# *Ecological impacts of an invasive predator explained and predicted by comparative functional responses*

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ORIGINAL PAPER

# Ecological impacts of an invasive predator explained and predicted by comparative functional responses

**Jaimie T. A. Dick · Kevin Gallagher · Suncica Avlijas · Hazel C. Clarke · Susan E. Lewis · Sally Leung · Dan Minchin · Joe Caffrey · Mhairi E. Alexander · Cathy Maguire · Chris Harrod · Neil Reid · Neal R. Haddaway · Keith D. Farnsworth · Marcin Penk · Anthony Ricciardi**

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**Abstract** Forecasting the ecological impacts of invasive species is a major challenge that has seen little progress, yet the development of robust predictive approaches is essential as new invasion threats continue to emerge. A common feature of ecologically damaging invaders is their ability to rapidly exploit and deplete resources. We thus hypothesized that the 'functional response' (the relationship between resource density and consumption rate) of such invasive species might be of consistently greater magnitude than those of taxonomically and/or trophically similar native species. Here, we derived functional responses of the predatory Ponto-Caspian freshwater 'bloody red' shrimp, *Hemimysis anomala*, a recent and ecologically damaging invader in Europe and N. America, in comparison to the local native analogues *Mysis salemaai* and *Mysis diluviana* in Ireland and Canada, respectively. This was conducted in a novel set of experiments involving multiple prey species in each geographic location and a prey species that occurs in both regions. The predatory functional responses of the invader were generally higher than those of the comparator native species and this difference was consistent across invaded regions. Moreover, those prey species characterized by the strongest and potentially de-stabilizing Type II functional responses in our laboratory experiments were the same prey species found to be most impacted by *H. anomala* in the field. The impact potential of

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*H. anomala* was further indicated when it exhibited similar or higher attack rates, consistently lower prey handling times and higher maximum feeding rates compared to those of the two *Mysis* species, formerly known as '*Mysis relicta*', which itself has an extensive history of foodweb disruption in lakes to which it has been introduced. Comparative functional responses thus merit further exploration as a methodology for predicting severe community-level impacts of current and future invasive species and could be entered into risk assessment protocols.

**Keywords** Biological invasion · Ecological impact · Functional response · Prediction · Risk assessment

## Introduction

Invasive species continue to jeopardize biodiversity and disrupt ecosystems (Lockwood et al. 2007; Davis 2009; Ricciardi et al. 2012). The most cost-effective approach to managing invasion threats is prevention (Leung et al. 2002), but effective allocation of limited resources towards this goal requires reliable forecasts of invasiveness and impact (Byers et al. 2002). Although there has been some progress in linking species characteristics to invasiveness (Kolar and Lodge 2001; van Kleunen et al. 2010; Keller et al. 2011), few advances have been made in developing methods for predicting the ecological impacts of invaders (Byers et al. 2002; NRC 2002; Ricciardi 2003; Lockwood et al. 2007; Davis 2009; but see Nentwig et al. 2009). Some physiological and life history correlates of ecological impact have been identified for terrestrial plants (McIntyre et al. 2005; Pysek et al. 2009), but attempts to use species traits to predict the outcomes of invasions in general have had modest success to date (Cronk and Fuller 1995; Lockwood et al. 2007; Davis 2009; van Kleunen et al. 2010).

Further, variation in morphological, genetic and behavioural characteristics across their invasive ranges have frustrated attempts to identify species traits that consistently predict invader impacts on recipient communities (Hayes and Barry 2008; Tecco et al. 2010). Presently, the only general predictive method available is to reference an invader's history of impact, an approach limited to invaders whose effects are already well documented (NRC 2002; Ricciardi 2003; Ricciardi et al. 2012). However, given that the rapid exploitation of resources is a trait commonly associated with high-impact invaders (Strayer et al. 1999; Byers et al. 2002; Johnson et al. 2008; Morrison and Hay 2011), valuable insights into their ecological impact could conceivably be derived from interspecific comparisons of their 'functional response'—i.e., the relationship between resource density and consumer uptake rate. Recently, it was suggested that introduced predators that are damaging to native communities might display higher functional responses than comparator native species (Bollache et al. 2008). We propose that comparative functional responses of invaders and natives offer a methodology to forecast the impacts of present and future invaders. Further, strong impacts may be predictable when new invaders exhibit functional responses that are consistently equivalent to, or higher than, those of known harmful invaders across different biogeographical regions. Should this be the case, comparative functional responses may also be a useful metric to include in risk assessment protocols (see Andersen et al. 2004).

