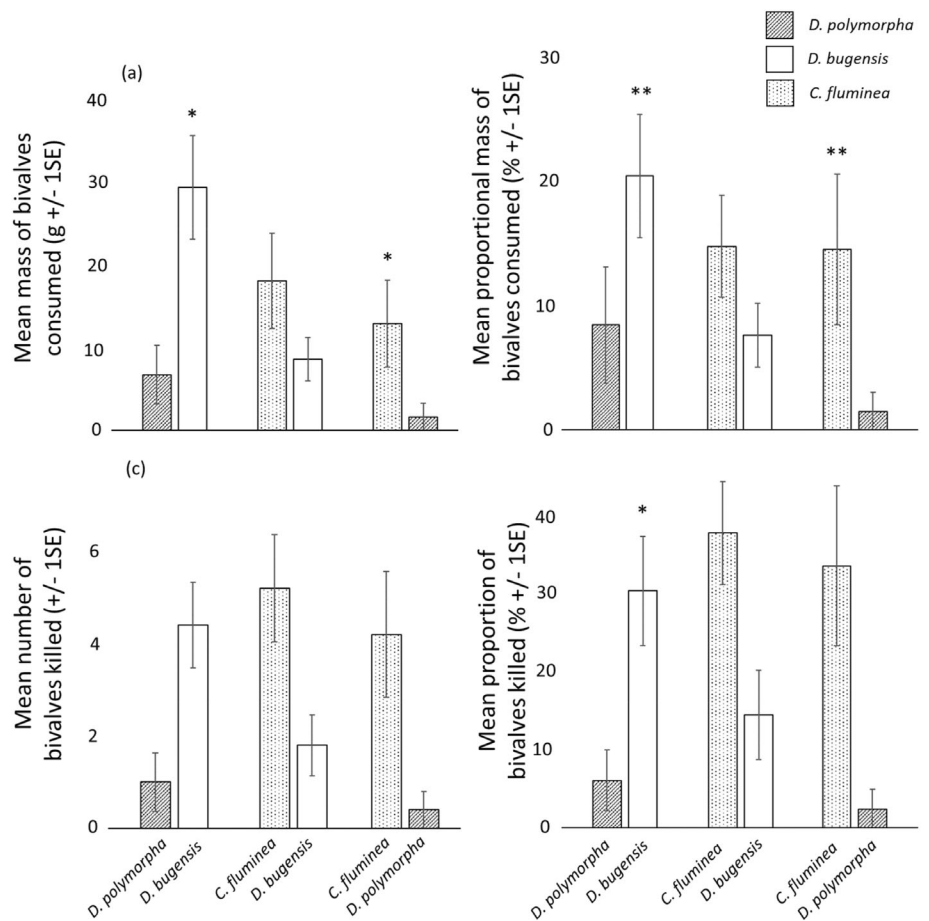
The results of these experiments demonstrate that invasive species, and in particular signal crayfish, can be effective predators of native and invasive fauna and provide supporting evidence that further spread of signal crayfish in the UK could cause deleterious impacts to both native and non-native bivalve populations through predation. Signal crayfish nonlethally consumed all native bivalve taxa tested and killed at least one bivalve specimen of each tested taxa (with the exception of *A. anatina*) during the experiments. This underlines the efficient predatory role of invasive signal crayfish in benthic communities (Mathers et al., 2016; Mathers et al., 2020) alongside the potential crayfish predation of cohabiting freshwater mussels (Czarnecki et al., 2011; Naddafi et al., 2007; Perry et al., 1997; Zu Ermgassen & Aldridge, 2011).

A greater number of invasive bivalves were killed by signal crayfish than native bivalves. Despite this difference in mortality rate, this does not mean that native bivalves are not at risk from crayfish predation. No consistent differences in the biomass of native versus invasive bivalves consumed were observed, with different mechanisms of predation observed between the native and invasive bivalves. Lethal opening of the shell and consumption of the mussel body was the dominant outcome of predation on invasive taxa, compared to the nonlethal damage (shell chipping) for native taxa, with a greater



FIGURE 3 (a) Native bivalve shells chipped by crayfish predation; (b) and (c) are magnified images of chipping at the margins of the shells [Color figure can be viewed at [wileyonlinelibrary.com](https://onlinelibrary.wiley.com)]

FIGURE 4 Biomass of bivalves consumed, (a), proportional biomass of bivalves consumed (b), number of bivalves killed (c) and proportional number of bivalves killed (d) by signal crayfish during experimental runs, of invasive species paired with invasive species. Significant differences are denoted by asterisks (* $p < 0.05$; ** $p < 0.01$)



proportion of surviving native bivalves suffering nonlethal damage than surviving invasive bivalves.

