Predicting the ecological impacts of a new freshwater invader: functional responses and prey selectivity of the 'killer shrimp', *Dikerogammarus villosus*, compared to the native *Gammarus pulex*

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SUMMARY

1. The ability to predict the likely ecological impacts of invasive species in fresh waters is a pressing research requirement. Whilst comparisons of species traits and considerations of invasion history have some efficacy in this respect, we require robust methods that can compare the effects of native and invasive species. Here, we utilise comparative functional responses and prey selectivity experiments to understand and predict the ecological impact of an invader as compared to a native.
2. We compared the predatory functional responses of an emerging invasive species in Europe, the 'killer shrimp', *Dikerogammarus villosus*, and an analogous native species, *Gammarus pulex*, towards three representative prey species: *Asellus aquaticus*, *Daphnia magna* and *Chironomus* sp. Furthermore, as ecological impact may be greater for invasive species with more indiscriminate feeding habits, we compared the selectivity for the three prey types between the invasive and native species.
3. In both the presence and absence of experimental habitats, large *D. villosus*, and those matched for body size with *G. pulex*, generally showed higher (Type II) functional responses than *G. pulex*, with the invasive species exhibiting higher maximum feeding rates. Further, *D. villosus* exhibited significantly more indiscriminate prey selection compared with *G. pulex*, a trait that became more evident as the invader increased in size. Differences in functional responses and prey selectivity were prey species specific, with higher to lower predicted impacts in the order *A. aquaticus*, *D. magna* and *Chironomus* sp. This is in accord with the impact of this invasive species on macroinvertebrates in the field.
4. We thus provide understanding of the known ecological impact of *D. villosus* and discuss the utility of the phenomenological use of comparative functional responses and resource use as a tool through which the potential ecological impacts of invasive species may be identified.

Keywords: community ecology, functional response, invasion, macroinvertebrate, predation

Introduction

The ability to predict the ecological consequences of species introductions is becoming increasingly important as biological invasions continue to be one of the main drivers of global biodiversity loss (Sala *et al.*, 2000; Ricciardi, 2007; Davis, 2009; Leung *et al.*, 2012; Strayer, 2012; Simberloff *et al.*, 2013). The effects of invasions include the local extinction of native species (e.g. Donlan & Wilcox, 2008), shifts in ecosystem function (e.g. Vander

Zanden, Casselman & Rasmussen, 1999; Strayer, 2012) and facilitation of other non-native species (Simberloff & von Holle, 1999; Bruno, Stachowicz & Bertness, 2003). The economic costs of invasions are also significant (Born, Rauschmayer & Brauer, 2005), with estimates from the U.S.A. and Europe attributing $120 billion and €12 billion per annum, respectively (Pimentel, Zuniga & Morrison, 2005; Kettunen *et al.*, 2008), and within the U.K., £26 million per annum has been attributed to the control of freshwater invasive species alone (Oreska & Aldridge, 2011). While research has provided some insight into predicting which species are likely to become established outwith their native range (e.g. Gallardo, Paz Errea & Aldridge, 2012), as well as an understanding of which traits might promote invasibility (e.g. Williamson & Fitter, 1996; Kolar & Lodge, 2001; van Kleunen *et al.*, 2010; Keller, Kocev & Dzeroski, 2011; Kulhanek, Ricciardi & Leung, 2011), the prediction of subsequent ecological impacts has remained more elusive (e.g. Ricciardi & Rasmussen, 1998; Parker *et al.*, 1999; Byers *et al.*, 2002; Strayer *et al.*, 2006; Kulhanek *et al.*, 2011; Strayer, 2012; Dick *et al.*, 2013a,b). Furthermore, predicting the ecological impacts of new and emerging invaders that have incomplete or indeed no invasion history is particularly challenging (Dick *et al.*, 2013b).

The ability of a novel species to become established within a community may depend on its relative foraging capabilities to pioneer previously un-utilised resources and/or its ability to use resources more efficiently and perhaps compete with resident species for available resources (MacArthur & Levins, 1967; Tilman, 1980). As resource use by invasive species may be much greater as compared to co-evolved resource use relationships of native species (e.g. predator/prey dynamics), the impact of invaders may be assessed by examining such differences (Dick *et al.*, 2013b). Therefore, a potential approach for assessing the ecological impacts of an invading species on a community is the comparison of its rate of resource uptake with that of a trophically analogous native species (Bollache *et al.*, 2008; Dick, Alexander & MacNeil, 2012; Dick *et al.*, 2013a,b). Such predatory capacity, and more generally the use of resources by consumers (see Dick *et al.*, 2013a), can be quantified by measuring the 'functional response' (Solomon, 1949; Abrams, 1990), the relationship between resource consumption rate (e.g. predation rate) and resource density (e.g. prey availability; Holling, 1966; Juliano, 2001). A Type I functional response describes a consumption rate that increases linearly with prey density and is associated with animals utilising a filter feeding mechanism (Jeschke, Kopp & Tollrian, 2004). A Type II functional response describes a consumption rate that increases with prey density and then gradually decelerates to an asymptote as handling time becomes a limiting factor (Holling, 1966). With Type III responses, prey experience a refuge from predation through, for example, the consumer switching to more abundant prey (Holling, 1966), or through refugia provided as a result of habitat complexity (Alexander *et al.*, 2012). Measurements of functional responses have been suggested as a mechanism through which species with the potential to become damaging invaders could be identified (e.g. Bollache *et al.*, 2008; Dick *et al.*, 2010, 2013a,b), as the type of functional response (Type II or III) has potential implications for resource (such as prey) population stability, as Type III functional responses are likely to be more stabilising towards prey populations, whereas Type II responses can be destabilising and lead to local extinctions of prey over certain ranges of density (Murdoch & Oaten, 1975; Juliano, 2001).

The form of functional response is not always fixed for a particular pair of interacting species, and many factors such as sediment type (Grant, 1984), light levels (Koski & Johnson, 2002) and habitat complexity (Alexander *et al.*, 2012) can affect forging success and prey vulnerability and, hence, alter the response type. It is therefore important to establish the form of functional response under variations in key environmental variables. In addition to this, as predators may respond differently to different prey types, empirical measurements of functional responses should be investigated over a range of prey types that encapsulate variations in prey morphology and behaviour. Further, differences in prey selection by predators are known to alter the composition of a community (e.g. Hambright & Hall, 1992; Alto *et al.*, 2009), and differential predation by invasive species in particular has been shown to have dramatic effects on ecosystem function (Vander Zanden *et al.*, 1999). The role of prey selection in the process of invasion may therefore also be particularly important when assessing the potential impacts of an invasive species.

Invasive species impact throughout terrestrial and aquatic environments, but the enhanced innate dispersal capabilities associated with aquatic organisms makes freshwater environments particularly susceptible (Dudgeon *et al.*, 2006; Vörösmarty *et al.*, 2010) and, notably, crustaceans are a particularly successful group at expanding their freshwater ranges (Gherardi, 2007). *Dikerogammarus villosus*, a freshwater amphipod native to the Ponto-Caspian region of Eastern Europe, has

undergone a dramatic range expansion across Western Europe in the last 20 years (Pockl, 2009). Extensive alterations to the structure of communities invaded by *D. villosus* (e.g. Dick & Platvoet, 2000; Dick, Platvoet & Kelly, 2002; MacNeil *et al.*, 2013) have resulted in the inclusion of this species among the 100 worst invasive species in Europe (www.europe-aliens.org) and it is likely that *D. villosus* will invade the North American Great Lakes (Ricciardi & Rasmussen, 1998; Bollache *et al.*, 2008). In September 2010, *D. villosus* was reported in the U.K. (MacNeil *et al.*, 2010), being discovered in a reservoir in the south east of England, in two locations in Wales (South West, U.K.; Madgwick & Aldridge, 2011), and more recently from Barton Broad in East England (Dirk Platvoet, pers comm.). Predicting the likely ecological impacts of this species is thus a high priority to inform management actions.

