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ORIGINAL PAPER

Predatory impacts of alien decapod Crustacea are predicted by functional responses and explained by differences in metabolic rate

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Abstract Alien predators can have large impacts on prey. It is important that we understand, and ideally predict, these impacts. Here, we compare predatory impacts of size-matched decapod crustaceans—invasive alien *Eriocheir sinensis* and *Pacifastacus leniusculus*, and native European *Austropotamobius pallipes*—and use this case study to inform methods for impact prediction. We quantify functional responses (FRs) on three macroinvertebrate prey species, examine switching behaviour, and measure metabolic rates as a possible mechanistic explanation for differences in predation. FRs show a consistent pattern: attack coefficients and maximum feeding rates are ordered *E. sinensis* ≥ *P. leniusculus* ≥ *A. pallipes* for all prey species. Attack coefficients of *E. sinensis* are up to 6.7 times greater than those of size-matched crayfish and maximum feeding rates up to 3.0 times greater. FR parameters also differ between the invasive and native crayfish, but only up to 2.6 times. We find no evidence of switching behaviour in crayfish but suggestions of negative switching in *E. sinensis*. Differences in FR parameters are mirrored by differences in routine, but not standard, metabolic rate. Overall, our data predict strong predatory impacts of *E. sinensis*, even relative to alien *P. leniusculus*. Strong impacts of *P. leniusculus* relative to *A. pallipes* may be driven more by body size or abundance than per capita effect. FRs vary between prey types in line with existing knowledge of impacts, supporting the use of FRs in quantitative, prey-specific impact predictions. MRs could offer a general mechanistic explanation for differences in predatory behaviour and impacts.

Keywords Freshwater · Invasive species · Biological invasions · Switching · Resource use

Introduction

Predation is a fundamental ecological interaction that can influence population dynamics and community structure (Wellborn et al. 1996; Chesson 2000; Hatcher et al. 2014). As well as informing basic ecological understanding, quantifying predatory interactions can inform applied management decisions, for example in the context of biocontrol (Symondson et al. 2002), conservation biology (Sutherland 1998) and biological invasions. The success and impact of alien species are often driven by resource use (Catford et al. 2009; Dick et al. 2014), and in particular by predatory interactions (Davis 2003; Salo et al. 2007; Sax and Gaines 2008). Thus, a quantitative understanding of predation by

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alien species is an important step in understanding and predicting impact in biological invasions (Dick et al. 2014) and consequently allocating limited management resources appropriately (Kumschick et al. 2012).

Predation can be described by a functional response (FR): the relationship between prey density N_0 and the rate of prey consumption N_e (Holling 1959). Holling's disk equation (Eq. 1) provides a simple functional response model.

$$N_e = aN_0/(1 + ahN_0) \tag{1}$$

There are two key FR parameters. Handling time (h) is the time needed for a predator to kill, ingest and digest a prey item. The attack coefficient (a) is the rate of successful search by a predator, or a measure of the rate of attacks that end in capture (Jeschke et al. 2002). Handling time is inversely related to the height of an FR curve, which describes the maximum possible rate at which prey can be consumed by a predator. Short handling times and correspondingly high FR curves are suggestive of high per capita impacts, which may translate into large population impacts in the field (Dick et al. 2013, 2017; Dodd et al. 2014; Xu et al. 2016). The attack coefficient defines the shape of an FR curve. When the attack coefficient is constant across prey densities, the FR is an asymptotically-declining Type II curve. Type II FRs are likely to be associated with the most severe impacts on prey populations because predation pressure remains high even at low prey densities (Murdoch and Oaten 1975; Juliano 2001). In contrast, a sigmoid Type III curve is generated when the attack coefficient is, at low prey densities, positively associated with prey density. Such a positive association could be mediated by predator learning, changes in foraging tactics, changing stimuli from prey, or structural complexity of habitats (Murdoch and Oaten 1975; Alexander et al. 2012).

When more than one prey type is present, attack coefficients can change with prey density if predators switch between prey types, attacking a more abundant prey type disproportionately more often that would be expected based on its abundance (Murdoch 1969). Detecting Type III FRs, or the factors that might lead to them, is important because they fundamentally change the consequences of predation for populations. For example, switching can reduce the likelihood of prey population extinction: because rare prey are attacked disproportionately infrequently, a low density refuge from predation is created (Murdoch 1969). However, switching could also maintain long-term predation pressure by sustaining predator populations when any single prey type becomes rare.

Metabolic rates (MRs) could provide a mechanistic explanation for predatory impacts. Metabolism refers to the enzymic processing of energy and materials within living organisms. MRs determine the rate of all biological activities (Brown et al. 2004). Generally, MR and food consumption should be positively associated: species with a high MR will require more food to fuel that metabolism, but may also be able to catch and process food more rapidly (Careau et al. 2008; Biro and Stamps 2010). In terms of FR parameters, a high MR necessitates a high maximum feeding rate (Rall et al. 2012) but could facilitate a shorter handling time (e.g. more energy available to fuel digestion) and a higher attack coefficient (e.g. more available energy to fuel movement and therefore encounter rates; Dell et al. 2014). Two fundamental measures of MR in ectotherms are standard (SMR) and routine (RMR). SMR reflects energy processing under minimal functional activity i.e. the minimum necessary to sustain life, or the idling cost of the individual's metabolic engine (largely the viscera). RMR reflects energy processing incorporating SMR and spontaneous, voluntary movements (Cech and Brauner 2011). To get an accurate picture of any feeding-metabolism relationship, it is important to measure both SMR and RMR: theoretically, one or the other or both could be related to feeding rate, depending on the predator's behaviour and physiology (Careau and Garland 2012).

Crustaceans are particularly successful as alien species and can exert strong impacts through a variety of mechanisms, including predation (Strayer 2010; Hänfling et al. 2011). In particular, decapod crustaceans are some of the most widely distributed and high-impact aliens in fresh waters (Karatayev et al. 2009; Strayer 2010). As flexible omnivores, they can impart impacts through predatory behaviour. Globally, two of the most successful and damaging alien decapods are the American signal crayfish *Pacifastacus leniusculus* (Dana 1852) and the Chinese mitten crab *Eriocheir sinensis* Milne Edwards 1853. Both species are biologically invasive having spread across large areas outside their native range, both can reach high densities in their novel range, and both have substantial ecological or economic impacts (Laverty et al. 2015).

Pacifastacus leniusculus is native to parts of North America but has been introduced and become a pest across much of Europe (Souty-Grosset et al. 2006). *Eriocheir sinensis* is native to the north-western Pacific but has been transported around the world, with key established populations on the west coast of the USA and in north-west Europe (Dittel and Epifanio 2009). Invasion by *P. leniusculus* can change community structure through a combination of competition, disease transmission and resource consumption (Crawford et al. 2006; Dunn et al. 2008; Twardochleb et al. 2013; Mathers et al. 2016). Evidence from mesocosms and field manipulations suggests *E. sinensis* may cause similar declines in macroinvertebrate populations through predation (Yu and Jiang 2005; Rudnick and Resh 2005; Rosewarne et al. 2016). However, our knowledge of these predatory impacts and their underlying mechanisms remains incomplete, especially for *E. sinensis* (Rosewarne et al. 2016).

