Deep impact: *in situ* functional responses reveal context-dependent interactions between vertically migrating invasive and native mesopredators and shared prey

DANIEL BARRIOS-O'NEILL*, JAIMIE T. A. DICK*, ANTHONY RICCIARDI[†], HUGH J. MACISAAC[‡] AND MARK C. EMMERSON*

Institute for Global Food Security, School of Biological Sciences, Queen's University Belfast, Belfast, U.K.
[†]*Redpath Museum, McGill University, Montreal, QC, Canada*
[‡]*Great Lakes Institute for Environmental Research, University of Windsor, Windsor, ON, Canada*

SUMMARY

1. The ecological effects of invasive species depend on myriad environmental contexts, rendering understanding problematic. Functional responses provide a means to quantify resource use by consumers over short timescales and could therefore provide insight into how the effects of invasive species vary over space and time. Here, we use novel *in situ* microcosm experiments to track changes in the functional responses of two aquatic mesopredators, one native and the other an invader, as they undergo diel vertical migrations through a lake water column.

2. The Ponto–Caspian mysid, *Hemimysis anomala*, a known ecologically damaging invader, generally had higher a functional response towards cladoceran prey than did a native trophic analogue, *Mysis salemaai*. However, this differential was spatiotemporally dependent, being minimal during the day on the lake bottom, and increasing at night, particularly inshore.

3. Because the functional response of the native predator was spatiotemporally consistent, the above pattern was driven by changes in the invader functional response over the diel cycle. In particular, the functional response of *H. anomala* was significantly reduced on the lake bottom during the daytime relative to night, and predation was especially pronounced in shallow surface waters.

4. We demonstrate the context dependency of the effects of an invasive predator on prey populations and emphasise the utility of functional responses as tools to inform our understanding of predator–prey interactions. *In situ* manipulations integrate experimental rigour with field relevance and have the potential to reveal how impacts manifest over a range of spatiotemporal scales.

Keywords: diurnal vertical migration, ecological impacts, functional response, *in situ* predation, invasive species

Introduction

Understanding how invasive species affect recipient communities remains a focal issue in ecology, yet there is a prevailing perception that such understanding will remain elusive (Gilpin, 1990; Williamson, 1999; Simberloff *et al.*, 2013), primarily because impacts are often strongly context dependent (Ricciardi *et al.*, 2013). Impacts may vary over space and time, where effects are modified by myriad environmental factors, both abiotic (e.g. temperature) and biotic (e.g. predator interference) (Barrios-O'Neill *et al.*, 2014; Dick *et al.*, 2014). In addition, the scale at which effects are considered will have a strong bearing on conclusions about their direction and magnitude, as is the case with diversity–invasibility relationships (Byers & Noonburg, 2003). For example, the effects of invasive species can change dramatically over decadal timescales (Strayer *et al.*, 2006). Little is known, however, about how effects may vary over much shorter timescales, despite the fact that seasonal heterogeneity and diurnal heterogeneity are fundamental to the structure and function of ecological communities, and are well known to mediate species interactions (Townsend & Risebrow, 1982; Viherluoto & Viitasalo, 2001). Spatial

Correspondence: Daniel Barrios-O'Neill, School of Biological Sciences, Queen's University Belfast, 97 Lisburn Road, Belfast, Antrim, BT9 7BL, U.K. E-mail: doneill952@qub.ac.uk

variations in effects are better understood at finer scales and can be linked to spatial heterogeneity, whether exogenous, that is, meditated by variation in abiotic conditions (Kestrup, Dick & Ricciardi, 2010), or endogenous, that is, mediated by the interactions and dispersal of species (Melbourne *et al.*, 2007). Even so, finely resolved data on spatial impacts are scarce, because many inferences about the impacts of invasive species are drawn from raw observations of range size and abundance (Ricciardi *et al.*, 2013).

Despite the complexities of biological invasions, efforts to understand their impacts have revealed some useful generalisations (Ricciardi, *et al.*, 2013). For example, the invasion history of a species can be a useful indicator of its potential impacts elsewhere (Grosholz & Ruiz, 1996; Kulhanek, Ricciardi & Leung, 2011), but this approach intrinsically lacks relevance to novel invaders. In contrast, certain ecological traits can be linked to invasiveness and perhaps also to impact (e.g. Pyšek *et al.*, 2012), thus providing a means by which to anticipate the effects of invaders *a priori*. However, trait-based approaches that rely solely on correlates between impact and the attributes of successful invaders may be confounded because they make no provision for how invaders interact with the recipient environment (Ricciardi *et al.*, 2013). Therefore, methodologies that have the capacity to unify species traits with specific environmental context dependencies could advance our understanding of impact.