To further explore this concept and its application, we conducted a novel inter-regional experiment to examine the functional responses of an invasive predator of emerging global significance, the Ponto-Caspian mysid 'bloody red' shrimp, *Hemimysis anomala* G.O Sars, which is spreading across continental Europe (Ketelaars et al. 1999; Ricciardi et al. 2012) and has recently invaded the UK (Holdich et al. 2006), Ireland (Minchin and Holmes 2008) and the North American Great Lakes (Ricciardi et al. 2012). In order to assess the potential ecological impact of this species, we compared its functional responses with those of other mysids, *Mysis salemaai* Audzijonyte & Väinölä, 2005 (native to Ireland) and *M. diluviana* Audzijonyte & Väinölä, 2005 (native to boreal North America). The latter are sister species in the *Mysis relicta* complex, which itself has an extensive invasion history and has caused biodiversity loss and foodweb disruptions in many lakes to which it has been introduced (Nesler and Bergersen 1991). We predicted that these crustacean predators would display Holling Type II functional responses, as such responses are most likely to be de-stabilizing with respect to prey populations (Murdoch and Oaten 1975) and thus would concur with observed patterns of prey species displacement in invaded systems (see Ketelaars et al. 1999; Ricciardi et al. 2012).

## Materials and methods

In Ireland, we collected *H. anomala* (8–14 mm body length) from Loughs Derg and Ree and the native *M. salemaai* (16–21 mm) from Loughs Derg and Neagh. In Canada, we collected *H. anomala* and *Mysis diluviana* (of similar respective size ranges as above) from the St. Lawrence River and Lakes Memphremagog and Oneida, respectively. All mysids were transported in opaque containers shielded from light, and experiments were conducted in the dark at 12 °C.

Prey types for our experiments were selected based on their documented importance in the diet of mysids (Nesler and Bergersen 1991; Ketelaars et al. 1999; Whall and Lasenby 2009; Ricciardi et al. 2012). In order to examine consistencies between field patterns and laboratory functional responses, we used prey species that have been shown to be significantly reduced in abundance in waterbodies following invasion by *H. anomala*, as well as species apparently less affected (see Ketelaars et al. 1999). In Ireland, prey were juvenile amphipods *Gammarus pulex* (1.5–2 mm), adult cladocerans *Daphnia pulex* (1–2.3 mm) and *Chydorus sphaericus* (0.3–0.8 mm), and the copepod *Cyclops abyssorum* (0.8–1.4 mm) from L. Neagh and laboratory stock. In Canada, the prey species were cladocerans *Ceriodaphnia quadrangula* (0.8–1 mm) from L. Memphremagog and *D. pulex* (1–2.3 mm) from laboratory stock. *Daphnia pulex* is a dominant member of lake planktonic communities throughout both Ireland and North America. Although the taxon is recognized as a circumarctic species complex (Colbourne et al. 1998), Irish and Canadian *D. pulex* populations are deemed to be sufficiently convergent (morphologically and ecologically; J. T. A. Dick and A. Ricciardi, personal observation) that they are useful prey for assessing the consistency of the predatory functional responses of *H. anomala*, both in absolute terms and in our inter-regional comparison with the two native *Mysis* spp.

