# Fortune favours the bold: a higher predator reduces the impact of a native but not an invasive intermediate predator

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## Summary

**1.** Emergent multiple predator effects (MPEs) might radically alter predictions of predatory impact that are based solely on the impact of individuals. In the context of biological invasions, determining if and how the individual-level impacts of invasive predators relates to their impacts in multiple-individual situations will inform understanding of how such impacts might propagate through recipient communities.

**2.** Here, we use functional responses (the relationship between prey consumption rate and prey density) to compare the impacts of the invasive freshwater mysid crustacean *Hemimysis anomala* with a native counterpart *Mysis salemaai* when feeding on basal cladoceran prey (i) as individuals, (ii) in conspecific groups and (iii) in conspecific groups in the presence of a higher fish predator, *Gasterosteus aculeatus*.

**3.** In the absence of the higher predator, the invader consumed significantly more basal prey than the native, and consumption was additive for both mysid species – that is, group consumption was predictable from individual-level consumption.

**4.** Invaders and natives were themselves equally susceptible to predation when feeding with the higher fish predator, but an MPE occurred only between the natives and higher predator, where consumption of basal prey was significantly reduced. In contrast, consumption by the invaders and higher predator remained additive.

**5.** The presence of a higher predator serves to exacerbate the existing difference in individual-level consumption between invasive and native mysids. We attribute the mechanism responsible for the MPE associated with the native to a trait-mediated indirect interaction, and further suggest that the relative indifference to predator threat on the part of the invader contributes to its success and impacts within invaded communities.

**Key-words:** emergent multiple predator effects, functional response, *Hemimysis anomala*, invasive species, trait-mediated interactions

## Introduction

Understanding and predicting how the impacts of invasive species propagate through recipient communities remains a key challenge in ecology (Kolar & Lodge 2001; Van Kleunen *et al.* 2010; Simberloff *et al.* 2013; Dick *et al.* in press). Determining individual-level traits that characterise successful invaders, such as high rates of resource consumption (Bollache *et al.* 2008; Dick *et al.* 2013), may fail to fully quantify such impacts because they do not account for how invaders interact with each other and with other species in recipient communities. For example, individual consumers can demonstrate both higher and lower *per capita* feeding rates as their density increases (Hassell 1978; Sommer 1992; Hansson *et al.* 2001).

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In addition, the presence of higher trophic level predators can modify feeding rates through a combination of density-mediation, i.e. predation and non-consumptive trait-mediation, where intermediate consumer phenotypes change as a result of predator threat (Peacor & Werner 2001; Werner & Peacor 2003). Although both mechanisms are well known to drive cascading effects down through food webs, there is accumulating evidence for the primacy of non-consumptive, trait-mediated indirect interactions (TMIIs; Abrams *et al.* 1996) over density mediation (Gabowski 2004; Schmitz, Krivan & Ovadia 2004; Trussell *et al.* 2004).

In the context of biological invasions where invasive species may replace or dominate native counterparts, asymmetries in the combination of density- and trait-mediated effects exerted by higher trophic level native predators have the potential to confound expectations of invader impact based solely on individual level traits. Non-consumptive effects are of particular importance in this respect, as the presence of higher predators has the capacity to reverse the efficacy of species feeding at lower trophic levels; the most effective consumers in isolation may become the least effective when faced with predator threat (Mowles, Rundle & Cotton 2011). Furthermore, it is necessary to account for the fact that higher predators may consume both intermediate and basal species with either positive or negative impacts on the latter (Finke & Denno 2005; Schmitz 2007; Schneider, Scheu & Brose 2012). In either case, these impacts can be non-additive (Sih, Englund & Wooster 1998; Griffen 2006), where the sum of individual predators' isolated impacts differs from the combined impact when predators interact. Such phenomena, collectively termed emergent multiple predator effects (MPEs; Sih, Englund & Wooster 1998), must be unravelled if we are to understand how individual level traits are expressed in multi-individual situations, be they intra-specific, inter-specific or, as is manifestly the case in the majority of natural communities, both.

Multiple predator effects are often quantified for single, or few, prey densities (Harvey, White & Nakamoto 2004; Griffen 2006; Van Son & Thiel 2006), but the magnitude of an MPE may vary with prey density, and in terms of prey population stability and viability, the specific shape of the relationship between prey density and prey consumption rate (i.e. the functional response) is as important as the magnitude (Williams & Martinez 2004). Although the use of functional responses is pervasive in ecology (Jeschke, Kopp & Tollrian 2002; Englund *et al.* 2011; Rall *et al.* 2012), they are infrequently used to quantify MPEs (but see Soluk 1993; Losey & Denno 1998), and are only recently being applied to understand and predict the impacts of invasive species (Bollache *et al.* 2008; Haddaway *et al.* 2012; Dick *et al.* 2013, in press).

Here, we use a comparative functional response-based approach (Dick *et al.* in press) to test whether two freshwater intermediate predators, the invasive Ponto-Caspian *Hemimysis anomala* Sars, 1907, and the native Irish *Mysis*

*salemaai* Audzijonyte & Väinölä (2005), exert different impacts on prey, as individuals, in conspecific groups and in conspecific groups in the presence of a higher fish predator, *Gasterosteus aculeatus* Linnaeus, 1758. These mysids represent an ideal study system with which to explore higher order interactions as, generally, mysids are gregarious, group-forming animals whose predatory efficacy is demonstrably related to their association with conspecifics (Hansson *et al.* 2001) which, in turn, can alter the non-consumptive effects exerted by higher predators (Lindén 2006). More specifically, whilst congeners of *M. salemaai* have themselves been implicated as damaging invaders (Spencer, McCelland & Stanford 1991), *H. anomala* is also known to have severe ecological impacts (Ketelaars *et al.* 1999; Ricciardi, Avlijas & Marty 2011), and is a more voracious predator of multiple prey species than *M. salemaai* (Dick *et al.* 2013).

First, we determine the individual-level functional responses of *H. anomala*, *M. salemaai* and *G. aculeatus* towards a common prey species, *Daphnia magna* Straus 1820. Then, we use these as a framework to explore how individual level impacts translate to impacts in multi-individual mixtures; we test the hypothesis that individual-level functional responses of these intermediate mysids predict their combined functional responses in groups, and explore how the presence of a higher predator alters the contribution of invader and native to impacts on basal prey.

## Materials and methods

### ANIMAL COLLECTION AND MAINTENANCE

During June 2012, invasive *Hemimysis anomala* and native *Mysis salemaai* were collected from Lough Derg, Co. Tipperary (52·90562°N, 8·34126°W); both species were closely matched for size (mean body mass/± SE = 19·3 mg/0·2 and 19·8 mg/0·2 respectively, $t_{98} = 1·73$, NS). Three-spined stickleback, *Gasterosteus aculeatus* (215·9 mg/2·6) were collected from Lough Neagh, Co. Armagh (54·49627°N, 6·38240°W). Each species was maintained separately in dechlorinated tap water at 12 °C on a reversed 12 D:12 L photoperiod (to facilitate daytime observation of nocturnal feeding) and supplied fish food flakes *ad libitum*, before being starved in isolation for 24 h prior to experimental trials.