Across Europe, the native white-clawed crayfish *Austropotamobius pallipes* (Lereboullet 1858) has declined over the past 40 years as alien crayfish, including *P. leniusculus*, have expanded their range (Dunn et al. 2008; Holdich et al. 2009; Füreder et al. 2010). More recent advancement of *E. sinensis* populations has created zones of overlap with *P. leniusculus*, and sympatry between *E. sinensis* and *A. pallipes* is also possible (Rosewarne et al. 2016). Thus, it is important to understand the relative ecological impacts of these species to appreciate how ecosystems have changed (or might change) as these species meet and replace each other. As a low-impact native analogue, *A. pallipes* also provides a baseline to contextualise the impact of the alien species.

Here, we aim to quantify the relative predatory impacts of *A. pallipes*, *P. leniusculus* and *E. sinensis* and investigate a possible mechanistic explanation for any differences. First, we compare laboratory-derived FRs on three macroinvertebrate prey types of differing morphology and behaviour (an amphipod crustacean, chironomid larvae and a gastropod mollusc). Predatory impacts may vary among prey species, so assessing FRs across a variety of prey species is important (Dick et al. 2014; Dodd et al. 2014). Second, we examine predation when more than one prey type is present—specifically the tendency of the predators to switch between similarly sized gastropods and amphipods. Third, we compare MRs (derived from oxygen consumption rates) between the three decapod species. We hypothesise that the alien species will have higher FR curves than *A. pallipes* in line with other invasive alien-native comparisons, and will show a greater tendency to switch between prey since diet flexibility may be a common trait of successful alien species (Sol et al. 2002; Weis 2010). We expect interspecific differences in MRs to mirror differences in feeding rates.

Methods

Experimental animals and husbandry

Decapods were collected by hand from established populations in the UK between 2013 and 2016. *A. pallipes* were collected from Adel Beck, Leeds (lat 53°51′18″N, long 1°34″26″W) under licenses from Natural England (#20131266 and #20144477). *P. leniusculus* were collected from Fenay Beck, Huddersfield (lat 53°38′29″N, long 1°43′51″W) under agreement with the UK Environment Agency. *Eriocheir sinensis* were collected from the River Thames at Chiswick (lat 51°29′17″N, long 0°14′44″W) under agreement with the Port of London Authority. The three experiments (FR, switching and MR) were run at different times on different batches of decapods, but all three species were tested simultaneously within each experiment.

Stock decapods were kept in a controlled environment room in the University of Leeds, at 14±0.2 °C (range) and under a 12:12 h light:dark cycle, for at least 2 weeks before use to allow acclimation to laboratory conditions and reduce the influence of any wild environmental cues (e.g. tidal cycles for *E. sinensis*; Gilbey et al. 2008). Stock tanks were communal by species, contained aerated aged tap water with excess PVC piping as shelter, and were supplied with Hikari® Crab Cuisine™ pellets and dried leaf litter (abscised *Acer pseudoplatanus* L. leaves) ad libitum.

A week before use in experiments, decapods were measured and isolated in individual plastic tanks (23 cm length, 15 cm width, 8 cm depth, with translucent white lids and sides covered in black plastic to minimise visual disturbance). Each tank was constantly aerated and contained one black PVC shelter (10 cm length, 5 cm diameter). Isolated animals were fed a standardised diet: four Hikari® Crab Cuisine™ pellets every other day, followed by starvation for 24 h before feeding experiments and 48 h before MR measurements.

Within each experiment, decapods were matched by overall body size (Section S1, Supplementary Information). We defined decapod body size as the first component from a principal components analysis on body mass and cmax (maximum carapace dimension: carapace length to tip of rostrum for crayfish; carapace width for crabs), explaining 88.7% of the variance in these parameters. Consequently, crabs were slightly heavier but shorter (cmax) than crayfish of similar body size. Across all experiments, mean ± SE decapod masses were: *A. pallipes* 10.6 ± 0.4 g; *P. leniusculus* 10.5 ± 0.3 g; *E. sinensis* 12.6 ± 0.4 g. Mean ± SE cmax was: *A. pallipes* 32.3 ± 0.4 mm; *P. leniusculus* 32.8 ± 0.3 mm; *E. sinensis* 30.9 ± 0.3 mm (see Table S1 for measurements of decapods used in each experiment).

Decapods were matched by overall body size for the feeding experiments because both the mass and body dimensions of predators relative to prey can affect predatory impact (Holling 1964; Nilsson and Brönmark 2000; Rall et al. 2012). Because the aim of this study was to relate MRs and predatory behaviour, we then analysed MRs of animals with a similar body size and mass to those used in FR experiments (Eq. 7). For other purposes, it may be more appropriate to compare mass-specific feeding and metabolic data (i.e. scaled to a common body mass). These analyses are presented in the Supplementary Information (Sections S5, S7 and S8). For the present study, they yield similar conclusions to analyses based on size-specific data.

Decapods used in experiments were in good condition (all limbs intact, no injuries to body) and free of visible parasites (Souty-Grosset et al. 2006). No decapods moulted within a week of use in any experiment, and typically not within two weeks. A mixture of male and female decapods of each species was used. Non-reproductive behaviours are generally similar between sexes in sub-adult crabs and crayfish (Taylor 2016).

For feeding experiments, three different prey species were used, chosen to represent differing motility and physical defence. Amphipods *Dikerogammarus villosus* (Sowinsky 1894) were collected from Grafham Water, Cambridgeshire (lat 52°17′52″N, long 0°18′44″W). Gastropods *Bithynia tentaculata* (L. 1758) were sourced from laboratory stocks, originating from various water bodies around Leeds. Chironomid larvae were sourced from a pet retailer in Leeds. For each prey species, animals in good condition and of similar size (Table 1) were blindly and haphazardly allocated to decapod predators. Uneaten and uninjured prey were returned to communal tanks and re-used.

Functional responses

Experimental design

FR data were obtained by providing an individual decapod with a known density of prey, allowing it to feed for 24 h and then calculating consumption based on the amount of prey remaining. FR experiments were run in the same controlled environment room as the stock tanks i.e. 14 ± 0.2 °C (range) and 12:12 h light:dark cycle.

Individual experimental tanks (dimensions as for isolation tanks) were set up containing three litres of aged tap water, approximately 150 glass stones (20 mm diameter, 9 mm height) to provide some structural complexity (Alexander et al. 2012) and a designated number of prey animals (Table 1). After 1 h to allow prey to settle, a single decapod was transferred from its isolation tank to each experimental tank.

After a 24 h feeding period, each tank was destructively sampled and remaining prey counted. We distinguished live prey, dead but complete prey, and identifiable parts of prey (fractions of animals). Consumption was calculated as the number of prey supplied minus all remaining flesh (whole and damaged prey). Killing was defined as prey that had been wholly or partially consumed i.e. excluding dead but undamaged prey assumed to reflect background mortality. Controls, to check background mortality, were tanks with prey but no predator (three replicate tanks per prey type per density, excluding chironomids at a density of 1200 tank^{-1}).