Experiments were conducted in cylindrical arenas of 7 cm diameter with 150 ml filtered lake water. In sets of controls without predators ($n = 3$ per density for all prey species), >98 % of prey survived. In Ireland, we introduced either single *H. anomala* or *M. salemaai* to *G. pulex* juveniles initially at prey densities of 4, 6, 8, 10, 16, 20 and 30 ($n = 3$ per density) and counted numbers eaten after 12 and 40 h. Since *H. anomala* predation showed no sign of an asymptote at prey density 30, densities were increased to 40, 80 and 140 with this prey species (Fig. 1a) and for all subsequent experiments, which were conducted for 12 h overnight in darkness (when mysids forage most actively). These methods were repeated with *H. anomala* and *M. diluviana* in Canada.

Mean prey eaten at 12 h was examined for each prey species in two-Factor ANOVAs with respect to 'predator species' and 'prey density'. There are numerous modelling approaches to the assessment of functional responses and choice of model may depend on whether a particular study is mechanistic or phenomenological in approach (Jeschke et al. 2002). Thus, the mechanistic application of parameters such as attack rate and handling time must be approached with extreme caution, or be supported with empirical measurements of parameter estimates (Caldow and Furness 2001; Jeschke et al. 2002; Jeschke and 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). Thus, to determine if the current predators displayed Type II (as opposed to Type III) functional responses, we used logistic regression to test for a negative linear coefficient (fitted using maximum likelihood) in the relationship between the proportion of prey eaten and prey density; on the other hand, a significantly positive first order term followed by a significantly negative second order term would have indicated a Type III response (Trexler et al. 1988; Juliano 2001). Further, we estimated values of '*a*' (attack rate), '*h*' (handling time) and maximum feeding rate ($1/hT$, where $T =$ experimental period) in R with Rogers' equation for prey depletion (Juliano 2001). Where prey density declines (i.e., in trials where prey are not replaced), the 'random predator equation' (Rogers 1972) is appropriate (Juliano 2001):

$$N_e = N_0(1 - \exp(a(N_e h - T))) \qquad (1)$$

where $N_e$ is the number of prey eaten, $N_0$ is the initial density of prey, $a$ is the attack constant, $h$ is the handling time and $T$ is the total time available. Owing to the implicit nature of the random predator equation, the Lambert W function was implemented to fit the model to the data (Bolker 2008). Bootstrapping was used to generate multiple estimates ($n = 30$) of the response parameters of attack rate $a$ and handling time *h* and maximum feeding rate (1/*hT*), which were then compared between *H. anomala* and the native *Mysis* spp. by *t* tests.

**Fig. 1** Functional responses of the invader *H. anomala* (*closed circles*) compared to the Irish native *M. salemaai* and the N. American native *M. diluviana* (open circles). Means are ± SE. Prey species are: **a** juvenile *G. pulex* (Ireland) at 12 h for *H. anomala* and 40 h for *M. salemaai*; **b** *D. pulex* (Ireland) at 12 h; **c** *C. sphaericus* (Ireland) at 12 h; **d** *C. abyssorum* (Ireland) at 12 h; **e** *C. quadrangula* (Canada) at 12 h; **f** *D. pulex* (Canada) at 12 h ▶