One promising trait-based methodology that can incorporate environmental context involves consideration of the relationship between resource use by invaders and their associated ecological impacts. Analysis of consumer functional responses (i.e. resource usage in relation to resource availability) provides a robust means to understand the stability of prey populations (Kalinkat *et al.*, 2013) and food webs (Williams & Martinez, 2004) and has a range of potential applications in invasion ecology (Dick *et al.*, 2014). A fundamental advantage of functional responses is their capacity to quantify the density dependence of the relationship between resource availability and usage, which avoids the pitfalls of snapshot assessments of resource usage (Dick *et al.*, 2014). Because functional responses underpin many concepts in ecology (e.g. Rall *et al.*, 2012), it is perhaps surprising that they have only recently been recognised as useful tools by invasion ecologists (Dick *et al.*, 2013; Barrios-O'Neill *et al.*, 2014). It is particularly apparent that functional responses could inform impact assessment frameworks *sensu* Parker *et al.* (1999), because they provide a rapid, tractable means of estimating the *per capita* effects of invaders, a fact which has not gone unnoticed in biologi-

cal control research (Zamani *et al.*, 2006). Moreover, functional responses can provide alternative insights into well-established hypotheses in the field by, for example, quantifying biotic resistance (MacNeil *et al.*, 2013).

The methods whereby functional responses are typically derived may provide only rudimentary insights into the context dependency of impact. Field-derived functional responses may intrinsically capture multiple context dependencies, but lack sufficient resolution of shape at low resource densities, which is crucial to mediating the stability of consumer–resource dynamics (Williams & Martinez, 2004; Kalinkat *et al.*, 2013). Furthermore, field-derived functional responses often combine data from a range of locations (e.g. Angerbjorn, Tannerfeldt & Erlinge, 1999), with the implicit assumption that functional responses are consistent over space and time. In contrast, laboratory-derived functional responses can provide such resolution and quantify specific context dependencies (e.g. Kestrup *et al.*, 2010), but may lack ecological realism (Aljetlawi, Sparrevik & Leonardsson, 2004). Thus, understanding whether and how functional responses vary spatiotemporally, both within and between habitats, remains a considerable challenge in contemporary ecology.

Here, we address this knowledge gap using *in situ* experimental microcosms to compare the functional responses of two aquatic invertebrate predators, both mysid shrimps, that have invaded habitats outside their native ranges: the Ponto–Caspian *Hemimysis anomala* Sars, 1907 and the glacial relict *Mysis salemaai* Audzijonytė and Väinölä, 2005. In Ireland, *H. anomala* has established within the native range of *M. salemaai*, where restricted waterbody size results in their co-occurrence (Minchin & Boelens, 2010). Previous laboratory studies demonstrated that *H. anomala* has consistently higher functional responses towards several prey species than does *M. salemaai* (Dick *et al.*, 2013; Barrios-O'Neill *et al.*, 2014). Both *H. anomala* and *M. salemaai* undergo diel vertical migration (DVM), which is a variable phenomenon, but generally involves aggregation close to the bottom during the daytime followed by dispersal upward towards the surface at night (Hays, 2003). We sought to understand how the ecological effects of these mysids manifest in the waterbodies they inhabit, by conducting *in situ* functional response trials designed to reflect realistic spatiotemporal distributions over their DVM cycles. We used *Daphnia magna* Straus, 1820 as a representative prey species because cladocerans are frequently adversely affected by introductions of mysids (Goldman *et al.*, 1979; Ketelaars *et al.*, 1999), and because cladocerans also undergo DVM (Southern & Gardiner, 1932). By transferring a rigorous laboratory-based methodology

into the field, we aimed to combine improved ecological realism with the capacity to adequately resolve functional response shape and, thus, explore the potential ecological effects of these predators on prey populations.

Methods

Animal collection and study site

During August 2012, we collected *Hemimysis anomala* and *Mysis salemaai* (wet weight $\pm$ SE = 18.6 mg $\pm$ 0.1 and 19.2 mg $\pm$ 0.2, respectively) from Lough Neagh, County Derry, Northern Ireland (54.71000°N, 6.49017°W) and Lough Derg, County Tipperary, Republic of Ireland (52.90556°N, 8.34158°W and 52.90782°N, 8.35553°W) using a combination of horizontal and vertical tows with a plankton net (1 m mouth diameter, 1 mm mesh size). Lough Derg is a mesotrophic lake with a maximum depth of 36 m which forms part of the Shannon River system. We selected this lough to conduct our *in situ* study because the deepest parts are close to the shore, and because the distributions of *H. anomala* and *M. salemaai* overlap on the lough (Minchin & Boelens, 2010).