Shell chipping was recorded on all tested native bivalve individuals and contributed at least 73.6% of the total biomass of *U. tumidus* consumed, whereas shell chipping was not recorded on any invasive bivalve where the shell had not been breached. This suggests that signal crayfish had a greater success rate at opening the shells of invasive taxa than native taxa, the shells of which may have provided a more robust defence. Shell thickness is an important defence in the predation of marine clams by swimming crabs (*Portunus trituberculatus*; Sun et al. 2017), with European green crabs (*Carcinus maenas*) attacking all encountered shelled prey, and rejecting those that remain unbroken after a certain number of opening attempts (Mascaro & Seed, 2001). However, *A. anatina* have thinner shells than *C. fluminea* (Ilarri, Souza, Modesto, Guilhermino, & Sousa, 2015), yet significantly fewer *A. anatina* shells were successfully opened than *C. fluminea*. It may be that whilst thin, the larger shells of the native bivalves were more physically difficult for crayfish to effectively handle (Machida & Akiyama, 2013). This requires further research, as it could have important implications for the predation of smaller juvenile *U. tumidus* and *A. anatina*, and thus the success of population expansion or reestablishment of native taxa where crayfish are present.

The shell chipping caused to larger mussels is consistent to results observed by Machida and Akiyama (2013), where predation on pearl mussels (*Margaritifera* spp.) resulted in the killing of small (< 10 mm)

mussels, but the most extensive damage was inflicted on larger (>50 mm) mussels. This highlights the importance of considering nonlethal effects of predator-prey relationships. In these experiments, whilst shell chipping was not fatal to native taxa during the experimental run, such shell weakening could take place over longer time periods in-situ, leading to attritional damage and increased lethal predation risk, such as from other crayfish individuals that could not otherwise penetrate an intact shell. Nonlethal impacts of predators are typically associated with mobility and changes in behaviour (Lima, 1998), and concern groups such as birds (e.g., Cresswell, 2008; Voelkl, Firth, & Sheldon, 2016), fish (e.g., Figueiredo et al., 2016), amphibians (e.g., Werner & Peacor, 2006), and snails (e.g., Trussell, Ewanchuk, Bertness, & Silliman, 2004; Werner & Peacor, 2006), which are able to actively evade predators. Bivalves have also been shown to be motile in response to different biotic (e.g., predation; Kobak, Kakareko, & Poznańska, 2010) and abiotic (e.g., hydrological conditions; Schwalb & Pusch, 2007) cues. However, these experiments demonstrate that nonlethal effects of predation to less-mobile taxa such as bivalves can also be accentuated, such as direct physical damage. Such direct physical damage may further inhibit the ability of bivalves to move or burrow, exposing them to further risks such as predation, biofouling, and entrainment.

Such risks to native bivalves were emphasised, as when crayfish were introduced to the mesocosms, they exhibited a strong predatory effort towards native taxa tested, being consistently observed

attempting to consume *U. tumidus* and *A. anatina* specimens prior to attempting to consume the invasive taxa. The native bivalves were larger than the invasive species that they were paired with, and previous experiments have also found signal crayfish preferring to predate on larger (> 50 mm) pearl mussel prey (Machida & Akiyama, 2013). Larger bivalves may have been passively selected over smaller invasive bivalves as they are easier to visually notice, or actively selected due to their greater energy potential. Larger bivalve prey have a greater soft tissue to shell ratio than smaller prey, and are thus more energy profitable (Prejs, Lewandowski, & Stańczykowska-Piotrowska, 1990), and prey selection is likely to reflect this prey profitability (Wong & Barbeau, 2005). This was also observed when crayfish were offered a choice of exclusively invasive bivalves, with significantly fewer *D. polymorpha* (mean individual mass 2.8 g) consumed than either other invasive taxa (mean individual mass of *D. bugensis* and *C. fluminea* 5.0 and 4.1 g, respectively).

Whilst the results considering the number of bivalves consumed and killed suggest a higher degree of native bivalve durability to signal crayfish predation, some caution should be taken. All native bivalves were physically damaged by signal crayfish, with all but one rejected following failure to breach the shell, potentially aided by the high abundance of other available prey. Whilst mesocosm experiments have shown the active selection of abundant over rare bivalve prey by rock crabs (*Cancer irroratus*; Wong & Barbeau, 2005), in natural settings, where prey is likely to be sparser than offered in mesocosm experiments, prey encounter rates may drive passive prey selection. This is likely to be accentuated by bivalve anti-predator defences not exhibited in these experiments. Both *C. fluminea* (Chang, Chang, Shih, Liu, & Lee, 2017) and Unionid mussels (Schwalb & Pusch, 2007) bury into substrates, which were not offered here, which serves as an effective anti-predator defence (Klocker & Strayer, 2004), meaning that the availability of burying mussels as prey items in-situ is likely to be further reduced. Dreissenid mussels also attach together to form druses as an anti-predator defence mechanism (Kobak et al., 2010). Whilst bivalves in these experiments were presented as singletons, rather than as druses, this has been shown not to influence signal crayfish foraging abilities on zebra mussels (Zu Ermgassen & Aldridge, 2011). In this respect, where food is scarcer in-situ, more time may be spent by crayfish to attempt to open and consume bivalve prey than in these experiments, resulting in a greater rate of directly lethal encounters between native bivalves and signal crayfish. Further, native taxa are likely to be encountered individually, whereas *Dreissena* spp. are found in druses, and *C. fluminea* are found in very high local population densities in invaded catchments (e.g., Pecorelli, 2018). Therefore, whilst more invasive individuals may be killed and consumed, a greater proportion will remain unaffected compared to the native species (Figure 2e), and so an equal predation rate may disproportionately reduce populations of the native taxa. This is supported by field surveys in the Sabor River, Portugal, where *Unio delphinus* and *A. anatina* were predated by signal crayfish, but invasive species were not (Meira et al., 2019).