*Daphnia magna* was used as a basal prey species in all trials; individuals were obtained from continuous laboratory cultures and transferred to holding tanks at 12 °C on a reversed 12 D:12 L photoperiod 10 d before trials. *D. magna* individuals were extracted from the holding tanks 24 h before trials by transferring cultures through 2 mm and 1 mm stacked sieves, yielding experimental animals with a wet weight of 2·9 mg/0·2 on the 1 mm sieve.

### ADDITIVE AND SUBSTITUTIVE EXPERIMENTAL DESIGNS

There is some debate as to the appropriateness of additive and substitutive experimental manipulations for quantifying emergent effects in ecological communities (Balvanera *et al.* 2006; Griffen 2006; O'Gorman, Enright & Emmerson 2008); substitutive

designs hold total predator abundance constant between single and multi-species mixtures, thereby removing it as an experimental confound, whereas additive designs use single predators, or single predatory-units, and compare these to mixtures of multiple predators or multiple predatory units. In this study we adopted an additive approach (Fig. 1a–e) for three reasons; first, due to the size difference between stickleback and mysids, their associated natural abundance and biomass should scale allometrically (Schneider, Scheu & Brose 2012). Second, substitutive designs only examine emergent effects between species relative to effects within species, and with mysids in particular, emergent conspecific effects are of clear importance. Finally, because mysid introductions often represent the insertion of a novel invertebrate planktivore into existing food webs (Spencer, McCelland & Stanford 1991), the ecological context is frequently additive, thus an equivalent design is necessary to understand the ecological consequences.
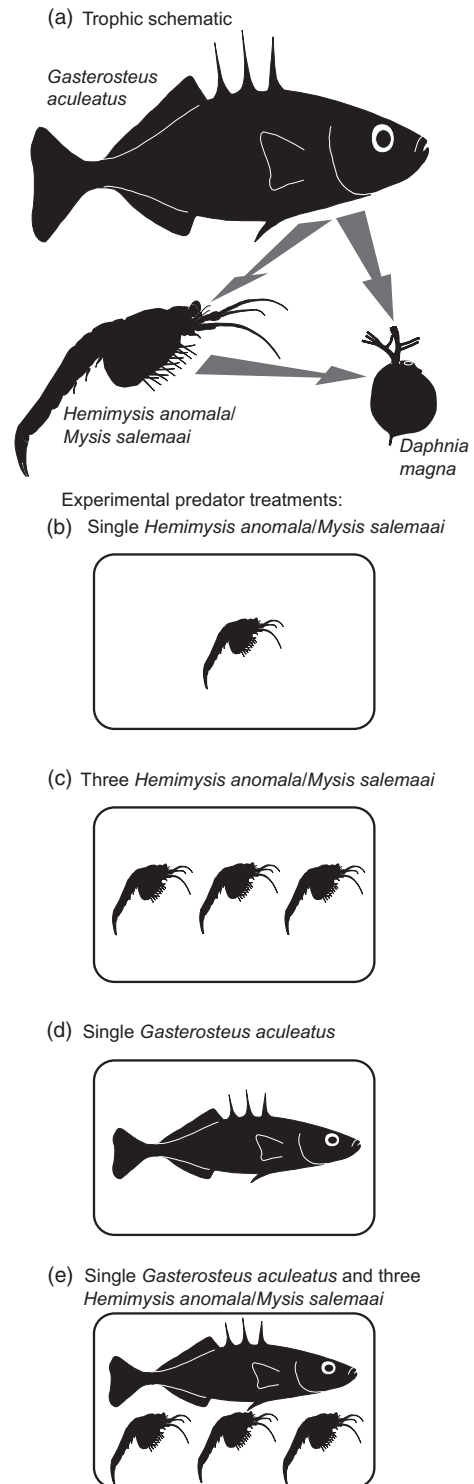
## EXPERIMENTAL TRIALS

Trials were conducted under 15 W red lights in arenas (22 × 22 cm) containing 4 L of dechlorinated tap water. Basal prey were introduced at seven densities (2, 4, 6, 8, 15, 30, 60, $n = 4$ each) 2 h before the introduction of predator treatments (Fig. 1b–e). Controls were predator-free arenas at all prey densities, $n = 4$ each. Trials were terminated after 3 h on removal of predators, after which surviving prey were counted.

Predation by *H. anomala* and *M. salemaai,* and intra-specific MPEs were compared by conducting trials with single predators and trials with groups of three conspecifics (Fig. 1b, c). *Per capita* consumption by single predators was multiplied by three (this value was capped at the maximum number of available prey) to generate estimates of additive group consumption for both species, which were compared with actual prey consumption by conspecific groups. To determine the presence of inter-specific MPEs between stickleback and conspecific mysid groups, trials were conducted with single stickleback predators and *D. magna* prey (Fig. 1d), combining prey consumption here with prey consumption from trials with mysid groups (also capped at maximum available prey); this gave estimates of additive inter-specific prey consumption, which were then compared with actual prey consumption by mixtures of interacting stickleback and conspecific mysid groups (Fig. 1e). Any mysids killed by stickleback were immediately replaced by individuals transferred from identical surplus mixtures; this ensured replacement mysids were in a comparable state of satiation and exposure to predatory threat. Pilot trials under experimental conditions indicated that maximal predation by stickleback in mixtures with either mysid species was not more than three individuals in three hours. Therefore, the necessary disturbance of mysid replacement was controlled for by extracting and / or replacing mysids with a dip net (or disturbing with a dip net in controls and single-stickleback treatments) such that there were always three similar disturbances throughout all trials. In trials involving mixtures of mysids and stickleback, we also recorded mysid mortality to quantify the direct effects of stickleback on invaders and natives.