Predators were re-used at different prey densities until each predator species x prey density

Table 1 Sizes and densities of prey supplied to predators in functional response (FR) experiments

Prey type	Length (mm) ± SE	Wet mass (mg) ± SE	Densities (prey.tank^{-1})
Amphipod	16.3 ± 3.0	46.8 ± 8.6	2, 5, 8, 12, 16, 25, 40, 80, 130, 180, 230, 280
Chironomid larva	8.7 ± 0.2	2.8 ± 0.2	2, 5, 8, 12, 16, 25, 40, 80, 220, 400, 600, 1200
Gastropod	9.4 ± 0.1	52.8 ± 1.6	2, 4, 8, 12, 16, 25, 40, 80, 150, 250

Mean lengths and masses estimated from a random sample of 30 prey items across replicate runs. Amphipod length was measured from photographs of animals in resting position, from rostrum tip to telson tip. Gastropod length was measured as the longest dimension of the shell, but mass refers only to the flesh (extracted from the shell). *Eriocheir sinensis* and *P. leniusculus* were supplied with chironomid larvae at additional densities of 140, 300 and 800

combination was replicated five (*B. tentaculata* prey) or six times (chironomid and *D. villosus* prey). Re-use led to pseudoreplication, but was a constraint enforced by the use of Endangered *A. pallipes*. However, no individual animal was used more than once at any prey density, and no more than eight times in total. Experimental design also minimised the influence of re-use on results. First, initial predator hunger levels were standardised by the set feeding/starvation schedule. Between uses, predators were returned to isolation tanks, fed with the standard ration (four Crab Cuisine™ pellets) for 24 h then starved for 24 h. Second, across uses of individual predators, the order of presentation of prey densities was randomised. Third, replicates were roughly blocked by time, such that within each block one replicate was run for all predator species x prey density combinations (except for 1200 chironomids.-tank^{-1}, an additional density tested after all others).

For logistical reasons and because of seasonal prey availability, each prey item was tested over a 1–2 month period at different times of year (*D. villosus* Nov–Dec, chironomids Jan–Feb; *B. tentaculata* Jun–Jul).

Statistical methods

All statistical analyses were carried out in R version 3.3.1 (R Core Team 2016) with $\alpha=0.05$ unless otherwise specified. We present analyses conducted using number of prey *consumed* as the response variable: because it is only prey consumed that fuel metabolic demand, this metric is more relevant than the number of prey killed when comparing predator physiology and there is partial consumption of prey (Section S4). Additional analyses using prey *killed* as the response variable, which is more relevant when considering effects on prey populations, yielded similar overall results (Section S4).

For each predator x prey species combination, FR type was determined by logistic regression (with quasibinomial errors) following Juliano (2001) and Alexander et al. (2012). Where results were ambiguous, fits for different FR types were compared using Akaike's Information Criterion (AIC) (Pritchard et al. 2017). Based on these analyses, all FRs were modelled as Type II curves. Maximum likelihood model fitting and parameter estimation were performed within the R package *frair* (*frair::frair_fit*; Pritchard et al. 2017) and used Rogers' random predator equation (Eq. 2; Rogers 1972) which modifies Holling's disk equation (Eq. 1) to account for the non-replacement of prey within trials.

$$N_e = N_0(1 - \exp(a(N_e h - T))) \tag{2}$$

where N_e is the number of prey consumed or killed, N_0 is the initial density of prey (prey.tank^{-1}), a is the attack coefficient (tanks.day^{-1}), h is the handling time (days.prey item^{-1}) and T is the total time available for predation (days). In practice, the *Lambert W* function is incorporated into Eq. 2 to make it solvable (Bolker 2008).

To visualise variability around fitted FR curves, 95% BCa confidence intervals were drawn from bootstrap populations generated from the original data (*frair::frair_boot*; $n=1999$). Following Juliano (2001), parameters were compared using indicator variables (*frair::frair_compare*). Because multiple pairwise comparisons were made within each prey type, significance was considered against Holm-Bonferroni corrected α values (Holm 1979).

Switching

Experimental design

The potential for predators to switch between alternative prey items depending on their relative density was investigated by presenting predators with *D. villosus* and *B. tentaculata* at a range of relative abundances. These prey items were chosen because they are similar in mass (Table 1) and will not prey upon each other.

Switching experiments followed a similar protocol to FR experiments (isolation and feeding, settlement of prey items in tanks with glass beads, similarly sized prey, same temperature and light regime, destructive sampling after 24 h feeding). The most important difference was that two prey types were presented simultaneously. A total of 280 individual prey were added to tanks at one of the following five ratios (*D. villosus* to *B. tentaculata*): 0.15:0.85, 0.35:0.65, 0.50:0.50, 0.65:0.35 or 0.85:0.15. As a further difference to the FR experiments, three days before experimental feeding each decapod was allowed to feed on 10 *D. villosus*, then two days before use allowed to feed on 10 *B. tentaculata*. Only individuals that consumed each prey type were used in switching experiments, such that all individuals had recent experience feeding on both prey types.

In the switching experiment, individual predators were only used once to ensure feeding was not differentially influenced by prior experience. Five replicates were run at each ratio for *A. pallipes*, six for *P. leniusculus* and eight for *E. sinensis*. Five controls, with no decapod predator, were run at the equal ratio (140 *D. villosus* and 140 *B. tentaculata*) to check prey survival.

Statistical methods

As for FRs, we present analyses using prey *consumed* (rounded to the nearest whole individual) as the response variable. Additional analyses carried out using prey *killed* as the response variable yielded similar results (Section S6).

Mean prey consumption (total number of individuals of both prey types) was compared between decapod species, using a quasipoisson generalised linear model and post hoc Tukey contrasts with Holm-Bonferroni adjustment of p values (*multcomp::glht*; Hothorn et al. 2016).

To detect switching, the observed proportions of prey in predator diets were compared with null proportions (assuming the absence of switching). This analysis used population proportions i.e. consumption by all predators of a species at each relative density. First, for each decapod species, electivity towards *D. villosus*, c, was determined using Eq. 3 (Murdoch and Oaten 1975).

$$c = N_{Dv}/N_{Bt} \tag{3}$$

where N_{Dv} and N_{Bt} are the total number of *D. villosus* and *B. tentaculata* consumed, by all predators of a species, when prey were equally available (ratio 0.50:0.50). *A. pallipes* did not consume any *B. tentaculata* in this situation, so an arbitary value of N_{Bt}=1 was used to allow estimation of c. A value of c =1 indicates no electivity (prey are consumed in equal numbers); $c > 1$ indicates electivity towards *D. villosus* and $c < 1$ electivity towards *B. tentaculata*. We describe c as electivity rather than preference, as it does not necessarily depend on a behavioural choice by the predator (Murdoch 1969).