In this study, we utilised recent advances in the demonstrated predictive power of comparative functional responses (see Dick *et al.*, 2013a,b), to forecast the likely impacts of *D. villosus* on native freshwater species, and supplemented this with prey selection experiments. Specifically, we investigated the relative predatory capacity of the invader, *D. villosus*, and an analogous native species, *Gammarus pulex*, by examining the functional responses and prey selectivity towards three common and representative prey types found in freshwater systems: an isopod, *Asellus aquaticus*, a cladoceran, *Daphnia magna* and a dipteran larva, *Chironomus* sp. Our aims were to establish whether (i)

functional responses differ between the invasive and native amphipods (comparing the larger invader with the native; as well, considering body size-matched individuals of the two species); (ii) functional responses are of Type II or Type III, and if these are influenced by environmental heterogeneity in the form of the presence or absence substrate, and; (iii) differences in prey selection exist between the native and invader.

Methods

Experimental organisms

Between September and November 2011, in Cambridgeshire (U.K.), the invasive amphipod *Dikerogammarus villosus* was collected from Grafham Water (Lat: 52° 18′ 36 N; Long: 0° 19′06 W) and the native amphipod *Gammarus pulex* from Duloe Brook (Lat: 52° 13′60 N; Long: 0° 22′36W). Juveniles of the isopod *Asellus aquaticus* were collected from nearby Pitsford Water (Lat: 52° 19′10 N Long: 0° 53′35 W), and the cladoceran *Daphnia magna* and the chironomid *Chironomus* sp. were bought from a commercial supplier (Livefishfood, Surrey, U.K.). All animals were kept in aquaria with water, substrate and plant material from source locations at 14 °C in a 10:14 h light/dark regime for 4 days prior to use in experiments, after which the amphipod predators were killed in 80% ethanol. The length (rostrum to urosome) and constant dry weight of all amphipods were then measured using a microscope and callipers.
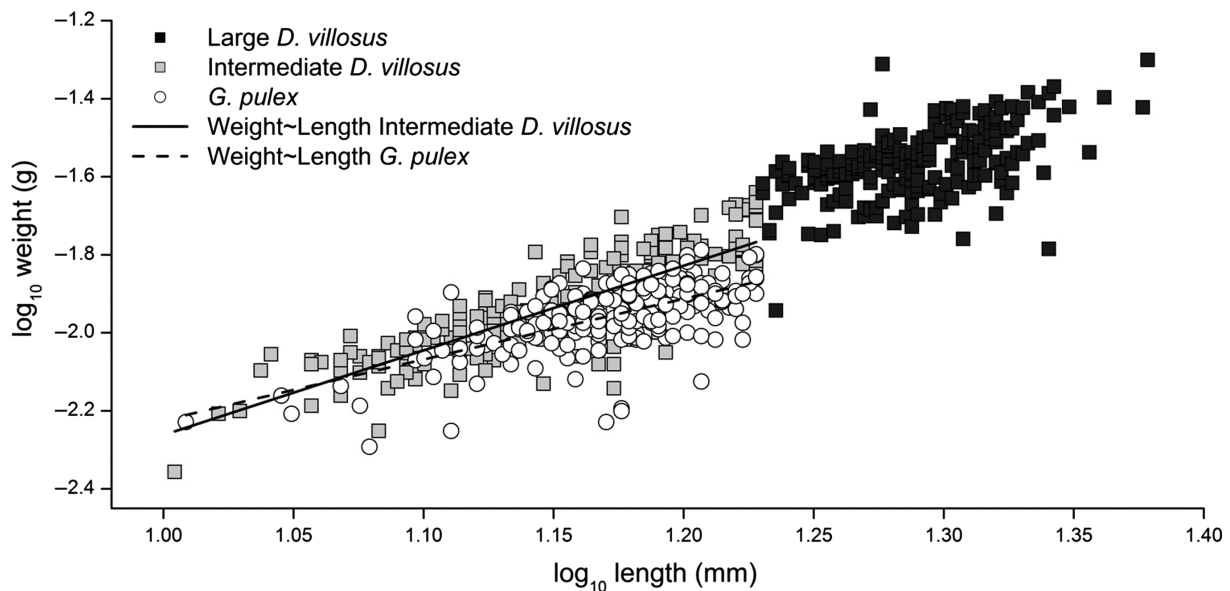

Fig. 1 Weight versus length relationships of the amphipod groups used in experiments.

Only amphipods free of obvious parasites were used in experiments (e.g. see Dick *et al.*, 2010). Amphipods were divided into three groups based on a visual assessment of body size; large *D. villosus*, intermediate *D. villosus* and large *G. pulex*. As intermediate *D. villosus* and large *G. pulex* are of comparable body length, this division allowed size matching of these two groups, thus removing body size as a confounding variable and allowing assessment of inherent species differences in predation rates. However, because *D. villosus* were generally heavier than *G. pulex* at equal body lengths (see Fig. 1), we used slightly shorter, heavier *D. villosus* and slightly longer, lighter *G. pulex*. One-factor ANOVA thus revealed significant differences in both length ($F_{2,693}$= 1267.6, $P < 0.001$) and weight ($F_{2,693}$=1037.4, $P < 0.001$) among the three species/size groups of amphipods, with 'large' *D. villosus* significantly longer (mean±SE, 19.4 mm ± 0.1) and heavier (28.7 mg ± 0.9) than 'intermediate' *D. villosus* (14.2 mm ± 0.1; 12.1 mg ± /0.2) and 'large' *G. pulex* (14.9 mm ± 0.1; 11.2 mg ± /0.1; Fig. 1, all $P < 0.001$). For intermediate-sized *D. villosus* and large *G. pulex*, further analysis by ANCOVA revealed a significant 'species × length' interaction effect ($F_{3,460}$=230.1, $P < 0.001$; Fig. 1), in line with our observation above. We thus used principal components analysis to reduce amphipod length and weight to an index of amphipod body size. The first principal component explained 84% of the variation in amphipod length and weight, providing a very good index of body size. A one-factor ANOVA of the extracted PC1 scores with respect to species revealed no significant difference in the body size of intermediate-sized *D. villosus* and large *G. pulex* used in the experiments ($F_{1,462}$=1.29, $P = 0.26$).

Single-prey experiments – predator functional responses

We presented individual male amphipods with a single-prey species of either *A. aquaticus* (mean ± SE 3.2 mm ± 0.1), *Daphnia magna* (3.3 mm ± 0.1) or *Chironomus* sp. (11.5 mm ± 0.2). *A. aquaticus* and *Chironomus* sp. were presented at nine densities (2, 4, 6, 8, 10, 16, 20, 30, 40 individuals; $n = 4$ per density), and *D. magna* at 11 densities (two additional densities of 70 and 140 individuals; $n = 4$), with or without substrate, in plastic experimental arenas (7.5 cm diameter) with 250 ml of water at 1 : 1 ratio from Grafham Water to Duloe Brook (amphipod source waters). 'With substrate' comprised a 10 mm length of plastic pond weed, anchored in 10 mm of sand (mean particle size 1 mm), on which lay one large stone (mean grain size = 40 mm) and two small stones (mean grain size = 20 mm). Replicates

were initiated at 17:00 h with the addition of an individual amphipod (starved for 24 h to standardise hunger) to the arena. Prey were already present in arenas, having been acclimatised for 3 h prior to the start of the trial. Replicates were terminated after 16 h (at 09:00) with the removal of the amphipod, which was then monitored for 24 h to assess survivorship and moulting. Amphipods that died or moulted before, during or within 24 h of the experiment were removed from analyses and the replicate rerun. We counted deaths due to predation as those prey either wholly or partially consumed or bitten to death (see Dick *et al.*, 2002). Control arenas were prey at each density with and without substrate ($n = 4$ for each combination) without amphipods present. Controls were run in parallel with predation groups.