## Results

In Ireland, *H. anomala* consumed significantly more of each of the four prey species offered than did the native *M. salemaai* (prey: juvenile *G. pulex* $F_{1,28} = 222.5$, $P < 0.001$, Fig. 1a; *D. pulex* $F_{1,40} = 95.5$, $P < 0.001$, Fig. 1b; *C. sphaericus* $F_{1,40} = 33.8$, $P < 0.001$, Fig. 1c; *C. abyssorum* $F_{1,40} = 3.5, P = 0.05$, Fig. 1d). More prey were eaten at higher prey densities (juvenile *G. pulex* $F_{6,28} = 13.4$, $P < 0.0001$, Fig. 1a; *D. pulex* $F_{9,40} = 5.9$, $P < 0.001$, Fig. 1b; *C. sphaericus* $F_{9,\ 40} = 90.5$, $P < 0.001$, Fig. 1c; *C. abyssorum* $F_{9,40} = 145.3$, $P < 0.001$, Fig. 1d) and there were significant 'predator species × prey density' interaction effects (juvenile *G. pulex* $F_{6,28} = 18.1$, $P < 0.001$, Fig. 1a; *D. pulex* $F_{9,40} = 4.1$, $P < 0.001$, Fig. 1b; *C. sphaericus* $F_{9,40} = 561.1$, $P < 0.001$, Fig. 1c; *C. abyssorum* $F_{9,40} = 3.1$, $P < 0.01$, Fig. 1d), reflecting the much steeper increase in numbers of prey eaten over the range of prey densities by *H. anomala* as compared to *M. salemaai*. In Canada, there was no significant difference in the mean numbers of *C. quadrangula* prey eaten by *H. anomala* and *M. diluviana* ($F_{1,40} = 2.1$, NS, Fig. 1e), but the invader consumed significantly more *D. pulex* than did the native ($F_{1,40} = 41.9$, $P < 0.0001$, Fig. 1f), as occurred with this prey species in Ireland (see Fig. 1b). Again, more prey were eaten at higher prey densities (*C. quadrangula* $F_{9,40} = 20.4$, $P < 0.01$, Fig. 1e; *D. pulex* $F_{9,40} = 12.7$, $P < 0.001$, Fig. 1f) and there were significant 'predator species x prey density' interaction effects (*C. quadrangula* $F_{9,40} = 2.2$, $P < 0.05$, Fig. 1e; *D. pulex* $F_{9,40} = 6.1$, $P < 0.001$, Fig. 1f).

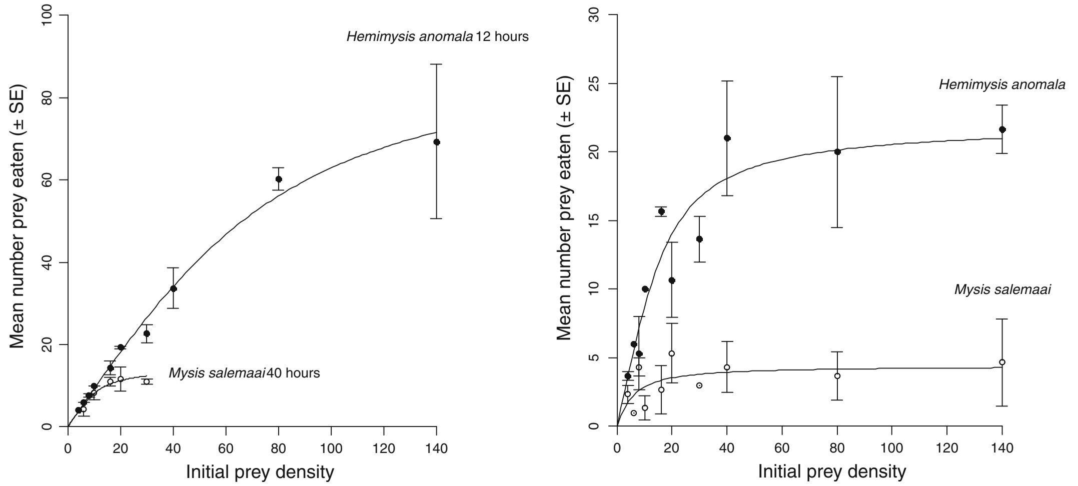
All three predators displayed potentially population de-stabilizing Type II functional responses (Fig. 1a–f; Table 1). In Ireland, *H. anomala* exhibited a significantly greater maximum feeding rate than *M. salemaai* for all prey species, with significantly lower handling times (or both higher attack rates and lower handling times; Table 1). While *H. anomala* and *M. diluviana* did not differ in mean number of *C. quadrangula* prey eaten, the latter predator had a significantly higher maximum feeding rate. As in Ireland, *H. anomala* in Canada had a significantly higher maximum feeding rate on *D. pulex* than did the native mysid (*M. diluviana*). Moreover, *H. anomala* in Canada exhibited similar differentials in functional responses and parameter values as in Ireland (see Fig. 1; Table 1).