## STATISTICAL ANALYSES

All statistical analyses were undertaken in R (R Core Team 2013). Here, we used functional response modelling not to gain



**Fig. 1.** (a) Trophic schematic indicating direction of interactions between predators and basal prey, and (b)–(e) predator treatments added to experimental arenas containing *Daphnia magna*.
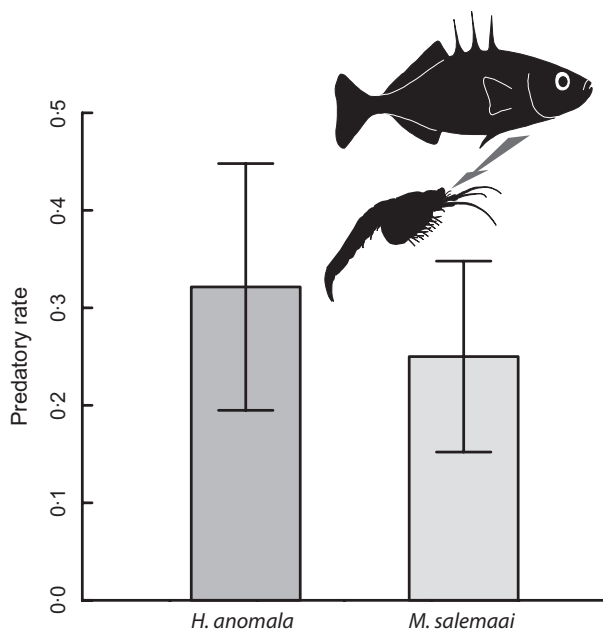
mechanistic insight into predator behaviour, as is frequently the case (Jeschke, Kopp & Tollrian 2002), but to understand the phenomenological consequences for prey populations. Functional response types were defined using logistic regression to determine the shape of the relationship between proportion of prey consumed and prey density for each data set. If the proportion of

prey consumed decreases with increasing prey density, then the logistic regression yields a significant negative first order term, and the functional response is appropriately described by a Type II model (Juliano 2001). Functional responses were subsequently modelled using maximum likelihood estimation (MLE; Bolker 2010) with the random predator equation, which assumes a Type II shape and accounts for the non-replacement of prey as they are consumed (Rogers 1972):

$$Ne = N0\,(1 - \exp\,(a\,(Neh - T))) \qquad \text{eqn 1}$$

where Ne is the number of prey eaten, N0 is the initial density of prey, $a$ is the attack rate, $h$ is the handling time and $T$ is the total time available.

Raw consumption data were non-parametrically bootstrapped ($n = 2000$), subsequently applying eqn (1) to each data set to construct 95% confidence intervals around the mean functional response curve of each predator treatment; MLE starting values of $a$ and $h$ for each bootstrapped data set were the same as those derived from the original data for each predator treatment. These analyses formed the basis of an integrated package for functional response analysis in R (frair; Pritchard 2013).

Generalised Linear Models (GLMs) assuming Poisson distributions were used to compare raw prey consumption between appropriate predator treatment pairings, with $z$-tests between coefficients used to ascribe significance – here no adjustment of α for multiplicity was used as all predator-treatment pairings were not logically comparable. A step-deletion procedure was used to select appropriate GLMs with $\chi^2$ used to compare residual deviance between models and, where appropriate, $\chi^2$ was reported to communicate a factor's relevance to the dependent variable.

## Results

Survival of *Daphnia magna* in controls averaged 99·8 % at 3 h, therefore we attribute most experimental mortality to predation. Where stickleback and groups of either *Hemimysis anomala* or *Mysis salemaai* were combined, neither mysid was more susceptible to stickleback predation ($\chi^2 = 0.25$, NS, Fig. 2), which occurred in only 29% of relevant trials, with mean number of mysids killed less than one for both *H. anomala* and *M. salemaai* (Fig. 2). Also, the initial prey density of *D. magna* had no effect on number of mysids consumed by stickleback ($\chi^2 = 0.32$, NS). Mysids spent time handling *D. magna* with their max-illipeds before consuming, whereas stickleback consumed *D. magna* whole. In trials where stickleback and mysids were combined, stickleback readily attacked both mysids and *D. magna*, although rarely consuming whole individuals when preying on mysids.

First-order terms derived from logistic regressions of proportions eaten were negative, indicating Type II functional responses in all cases (Table 1). Correspondingly, maximum likelihood estimations of attack rates, $a$, and handling times, $h$, derived from eqn (1) were all significant at the $P < 0.05$ level (Table 1).

When feeding alone, *H. anomala* consumed significantly more *D. magna* than did *M. salemaai* ($z = 4.48$,



**Fig. 2.** Predatory interactions between the higher fish predator *Gasterosteus aculeatus* and the intermediate mysid predators *Hemimysis anomala* and *Mysis salemaai* during relevant experimental trials. Values are mean numbers of mysids killed ± SE. Those mysids killed were replaced (see text for details).

**Table 1.** Parameter estimates and associated probabilities of first order terms from logistic regressions of proportions of prey consumed, alongside maximum likelihood estimations and associated probabilities of the parameters $a$ and $h$ from the random predator eqn (1)

| Predators | Actual/predicted data | First order term, $P$ | $a$ | $P$ | $h$ | $P$ |
|---|---|---|---|---|---|---|
| 1 *H. anomala* | Actual | −0·027, <0·001 | 0·785 | <0·001 | 0·144 | <0·001 |
| 1 *M. salemaai* | Actual | −0·017, 0·011 | 0·194 | <0·001 | 0·127 | 0·02 |
| 1 *G. aculeatus* | Actual | −0·024, <0·001 | 0·796 | <0·001 | 0·088 | <0·001 |
| 3 *H. anomala* | Actual | −0·029, <0·001 | 1·672 | <0·001 | 0·037 | <0·001 |
| 3 *H. anomala* | Predicted | −0·030, <0·001 | 2·007 | <0·001 | 0·041 | <0·001 |
| 3 *M. salemaai* | Actual | −0·011, 0·016 | 0·52 | <0·001 | 0·027 | 0·008 |
| 3 *M. salemaai* | Predicted | −0·002, <0·001 | 0·7 | <0·001 | 0·045 | <0·001 |
| 3 *H. anomala*, 1 *G. aculeatus* | Actual | −0·021, <0·001 | 1·742 | <0·001 | 0·017 | <0·001 |
| 3 *H. anomala*, 1 *G. aculeatus* | Predicted | −0·008, 0·036 | 2·161 | <0·001 | 0·022 | <0·001 |
| 3 *M. salemaai*, 1 *G. aculeatus* | Actual | −0·001, 0·015 | 0·532 | <0·001 | 0·026 | 0·013 |
| 3 *M. salemaai*, 1 *G. aculeatus* | Predicted | −0·023, <0·001 | 1·402 | 0·001 | 0·004 | <0·001 |

*H. anomala*, *Hemimysis anomala* ; *M. salemaai*, *Mysis salemaai*; *G. aculeatus*, *Gasterosteus aculeatus*.