Second, for each decapod species and at each relative prey density, the expected proportion of *D. villosus* in the predator diet under the null hypothesis of no switching, $P_{Dv\ (null)}$, was calculated using Eq. 4 (Murdoch and Oaten 1975).

$$P_{Dv(null)} = cF_{Dv}/(1 - F_{Dv} + cF_{Dv}) \tag{4}$$

where F_{Dv} is the proportion of *D. villosus* in the available food. Expected numbers of *D. villosus* and *B. tentaculata* in predator diets were then calculated, using $P_{Dv\ (null)}$ and observed total consumption. Finally, expected and observed prey numbers were compared using Fisher's exact tests (*fisher.test*). If the proportion of *D. villosus* in the diet was lower than the null proportion when *D. villosus* was relatively rare, but higher than the null when *D. villosus* was relatively common, we would conclude that switching had occurred (Murdoch 1969).

The above calculations assume that absolute and relative prey densities do not change over time: a reasonable assumption for our data. The high prey densities ensured that in 83% of trials < 20% of the prey were consumed (and in 99% of trials < 30% of prey were consumed) and wide spacing of relative prey densities meant that final relative densities never became more extreme than adjacent starting densities. Neither prey species was completely consumed in any replicate trial. We also note that these tests will be subject to high Type I error rates: there is variation around c (because it is estimated from sample data) that is not incorporated into estimates of null consumption. However, given limited significance in the results this does not affect our overall conclusions.

Metabolic rates

Experimental design

As a proxy for MRs, oxygen consumption rates ($\dot{M}O_2$) of individual decapods were measured in a custom made intermittent-flow respirometer (following Quetin 1983 and Svendsen et al. 2016; see Section S2 for diagram). In brief, the respirometer was a PVC food storage container that was airtight when clipped shut and enclosed 505 ml of water. The chamber contained a magnetic stir bar to mix water during measurements and a PVC shelter (6 cm length, 4.5 cm diameter) to minimise stress. An optical dissolved oxygen (DO) probe (YSI ProODO, YSI Incorporated, OH) was inserted into the chamber through a rubber seal. Plastic mesh separated the decapod from the stir bar and DO sensor cap. One piece of inflow silicone tubing (40 mm length, 3 mm internal diameter) connected the chamber to a flush pump (Sacem BIP 4W) via an air trap, whilst another 40 mm length of tubing provided an outflow. The chamber and attachments were submerged in a water bath, which was constantly aerated and contained a combined filter/ultraviolet light (All Pond Solutions, Middlesex, UK) to continually mix the water bath and minimise microbial growth. The entire setup was housed in an incubator with the same temperature (14.0 ± 0.3 °C range) and photoperiod (12:12 h) as the controlled environment room. Housing in a separate incubator ensured complete standardisation of visual and acoustic cues during measurements.

Prior to measurement, decapods were isolated for one week and fed a standardised diet (as for FR experiments), including a 48 h starvation period before measurement to minimise the influence of digestive processes on MR. An individual animal was transferred in water (to avoid introducing air bubbles) to the respirometer at 20:00 h. After a 5 h acclimation period, which allowed $\dot{M}O_2$ to stabilise, measurements were taken every 20 min (*E. sinensis*) or 30 min (crayfish) within automated 50 min cycles (Section S2). Temperature- and pressure-compensated [DO] (mg O_2 L^{-1}), along with temperature (°C) and pressure (mmHg) separately, were logged every 20 s via YSI's Data Manager Software. At the same time, animals were recorded by webcam (Logitech Pro 9000 and Webcam XP 5 software). Eighteen cycles were completed for each animal: nine in the light and nine in the dark. *E. sinensis* were allocated a shorter measurement phase than crayfish because pilot studies suggested their $\dot{M}O_2$ was higher. The chosen measurement phase durations ensured oxygen pressures in the respirometer never dropped below 80% but R^2 values of fitted lines (see below) remained high (≥ 0.88) even when $\dot{M}O_2$ was low.

Due to equipment limitations, only one individual could be measured per day. MR was measured for eight *A. pallipes*, 12 *P. leniusculus* and 10 *E. sinensis*. The order in which individuals of each species were tested was randomised to remove any confounding temporal effects. To minimise microbial growth, respirometry equipment was scrubbed in a weak (0.5%) bleach solution and allowed to dry between uses.

Statistical methods

For each individual, [DO] measurements over time were split by eye into the longest possible linear sections. A least-squares regression line (with $R^2 \geq 0.88$) was fitted to each section in Microsoft Excel. Some short sections (≤ 3 min) with unstable [DO] readings, and thus poor regression fits, were omitted from analyses. $\dot{M}O_2$ for each section was calculated according to Eq. 5, suitable for closed-system respirometers (adapted from Cech and Brauner 2011):

$$\dot{M}O_2 = m \times (V_t - V_c) \times 3600 \tag{5}$$

where $\dot{M}O_2$ is oxygen consumption rate (mg O_2 h^{-1}), m is the gradient of the linear decline in oxygen concentration (mg O_2 L^{-1} s^{-1}), V_t is the total volume of the respirometer chamber (0.505 L) and V_c is the volume of each individual crayfish (determined by displacement immediately after $\dot{M}O_2$ measurement). $\dot{M}O_2$ was uncorrected for background respiration, as controls (respirometer with no decapod) indicated this was negligible.

Each individual's lowest recorded $\dot{M}O_2$ across all sections was taken as an estimate of its SMR. Where possible, webcam recordings were used to verify that this coincided with a period of minimal activity. Two *E. sinensis* were probably active during all measurements, so SMR was not recorded. Each individual's RMR was estimated as a weighted average of $\dot{M}O_2$ values across all sections, overall and separately for the light and dark phases (Eq. 6):

$$RMR = \left(\sum_{s=1}^{n}\left(\dot{M}O_{2(s)} \times t_s\right)\right)/\mathrm{T} \qquad (6)$$

where $\dot{M}O_{2(s)}$ is the oxygen consumption rate for section s, t_s is the duration of section s, and T is the total duration of all sections. Thus, RMR incorporates periods of activity as well as periods of rest.

MR and $\dot{M}O_2$ are strongly mass-dependent (Cech and Brauner 2011). In order to interpret consumption data from FR experiments, MRs were adjusted to the mean mass of animals used in FR trials using Eq. 7 (adapted from Cech and Brauner 2011).

$$MR_{(massFR)} = MR \times (massFR/massMR)^b \qquad (7)$$

where *massFR* is the mean mass (g) of each species across all FR trials (*A. pallipes* 10.4 g, *P. leniusculus* 10.1 g, *E. sinensis* 12.0 g), *massMR* is the mass (g) of an individual animal used in metabolism experiments, and *b* is a scaling exponent for MR against mass. In the absence of a complete set of species- and rate-specific values for *b*, all adjustments were made using *b*=0.71 based on the field MR of *Orconectes rusticus* crayfish (McFeeters et al. 2011).

Mass-adjusted MRs (Eq. 7) were compared between species using ANOVA and post hoc Tukey contrasts with Holm-Bonferroni correction of *p* values (*multcomp::glht*). We initially built full models containing species and sex and their interaction, but these were simplified by stepwise deletion of terms to contain species only (Crawley 2007). Within species, mass-adjusted diurnal and nocturnal MRs were compared using paired *t* tests.