Samples were separated by species and transferred into 50 L covered opaque holding tanks situated at a shoreside location on Lough Derg (52.90523°N, 8.34507°W). *Daphnia magna* was used as prey in all trials, maintained in culture at Queen's University Belfast and transported in identical holding tanks to this shoreside location. Each holding tank was filled with 40 μm filtered lough water that was changed daily, thus maintaining similar temperatures to ambient surface temperatures in Lough Derg over the duration of the study (tanks: 17.1 °C $\pm$ 0.03, lough surface: 16.9 °C $\pm$ 0.06). Because *D. magna* generally exceeds the size of other cladocerans, we ensured some relevance as a representative prey item by extracting a smaller size class for use in trials: individuals were obtained from the holding tanks before trials by transferring cultures through 2 mm and 1 mm stacked sieves, yielding experimental animals of 2.7 mg $\pm$ 0.2 on the 1 mm sieve. Tanks containing mysids were supplied *ad libitum* with a mixture of locally sourced zooplankton and cultured *D. magna*. Tanks containing *D. magna* were supplied every third day with a feed solution of finely ground alfalfa, baker's yeast and trout chow at a ratio of 1 mL of feed solution to 1.5 L of holding tank water.

In situ functional responses: experimental design

We sought to derive *in situ* functional responses for this mysid–cladoceran study system where, as far as

practically possible, both predators and prey were exposed to ambient cues, particularly because non-lethal cues consistently invoke antipredator responses in aquatic invertebrates (Paterson *et al.*, 2013). Therefore, all trials were conducted in purpose-built arrays constructed from clear polycarbonate sheeting, supporting grids of 50 × 200 mL clear plastic containers (hereafter chambers), into which 6 cm diameter windows were cut and sealed with 40 μm nylon mesh and non-toxic clear aquatic silicone (Fig. 1). Previous laboratory studies have demonstrated that meshed chambers of this kind allow the transmission of ambient cues to predators and prey (e.g. Alexander, Dick & O'Connor, 2013). Each array was deployed vertically on a buoyed line during experimental trials. Two sites on Lough Derg were selected to deploy arrays (Fig. 1); a shallow site (site 1, 52.90556°N, 8.34158°W, 4 m deep) and a deep site close to the deepest part of the lough (site 2, 52.90782°N, 8.35553°W, 22 m deep). Prior to deployment, arrays were prepared at the shoreside location; trials were initiated on the introduction of single mysid predators into chambers filled with 40 μm filtered lough water and containing *D. magna* prey at one of seven densities (2, 4, 6, 8, 15, 25 and 40, *n* = 3 each). Controls with no predators consisted of densities 2, 15 and 40 (*n* = 3 each). Predator–prey combinations and controls were randomly distributed on arrays, and all chambers were sealed with lids before deployment. Arrays were subsequently deployed within 15 min of the initiation of trials at five 'locations' (here, location refers to both time and space) reflecting a typical DVM cycle over 24 h (i.e. distributed through the water column during night time and aggregated close to the bottom during daytime) (Fig. 1). Thus, locations for functional response trials were as follows: on the bottom during daytime at the shallow and deep sites (3 m and 20 m, respectively) and, during night, on the surface (1 m) at both sites, as well as on the bottom at the deep site. The latter location reflects the fact that mysids still occur in deeper water during the night, despite a general migration towards the surface (Southern & Gardiner, 1932).

Trials were terminated after 6 h on retrieval of the arrays and removal of predators, after which surviving *D. magna* were counted.