Mixed prey experiments – predator selectivity

Individual male amphipods (starved for 24 h) were presented with equal proportions of *A. aquaticus*, *D. magna* and *Chironomus* sp. (prey sizes as before) at ten densities (1 of each prey type, 2 of each prey type, up to 10 of each prey type; $n = 4$ per density). Experimental arenas were as above, with and without substrate and containing 250 ml of mixed amphipod source water. As in the previous experiment, prey were added 3 h prior to the start of the trial at 17.00 h and replicates were terminated after 16 h (at 09:00) with the removal of the amphipod (which was then monitored for 24 h as before). Again, we counted deaths due to predation as those prey either wholly or partially consumed or bitten to death (see Dick *et al.*, 2002). Once again, controls were experimental arenas (with and without substrate) containing prey without predators present.

Statistical analyses

Single-prey experiments – predator functional response. Mean number of prey eaten was examined separately for *A. aquaticus*, *D. magna* and *Chironomus* sp. with respect to three factors [amphipod group (large *D. villosus*, intermediate *D. villosus* and large *G. pulex*), prey density (see above) and substrate type (with/without substrate)] in a general linear model with negative binomial error structure and Tukey *post hoc* tests.

There are numerous modelling approaches to assess functional responses, and model choice may depend on whether a particular study is mechanistic or phenomenological in approach (Jeschke, Kopp & Tollrian, 2002). Thus, the mechanistic application of parameters such as

attack rate and handling time must be approached with caution or be supported with empirical measurements of parameter estimates (Caldow & Furness, 2001; Jeschke *et al.*, 2002; Jeschke & Hohberg, 2008). Phenomenological use of these parameters does, however, provide a tool to examine differences in functional response types and parameter estimates in comparative or factorial experiments and this is the approach taken here (see also Alexander *et al.*, 2012; Dick *et al.*, 2013a). Thus, to determine whether the current predators displayed Type II as opposed to Type III functional responses, we used logistic regression to test for, in the case of Type II responses, a significant negative linear coefficient in the relationship between the proportion of prey eaten and prey density, and in the case of Type III responses, a significant positive first-order term followed by a significant negative second-order term (Trexler, McCulloch & Travis, 1988; Juliano, 2001). As we did not replace prey during the experiments, and consequently prey density declined as prey were consumed, for a Type II functional response, the 'random predator equation' (Rogers 1972) is appropriate (Juliano, 2001):

$$N_e = N_o(1 - \exp(a(N_e h - T))) \qquad 1$$

where N_e is the number of prey eaten, N_0 is the initial prey density, a is the attack constant, h is the handling time and T is the total time available. Estimated maximum feeding rate was estimated as $1/hT$. The Type II functional response was modelled using maximum likelihood estimation (Bolker, 2010). We did not find any Type III functional responses in the present study, but see Alexander *et al.* (2012) for their modelling.

Following the model fitting, bootstrapping was used to generate multiple estimates ($n = 30$) of the response parameter of maximum feeding rate ($1/hT$), which was then compared for each prey type separately with respect to amphipod group and substrate conditions (two-factor ANOVA and Tukey *post hoc* tests). When data were non-normal (Shapiro–Wilks test, $P < 0.05$) and heteroscedastic (Bartlett's test, $P < 0.05$), parameter estimates were ($x' = \log_{10}(x + 1)$) transformed.

Mixed prey experiments – predator selectivity. The proportion of each prey type eaten relative to the total number of prey items provided was calculated and then reduced to an index of prey selectivity using principal components analysis (PCA). We tested prey selection differences for all amphipod groups based on the first two extracted principal component scores with respect to amphipod group, prey density and substrate conditions (three-factor ANOVA and Tukey HSD *post hoc* tests).

The origin of the two PC axes represents the point in PC space where there is no prey selection (i.e. all prey types are eaten in equal proportion), thus increasing distance from the origin is representative of a move from an indiscriminate feeding strategy (i.e. no prey selection) to a selective feeding strategy (i.e. selection for specific prey type). Feeding strategy was measured as the distance from the origin to each point in PC space (i.e. the PC1, PC2 co-ordinate). We tested feeding strategy with respect to amphipod group, prey density and substrate conditions (three-factor ANOVA and Tukey HSD *post hoc* tests).

All statistical analyses were performed in R, version 2.13.1 (R Development Core Team, 2010).

Results

Single-prey experiments – predator functional responses

Prey survivorship in control arenas was high (*A. aquaticus*, 100% without substrate, 95.5% ± 0.02 SE with substrate; *D. magna*, 98.5% ± 0.01 SE without substrate, 98.7% ± 0.01 SE with substrate; *Chironomus* sp., 98.2% ± 0.01 SE without substrate, 99.1% ± 0.01 SE with substrate). The majority of deaths in experimental arenas were thus the result of amphipod predation. This was further evidenced through observations of direct predation by both predator species as well as the presence of partly consumed prey in experimental arenas following the removal of the amphipod.

Prey: Asellus aquaticus. The minimum model revealed a significant two-way interaction between amphipod species and *A. aquaticus* density (Table 1; Fig. 2a). This reflected the increased disparity between amphipod species in mean prey consumed at higher densities (Fig. 2a).

Table 1 Minimum models (AIC method) of the relationship between mean prey consumed and amphipod group, supplied prey density and substrate conditions. Amphipod = amphipod group (three levels), density = prey density (nine levels for *Asellus aquaticus* and *Chironomus* sp., and 11 levels for *Daphnia magna*), substrate = substrate conditions (two levels) and '*'denotes an interaction