$P$ <0·001), and had a higher functional response, but 95% confidence intervals overlapped above prey densities of 22 (Fig. 3a); here, higher consumption at lower prey densities by *H. anomala* manifested as a result of a higher attack rate, which was comparable with that of the larger stickleback (Table 1), whose functional response towards basal prey is shown in Fig 3b. When feeding in conspecific groups, *H. anomala* consumed significantly more *D. magna* than did *M. salemaai* ($z = 4.48$, $P$ <0·001) and the invader had a higher functional response, but here 95% confidence intervals overlapped only above prey densities of 37 (Fig. 4a). Again, the higher consumption by invasive conspecifics is attributable to higher attack rates, as handling times were comparable (Table 1). No emergent MPEs were apparent for either invader or native when feeding in conspecific groups, as consumption by groups was not significantly different to that predicted from additive estimates derived from single predator consumption (*H. anomala*; $z = 0.14$, NS, *M. salemaai*;
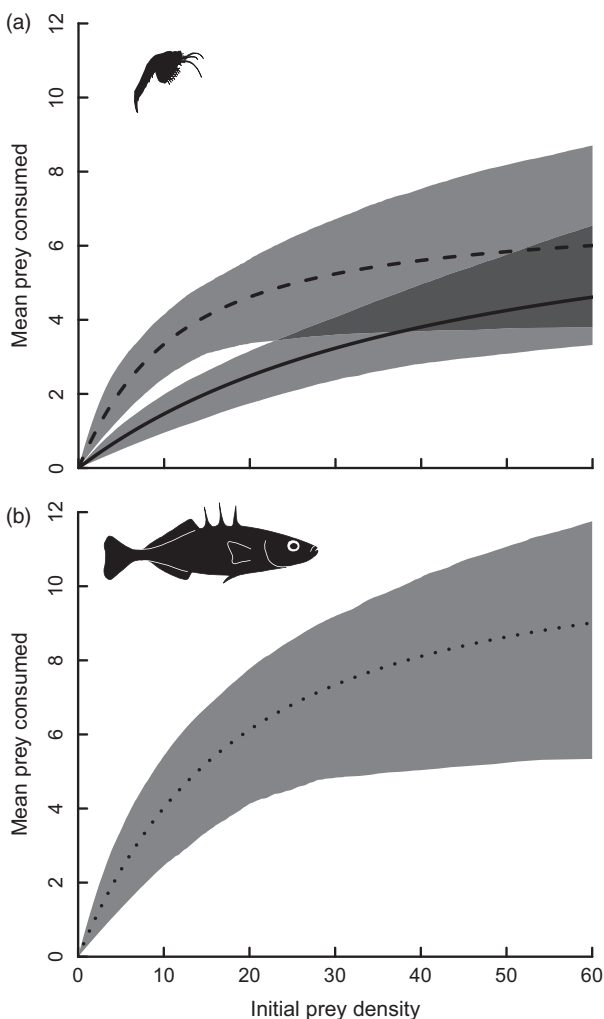


**Fig. 3.** Single predator functional responses towards *Daphnia magna* of (a) *Hemimysis anomala* (dashed line) and *Mysis salemaai* (solid line) and (b) *Gasterosteus aculeatus* (dotted line). Shaded areas are bootstrapped 95 % confidence intervals.
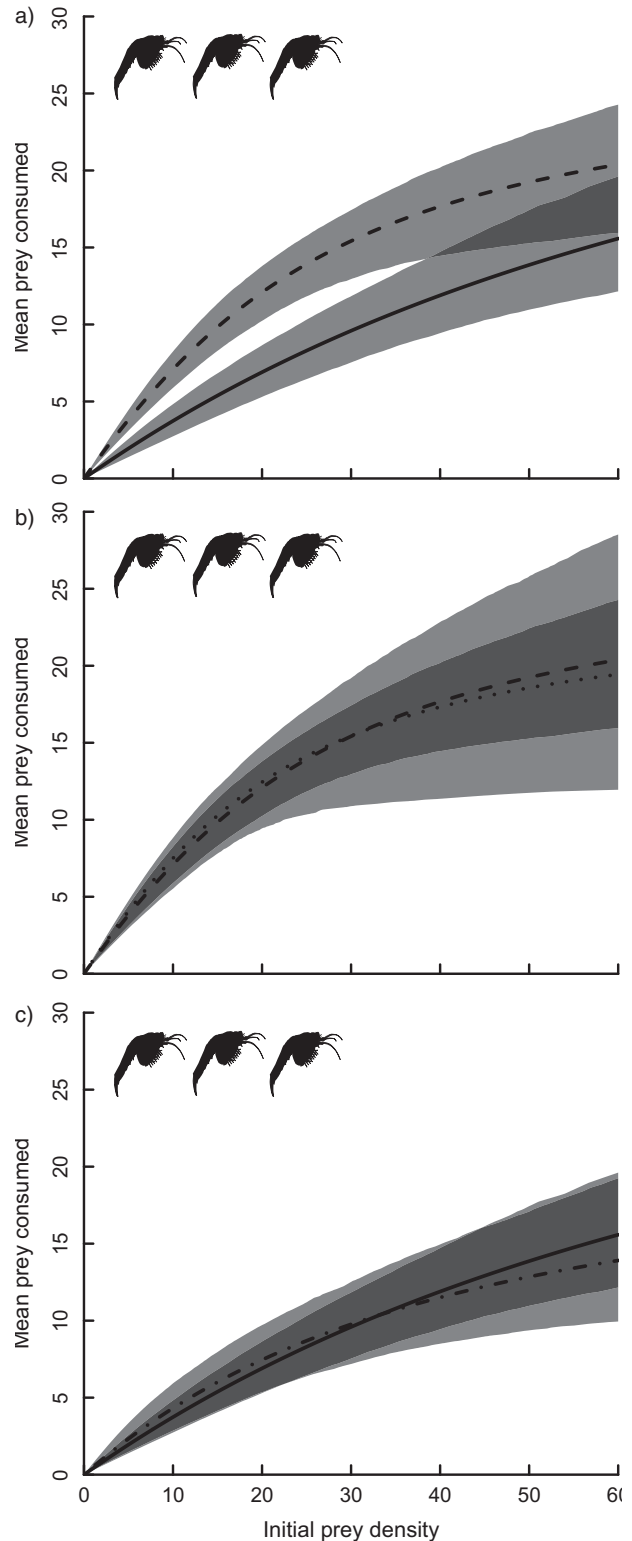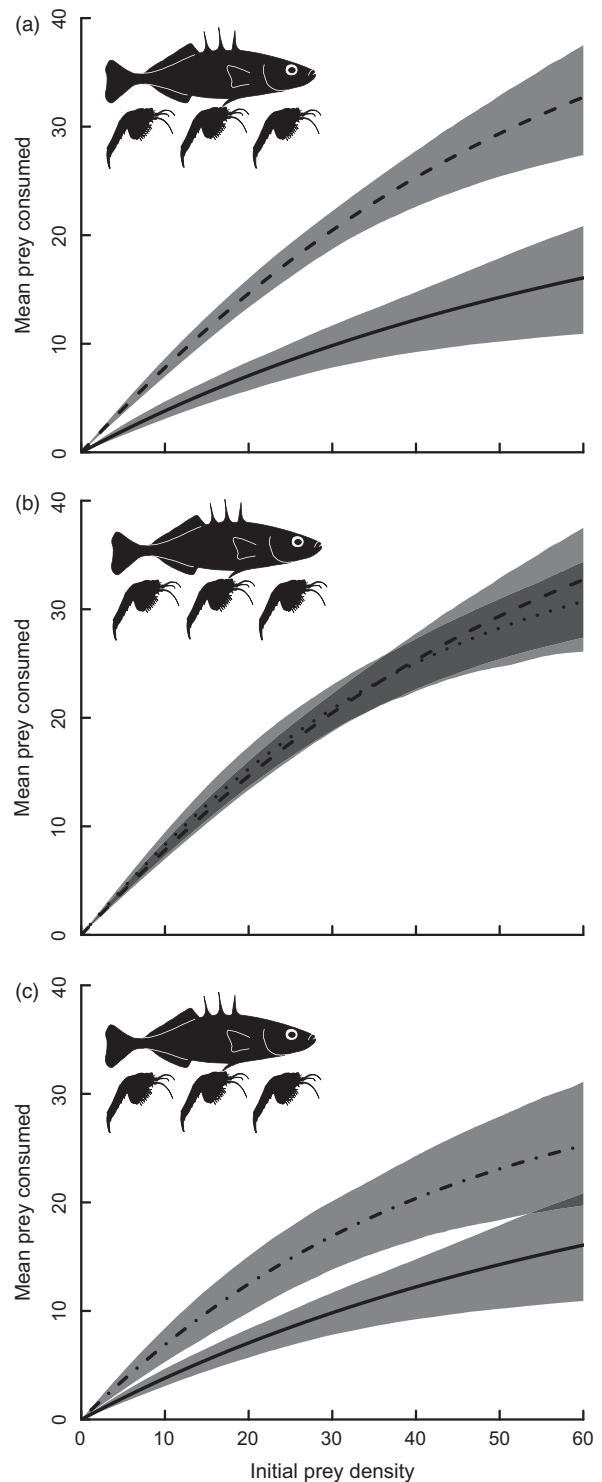