Statistical methods

All statistical analyses were undertaken using R (R Development Core Team, 2013). Generalised linear models (GLMs) were used to assess the consumption of
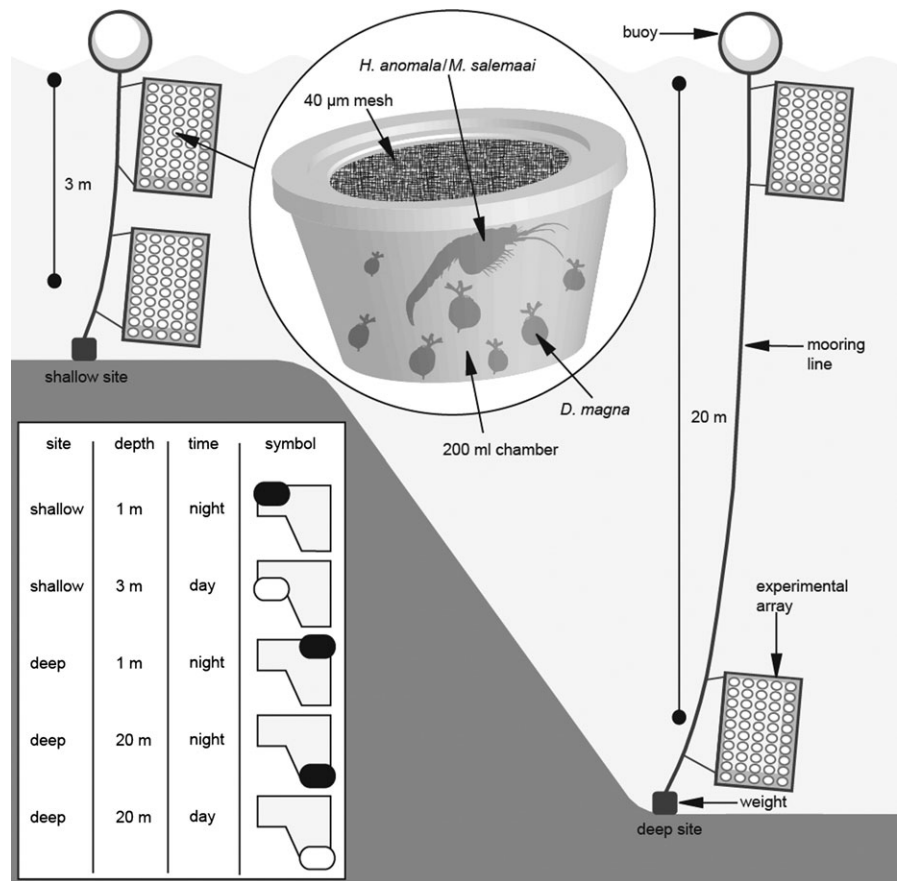
Fig. 1 Schematic representation of experimental design. Six hour *in situ* functional response trials were conducted at a shallow and a deep site during the day and night, reflecting the diurnal migration pattern of *Hemimysis anomala* and *Mysis salemaai* and their prey (i.e. distributed through the water column at night and aggregated on the bottom during the day). Schematic and chamber inset not to scale.

D. magna by mysid predators among all array locations. Then, after using logistic regression to determine the appropriate functional response types (see Juliano, 2001), we fitted functional response curves using maximum likelihood estimation (MLE; Bolker, 2010). Nonparametric bootstrapping was used to construct 95% confidence intervals around functional response curves and their associated parameters (Pritchard, 2013).

Consumption of Daphnia magna by mysid predators

To compare prey consumption between invaders and natives at single array locations, and also to compare consumption by invaders and natives among all array locations, GLMs assuming quasi-Poisson distributions (because count data were overdispersed) were used. For pairwise comparisons of consumption by invaders and natives at single array locations, GLMs contained the factors 'predator species' (two levels) and 'prey density' (seven levels) and t values were used to compare linear coefficients. Here, we make no adjustment of α for multiplicity. To compare consumption by invaders or natives among all locations in their DVM cycle, maximal

GLMs which contained the factors 'array location' (five levels: Fig. 1), 'prey density' (seven levels) and their associated interaction were simplified stepwise using F tests. If 'array location' was required by the minimum adequate model, then *post hoc* comparisons of linear coefficients with Tukey's HSD method were used to identify specific differences.

Functional responses of mysid predators

To fit appropriate functional response models to the data, we first used logistic regressions to determine the shapes of the relationships between proportional prey consumption and prey density. Where proportional consumption declines with increasing prey density, the logistic regression yields a significant negative first-order term, and the functional response is appropriately described by a Type II hyperbola. Proportional consumption which is described by a significant positive first-order term followed by a significant second-order term indicates that the functional response is appropriately described by a sigmoidal Type III model (Juliano, 2001). Because the logistic regressions for both

Table 1 Functional response model selection results for *Hemimysis anomala* and *Mysis salemaai* at each array location using logistic regressions of the proportion of *Daphnia magna* consumed with initial density of *D. magna* (see text for further details)