Whilst there were few additional trends in the native versus invasive bivalve feeding trials, further differences were observed when crayfish were offered a choice of invasive bivalves. In these

experiments, *D. polymorpha* were more robust to crayfish predation, being consumed, killed, and damaged significantly less than either *D. bugensis* or *C. fluminea*. *D. polymorpha* are widespread throughout the UK (Aldridge, Elliott, & Moggridge, 2004), and where crayfish predation rates are limiting factors in rivers, the preferential selection of prey other than *D. polymorpha* by crayfish could contribute to their wider distribution. Such relationships could be important considering *D. polymorpha* invasions have been associated with several negative impacts in UK freshwaters, such as commensal facilitation of omnivorous, invasive Ponto-Caspian amphipods (e.g., *Dikerogammarus* spp.; Gallardo & Aldridge, 2015), and the physical smothering of benthic habitats and native bivalve shells (Ricciardi et al., 1998; Sousa et al., 2011).

To elucidate associated risks for native bivalve taxa such as *U. tumidus* and *Anadonta anatina*, more research on crayfish and non-native bivalve interactions is needed. Globally, native bivalves are in decline (Lopes-Lima et al., 2014; Lydeard et al., 2004), in part due to invasion by alien bivalve (Burlakova et al., 2000; Ferreira-Rodríguez et al., 2018; Ricciardi et al., 1998; Sousa et al., 2014; Strayer & Malcom, 2007) and crayfish (Mathers et al., 2016; Mathers et al., 2020; Turley et al., 2017) species. The results of these experiments emphasise the role of signal crayfish as predators to bivalve communities and show some of the potential mechanisms through which resultant changes to bivalve communities occur. It is worth underlining that signal crayfish predation exerted different pressures on native and invasive bivalve taxa. Whilst a greater number of invasive individual bivalves were killed compared to native bivalves, a greater number were also left undamaged, whereas all native bivalves received physical damage (shell chipping). Nonlethal behavioural responses to predators can result in reduced feeding time in bivalves (Dzierżyńska-Białończyk, Jermacz, Zielska, & Kobak, 2019; Kobak, Poznańska, & Kakareko, 2012; Naddafi et al., 2007; Smee & Weissburg, 2006) and thus growth rate (Nakaoka, 2000), which can have negative implications for survivorship and fecundity (Nakaoka, 1994), and stress leading to other mortality factors (McCauley, Rowe, & Fortin, 2011). These long-term effects may also be observed through nonlethal physical effects of predation (injury) observed in these experiments. Given the associated higher fecundity and growth rates of aquatic invasive species (Morrison & Hay, 2011; Vila-Gispert, Alcaraz, & García-Berthou, 2005), and the observed initial targeting and increased physical damage of larger native bivalves, these nonlethal effects may play an important role in the deleterious long-term implications for native bivalve communities associated with invasive taxa.

This research has suggested, through lethal and nonlethal effects, different predation outcomes on invasive and native bivalve species, which may have life history and thus population success effects on the tested taxa. Previous research considering interactive effects between invasive species has largely considered taxa from the same co-evolutionary region (e.g., Ponto-Caspian invasional meltdown; Ricciardi, 2001; Gallardo & Aldridge, 2015), but this research has supported the concept that there may be potential interactive effects between species from different geographic regions (signal crayfish, North America; Dreissenid mussels, Ponto-Caspian; *C. fluminea*,

southeast Asia), as proposed in Simberloff and Von Holle (1999). In an increasingly globalised world, where invasive species introductions occur from multiple geographic regions, future research must consider the potential impact of invasive species not from the same co-evolutionary region to better understand the dynamics of geographically diverse biological invasions.

5 | CONCLUSION

Whilst there was no consistent difference in the biomass of invasive versus native bivalves consumed, the mechanism of predation was consistently different, with 18.2% of invasive individuals being lethally predated, and 81.8% being left undamaged, compared to 98.9% of native bivalves receiving nonlethal predatory effects, in the form of shell chipping, which may have lasting life history effects. The use of mesocosms in ecological studies has previously been criticised for not replicating the natural environment (e.g., Skelly, 2002; Skelly & Kiesecker, 2001; Underwood, 1986), but these experiments demonstrate their importance in understanding the mechanisms behind associations found in the field. The majority of field research considering species invasions, and in particular macroinvertebrate predation, considers purely lethal effects inferred from invertebrate presence/absence data. These experiments have demonstrated significant interactive effects between native and invasive species at the behavioural level. This emphasises the need for further mesocosm and in-situ studies at both the behavioural and population level to better understand the processes of predation by invasive species, which may have substantial nonlethal effects on the life history of endangered taxa.

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DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the supplementary material of this article.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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