## Discussion

### Functional response experiments

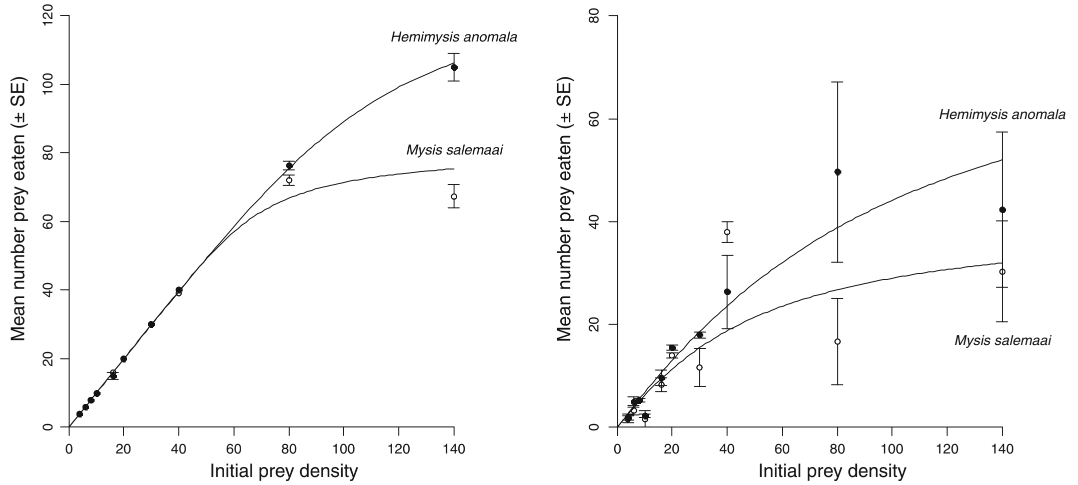
If the most damaging invaders are characterized by an ability to rapidly consume and deplete resources (e.g. Funk and Vitousek 2007; Johnson et al. 2008; Morrison and Hay 2011), then the classical 'functional response' of Holling (1959) offers a method whereby invader impacts can be examined not only in absolute terms but in relative terms with a comparator—which we contend should be taxonomically and/or trophically analogous native species. Using such native comparators is much more practical and powerful than trying to collate data for unsuccessful or inconspicuous invaders, which are necessarily scarce. Indeed, it is logical that where invasive species show functional responses of greater magnitude than natives, the resource (such as prey) is likely to be depleted to a greater degree, equating to a greater ecological impact.

Overall, the invasive mysid *H. anomala* showed dramatically higher predatory functional responses than did native mysids. This pattern occurred over a range of prey species and in spite of individuals of *H. anomala* being considerably smaller than the *Mysis* spp. Given that species of the *M. relicta* group are themselves highly disruptive invaders (Ketelaars et al. 1999; Nesler and Bergersen 1991; Ricciardi et al. 2012) and are known to have a strong structuring effect on communities even within their native range (Nero and Sprules 1986), our results signify a high impact potential for *H. anomala*. Indeed, although *H. anomala* has a much more recent invasion history,