**Fig. 4.** Predicted and actual functional responses of three mysids towards *Daphnia magna*: (a) actual functional responses of three *Hemimysis anomala* (dashed line) and three *Mysis salemaai* (solid line); (b) actual functional response of three *H. anomala* (dashed line) and predicted functional response for this species (dotted line) based on Fig. 3a data; (c) actual functional response of three *M. salemaai* (solid line) and predicted functional response for this species (dash-dotted line) based on Fig. 3a data. Shaded areas are bootstrapped 95 % confidence intervals.

$z = 0.11$, NS). Accordingly, 95% confidence intervals overlapped for actual and predicted group functional responses over the entire range of prey densities for both *H. anomala* (Fig. 4b) and *M. salemaai* (Fig. 4c). Consumption of *D. magna* by the stickleback and *H. anomala* mixture was significantly higher than by the stickleback and *M. salemaai* mixture ($z = 18.06$, $P < 0.001$), and here 95% confidence intervals did not overlap at all for the functional response curves (Fig. 5a). The functional response parameters reflected this difference, as attack rates were higher and handling times were shorter in the invasive mixture (Table 1). No emergent MPE occurred between *H. anomala* groups and stickleback (Fig. 5b), as actual prey consumption by this mixture was additive, i.e. not significantly different from predictions derived from combining prey consumption by stickleback and *H. anomala* groups ($z = 0.04$, NS), and the 95% confidence intervals for the predicted and actual functional responses of this mixture overlapped throughout the entire range of prey densities (Fig. 5b). In contrast, an emergent MPE was apparent for the stickleback and *M. salemaai* mixture (Fig. 5c), as predicted prey consumption derived from combining prey consumption by stickleback and *M. salemaai* groups was significantly higher than actual prey consumption for this mixture ($z = 5.20$, $P < 0.001$). Further, the actual functional response was lower than the predicted functional response for this mixture, where 95% confidence intervals overlapped only at the highest prey densities (Fig. 5c) and actual attack rates were lower, whilst actual handling times were longer (Table 1).

## Discussion

As ecological communities almost exclusively consist of multiple predators feeding on shared prey resources (Sih, Englund & Wooster 1998), accounting for emergent intra- and inter-specific MPEs is essential for understanding, and perhaps ultimately predicting, the impacts of invasive predators. Here we demonstrate that the invasive *Hemimysis anomala* has a higher functional response towards prey, *Daphnia magna*, than does its native counterpart, *Mysis salemaai*. We also find that predatory impacts of conspecific groups of both *H. anomala* and *M. salemaai* are additive, as they are well predicted by the impacts of individuals. However, the range of prey densities at which functional responses did not overlap for invaders and natives increased between individual and group-level functional responses, reiterating the importance of considering impacts in an ecologically relevant manner. Here, individual-level functional responses may underestimate the difference between invader and native, even before the influence of a higher predator is quantified. Indeed, the presence of the higher predator, *G. aculeatus*, elicited an emergent impact-reducing MPE within the native mixture; in contrast, the invasive mixture resulted in additive impacts on the basal prey.



**Fig. 5.** Predicted and actual functional responses of three mysids and one *Gasterosteus aculeatus* towards *Daphnia magna*: (a) actual functional responses of three *Hemimysis anomala* and one *G. aculeatus* (dashed line) and three *Mysis salemaai* and one *G. aculeatus* (solid line); (b) actual functional response of three *H. anomala* and one *G. aculeatus* (dashed line) and predicted functional response for this mixture (dotted line) based on Fig. 3b and Fig. 4a data; (c) actual functional response of three *M. salemaai* and one *G. aculeatus* (solid line) and predicted functional response for this mixture (dash-dotted line) based on Fig. 3b and Fig. 4a data. Shaded areas are bootstrapped 95 % confidence intervals.

Importantly, the higher predator showed no preference for either mysid species as prey, thus we suggest that the MPE associated with the higher predator and native *M. salemaai* is the result of predator avoidance behaviour, i.e. a trait-mediated indirect interaction (TMII), whereas the invasive *H. anomala* appears to be less influenced by the same predator threat. Typically, such pronounced differences amongst species occupying the same functional niche correspond directly to differences in vulnerability to predation (Mowles, Rundle & Cotton 2011), but here this is clearly not the case. Although cascading effects are classically considered to be driven by density-mediated indirect interactions (DMIIs; Abrams 1995; Abrams *et al.* 1996), a growing body of evidence highlights the importance of TMIIs (Schmitz, Krivan & Ovadia 2004) which, in many instances, are the primary drivers of cascades (Gabowski 2004; Trussell, Ewanchuk & Matassa 2006; Zhao *et al.* 2013). Even so, the relative contributions of DMIIs and TMIIs to the net effects of predators remains a source of some debate; in part, because interplay between the state-dependence and allometry of predator-prey relationships, as well as the breadth of prey habitat use relative to predators, all impinge on resulting net effects (Ovadia & Schmitz 2002; Schmitz, Krivan & Ovadia 2004). Ultimately, however, the absolute limits of predator-prey interactions can be abstracted and defined primarily by body-mass ratios (Brose 2010; Schneider, Scheu & Brose 2012). We note that the function of *G. aculeatus*, both as a competitor and predator of mysids, is usefully viewed in this context, particularly because *G. aculeatus* rarely consumed whole mysids. As *G. aculeatus* showed no preference for mysids at lower basal prey densities (where mysids represent a larger proportion of the total available prey), we speculate that mysids represent a sub-optimal prey type and size for the higher predator, and that any associated predation can be viewed as interference competition.