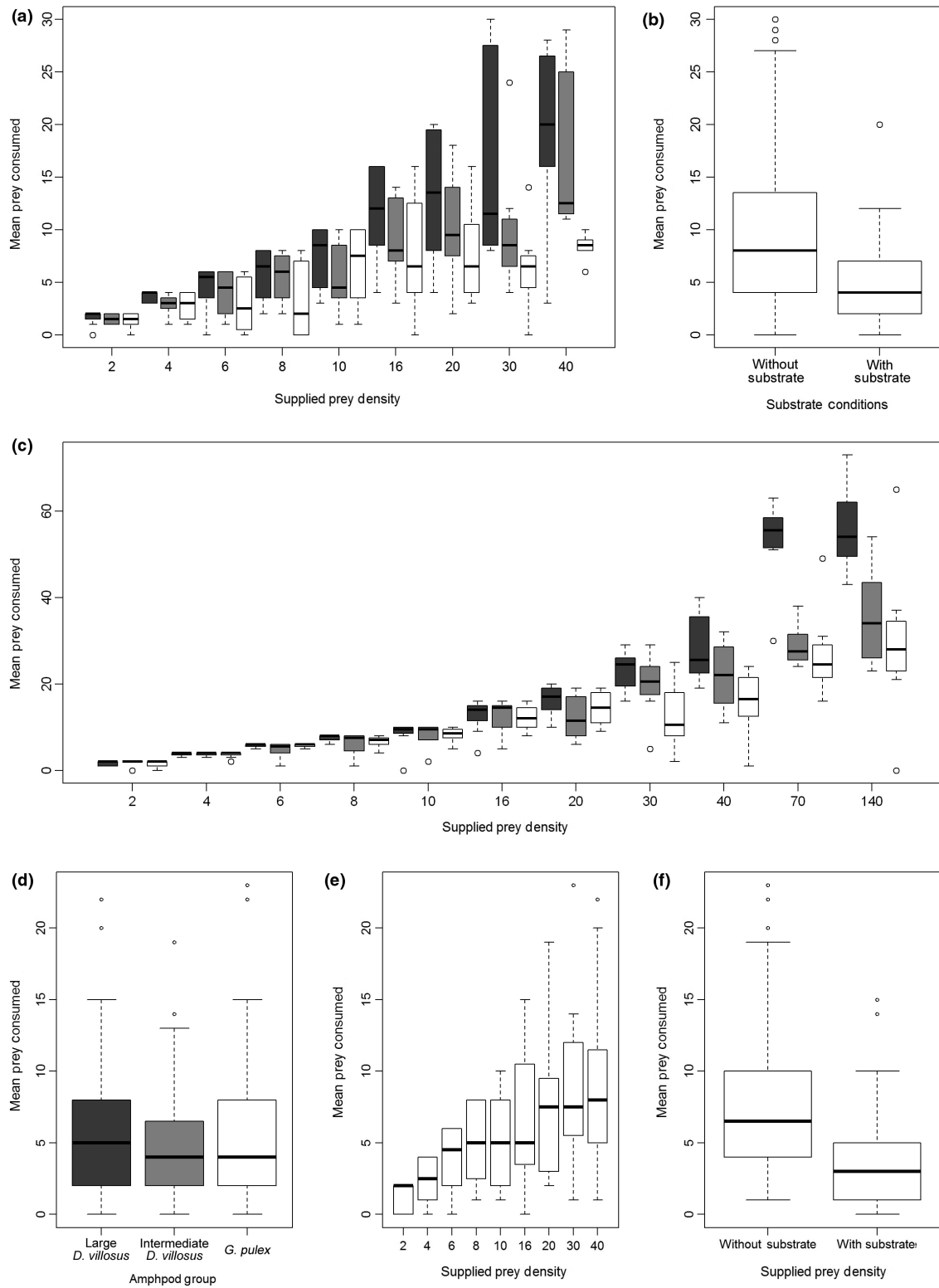| Prey	Factor	$X^2_{\text{Wald(d.f.)}}$	P
A. aquaticus	Amphipod * Density	7238.970 $_{(27,188)}$	0.040
	Substrate	190.788 $_{(1,188)}$	<0.001
D. magna	Amphipod * Density	17981 $_{(33,231)}$	0.011
Chironomus sp.	Amphipod	14.946 $_{(2,204)}$	0.060
	Density	1386.051 $_{(9,204)}$	<0.001
	Substrate	124.472 $_{(1,204)}$	<0.001

Fig. 2 Interaction and main effects of mean prey consumed and experimental conditions for the three amphipod groups (dark grey = large *Dikerogammarus villosus*, light grey = intermediate *D. villosus*, white = *Gammarus pulex*); (a) interaction between increasing prey density and amphipod group on mean *Asellus aquaticus* consumed, (b) mean *A. aquaticus* consumed under different substrate conditions, (c) interaction between increasing prey density and amphipod group on mean *Daphnia magna* consumed, (d) mean *Chironomus* sp. consumed by different amphipod groups, (e) mean *Chironomus* sp. consumed under different prey densities, (f) mean *Chironomus* sp. consumed under different substrate conditions.

Table 2 Linear coefficient from logistic regression analysis for large and intermediate *Dikerogammarus villosus* and large *Gammarus pulex* with substrate absent (−) and present (+) (all $P < 0.001$ unless specified)

Prey	Substrate	Lg. *D. villosus*	Int. *D. villosus*	*G. pulex*
A. aquaticus				
	−	−0.12	−0.05	−0.11
	+	−0.03	−0.02	*−0.01*
			($P = 0.002$)	($P = 0.422$)
D. magna				
	−	−0.02	−0.02	−0.02
	+	−0.02	−0.01	−0.02
Chironomus sp.				
	−	−0.09	−0.08	−0.07
	+	−0.02	−0.04	−0.02

At high densities (30 and 40), large *D. villosus* consumed significantly more *A. aquaticus* ($Z = 4.033$, $P = 0.014$; $Z = 3.754$, $P = 0.037$ respectively) compared with G. pulex, and intermediate *D. villosus* consumed more *A. aquaticus* at density 40 ($Z = 4.199$, $P < 0.01$). Significantly more *A. aquaticus* were consumed when substrate was absent as compared to present ($Z = 7.15$, $P < 0.001$; Table 1, Fig. 2b).

Logistic regression revealed significant negative estimates of the linear coefficient for all predator/*A. aquaticus* prey groups (except for *G. pulex* with substrate present; see Table 2); therefore, most amphipod groups exhibited Type II functional responses (Fig. 3a). Large *D. villosus* had a significantly greater maximum feeding rate compared with both intermediate *D. villosus* and *G. pulex* (between which there was no difference, Table 3, Fig. 4a). The significant 'amphipod group x substrate' interaction (Table 3, Fig. 4a) indicated higher feeding rates of *D. villosus* compared with *G. pulex* where no substrate was present, but the opposite when substrate was present (Fig. 4a).

Prey: Daphnia magna. The minimum model revealed a significant two-way interaction between amphipod species and *D. magna* density (Table 1; Fig. 2c). This reflected the increased disparity between amphipod species in mean prey consumed at higher densities (Fig. 2c). Significant differences in mean prey consumed between the native and invasive species as a result of body size differences became apparent at prey density of 30 ($Z = 3.804$, $P = 0.043$) and continued up to a prey density of 140 (40, $Z = 3.844$, $P = 0.037$; 70, $Z = 5.097$, $P < 0.001$; 140, $Z = 4.868$, $P < 0.001$). The presence of substrate did not significantly influence the mean number of *D. magna* consumed (Table 1).

Logistic regression revealed significant negative estimates of the linear coefficient (Table 2); therefore, all predator prey groups exhibited Type II functional responses (Fig. 3b). Both size groups of *D. villosus* had significantly greater maximum feeding rates than *G. pulex* and large *D. villosus* significantly greater than intermediate *D. villosus* (Table 3; Fig. 4b). There were no differences in maximum feeding rate in the presence or absence of substrate, and there was no significant 'amphipod group x substrate' interaction (Table 3).

Prey: Chironomus sp. The minimum model revealed no significant interactions between amphipod, prey density and substrate type. There was a strong trend for a significant difference in the mean number of *Chironomus* sp. consumed among amphipod groups (Table 1, Fig. 2d). Mean number of *Chironomus* sp. consumed was significantly greater at higher densities (Table 1, Fig. 2e) and significantly more *Chironomus* sp. were consumed in the absence of substrate compared with the presence of substrate (Table 1; Fig. 2f).

Logistic regression revealed significant negative estimates of the linear coefficient (Table 2); therefore, all predator/*Chironomus* sp. groups exhibited Type II functional responses (Fig. 3c). Maximum feeding rate of large *D. villosus* and *G. pulex* was significantly higher than intermediate *D. villosus,* and there was no significant difference between the maximum feeding rate of large *D. villosus* and *G. pulex* (Table 3; Fig. 4c). There were no differences in maximum feeding rate in the presence or absence of substrate, and there was no significant 'amphipod group x substrate' interaction (Table 3).