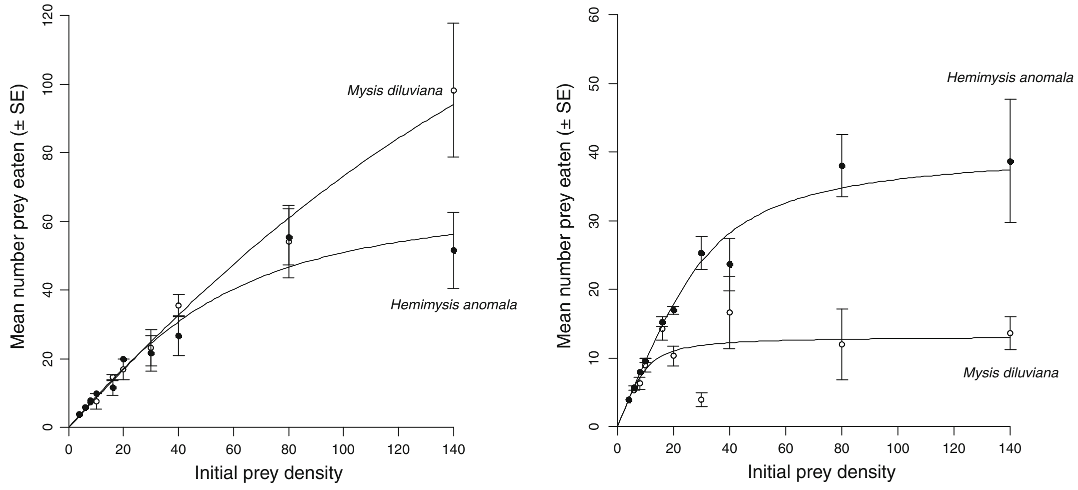
**(a)** Prey = *Gammarus pulex* (Ireland)

**(b)** Prey = *Daphnia pulex* at 12 hours (Ireland)



**(c)** Prey = *Chydorus sphaericus* at 12 hours (Ireland)

**(d)** Prey = *Cyclops abyssorum* at 12 hours (Ireland)



**(e)** Prey = *Ceriodaphnia quadrangula* at 12 hours (Canada)

**(f)** Prey = *Daphnia pulex* at 12 hours (Canada)

**Table 1** Functional response parameters for *H. anomala*, *M. salemaai* and *M. diluviana* with a range of prey species

| Location | Prey species | Metric | *Predator species* | | *t* | *P* |
|---|---|---|---|---|---|---|
| | | | *H. anomala* (invader) | *M. salemaai* (native) | | |
| Ireland | *G. pulex* | lc | −0.018 | −0.106 | – | Both <0.001 |
| | | a | 3.05 (0.12) | 3.65 (0.23) | 2.3 | <0.03 |
| | | h | 0.01 (0.0008) | 0.07 (0.002) | 22.2 | <0.001 |
| | | 1/*hT* | 8.96 (0.48) | 0.39 (0.018) | 17.9 | <0.001 |
| | *D. pulex* | lc | −0.022 | −0.019 | – | Both <0.001 |
| | | a | 3.98 (0.24) | 1.38 (0.18) | 8.6 | <0.001 |
| | | h | 0.05 (0.001) | 0.23 (0.01) | 15.7 | <0.001 |
| | | 1/*hT* | 1.82 (0.04) | 0.39 (0.02) | 32.6 | <0.001 |
| | *C. sphaericus* | lc | −0.032 | −0.041 | – | Both <0.001 |
| | | a | 6.96 (0.32) | 9.76 (0.22) | 7.2 | <0.001 |
| | | h | 0.007 (0.0001) | 0.01 (0.0001) | 27.9 | <0.001 |
| | | 1/*hT* | 5.73 (0.1) | 3.4 (0.03) | 22.5 | <0.001 |
| | *C. abyssorum* | lc | −0.011 | −0.014 | – | Both <0.001 |
| | | a | 1.25 (0.04) | 1.2 (0.04) | 0.94 | NS |
| | | h | 0.01 (0.001) | 0.02 (0.001) | 7.1 | <0.001 |
| | | 1/*hT* | 4.69 (0.54) | 1.75 (0.06) | 5.4 | <0.001 |
| Location | Prey species | Metric | *Predator species* | | *t* | *P* |
| | | | *H. anomala* (invader) | *M. diluviana* (native) | | |
| Canada | *C. quadrangula* | lc | −0.018 | −0.007 | – | Both <0.001 |
| | | a | 2.75 (0.15) | 2.23 (0.08) | 3.2 | <0.003 |
| | | h | 0.01 (0.001) | 0.006 (0.0005) | 10.1 | <0.001 |
| | | 1/*hT* | 6.21 (0.3) | 16.6 (1.88) | 5.4 | <0.001 |
| | *D. pulex* | lc | −0.022 | −0.024 | – | Both <0.001 |
| | | a | 4.15 (0.17) | 4.83 (0.24) | 2.3 | <0.03 |
| | | h | 0.02 (0.001) | 0.08 (0.001) | 27.6 | <0.001 |
| | | 1/*hT* | 3.39 (0.08) | 1.12 (0.02) | 24.5 | <0.001 |