Although a broad, size-based approach to quantify predator-prey dynamics has the capacity to progress our understanding of impact in food webs (Schneider, Scheu & Brose 2012), we also highlight the need to consider fine-scale behavioural and ecological context. Historically, mysids have been deliberately introduced into new habitats precisely because they represent an ideal prey size and type for larger fish predators. However, as a result of diurnal habitat shifts on the part of the mysids, the ecosystem-level consequence is often a prevalence of competition over predation and an associated decline in fish abundance (Spencer, McCelland & Stanford 1991; Ricciardi, Avlijas & Marty 2011). It is apparent, then, that any experimental manipulations designed to inform our understanding of impact in species that undergo significant habitat shifts must reflect the appropriate context. For example, it is clear that increased light levels would probably increase the predatory efficacy of *G. aculeatus*, towards both mysids and cladocerans (Townsend & Risebrow 1982), but the low light levels used in this study

reflect the fact that these intermediate and basal prey primarily encounter limnetic *G. aculeatus* in inshore surface waters during the night (Southern & Gardiner 1932). In addition, the basal prey concentrations used in our experimental trials fall well within natural abundances found in the field, typically between 1 and 100 individuals $L^{-1}$ (Southern & Gardiner 1932; Pociecha, Higgins & McCarthy 2010). Therefore, we contend that the results presented here should not simply be viewed as an artefact of coercing mixtures of species that lack real-word relevance.

The 'adaptive lag' (Carlsson, Sarnelle & Strayer 2009) of native predator assemblages is one possible mechanism which may facilitate the rapid spread and establishment of non-native species, both because native predators may not recognise a novel resource and because invaders may be indifferent to novel predator threat, but here we note that *G. aculeatus* co-occurs with both mysids in their respective native environments. Thus, we cannot attribute the apparent lack of a TMII associated with invasive *H. anomala* to differences in evolutionary experience. Although the precise mechanisms by which density- and trait-mediated interactions combine to elicit net impacts are necessarily masked, particularly as multiple higher order interactions can yield net additivity (Sih, Englund & Wooster 1998), the consequences for prey populations are clear; in this example, the presence of a higher predator exacerbates the difference in impact between invasive *H. anomala* and native *M. salemaai,* and the observed overlap in individual-level functional responses at high prey densities is attenuated, or eliminated, in multiple-individual mixtures.

Emergent MPEs have been observed to increase in magnitude with increasing prey density in studies that have incorporated prey density into experimental design (Soluk 1993; Losey & Denno 1998). Similarly, this study reiterates the importance of such an experimental approach, given the variety of conclusions which could be drawn from a single prey density using these data (see also Dick *et al.* in press). It is apparent that differences in functional response shape and magnitude, at lower prey densities in particular, have the capacity to drive substantial changes in prey populations. Generally, ecologists consider Type III functional responses to impart stability to prey populations, whilst Type II functional responses are regarded as de-stabilising (Murdoch & Oaten 1975; Wennhage 2002; Taylor & Collie 2003; Rall, Guill & Brose 2008; Alexander *et al.* 2012). However, Williams & Martinez (2004) assert that the difference between what constitutes a stabilising or de-stabilising relationship, both at a population and ecosystem level, is far more subtle than this, and they challenge empiricists to develop experimental designs capable of detecting these subtleties. Our experimental design focuses on lower prey densities for this very reason, and we suggest that the discernible difference between the functional responses of *H. anomala* and *M. salemaai* at lower prey densities contributes to the difference in known field impacts between these species.

From its native range in the Ponto-Caspian region of eastern Europe, *H. anomala* has spread rapidly throughout western Europe (Ketelaars *et al.* 1999; Bij de Vaate *et al.* 2002; Minchin & Boelens 2010) and North America (Ricciardi, Avlijas & Marty 2011). Species in the *Mysis relicta* group, of which *M. salemaai* is a member (Audzijonyté & Väinölä 2005), are known to have deleterious ecological impacts that can propagate to the highest trophic levels (Spencer, McCelland & Stanford 1991; Ricciardi, Avlijas & Marty 2011). Introduced populations of *H. anomala*, however, have known field impacts that are even more pronounced (Dick *et al.* 2013), often leading to the elimination of prey species (Ketelaars *et al.* 1999). *H. anomala* individuals were previously shown to have higher functional responses towards multiple prey species than comparator species in the *M. relicta* group (Dick *et al.* 2013), but this study examined only individual-level functional responses. The current study indicates that when placed in the broader community, the impacts of *M. salemaai*, as natives or invaders, may be somewhat ameliorated by higher predators through a combination of direct and non-consumptive mechanisms, whereas the impacts of invasive *H. anomala* may be primarily ameliorated via direct mechanisms. As studies have indicated that predator avoidance behaviour in gregarious mysids is more pronounced in individuals than in groups (Lindén 2006), the ecological consequences of direct and non-consumptive effects will primarily relate to the group level. Further, the risk-foraging trade-offs that result from predator avoidance can result in reduced growth and fecundity (Lima 1998), and *M. salemaai* is only capable of producing one brood per year, whereas *H. anomala* can produce up to four (Minchin & Boelens 2010). Thus, the higher *per capita* impact of this invader may facilitate its ability to maintain higher population densities, further exacerbating impacts within invaded communities. Considering how these observed differences between invader, native and their immediate interactors, propagate into the wider food web is clearly speculative, but two salient points are apparent; weak interactors and predator interference tend to stabilise predator-prey dynamics and food webs (McCann 2000; Arditi *et al.* 2004; Rall, Guill & Brose 2008). Thus, the mechanisms by which *H. anomala*, and perhaps other successful invasive predators, de-stabilise food webs may be threefold; first, by virtue of being stronger interactors than native equivalents, second, by reducing net predator interference and third, by eliminating other species, thereby increasing the average interaction strength within a food web.