Mixed prey trials

Prey survivorship in control arenas was high (*A. aquaticus*, 99.4% ± 0.01 SE without substrate, 97.8% ± 0.01 SE with substrate; *D. magna*, 98.2% ± 0.01 SE without substrate, 98.7% ± 0.01 SE with substrate; *Chironomus* sp., 95.6% ± 0.03 SE without substrate, 99.2% ± 0.01 SE with substrate); thus, experimental deaths were the result of amphipod predation.

The first and second scores from the PCA of prey selectivity explained 59 and 39% of the variation, respectively, accounting for a total of 97% of the total variation in prey selectivity. PC1 was positively loaded (+0.739) for *D. magna* selection and negatively loaded for *Chironomus* sp. (−0.605) and *A. aquaticus* (−0.296); thus, a large positive PC1 score was indicative of predatory selection for *D. magna*, while a small PC1 score was indicative of
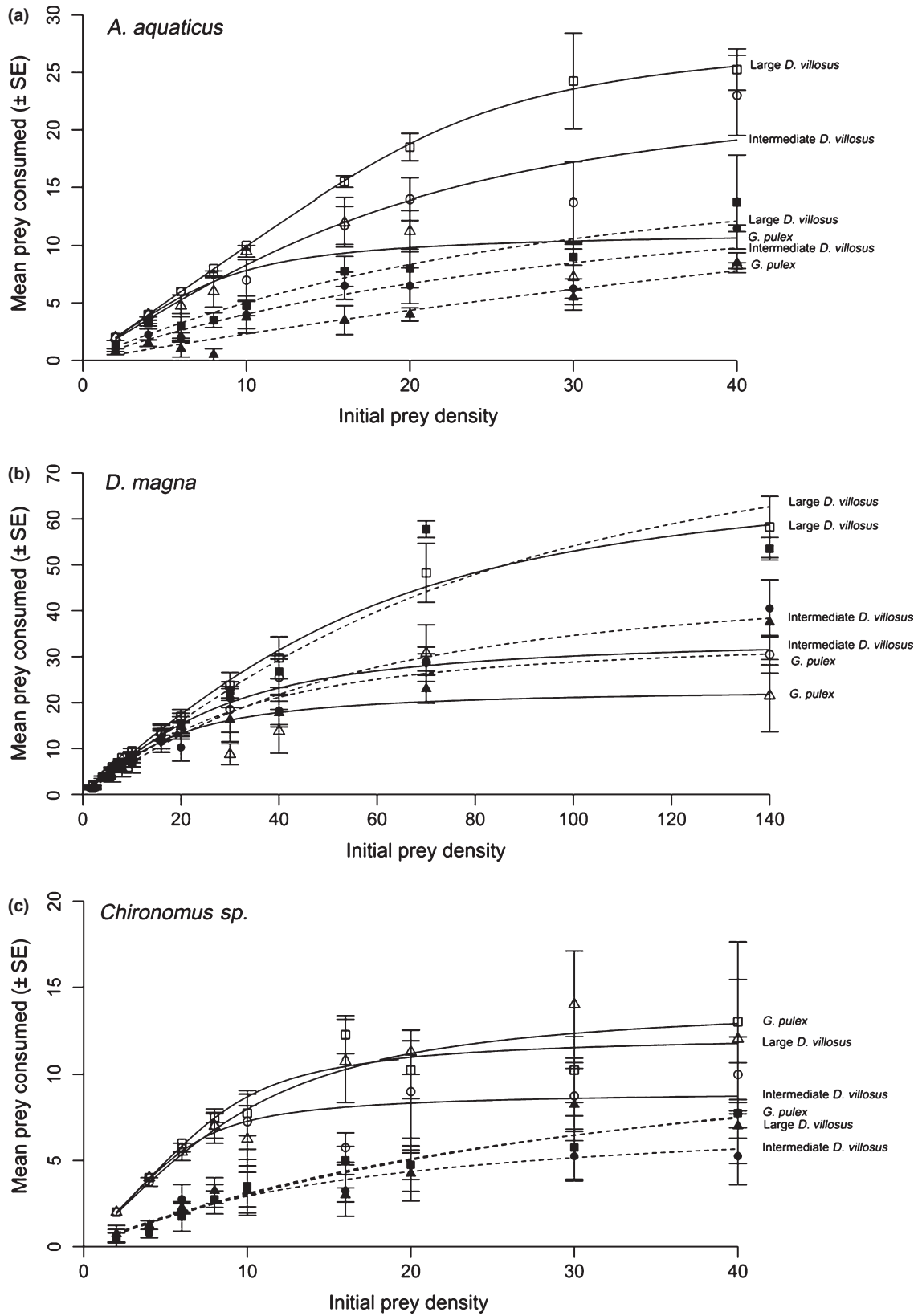
Fig. 3 Functional responses of large *Dikerogammarus villosus* (squares), intermediate *D. villosus* (circles) and *Gammarus pulex* (triangles) in simple (open symbols, solid line) and complex (closed symbols, dashed line) substrate arenas with (a) *Asellus aquaticus*, (b) *Daphnia magna* and (c) *Chironomus* sp. prey.

Table 3 ANOVA models for bootstrap generated values of maximum feeding rate with amphipod group and substrate conditions (amphipod = amphipod group (three levels), substrate = substrate conditions (two levels) and '*' denotes an interaction). Non-significant terms are detailed in greyed italics

Prey	Factor	$F_{(d.f.)}$	P
A. aquaticus	Amphipod	7.119 $_{(2,174)}$	0.001
	Substrate	*<0.001 $_{(1,174)}$*	*0.999*
	Amphipod * substrate	42.467 $_{(2,174)}$	<0.001
D. magna	Amphipod	460.589 $_{(2,174)}$	<0.001
	Substrate	123.672 $_{(1,174)}$	<0.001
	Amphipod * substrate	0.997 $_{(2,174)}$	0.371
Chironomus sp.	Amphipod	24.321 $_{(2,174)}$	<0.001
	Substrate	*0.010 $_{(1,174)}$*	*0.922*
	*Amphipod * substrate*	*0.903 $_{(2,174)}$*	*0.407*

predatory selection for *Chironomus* sp. and *A. aquaticus*. PC1 scores could therefore be interpreted as an index of selectivity for the pelagic (*D. magna*) versus benthic prey (*Chironomus* sp. and *A. aquaticus*). PC2 scores were positively loaded for selection for *A. aquaticus* (+0.841) and negatively loaded for *Chironomus* sp. selection (−0.532) (loading for *D. magna* was negligible, −0.099); thus, large PC2 scores were indicative of selection for *A. aquaticus* and small scores indicative of selection for *Chironomus* sp. PC2 scores could therefore be interpreted as an index of selection for the two different benthic prey types (*A. aquaticus* and *Chironomus* sp.).