*lc* linear coefficient from logistic regression, with *P* values, $a$ = attack rate, $h$ = handling time, $1/hT$ = estimated maximum feeding rate, presented as means with standard errors in parentheses, raw data from multiple parameter estimates derived from bootstrapping, with *t* tests and *P* values ($df = 58$ in all cases)

it has been implicated in dramatic changes in zooplankton communities in European waterbodies (Ketelaars et al. 1999; Ricciardi et al. 2012), supporting our prediction. In addition, the differential magnitudes in functional responses and associated parameters of *H. anomala* were consistent in Ireland and Canada, further suggesting that this species will impact aquatic communities across much of the geographic range of its invasion. This inter-regional consistency of the invader functional response indicates that this species trait has advantages as a predictive tool over other traits that have been shown to vary across a species' range (NRC 2002; see also van Kleunen et al. 2010).

*Hemimysis anomala* and *M. diluviana* in Canada did not differ in mean numbers of prey eaten with respect to *C. quadrangula*, with the invader having a higher attack rate, but the native a lower handling time—yielding a higher maximum feeding rate (Table 1). On the other hand, *H. anomala* was consistently higher than *Mysis* spp. in its mean number of prey eaten and had higher maximum feeding rates for the other five prey species utilized in our experiments. The functional response methodology therefore should not rely on only one or very few potential prey items, but instead use multiple prey species that span taxonomic and trophic groups. This will also give the benefit of predicting which species are likely to be impacted more so by the invader than natives, as well as which prey species may escape such impact (see below). Thus, the use of multiple potential prey items can refine the predictive capacity of the method.

### Type II versus Type III functional responses

The distinction between Type II and Type III functional responses, and hence whether predators will likely de-stabilize or stabilize prey populations, relies on examining prey consumption rates at low prey densities (Juliano 2001). We utilised prey numbers down to as low as four individuals in relatively large volumes of water to ensure that we could identify any inflection of the functional response curves at low prey densities that would describe a Type III response. However, we clearly see a Type II response in each case in Fig. 1 and Table 1, and this is corroborated by the associated statistical analyses. It is also noteworthy in this respect that prey were not replaced as they were consumed in this experiment, thus where all prey were consumed (as they often were at the lower densities; see Fig. 1), the number of prey in such replicates fell to the last individual before it too was consumed. If these predators exhibited Type III functional responses, we would instead see few, if any, prey eaten at low densities and then a rise in proportion eaten at higher densities; but this is not the case and we see Type II responses, as we predicted, where most and usually all prey are consumed at low densities. Type II responses are likely to be de-stabilizing with respect to prey populations (Murdoch and Oaten 1975), as prey do not escape predation at low prey densities—in contrast to Type III functional responses whereby prey are under-consumed at low prey densities (Juliano 2001). Accordingly, cladocerans such as *Daphnia* spp. and *C. sphaericus* both virtually disappeared in European lakes shortly after invasion by *H. anomala* (Ketelaars et al. 1999; Borcherding et al. 2006; Ricciardi et al. 2012), whereas copepods were less affected. These field observations match our laboratory experimental findings, whereby the functional responses toward cladocerans were much greater than that toward the copepod. Similar conclusions can be made for the *Mysis* spp., which are also known to severely reduce zooplankton abundance following invasion (Nesler and Bergersen 1991; Ricciardi et al. 2012). Indeed, our experimental results show a Type II functional response for *Mysis* towards such prey, albeit of generally much lesser magnitude, suggesting that *H. anomala* will be even more disruptive to food webs. Future studies should, however, incorporate multiple prey species presented simultaneously to individual predators to test for 'switching' among prey species, plus environmental heterogeneity, as both may have effects on functional response types (e.g see Akre and Johnson 1979; Alexander et al. 2012).