Predator	Site	Depth	Time	Logistic regression Type II		Logistic regression Type III	
				1st term	P	Terms: 1st, 2nd	P: 1st, 2nd
H. anomala	Shallow	1 m	Night	−0.066	<0.001	0.062, −0.002	0.483, 0.153
M. salemaai	Shallow	1 m	Night	−0.050	<0.001	−0.073, 0.000	0.105, 0.595
H. anomala	Shallow	3 m	Day	−0.017	0.052	−0.116, 0.002	0.010, 0.025
M. salemaai	Shallow	3 m	Day	−0.033	<0.001	−0.193, 0.003	<0.001, 0.001
H. anomala	Deep	1 m	Night	−0.030	<0.001	−0.100, 0.001	0.096, 0.231
M. salemaai	Deep	1 m	Night	−0.067	<0.001	−0.069, 0.000	0.194, 0.993
H. anomala	Deep	20 m	Night	−0.025	0.029	−0.353, 0.006	<0.001, <0.001
M. salemaai	Deep	20 m	Night	−0.059	<0.001	−0.167, 0.002	0.002, 0.036
H. anomala	Deep	20 m	Day	−0.068	<0.001	−0.262, 0.004	<0.001, 0.005
M. salemaai	Deep	20 m	Day	−0.045	<0.001	−0.086, 0.001	0.068, 0.370

predators at all locations yielded negative first-order terms (Table 1), functional responses were subsequently modelled using MLE 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):

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

where N_e is the number of prey eaten, N_0 is the initial density of prey, a is the attack or capture rate, h is the handling time and T is the total time available.

To construct 95% confidence intervals around functional response curves and their associated parameters, data sets were nonparametrically bootstrapped ($n = 2000$) and eqn 1 was fitted to each bootstrapped data set using starting values of a and h from the original MLE. Because bootstrapping allows data to be considered in terms of populations, as opposed to samples, a lack of overlap between 95% confidence intervals is sufficient to ascribe significance to differences between treatments without recourse to parametric tests. Therefore, we present both functional responses and their associated model parameters graphically with 95% confidence intervals to quantify differences between invaders and natives at the same array location, and also for invaders and natives among all array locations.

Results

Control *Daphnia magna* survival was 100% after 6 h at all control densities, at both sites and at all locations; therefore, we deemed all experimental mortality to be a result of mysid predation. Although predation was impossible to observe directly, it was also evidenced by the partial remains of prey.

Consumption of Daphnia magna by mysid predators

Hemimysis anomala consumed significantly more *Daphnia magna* than did *Mysis salemaai* at all locations during the night (see Fig. 2a–c): at the shallow site on the surface ($t = 5.10$, $P < 0.001$), at the deep site on the surface ($t = 2.43$, $P = 0.015$) and at the deep site on the bottom ($t = 3.60$, $P < 0.001$). In contrast, on the bottom during the day (see Fig. 3a,b), there were no significant differences in consumption of *D. magna* by *H. anomala* and *M. salemaai* at either shallow ($t = 0.89$, NS) or deep ($t = 1.82$, NS) sites.

Notably, predation by *M. salemaai* was consistent among all locations because the factor 'array location' could be removed from the minimum GLM ($F_{4, 103} = 2.03$, NS). In contrast, consumption of *D. magna* by *H. anomala* was markedly asymmetric among locations, because the factor 'array location' was required in the minimum GLM ($F_{4, 103} = 7.67$, $P < 0.001$). Differences were driven by a relative reduction in feeding by *H. anomala* at both sites on the bottom during daytime (Fig. 2a–c with Fig. 3a,b). In particular, consumption was lower on the bottom at the shallow site during daytime than at all locations during the night, at the deep site both on the bottom ($P < 0.001$) and on the surface ($P = 0.002$), and at the shallow site on the surface ($P < 0.001$). Consumption was also lower at the deep site on the bottom during daytime than at the shallow site on the surface during the night ($P = 0.031$).