The three-way ANOVA of PC1 revealed significant differences in mean prey selectivity for benthic (*A. aquaticus* and *Chironomus* sp.) and pelagic prey (*D. magna*) types, among amphipod groups, under different substrate conditions and with supplied prey density (Table 4, Fig. 5). Overall, *G. pulex* exhibited a significantly more positive selection for pelagic prey types compared with intermediate *D. villosus* (Fig. 5). There was, however, no significant difference in benthic/pelagic prey selection between *G. pulex* and large *D. villosus* (Table 4), and there were no differences between the two sizes of *D. villosus* (Fig. 5). There was a significant effect of substrate presence on benthic/pelagic prey selection, with a significant change from a benthic prey selection in the absence of substrate to a pelagic prey selection in the presence of substrate

Fig. 4 Maximum feeding rates (mean prey consumed per hour ± SE) for the three prey species for large *Dikerogammarus villosus* (dark grey), intermediate *D. villosus* (mid grey) and large *Gammarus pulex* (light grey) for the three prey species, (a) *Asellus aquaticus*, (b) *Daphnia magna* and (c) *Chironomus* sp., with and without substrate. Different letters indicate significant differences (*P* < 0.05).
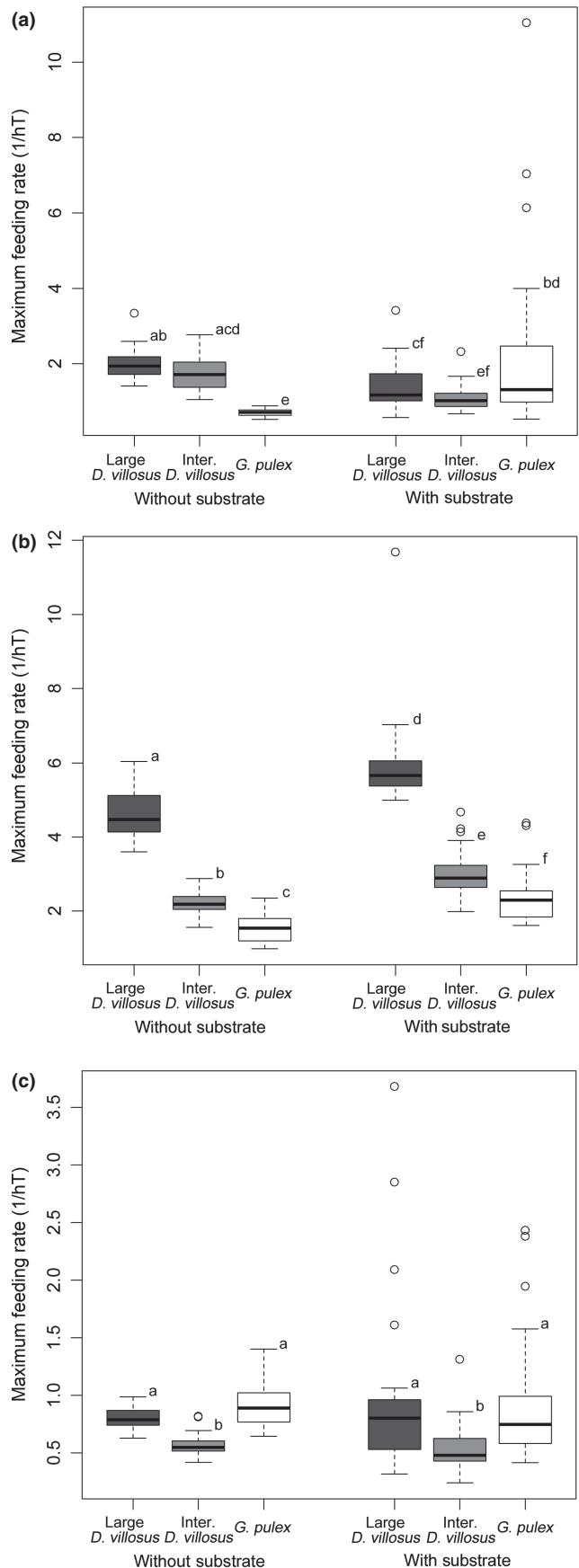
Table 4 ANOVA models for prey selection (principal component scores) and predatory generalism (see text for details) with amphipod group, supplied prey density and substrate conditions (amphipod = amphipod group (three levels), density = prey density (nine levels for *Asellus aquaticus* and *Chironomus* sp., and 11 levels for *Daphnia magna*), substrate = substrate conditions (two levels) and '*'denotes an interaction). Non-significant terms are detailed in greyed italics

Selectivity	Factor	F(d.f.)	P
Benthic versus Pelagic			
	Amphipod	4.306 (2,180)	0.015
	Substrate	181.435 (1,180)	<0.001
	Density	3.337 (9,180)	<0.001
	*Amphipod * substrate * density*	*0.906 (18,180)*	*0.572*
	*Amphipod * substrate*	*1.547 (2,180)*	*0.216*
	*Amphipod * density*	*0.263 (18,180)*	*0.999*
	*Density * substrate*	*1.310 (9,180)*	*0.235*
A. aquaticus versus *Chironomus* sp.			
	Amphipod	15.986 (2,180)	<0.001
	Substrate	*0.448 (1,180)*	*0.504*
	Density	*1.665 (9,180)*	*0.100*
	*Amphipod * substrate * density*	*1.443 (18,180)*	*0.116*
	*Amphipod * substrate*	*1.762 (2,180)*	*0.175*
	Amphipod * density	2.460 (18,180)	0.001
	*Density * substrate*	*1.057 (9,180)*	*0.397*
Generalism			
	Amphipod	10.350 (2,180)	<0.001
	Substrate	8.956 (1,180)	0.003
	Density	2.700 (9,180)	0.005
	*Amphipod * substrate * density*	*1.090 (18,180)*	*0.366*
	Amphipod * substrate	3.214 (2,180)	0.043
	*Amphipod * density*	*0.333 (18,180)*	*0.999*
	Density * substrate	7.295 (9,180)	<0.001

(Fig. 5). Increasing prey density moved predatory selection towards benthic prey types (Fig. 5).

The three-way ANOVA of PC2 revealed significant differences in mean prey selectivity for the two benthic prey (*A. aquaticus* and *Chironomus* sp.) among amphipod groups (Fig. 5). *G. pulex* exhibited significantly greater selection for *Chironomus* sp. compared with both *D. villosus* groups (Fig. 5). There was no difference in selection for benthic prey between the two *D. villosus* groups. A significant 'amphipod group x prey density' interaction reflected the greater increasing selection for *Chironomus* sp. at higher prey density by *G. pulex* compared with the two *D. villosus* groups, which exhibited a greater selection for *A. aquaticus* at high prey density. The presence/absence of substrate had no statistically significant effect on differences in benthic prey selectivity.

Feeding strategy (measured as the distance from the origin of PC1 and PC2) differed significantly among amphipod groups, under different substrate conditions and with prey density (Table 4). *G. pulex* was significantly more selective compared with both groups of *D. villosus* (Fig. 6) that were significantly more indiscriminate in their feeding strategy, and large *D. villosus* was more indiscriminate than intermediate *D. villosus* (Fig. 6a). Amphipods showed a significantly more selective feeding strategy in the presence of substrate (Table 4, Fig. 6b) and with increasing prey density (Fig. 6c). There was a significant 'amphipod group x substrate' interaction (Table 4) reflecting the greater
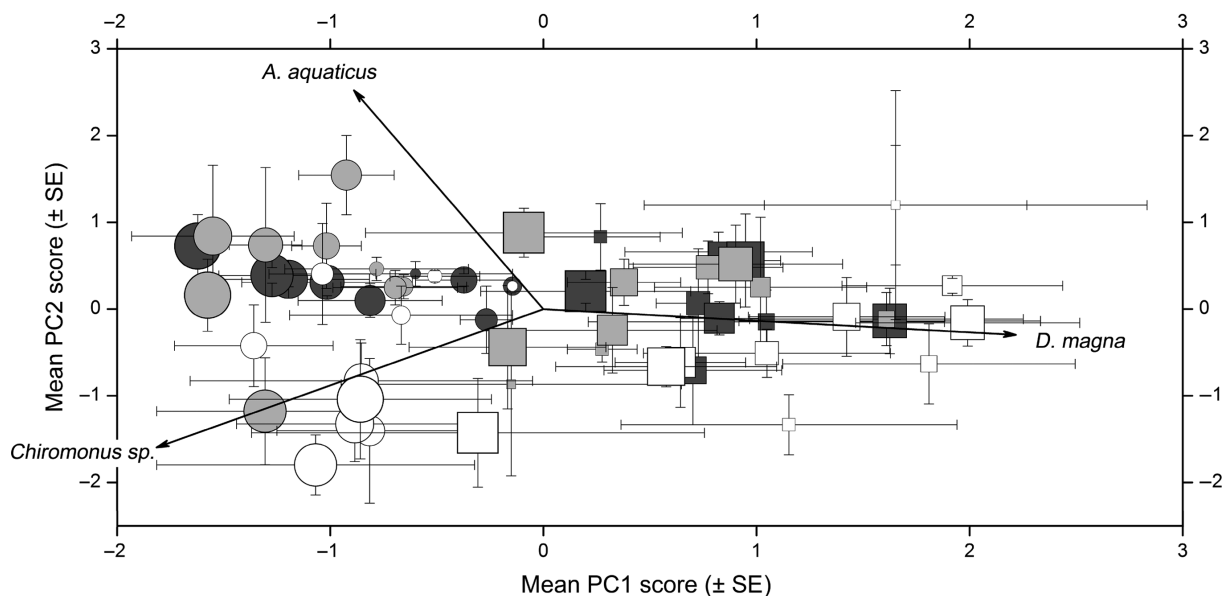