### Functional responses as a tool for forecasting impact

The present study demonstrates the potential value of comparative functional responses in explaining and predicting the impact of one particular invader, as revealed by comparisons with two native species in two disparate geographical locations and with a range of prey species. Whilst here we have studied one invasive species, we have in fact considered two geographically distant populations of this invader. Invasive populations, rather than species, are arguably a more appropriate level of comparison for trait-based studies (Colautti and MacIsaac 2004).

Further demonstrations of consistency in functional response comparisons with other invader/native species pairings are needed to assess the broad applicability of our method. There exist, however, several studies that are consistent with our hypothesis that high impact invaders will have higher functional responses than analogous natives, although these studies were often designed to answer different questions. The most closely allied study showed that the invasive 'killer shrimp', *Dikerogammarus villosus*, has a higher functional response towards one prey species than do a range of other amphipods (Bollache et al. 2008), and similar conclusions were made for comparisons of an invasive and a native crayfish (Haddaway et al. 2012). However, neither study explicitly linked differential functional responses to actual field patterns of impact on prey species, as we have done here. In another recent study, the co-existence patterns of two intra-guild predators, a native amphipod and an invasive amphipod, were partly explained by our functional response method, which revealed that the native withstood replacement by the invader by preying more heavily on the invader's juveniles (Kestrup et al. 2011). Further, the biological control potential of an introduced parasitoid was assessed as 'high' relative to that of an indigenous species using comparisons of functional responses at different temperatures (Jones et al. 2003). Functional responses have also been derived for introduced species but without native comparators, and they have still been useful in explaining impacts on prey species in the field (Hoof and Bollens 2004; Jones et al. 2011). Finally, functional responses may be useful in testing other hypotheses in invasion ecology, such as enemy release (Dick et al. 2010) and biotic resistance (Twardochleb et al. 2012). Thus, although there are currently insufficient studies for a formal meta-analysis, there is increasing evidence that comparative functional responses may predict invasive species impacts in invaded communities.

Our approach could complement and extend traditional correlative approaches to understanding and predicting invader success (e.g. see van Kleunen et al. 2010) by offering a more process oriented and cause/effect centered consideration. Comparative functional responses could be employed in studies of introduced predators, in situations where consumptive demand is recognized as a major driver of impact (Johnson et al. 2008). Moreover, this method can be employed using diverse taxonomic and trophic groups, as functional responses may be derived for any organism's utilization of resources (e.g for herbivores; Farnsworth et al. 2002). Indeed, our comparative functional responses of predatory animals resembles the 'resource use efficiency' concept as applied to plants (Funk and Vitousek 2007). Finally, this approach may prove to be useful as a risk assessment tool for prioritizing management actions towards future invasion threats (see Andersen et al. 2004). As the spiralling economic costs of invasive species are now becoming apparent (e.g. estimated at £1.7 Billion annually to Great Britain; Williams et al. 2010), a method that can effectively identify the most damaging invaders should be further explored with respect to costs and benefits. We contend that functional responses as measured in the laboratory in this study are relatively inexpensive and could become more efficient with, for example, automated counts of prey depletion (e.g. taking prey counts from digital photographs and using tracking software such as '*Tracksys*'). However, functional responses can also be measured in field situations utilising survey data and observation (e.g. Smout et al. 2010), field video recording (e.g. Schenk and Bacher 2002), gut contents analyses (e.g. Jones et al. 2011), and scat analyses (e.g. Middlemas et al. 2006). There may also be a role for stable isotope analysis and qPCR in determining predator consumption as part of deriving functional responses. As prevention is more cost effective than attempting to control or mitigate invasions after the fact, we encourage further investigation and development of our comparative functional response methodology for use as an invasive species management tool.

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