Finally, we highlight the utility of comparative functional response studies as tools to inform our understanding of invasions (Bollache *et al.* 2008; Dick *et al.* 2013, in press), particularly through their potential to quantify MPEs and TMIIs (McCoy, Stier & Osenberg 2012; Alexander, Dick & O'Connor in press), which must be addressed if we are to develop a predictive capability to describe how existing, emerging and potential invasive predators might impact on recipient communities.

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## References

Abrams, P.A. (1995) Implications of dynamically variable traits for identifying, classifying, and measuring direct and indirect effects in ecological communities. *The American Naturalist*, **146**, 112–134.

Abrams, P.A., Menge, B.A., Mittelbach, G.G., Spiller, D. & Yodzis, P. (1996) The role of indirect effects in food webs. *Food Webs: Integration of Patterns and Dynamics* (eds G.A. Polis & K.O. Winemiller), pp. 371–395. Chapman & Hall, New York.

Alexander, M.E., Dick, J.T.A. & O'Connor, N.E. (in press) Trait-mediated indirect interactions in a marine intertidal system as quantified by functional responses. *Oikos*, doi: 10.1111/j.1600-0706.2013.00472.x.

Alexander, M.E., Dick, J.T.A., O'Connor, N.E., Haddaway, N.R. & Farnsworth, K.D. (2012) Functional responses of the intertidal amphipod *Echinogammarus marinus*: effects of prey supply, model selection and habitat complexity. *Marine Ecology Progress Series*, **468**, 191–202.

Arditi, R., Callois, J.M., Tyutyunov, Y. & Jost, C. (2004) Does mutual interference always stabilize predator–prey dynamics? A comparison of models. *Comptes Rendus Biologies*, **327**, 1037–1057.

Audzijonyté, A. & Väinölä, R. (2005) Diversity and distributions of circumpolar fresh- and brackish-water *Mysis* (Crustacea: Mysida): descriptions of *M. relicta* Lovén, 1862, *M. salemaai* n. sp., *M. segerstralei* n. sp. and *M. diluviana* n. sp., based on molecular and morphological characters. *Hydrobiologia*, **544**, 89–141.

Balvanera, P., Pfisterer, A.B., Buchmann, N., He, J.S., Nakashizuka, T., Raffaelli, D. *et al.* (2006) Quantifying the evidence for biodiversity effects on ecosystem functioning and services. *Ecology Letters*, **9**, 1146–1156.

Bij de Vaate, A., Jazdzewski, K., Ketelaars, H.A.M., Gollasch, S. & Van der Velde, G. (2002) Geographical patterns in range extension of Ponto-Caspian macroinvertebrate species in Europe. *Canadian Journal of Fisheries and Aquatic Sciences*, **59**, 1159–1174.

Bolker, B.M. (2010) *bbmle: Tools for General Maximum Likelihood Estimation*. R Package. http://www.cran.rproject.org/.

Bollache, L., Dick, J.T.A., Farnsworth, K.D. & Montgomery, I.W. (2008) Comparison of the functional responses of invasive and native amphipods. *Biology Letters*, **4**, 166–169.

Brose, U. (2010) Body-mass constraints on foraging behaviour determine population and food-web dynamics. *Functional Ecology*, **24**, 28–34.

Carlsson, N.O., Sarnelle, O. & Strayer, D.L. (2009) Native predators and exotic prey – an acquired taste? *Frontiers in Ecology and the Environment*, **7**, 525–532.

Dick, J.T.A., Gallagher, K., Avlijas, S., Clarke, H.C., Lewis, S.E., Leung, S. *et al.* (2013) Ecological impacts of an invasive predator explained and predicted by comparative functional responses. *Biological Invasions*, **15**, 837–846.

Dick, J.T.A., Alexander, M.E., Jeschke, J.M., Ricciardi, A., MacIsaac, H.J., Robinson, T.B. *et al.* (in press) Advancing impact prediction and hypothesis testing in invasion ecology using a comparative functional response approach. *Biological Invasions*, DOI 10.1007/s10530-013-0550-8.

Englund, G., Ohlund, G., Hein, C.L. & Diehl, S. (2011) Temperature dependence of the functional response. *Ecology Letters*, **14**, 914–921.

Finke, D.L. & Denno, R.F. (2005) Predator diversity and the functioning of ecosystems: the role of intraguild predation in dampening trophic cascades. *Ecology Letters*, **8**, 1299–1306.

Gabowski, J.H. (2004) Habitat complexity disrupts predator – prey interactions but not the trophic cascade on oyster reefs. *Ecology*, **85**, 995–1004.

Griffen, B.D. (2006) Detecting emergent effects of multiple predator species. *Oecologia*, **148**, 702–709.

Haddaway, N.R., Wilcox, R.H., Heptonstall, R.E.A., Griffiths, H.M., Mortimer, R.J.G., Christmas, M. *et al.* (2012) Predatory functional response and prey choice identify predation differences between native/invasive and parasitised/unparasitised crayfish. *PLoS ONE*, **7**, e32229.

Hansson, S., De Stasio, B., Gorokhova, E. & Mohammadian, M. (2001) Ratio-dependent functional responses - tests with the zooplanktivore *Mysis mixta. Marine Ecology Progress Series*, **216**, 181–189.

Harvey, B.C., White, J.L. & Nakamoto, R.J. (2004) An emergent multiple predator effect may enhance biotic resistance in a stream fish assemblage. *Ecology*, **85**, 127–133.

Hassell, M.P. (1978) *The Dynamics of Arthropd Predator-Prey Systems*. Priceton University Press, Princeton, NJ.

Jeschke, J., Kopp, M. & Tollrian, R. (2002) Predator functional responses: discriminating between handling and digesting prey. *Ecological Monographs*, **72**, 95–112.

Juliano, S.A. (2001) Nonlinear curve fitting. *Design and Analysis of Ecological Experiments*, 2nd edn (eds S.M. Scheiner & J. Gurevitch), pp. 178–196. Oxford University Press, Oxford.

Ketelaars, H.A.M., Lambregts-van de Clundert, F.E., Carpentier, C.J., Wagenvoort, A.J. & Hoogenboezem, W. (1999) Ecological effects of the mass occurrence of the Ponto–Caspian invader, *Hemimysis anomala* G.O. Sars, 1907 (Crustacea: Mysidacea), in a freshwater storage reservoir in the Netherlands, with notes on its autecology and new records. *Hydrobiologia*, **394**, 233–248.

Kolar, C.S. & Lodge, D.M. (2001) Progress in invasion biology: predicting invaders. *Trends in Ecology & Evolution*, **16**, 199–204.

Lima, S.L. (1998) Nonlethal effects in the ecology of predator-prey interactions. *BioScience*, **48**, 25–34.

Lindén, E. (2006) The more the merrier: swarming as an antipredator strategy in the mysid *Neomysis integer. Aquatic Ecology*, **41**, 299–307.