Fig. 5 Prey selection (mean PC score ± SE) differences among the amphipod groups (dark grey = large *Dikerogammarus villosus*; light grey = intermediate *D. villosus*; white = *Gammarus pulex*) with and without substrate (respectively, squares and circles) with increasing prey density (size of shape relative to prey density - see text for further detail). Arrows indicate the direction of loading for each of the three prey types.
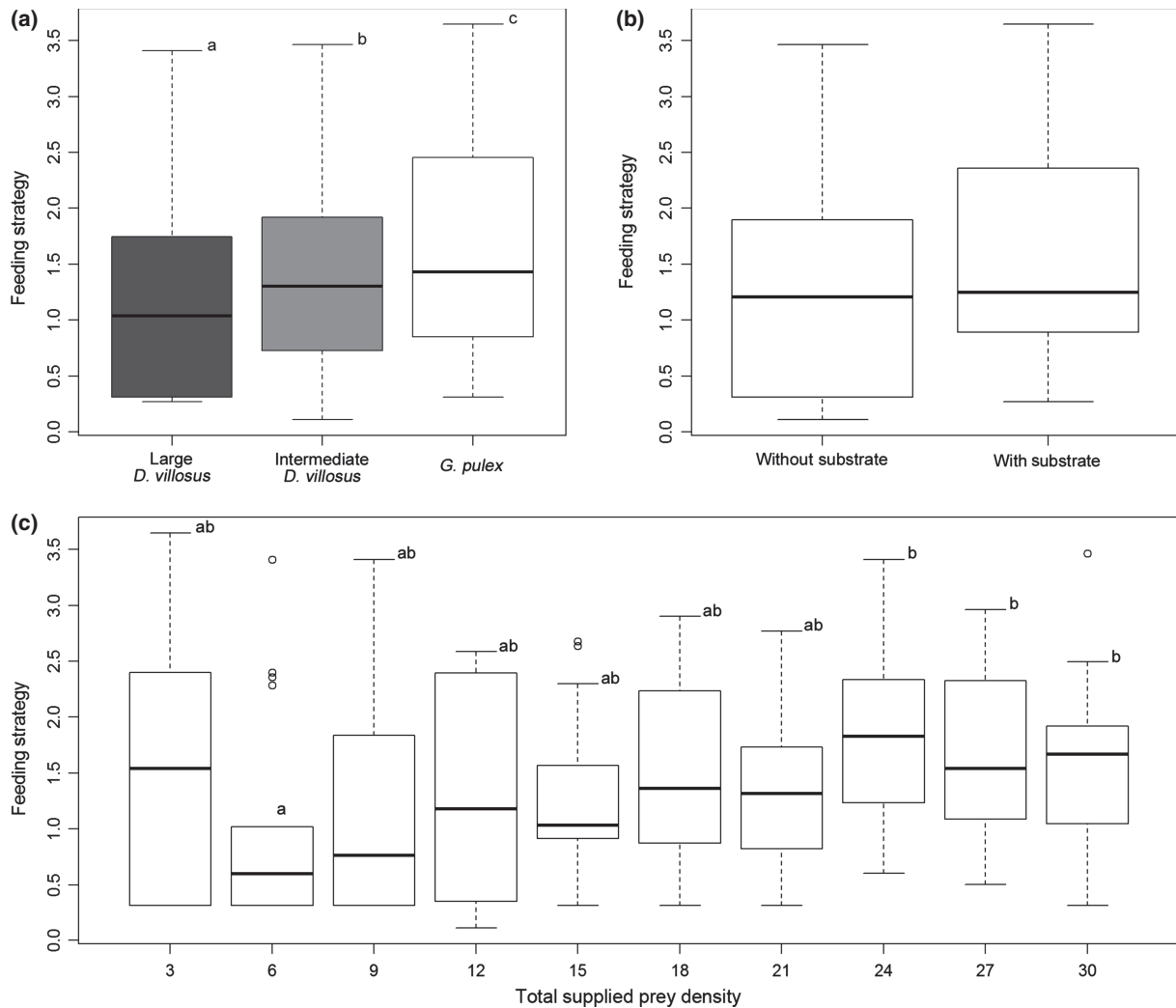
Fig. 6 Predator generalism (measured as distance from the origin, increasing distance from the origin equates to a move from indiscriminate feeding to selective feeding) differences (a) among amphipod groups; (b) in the absence or presence of substrate and; (c) with increasing supplied prey density.

disparity between large *D. villosus* and *G. pulex* compared with intermediate *D. villosus*, which was less likely to change feeding strategy in the presence of substrate. There was a significant 'prey density x substrate' interaction (Table 4) indicating a greater difference in selective feeding at higher prey densities in the absence of substrate compared with that of in the presence of substrate.

Discussion

The development of tools that can forecast the ecological impacts of invasive species on recipient communities is a major objective of invasion ecology research that has seen limited success (e.g. see Ricciardi, 2003; Lockwood, Hoopes & Marchetti, 2007; Davis, 2009; Dick *et al.*,

2013a,b; but see Nentwig, Kuhnel & Bacher, 2009). In this study, we make use of a comparative functional response methodology to assess relative use of resources by invasive and native species, as well as examining prey selectivity, to predict the likely ecological impacts on native prey of the 'killer shrimp', *Dikerogammarus villosus*, newly invasive in the U.K. (MacNeil *et al.*, 2010) and likely to invade outside of Europe, such as the North American Great Lakes (Ricciardi & Rasmussen, 1998; Bollache *et al.*, 2008). Under our experimental conditions, both the invader *D. villosus* and the native *G. pulex* exhibited Type II functional responses towards three prey species, *Asellus aquaticus*, *Daphnia magna* and *Chironomus* sp. Furthermore, this form of response was conserved with the addition of substrate, counter to a number of studies that report a shift to Type III

functional responses in gammarids and other predators under such conditions of habitat heterogeneity (see Alexander *et al.*, 2012). This may be important for prey at the population level, as Type III functional responses tend to be stabilising, whereas Type II responses may destabilise prey populations over certain ranges of density (Murdoch & Oaten, 1975; Juliano, 2001). Such functional response results are congruous with the known ecological impacts of both species, which show negative abundance relationships with many macroinvertebrates that have led to local and regional extinctions (Dick & Platvoet, 2000; Kelly *et al.*, 2006; MacNeil *et al.*, 2013).