Results

Functional responses

Prey survivorship in the presence of decapods was significantly lower than survivorship in control treatments (*D. villosus* 75.9% vs. 97.1%, chironomids 37.5% vs. 94.5%, *B. tentaculata* 83.6% vs. 97.4%; χ^2 tests for these overall proportions and for each decapod species separately all $p < 0.001$). Thus, we infer that the decapods were acting as predators (not just scavenging dead prey) in the experimental arenas. Predation was also directly observed in separate tanks.

Using prey consumption as the response variable, FRs for all predator x prey species combinations were best described by a Type II curve. In most logistic regressions of proportional consumption against prey density, the first order term was significantly negative (Table S3.1). In two regressions, where the first order term was negative but not significantly different from zero (*E. sinensis* consuming chironomid larvae $p=0.169$ and *A. pallipes* consuming *B. tentaculata* $p=0.050$), AIC values were lower for Type II than Type I fits.

Across all prey items, *E. sinensis* had a significantly greater attack coefficient than both crayfish species (*z* tests, $p \leq 0.012$ for all comparisons): at least 2.2 times that of *A. pallipes* on all prey types, and between 1.2 (on chironomids) and 4.1 (on *B. tentaculata*) times that of *P. leniusculus* (Table 2). In addition, the attack coefficient of *P. leniusculus* was at least 1.7 times greater than that of *A. pallipes* on all prey items, and always significantly greater (*z* tests, $p \leq 0.007$ for all comparisons). Higher attack coefficients are manifested as steeper initial rises in FR curves (i.e. greater predation rates at low prey densities; Fig. 1).

Eriocheir sinensis had a high maximum feeding rate (1/*h*T) on all prey items, by virtue of its short handling time (Table 2). The maximum feeding rate of *E. sinensis* was significantly higher than the maximum feeding rate of both crayfish species when *D. villosus* or chironomid larvae were prey (*z* tests, $p < 0.001$ for all comparisons; Table S3.2): at least 2.9 times higher on *D. villosus* (72 vs. 24−25 amphipods.day^{-1}) and at least 1.9 times higher on chironomid larvae (647 vs. 303−346 chironomids.day^{-1}). With *B. tentaculata* as prey, *E. sinensis* had a higher feeding rate than *A.*

Table 2 Estimates of functional response (FR) parameters for decapod predators consuming each of three macroinvertebrate prey species, extracted from Rogers' random predator equation fitted to data in the *frair* package (Pritchard et al. 2017)

Prey	Decapod	*a*	SE	Diff.	*h*	SE	1/*h*T	Diff.
Amphipod	*A. pallipes*	0.721	0.082	a	4.177×10^{-2}	2.560×10^{-3}	23.9	a
	P. leniusculus	1.905	0.195	b	4.078×10^{-2}	1.733×10^{-3}	24.5	a
	E. sinensis	2.529	0.154	c	1.394×10^{-2}	4.145×10^{-4}	71.7	b
Chironomid	*A. pallipes*	2.444	0.088	A	3.298×10^{-3}	6.332×10^{-5}	303.2	A
	P. leniusculus	4.382	0.130	B	2.888×10^{-3}	3.610×10^{-5}	346.3	B
	E. sinensis	5.456	< 0.001	C	1.546×10^{-3}	1.284×10^{-5}	647.0	C
Gastropod	*A. pallipes*	0.298	0.043	α	5.669×10^{-2}	7.208×10^{-3}	17.6	α
	P. leniusculus	0.494	0.058	β	4.515×10^{-2}	4.203×10^{-3}	22.1	α
	E. sinensis	2.006	0.227	γ	4.528×10^{-2}	2.567×10^{-3}	22.1	α

a attack coefficient (tanks.day^{-1}), *h* handling time (days.prey item^{-1}), 1/*h*T maximum feeding rate (prey.day^{-1}) where T=time in days, SE standard error. Within each prey item and for each parameter, different letters in the *Diff.* column indicate significantly different parameters (based on indicator variable comparisons, and after Holm-Bonferroni correction for multiple comparisons)

pallipes, but not significantly so (22 vs. 18 snails.day^{-1}, $z=1.49$, $p=0.136$) and a similar feeding rate to *P. leniusculus* (22 snails.day^{-1}, $z=-0.02$, $p=0.984$). Considering the two crayfish species, *P. leniusculus* had a higher maximum feeding rate than *A. pallipes* on all prey items (1.03 times higher on *D. villosus*, 1.1 times higher on chironomid larvae and 1.3 times higher on *B. tentaculata*; Table 2), but only significantly so on chironomid larvae ($z=6.39$, $p < 0.001$; Table S3.2).

Switching

Prey survivorship in controls, containing 140 of each prey animal, was high (*D. villosus* 96.8% and *B. tentaculata* 99.7%). Thus, as for FR experiments, we infer that the decapods were acting as predators (not just scavenging dead prey) in the experimental arenas.

In the switching experiments, *E. sinensis* consumed significantly more prey in total (across all relative densities mean ± SE individuals consumed=50.3 ± 3.2) than *P. leniusculus* (18.1 ± 1.7) and *A. pallipes* (18.6 ± 1.1) (Tukey adjusted $p < 0.001$ for both). The crayfish species did not differ in the total number of prey consumed (Tukey adjusted $p=0.883$).

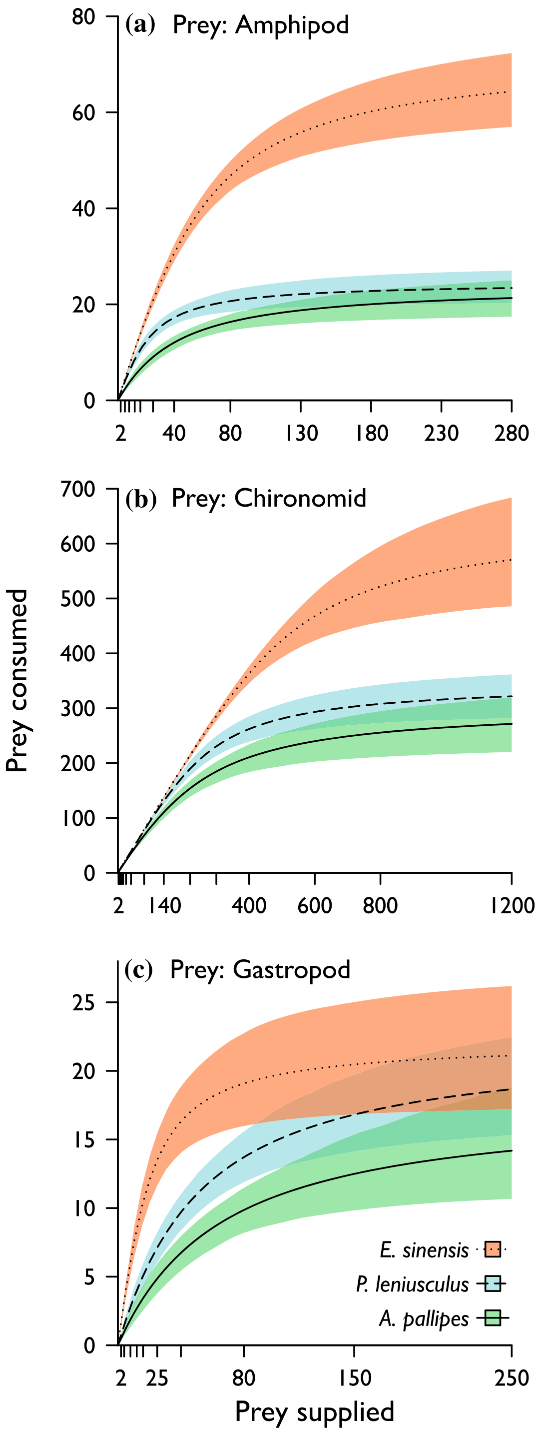
All decapods showed strong electivity towards *D. villosus* when both prey types were equally common: *D. villosus* formed a significantly greater proportion of the diet than would be expected under random feeding (*A. pallipes* $c=96.0$; *P. leniusculus* $c=26.3$; *E. sinensis* $c=16.1$; binomial tests of proportion of *D. villosus* in diet=0.5, $p < 0.001$ for all three predator species). As electivity≠1, the null hypothesis for switching (Eq. 4) yields a non-linear curve on a plot of proportional consumption against availability of *D. villosus* (Fig. 2). The observed proportion of *D. villosus* in the diet did not differ from null expectations for either crayfish species at any prey density (Fig. 2). For *E. sinensis*, the observed proportion of *D. villosus* in the diet only differed from null expectations at one relative prey density (0.35; Fisher's exact test $p=0.016$).