Losey, J.E. & Denno, R.F. (1998) Positive predator – predator interactions: enhanced predation rates and synergistic suppression of aphid populations. *Ecology*, **79**, 2143–2152.

McCann, K.S. (2000) The diversity-stability debate. *Nature*, **405**, 228–233.

McCoy, M.W., Stier, A.C. & Osenberg, C.W. (2012) Emergent effects of multiple predators on prey survival: the importance of depletion and the functional response. *Ecology Letters*, **15**, 1449–1456.

Minchin, D. & Boelens, R. (2010) *Hemimysis anomala* is established in the Shannon River Basin District in Ireland. *Aquatic Invasions*, **5**, S71–S78.

Mowles, S.L., Rundle, S.D. & Cotton, P.A. (2011) Susceptibility to predation affects trait-mediated indirect interactions by reversing interspecific competition. *PLoS ONE*, **6**, e23068.

Murdoch, W.W. & Oaten, A. (1975) Predation and population stability. *Advances in Ecological Research*, **9**, 1–131.

O'Gorman, E.J., Enright, R.A. & Emmerson, M.C. (2008) Predator diversity enhances secondary production and decreases the likelihood of trophic cascades. *Oecologia*, **158**, 557–567.

Ovadia, O. & Schmitz, O.J. (2002) Linking individuals with ecosystems: experimentally identifying the relevant organizational scale for predicting trophic abundances. *Proceedings of the National Academy of Sciences of the United States of America*, **99**, 12927–12931.

Peacor, S.D. & Werner, E.E. (2001) The contribution of trait-mediated indirect effects to the net effects of a predator. *Proceedings of the National Academy of Sciences of the United States of America*, **98**, 3904–3908.

Pociecha, A., Higgins, T. & McCarthy, K. (2010) A preliminary study on the plankton assemblages of Lough Derg (Ireland) during a winter-spring season. *Oceanological and Hydrobiological Studies*, **39**, 145–154.

Pritchard, D.W. (2013) frair: a package for functional response analysis in R. Under development on GitHub: https://github.com/dpritchard/frair.

R Development Core Team (2013) *R: A language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-project.org/.

Rall, B.C., Guill, C. & Brose, U. (2008) Food-web connectance and predator interference dampen the paradox of enrichment. *Oikos*, **117**, 202–213.

Rall, B.C., Brose, U., Hartvig, M., Kalinkat, G., Schwarzmüller, F., Vucic-Pestic, O. *et al.* (2012) Universal temperature and body-mass scaling of feeding rates. *Philosophical Transactions of the Royal Society of London Series B, Biological Sciences*, **367**, 2923–2934.

Ricciardi, A., Avlijas, S. & Marty, J. (2011) Forecasting the ecological impacts of the *Hemimysis anomala* invasion in North America: lessons from other freshwater mysid introductions. *Journal of Great Lakes Research*, **38**, 7–13.

Rogers, D. (1972) Random search and insect population models. *Journal of Animal Ecology*, **41**, 369–383.

Schmitz, O.J. (2007) Predator diversity and trophic interactions. *Ecology*, **88**, 2415–2426.

Schmitz, O.J., Krivan, V. & Ovadia, O. (2004) Trophic cascades: the primacy of trait-mediated indirect interactions. *Ecology Letters*, **7**, 153–163.

Schneider, F.D., Scheu, S. & Brose, U. (2012) Body mass constraints on feeding rates determine the consequences of predator loss. *Ecology Letters*, **15**, 436–443.

Sih, A., Englund, G. & Wooster, D. (1998) Emergent impacts of multiple predators on prey. *Trends in Ecology & Evolution*, **13**, 350–355.

Simberloff, D., Martin, J.L., Genovesi, P., Maris, V., Wardle, D.A., Aronson, J. *et al.* (2013) Impacts of biological invasions: what's what and the way forward. *Trends in Ecology & Evolution*, **28**, 58–66.

Soluk, D.A. (1993) Multiple predator effects: predicting combined functional responses of stream fish and invertebrate predators. *Ecology*, **74**, 219–225.

Sommer, U. (1992) Phosphorus-limited *Daphnia*: intraspecific facilitation instead of competition. *Limnology and Oceanography*, **37**, 966–973.

Southern, R. & Gardiner, A.C. (1932) Reports from the Limnological Laboratory. II. The diurnal migrations of the crustacea of the plankton in Lough Derg. *Proceedings of the Royal Irish Academy Section B: Biological, Geological, and Chemical Science*, **40**, 121–159.

Spencer, C.N., McCelland, B.R. & Stanford, J.A. (1991) Shrimp stocking, salmon collapse, and eagle displacement. *BioScience*, **44**, 14–21.

Taylor, D.L. & Collie, J.S. (2003) Effect of temperature on the functional response and foraging behavior of the sand shrimp *Crangon septemspinosa* preying on juvenile winter flounder *Pseudopleuronectes americanus. Marine Ecology Progress Series*, **263**, 217–234.

Townsend, C.R. & Risebrow, A.J. (1982) The influence of light level on the functional response of a zooplanktonivorous fish. *Oecologia*, **53**, 293–295.

Trussell, G.C., Ewanchuk, P.J. & Matassa, C.M. (2006) Habitat effects on the relative importance of trait- and density-mediated indirect interactions. *Ecology Letters*, **9**, 1245–1252.

Trussell, G.C., Ewanchuk, P.J., Bertness, M.D. & Silliman, B.R. (2004) Trophic cascades in rocky shore tide pools: distinguishing lethal and nonlethal effects. *Oecologia*, **139**, 427–432.

Van Kleunen, M., Dawson, W., Schlaepfer, D., Jeschke, J.M. & Fischer, M. (2010) Are invaders different? A conceptual framework of comparative approaches for assessing determinants of invasiveness. *Ecology Letters*, **13**, 947–958.

Van Son, T.C. & Thiel, M. (2006) Multiple predator effects in an intertidal food web. *Journal of Animal Ecology*, **75**, 25–32.

Wennhage, H. (2002) Vulnerability of newly settled plaice (*Pleuronectes platessa* L.) to predation: effects of habitat structure and predator functional response. *Journal of Experimental Marine Biology and Ecology*, **269**, 129–145.

Werner, E.E. & Peacor, S.D. (2003) A review of trait-mediated indirect interactions in ecological communities. *Ecology*, **84**, 1083–1100.

Williams, R.J. & Martinez, N.D. (2004) Stabilization of chaotic and non-permanent food-web dynamics. *The European Physical Journal B – Condensed Matter and Complex Systems*, **38**, 297–303.

Zhao, C., Griffin, J.N., Wu, X. & Sun, S. (2013) Predatory beetles facilitate plant growth by driving earthworms to lower soil layers. *The Journal of Animal Ecology*, **82**, 749–758.