The invader, *D. villosus*, had significantly higher functional responses, with greater maximum feeding rates, towards both *A. aquaticus* and *D. magna*. There was, however, less of a difference between the invasive and native amphipod functional responses towards *Chironomus* sp. We thus predict greater ecological impacts for the former two prey species than for the latter. Indeed, there is some field evidence that the presence of Asellidae is more affected than other taxa, including Chironomidae, when *D. villosus* invades (MacNeil *et al.*, 2013). The overall higher predatory rate of *D. villosus* may be attributed to a number of factors, including relatively larger antennae and mouthparts (Platvoet, 2007; Mayer *et al.*, 2009; Stoffels *et al.*, 2011), differences in physiology (Maazouzi *et al.*, 2011) and resource assimilation rates (Gergs & Rothhaup, 2008). In addition to this, *D. villosus* attains a greater maximum size in comparison with *G. pulex* (the former can be approximately 20% longer and twice as heavy); thus, species specific differences are amplified by the greater maximum body size of the invader. *D. villosus* also demonstrates a tendency for partial predation of prey, a phenomena that has been observed and photographed in this species (see Dick *et al.*, 2002). The greater maximum feeding rate of *G. pulex* compared with *D. villosus* towards *A. aquaticus* in the presence of substrate may be indicative of different hunting strategies, such as active searching versus sit-and-wait, but further research is required to unravel this.

Our prey selectivity experiment further highlighted the differences in predatory behaviour between the invasive and native amphipods. Compared with the native amphipod *G. pulex*, *D. villosus* was more selective of the benthic prey and was specifically more selective of *A. aquaticus*, a feeding strategy that was amplified at higher prey densities. This differential prey selectivity for *A. aquaticus*, coupled with the greater maximum feeding rate of the invader on this prey type, indicates that any impact on *A. aquaticus* populations would, under natural conditions, likely be amplified to a

greater degree when compared with *Chironomus* sp. populations following invasion. In fact, *Chironomus* sp. populations might not be especially impacted following the invasion of *D. villosus*, given the similarity in maximum feeding rate between the native and invasive species and the lack of positive selection for *Chironomus* sp. by the invader. J. Dodd (personal observation) found that in two adjacent, uninvaded reservoir systems, *A. aquaticus* represented 34–64% and *Chironomus* sp. represented 1–11% of the biomass of the macroinvertebrate community. This was in stark comparison with a complete lack of detection of both *A. aquaticus* and *Chironomus* sp. in Grafham water, the invaded reservoir, where 97% of the biomass of the macroinvertebrate community was represented by *D. villosus*. This pattern of field observation supports the results reported in this study and could tentatively indicate potential effects on ecosystem function. The increased predatory impact on *A. aquaticus* by *D. villosus* in invaded lake systems could result in changes to energy transfer in food webs (MacNeil *et al.*, 2011). *A. aquaticus* has been described to use a wide resource base (Moog, 2002), but are generally described as detritivores (Adcock, 1979). Their role in the food web is the facilitation of energy transfer between trophic levels through the processing of allochthonous material (Adcock, 1979). The mechanisms through which some types of this material are processed have been shown to differ between *A. aquaticus*, *G. pulex* and *D, villosus*, with the latter showing a much lesser processing efficiency than the two former species (MacNeil *et al.*, 2011). *A. aquaticus*, *D. magna* and *Chironomus* sp. are also prey for lake dwelling fish species, and both Cladocerans and Chironomidae form a large component of fish diet in Grafham Water (Lindsey & Lowe, 2001). The routes of energy transfer within food webs form the basis of how an ecosystem functions (Hooper *et al.*, 2005); thus, changes in the energy transfer route may have serious consequences on the stability (Hooper *et al.*, 2005) and resilience (Richmond, Breitburgh & Rose, 2005) of a system invaded by *D. villosus*. Indeed, both the change in the availability of *A. aquaticus*, *D. magna* and *Chironomus* sp. and the increased availability of *D. villosus* as an alternative food resource, has the potential to drive evolutionary change within some species of lake dwelling fish, for example Arctic charr, *Salvalinus alpinus*, which have been shown to be particularly susceptible to resource use-driven speciation (Adams & Huntingford, 2004; Knudsen *et al.*, 2011).

Predatory differences between the invader and native amphipods on the pelagic *D. magna* are complex, with the invader showing a greater maximum feeding rate

compared with the native species when presented with a single-prey type; however, when presented with multiple prey types, the invasive *D. villosus* exhibited lower selection for this prey species when compared with *G. pulex*. It is therefore likely that potential amphipod impacts on *D. magna* under natural conditions are likely to show greater variation depending on the availability of other food resources.

In addition to differences in specific prey types, *D. villosus* also exhibited differences in feeding strategy when compared with *G. pulex*. *D. villosus* was significantly more indiscriminate in prey selection, a tendency that became stronger as the invader increased in size. The indiscriminate use of available resources has been highlighted as another trait that may confer an advantage to invasive species (Romanuk *et al.*, 2009; Hänfling, Edwards & Gherardi, 2011; Keller *et al.*, 2011), and the reasons surrounding such an increase in generalist feeding ability of *D. villosus* are likely to be similar to those physical advantages conferring a greater maximum feeding rate on this species, such as larger, more powerful mouth parts and larger antennae, as detailed above.

The combination of functional response studies and prey selection experiments has the potential to not only indicate those native species most at risk of impact following invasion by a novel species, but also the degree to which such groups are likely to be affected. There is growing support that functional response analysis in particular provides reliable predictions of such invader impact (see Dick *et al.*, 2013a,b) and has indicated that invasive species may in general have higher functional responses compared with native species (e.g. for parasitoids; Greenberg, Legaspi & Jones, 2001; Jones *et al.*, 2003). While direct comparisons of invasive and native species functional responses are rare, Haddaway *et al.* (2012) showed that an invasive crayfish has a higher functional response than a native, although this was not directly related to field impacts on prey. However, most recently, Dick *et al.* (2013a) show that the invasive 'bloody red shrimp', *Hemimysis anomala*, has a higher functional response than analogous native species and that the greatest differentials in functional responses were associated with the prey that suffered the greatest field impacts. Further, Dick *et al.* (2013a) show that this difference in functional responses is consistent across the geographical range of the invader. Functional response techniques can offer some advantages over trait-based predictions (e.g. see Sakai *et al.*, 2001), by providing predictions of the potential consequences for specific prey. However, it is likely that the best information will be generated using these techniques in concert; trait-based

information can be gathered simply (e.g. Kolar & Lodge, 2001) and inform which species need further investigation through functional response models.

Risk assessments for invasive species require some element of likely ecological impact, but without an invasion (and hence impact) history, this is difficult to derive (see Leung *et al.*, 2012). Comparative functional responses have been utilised in the field of biocontrol to assess the efficacy of native and introduced biocontrol agents (Fernandez-Arhex & Corley, 2003; Madadi *et al.*, 2011). We suggest that comparative functional responses provide a powerful route to investigate the impact of existing, emerging and potential invasive species. Furthermore, functional responses and resource selection can be derived for consumers other than predators (e.g. Hobbs *et al.*, 2003; Sarnelle & Wilson, 2008), their derivation can be in the laboratory or field, and the method is widely applicable across taxonomic and trophic groups (see also Dick *et al.*, 2013a,b). Ultimately, further exploration of these ideas could move invasion ecology from a descriptive to a more predictive science.

Acknowledgments

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