Metabolic rates

Here we present analyses using MRs adjusted to the mass of animals used in FR experiments (Eq. 7). These are therefore MRs of decapods with a similar body size, but not a similar mass. For comparisons of MRs scaled to a common mass, see Section S8.

Mean ± SE SMRs were *A. pallipes* 0.31 ± 0.04 mg O_2 h^{-1}, *P. leniusculus* 0.30 ± 0.02 mg O_2 h^{-1}, *E. sinensis* 0.34 ± 0.03 mg O_2 h^{-1}. There was no difference in these SMRs between the three decapod species (Fig. 3a; ANOVA $F_{2,25}=0.68$, $p=0.515$).

In contrast to SMR, RMR (calculated across both day and night) did differ between species (ANOVA $F_{2,27}=15.61$, $p < 0.001$). Mean ± SE RMRs were *A. pallipes* 0.50 ± 0.06 mg O_2 h^{-1}, *P. leniusculus* 0.75 ± 0.08 mg O_2 h^{-1}, *E. sinensis* 1.25 ± 0.13 mg O_2 h^{-1}. The RMR of *E. sinensis* was signifcantly greater than



◀**Fig. 1** Functional response curves of size-matched *A. pallipes* (green areas, solid lines), *P. leniusculus* (blue areas, dashed lines) and *E. sinensis* (orange areas, dotted lines) on (**a**) *D. villosus*; n=6 per density (**b**) chironomid larvae; n=6 per density (**c**) *B. tentaculata*; n=5 per density. Curves were modelled in *frair* using Rogers' random predator equation. Shaded areas show 95% bootstrapped BCa confidence intervals for each curve

that of *P. leniusculus* (1.7 times higher; Tukey adjusted p=0.004), which in turn had a significantly greater RMR than *A. pallipes* (1.5 times higher; Tukey adjusted p=0.015).

RMRs of the alien species were significantly higher at night than during the day (*E. sinensis* paired t=3.09, df=9, p=0.013; *P. leniusculus* t=4.83, df=11, $p<0.001$), whilst the RMR of *A. pallipes* was marginally lower at night than during the day (t=−2.02, df=7, p=0.083). Consequently, during the day RMR did not differ between the crayfish (Fig. 3b; Tukey adjusted p=0.61) but *E. sinensis* had a higher RMR than both crayfish species (Tukey adjusted $ps \leq 0.002$; overall ANOVA $F_{2,27}$=11.74, $p<0.001$). At night, RMR differed between all species pairs (Fig. 3c; Tukey adjusted $ps \leq 0.037$; overall ANOVA $F_{2,27}$=21.53, $p<0.001$).

Discussion

This paper combines experimentally determined FRs, switching behaviour and MRs to understand the predatory impacts of freshwater decapod crustaceans. We provide quantitative data on the relative impact of important invasive alien species and a native non-invasive analogue. Our data highlight the potential for strong, previously underappreciated predatory impacts by *E. sinensis*. Our data suggest differences in activity levels (reflected in RMR) could provide a mechanistic explanation for differences in predatory consumption and impacts of alien species.

Our FR experiments, supported by total consumption in our switching experiments, indicate that *E. sinensis* is a more voracious predator than both native and alien crayfish. Rosewarne et al. (2016) reported that *E. sinensis* had a higher FR than *P. leniusculus* and *A. pallipes*. However, we demonstrate that relative impact of *E. sinensis* may be much greater than previously thought, with an attack coefficient up to 6.7 times, and maximum feeding rate up to 3.0 times, that of a similarly sized crayfish (Table 2). Our data also suggest the relatively high impact of *E. sinensis* is conserved across prey types. This is clearly

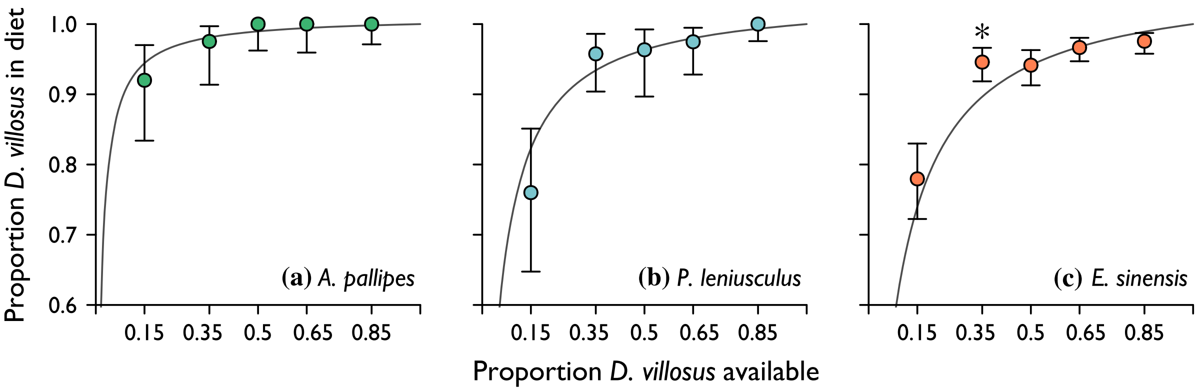


Fig. 2 Proportion of *D. villosus* in the diet of size-matched decapod predators at varying relative densities of *D. villosus* to *B. tentaculata*. At all relative densities, total prey density was fixed at 280 tank^{-1}. Note that the y axes begin at 0.6. Points are population proportions with 95% binomial confidence intervals. Curves are expected proportions in the absence of preference, based on consumption when prey types are equally available. Asterisk indicates significant deviation from null hypothesis (Fisher's exact tests on numbers of prey consumed, without correction for multiple testing)