Functional responses of mysid predators

Hemimysis anomala had higher functional responses towards *Daphnia magna* than did *Mysis salemaai* at all locations during the night: at the shallow site on the
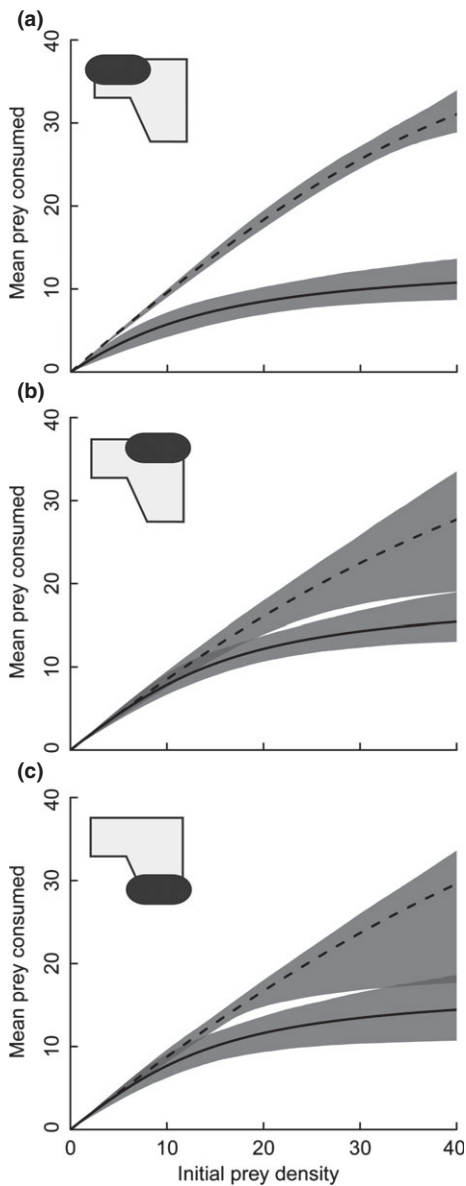
Fig. 2 Functional responses of *Hemimysis anomala* (dashed lines) and *Mysis salemaai* (solid lines) towards *Daphnia magna* at three locations during the night: (a) 1 m at the shallow site, (b) 1 m at the deep site and (c) 20 m at the deep site. Shaded areas are bootstrapped 95% confidence intervals.

Fig. 3 Functional responses of *Hemimysis anomala* (dashed lines) and *Mysis salemaai* (solid lines) towards *Daphnia magna* at two locations during the day: (a) 3 m at the shallow site and (b) 20 m at the deep site. Shaded areas are bootstrapped 95% confidence intervals.

surface (Fig. 2a), at the deep site on the surface (Fig. 2b) and at the deep site on the bottom (Fig. 2c). Although predator functional responses were similar at both sites on the bottom during the day (Fig. 3a,b), bootstrapped 95% confidence intervals revealed more subtle differences. Specifically, confidence intervals were divergent between invader and native functional responses for the entire range of prey densities only at the shallow site on the surface during the night (Fig. 2a). In contrast, invasive and native functional responses were not
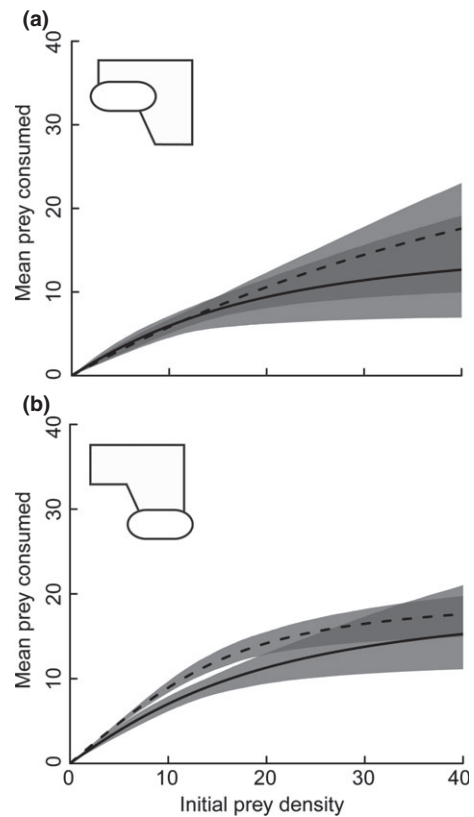
significantly different at the same site on the bottom during the day, as 95% confidence intervals overlapped throughout (Fig. 3a). At all other locations, the overlap of native and invasive functional responses was dependent on prey density (Figs 2b,c and 3b).