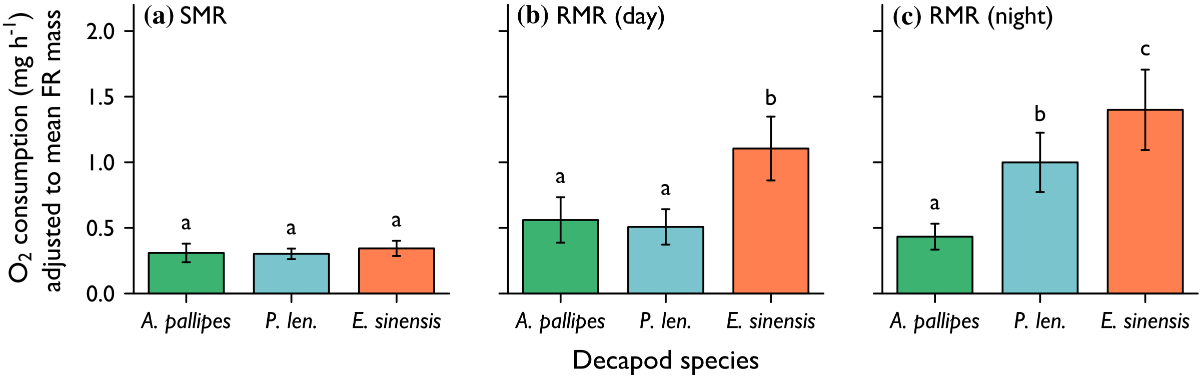


Fig. 3 Mass-adjusted (to mean mass of animals used in FR experiments) oxygen consumption rates of decapod crustaceans, as proxies for metabolic rates. **a** Standard metabolic rate (SMR): the lowest recorded $\dot{M}O_2$ associated with minimal activity **b** diurnal routine metabolic rate (RMR): a weighted average of all $\dot{M}O_2$ measurements during the light phase and **c** nocturnal RMR: a weighted average of all $\dot{M}O_2$ measurements during the dark phase. Letters indicate significant differences (within panels) based on Tukey contrasts with Holm-Bonferroni correction of *p* values. Bars show means ± 2 SE. *P. len.*—*Pacifastacus leniusculus*

true for amphipods and chironomids. There was a similar trend for gastropods, although maximum feeding rate on these thick-shelled, operculate snails was limited somewhat by the time taken to extract and ingest the flesh (pers. obs.; Mills et al. 2016). In the field, strong predation pressure from *E. sinensis* whether prey are abundant (small *h*) or rare (large *a*) could lead to prey population decline or extinction. Interestingly, when prey species are themselves alien, predation by *E. sinensis* could provide biotic resistance to subsequent invasions (Twardochleb et al. 2012).

Considering the crayfish species, our FR data suggest per capita predation by alien *P. leniusculus* consistently exceeds that of *A. pallipes* on a range of prey types. *Pacifastacus leniusculus* had a significantly higher attack coefficient than *A. pallipes* on all prey items, reflecting a steeper initial rise of the FR curve—even with the constraints on the curves at low densities imposed by our non-replacement design (Dick et al. 2014). Thus, our data suggest *P. leniusculus* is a more effective predator when prey are rare, and will exert high predation pressure when prey populations are most vulnerable to additional mortality (Murdoch and Oaten 1975). Alien *P.*

leniusculus also had a higher maximum feeding rate than *A. pallipes* on all prey items, in accord with previous studies using *G. pulex* as prey (Haddaway et al. 2012; Rosewarne et al. 2016) and the general pattern emerging from FR studies in invasion ecology (Dick et al. 2017). However, this difference was only significant on chironomid prey, and differences were generally small in magnitude (up to 1.3 times higher in *P. leniusculus*) relative to the differences observed between *E. sinensis* and the two crayfish species.

Differences in FRs on each prey species also match previous observations of predatory impact. For example, *E. sinensis* had an especially high maximum feeding rate on amphipods: at least 2.9 times greater than the crayfish. Accordingly, in mesocosm experiments amphipods were the only prey group that *E. sinensis* affected more strongly than *P. leniusculus* (Rosewarne et al. 2016). Amphipods and other motile taxa may be amongst the least affected by crayfish in the field (Crawford et al. 2006; Mathers et al. 2016), so we would expect their FRs to be low. *Eriocheir sinensis* also had a relatively high feeding rate on chironomid larvae: at least 1.9 times greater than the crayfish. In field or mesocosm studies, chironomids have been found to be strongly affected by *E. sinensis* (Yu and Jiang 2005; Rudnick and Resh 2005; Czerniejewski et al. 2010) but are amongst the macroinvertebrate taxa least affected by crayfish predation (Nyström et al. 1996; Twardochleb et al. 2013; but see Crawford et al. 2006). Meanwhile, the decapod species had more similar maximum feeding rates on gastropod prey (Table 2). This agrees with field or mesocosm observations that gastropods are amongst the macroinvertebrates least affected by *E. sinensis* predation (Yu and Jiang 2005) and most affected by crayfish predation (Lodge et al. 1994; Twardochleb et al. 2013), and that the decapods may have similar overall impacts on gastropod populations (Rosewarne et al. 2016). The FR of *E. sinensis* on gastropods may be low compared to its FR on amphipods or chironomids whilst the FR of the crayfish may be relatively high, bringing the crab and crayfish FRs closer together for gastropods than for other prey types.

Through its effects on both predator and prey behaviour, structural habitat complexity can modify the shape of FRs. In particular, it often reduces predation rates at low prey densities—by disrupting predator movement, providing a physical refuge for prey or facilitating camouflage—to generate a Type III FR (Alexander et al. 2012; Barrios-O'Neill et al. 2015). However, there was no evidence of this effect in our experiments. FRs were Type II, as in previous experiments of decapod predation in simple habitats (Haddaway et al. 2012; Rosewarne et al. 2016). The structural complexity we provided may have had no effect on predator or prey behaviour (e.g. the decapods were large enough to walk over the beads, and could reach through gaps with their legs or pereopods) or may have even facilitated predation at low prey densities (e.g. by restricting prey movement).

Our data support the use of FRs as a simple, cost-effective tool for rapid assessment of invader impacts, as explained by Dick et al. (2014) and supported by the analysis of Dick et al. (2017) in which high impact alien species had higher FRs than native analogues in 18 of 22 studied consumer-resource pairs. At one level, our data support the use of comparative FRs on a single prey type to rapidly score impact potential, because similar conclusions regarding relative FR shape and height were drawn for all of our prey types. At another level, because the details of our FRs were sensitive to prey type in accord with observations in more natural situations, our data support the use of FRs to make specific predictions about magnitude of impact on different prey groups (Dick et al. 2013; Dodd et al. 2014). However, further field data would be useful to verify this relationship.

Although simple FRs (based on individual, size-matched predators feeding on single prey types) are a robust starting point for predicting alien species' impacts, several additional factors could modulate the field impacts of our focal decapods—generally or in specific contexts. First, interspecific differences in both body size and abundance could augment the per capita effect of *E. sinensis* and *P. leniusculus* relative to *A. pallipes* (Parker et al. 1999; Pintor et al. 2009). The alien decapods grow to larger sizes than *A. pallipes* (Souty-Grosset et al. 2006; Dittel and Epifanio 2009). Larger animals generally eat more, owing to positive relationships between body size and traits such as metabolic rate, reaction distance and exploratory speed (Brown et al. 2004; Rall et al. 2012; Hirt et al. 2017). Second, aquatic alien species reach higher densities than natives on average (Hansen et al. 2013), and this is probably the case for *E. sinensis* and *P. leniusculus* relative to *A. pallipes* (Guan 2000; Demers et al. 2003; Rudnick et al. 2003). The impact of a population of predators generally increases with abundance (Parker et al. 1999), although the effect may be less than additive if mutual interference reduces the per capita impact of individual predators (Pintor et al. 2009; Médoc et al. 2013). Third, predatory impacts might be affected by the consumption of non-animal food sources (Médoc et al. 2018). All of our studied decapods are opportunistic omnivores, consuming leaf litter and other detritus even when animal prey are present (Bondar et al. 2005; Rudnick and Resh 2005; Haddaway et al. 2012; Rosewarne et al. 2016), although the precise balance between predation, herbivory and detritivory may be context-dependent (Larson et al. 2017). Future work should quantify how predatory FRs are affected by these factors—and others such as temperature, structural complexity, higher predators and parasites—that were beyond the scope of the present study.

Data on predator switching could complement single-species FRs to improve impact predictions. Switching—changing electivity towards prey types as their relative densities change—was not definitively observed in any of our decapod predator species. The proportion of *D. villosus* and *B. tentaculata* in crayfish diets always matched null expectations, assuming no switching. This implies that in the field, predation pressure on a single prey type could be maintained even when it becomes rare, potentially leading to local prey extinction (Murdoch and Oaten 1975): switching will not temper impacts on any single prey species. *Eriocheir sinensis* may exert particularly strong predation pressure on rare prey since it showed a tendency towards negative prey switching i.e. higher than expected proportional consumption of *D. villosus* when it is the less abundant prey (see also Section S7: smaller crabs with longer gastropod handling times showed the tendency even more clearly). Negative switching could help to explain the large impacts of *E. sinensis* on mesocosm populations of amphipods (Rosewarne et al. 2016). However, we encourage further investigation of switching with prey items that are more similar in defence strategies and handling time, thus eliciting weaker predator electivity. Switching may be more likely in such situations (Murdoch and Oaten 1975).

Our data indicate that that MRs could provide a mechanistic explanation for the observed differences in feeding rates and, by extension, differences in impacts of alien species on prey populations. There were large interspecific differences in the RMR of similarly sized decapods: *E. sinensis* had a greater RMR than the crayfish species, and *P. leniusculus* had a greater RMR than *A. pallipes* (driven by greater nocturnal activity). These results also held when MRs were adjusted to a common mass (Section S8). Together, our RMR and FR data indicate positive associations between the supporting traits of activity, RMR and feeding rate across species. An active species with a high RMR both needs to feed at a higher rate and is able to feed at a higher rate: it needs to fuel the high rate of energy processing, but is able to do so because it has more energy available for movement (which could increase encounter rates and attack coefficients; Dell et al. 2014; Hirt et al. 2017) and more energy available for physiological processes such as digestion (which could reduce handling times; Millidine et al. 2009). Accordingly, observed interspecific differences in RMR match the rank order of differences in feeding rate (cf. Careau et al. 2008; Rall et al. 2012), whilst webcam recordings suggest that the differences in RMR were related to activity in the respirometer. The higher RMR of *E. sinensis* and *P. leniusculus* at night is also consistent with their known nocturnal activity (Styrishave et al. 2007; Gilbey et al. 2008), and may be associated with higher predatory impacts on nocturnal than diurnal prey. We acknowledge confinement in a respirometer may have influenced activity levels and hence RMR (Careau et al. 2008; Toscano and Monaco 2015), so encourage further investigation of activity in more natural scenarios.

In contrast to RMR, SMR did not significantly differ between size-matched decapods (again, this was also true for mass-matched decapods; Section S8). Furthermore, differences in SMR were small in magnitude (*E. sinensis* SMR only around 1.1 times that of the crayfish) relative to differences in maximum feeding rate (at least 1.9 times on amphipods and chironomids). Thus SMR and RMR are apparently unrelated across the decapod species, suggesting the core metabolic engine (providing the energy for vital bodily functions and tissue maintenance) runs at a similar rate in all the species and supporting our inference that high feeding rates were associated with activity and metabolism *above and beyond* SMR. In other words, the maximum rate of energy processing is independent of the size of core metabolic engine (independent model of Careau and Garland 2012). Note the implication for explaining species' impacts or interactions using MR: rates that include activity, such as field or RMRs, should be more closely related to real-world impacts than basal or SMRs (e.g. Lohr et al. 2017).

As well as being related to impact, FRs and MRs might be related to invasion success (Lagos et al. 2017), although less strongly and in variable directions. High resource consumption rates, sometimes measured explicitly as FRs, are associated with success of alien species at various stages of the invasion process (Catford et al. 2009; Xu et al. 2016; McKnight et al. 2017). High MRs might be linked to fast life history traits that can confer invasion success e.g. high activity levels, faster growth and greater reproductive rates (Lindqvist and Huner 1999; Sakai et al. 2001; Ricklefs and Wikelski 2002; McKnight et al. 2017). However, species with a fast life history, linked to high MRs and/or FRs, could struggle to invade marginal environments where resources are not abundant. Invasions might be transient if a species' high energetic requirement reduces its ability to tolerate stressful periods (Alpert 2006). Perhaps the high FR and MR of *E. sinensis* contributes to its observed boom and bust population dynamics (Rudnick et al. 2003)?

Quantitative evidence of alien species' impacts is an important factor for making decisions about their management (Kumschick et al. 2012). Our data provide novel evidence for two important invasive alien decapods in Europe. *Eriocheir sinensis* and *P. leniusculus* had consistently high predatory impacts on a range of macroinvertebrate prey relative to the impact of *A. pallipes*, associated with differences in RMR. The difference in per capita effect between the crayfish species was relatively small, although *P. leniusculus* could have a stronger impact in the field owing to its greater abundance and/or body size. Meanwhile, the per capita effect of *E. sinensis* was exceptionally high on soft-bodied prey and it showed some evidence of negative switching onto soft-bodied prey, highlighting predation as an underappreciated mechanism by which *E. sinensis* could cause large impacts. Data from more natural settings are desirable, but our laboratory data support the use of FRs, and potentially RMRs, as part of a toolbox to predict and understand alien species' impacts.

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Author Contributions NGT and AMD conceived and designed the experiments. NGT performed the experiments, analysed the data and wrote the manuscript. NGT and AMD edited the manuscript.

Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethics statement All applicable institutional and/or national guidelines for the care and use of animals were followed.

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