Bootstrapped estimates of attack rates and handling times corroborated the lack of differences and hence observed consistency of predatory activity by *M. salemaai*, because 95% confidence intervals overlapped among all locations, both for attack rates (Fig. 4a–e, filled circles) and handling times (Fig. 4f–j, filled circles), although handling times were longest on the surface at the shallow site (Fig. 4f, filled circle). On the other hand, estimates of attack rates and handling times for *H. anomala* were more variable among locations. Attack rates were lower at the shallow site on the bottom during the day than at all locations during the night (Fig. 4d and a–c, respectively, open circles), whilst handling times were longer at the deep site on the bottom during the day than at all locations during the night (Fig. 4j,f–h, respectively, open circles). The attack rates of invasive
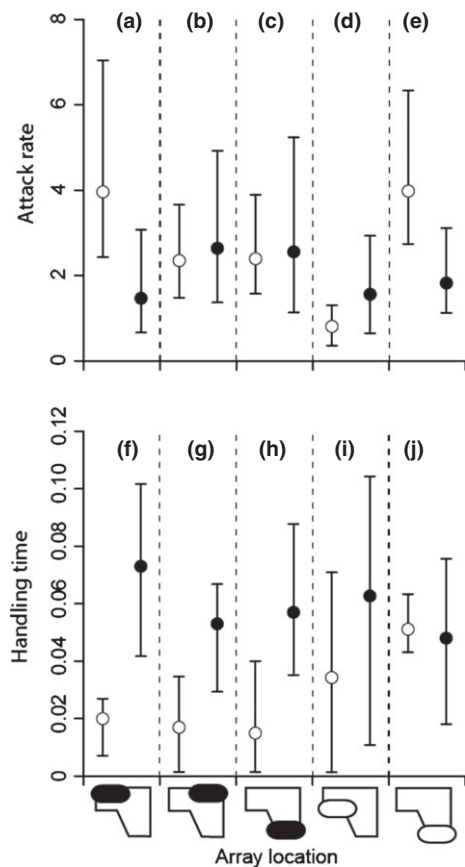
Fig. 4 Estimates of predator attack rates (top) and handling times (bottom) at each array location derived from eqn 1. Open circles are *Hemimysis anomala*, and filled circles are *Mysis salemaai*. Bars are bootstrapped 95% confidence intervals.

and native mysids exhibited a degree of overlap at each location (Fig. 4a–e); thus, observed differences in functional responses were driven primarily by the shorter handling times of the invader during the night (Fig. 4f–h). Although the handling times of the invader exhibited some degree of overlap with those of the native during night, they were consistently shorter, significantly so inshore on the surface (Fig. 4f).

Discussion

We demonstrate that the invasive mysid *Hemimysis anomala* has generally higher functional responses over its diurnal vertical migration (DVM) cycle than does the native species *Mysis salemaai*, corroborating previous laboratory findings (Dick *et al.*, 2013; Barrios-O'Neill *et al.*, 2014). Crucially, however, we highlight the context dependency of these functional responses; the impacts of *H. anomala* were particularly asymmetric over its DVM cycle, with a marked reduction in feeding on the

bottom during daytime and higher feeding during the night, particularly at the shallow site. In contrast, *M. salemaai* fed consistently over its DVM cycle, demonstrating the higher relative importance of daytime predatory activity for this species. Further, the broad consistency of evidence for the ecological effects of *H. anomala* between laboratory manipulations (Dick *et al.*, 2013; Barrios-O'Neill *et al.*, 2014), field manipulations and field surveys (Ketelaars *et al.*, 1999) alludes to the potential value of functional responses as a tool to inform assessments of impact.

In large waterbodies, *H. anomala* is essentially littoral, being found at a maximum depth of 50 m during the daytime (but frequently much shallower), whilst *Mysis* spp. generally occur further offshore (Ricciardi, Avlijas & Marty, 2011). However, in Irish waterbodies where *M. salemaai* is native and *H. anomala* is an established invader, maximum depths rarely exceed 30 m, resulting in a high degree of spatial overlap between these species (Minchin & Boelens, 2010). Emerging evidence for the seasonally mediated presence of *M. salemaai* in the littoral zone of some lakes (Penk & Minchin, 2014), combined with evidence of profundal aggregations of *H. anomala* (Ketelaars *et al.*, 1999), highlights the need to better understand the consequences of interactions of these species – with each other and with prey. Nevertheless, even in relatively small waterbodies such as Lough Derg, *H. anomala* is more prevalent in the shallows, whilst *M. salemaai* is common in deeper areas. Thus, we may speculate that observed differences in predatory behaviour manifest primarily because of the typical distributions of these species in larger systems; in the case of the invader, daytime aggregation in the littoral zone may necessitate reduced activity because its visually orientated potential predators may be more effective in well-lit conditions (Hays, 2003). Conversely, where native mysids have the available depth, daytime migrations into deep water may result in a perpetual refuge effect, where the abundance and/or efficacy of its predators is continuously limited. Therefore, where these species co-occur as a result of waterbody size and morphology, endogenous behaviour may determine how their impacts manifest. Indeed, although there is some debate as to the extent to which mysids rely on vision to capture prey (Viherluoto & Viitasalo, 2001), predator avoidance behaviour may ultimately dictate maximal feeding (Paterson *et al.*, 2013; Barrios-O'Neill *et al.*, 2014), regardless of ambient light. Notably, Barrios-O'Neill *et al.* (2014) found evidence for predator avoidance behaviour in *M. salemaai* but not *H. anomala* during low-light trials. These findings and those of the current

study suggest that predator avoidance behaviour by *H. anomala* has an overarching diurnal component, whilst predator avoidance behaviour by *M. salemaai* is a relatively consistent feature over diurnal periods.

Although absolute results derived from experimental chambers such as these may reasonably be seen as an artefact of containment, as has been highlighted by other *in situ* studies (e.g. Wilhelm, Schindler & Mcnaught, 2000), valuable information lies not in the absolute, but in the relative values. Here, relative differences between native and invasive mysids over diurnal periods highlight the subtleties of predatory behaviour and yield insight into how both species exert effects on prey populations. However, we caution against absolute interpretations of these findings because the manipulations preclude important components of real-world interactions, such as multiple predator effects and prey selectivity (Barrios-O'Neill *et al.*, 2014; Dodd *et al.*, 2014), and we have no means to quantify the contribution of environmental cues to the overall response. Similarly, whilst both the invader and native mysids exhibited Type II responses, such responses are not synonymous with the extinction of prey populations (MacNeil *et al.*, 2013) and may be artefacts of containment (Murdoch, 1972). Type II responses may exert destabilising effects on predator–prey dynamics by increasing the importance of recruitment rates within prey populations (Sinclair *et al.*, 1998). Thus, in some oligotrophic systems, mysids have caused cladoceran extinctions (Goldman *et al.*, 1979), whilst in more productive systems, coexistence occurs (Southern & Gardiner, 1932). Ultimately, the utility of quantifying functional responses lies in the ability to rapidly assess the numerous ways in which invaders may interact with recipient communities. For example, the relative consistency of the functional response of *M. salemaai* demonstrates that its effects on benthic and diurnally migrating prey communities in deep water may be at least as important as its effects on prey higher in the water column.

The value of an in situ approach to understanding context-dependent variation

The shape and magnitude of predator–prey interactions are considered crucial determinants of population and food-web stability, resulting in the incorporation of functional responses into contemporary modelling approaches (Williams & Martinez, 2004; Vucic-Pestic *et al.*, 2010; Kalinkat *et al.*, 2013). But we know very little about how functional responses vary in time and space under different environmental conditions, in spite of the well-recognised dynamic nature and context dependency of species interactions (Powers & Kittinger, 2002; Leahy *et al.*, 2011). Laboratory studies may yield broad insight into how, for example, light intensity (Townsend & Risebrow, 1982) impinges on functional response shape and magnitude, but it is also apparent that predator–prey dynamics hinge on very small changes in the functional response (Williams & Martinez, 2004). Altogether, the value of an *in situ* approach is evident, particularly when considering the sensitivity of predator–prey dynamics in conjunction with the fact that natural systems are replete with cues that shape the outcomes of interactions and prey fitness (Orrock *et al.*, 2013; Paterson *et al.*, 2013). Conceptually, predator–prey interactions can be thought to map over habitats at various spatiotemporal scales, and therefore resolving interactions at the appropriate scale may inform our understanding of the persistence and stability of food webs. This point is particularly relevant to risk assessments concerned with how novel species will affect recipient communities, because spatial and temporal changes in interactions and subsequent impacts are characteristic of invasions (Byers & Noonburg, 2003; Strayer *et al.*, 2006).

It is clear that not all study systems will be practically amenable to *in situ* manipulations. Nevertheless, the scope for application remains broad, and functional responses are not specific to predator–prey systems (e.g. they are well demonstrated in herbivores; Gross *et al.*, 1993). Further, although the present study highlights functional response dynamics at a diurnal scale, there is clearly scope within this mysid study system to address questions relating to seasonal (Penk & Minchin, 2014), ontogenetic, allometric (Boscarino *et al.*, 2012) and prey-specific (Dick *et al.*, 2013) interaction patterns. Broadly, then, the range of potential applications across invasion science as a whole is likely to be similarly diverse. Additionally, functional responses are relatively rapidly derived, thus providing a tractable proxy to inform assessments of impact. There is a clear need for proxies of this kind, as limited resources are available to study and manage the burgeoning number of invasions, and there is growing pressure to prioritise (Hulme *et al.*, 2013). Managers and researchers alike require reliable methods with which to assess impact without recourse to extensive, time-consuming analysis of entire ecosystems.

Acknowledgment

References

Alexander M.E., Dick J.T.A. & O'Connor N.E. (2013) Trait-mediated indirect interactions in a marine intertidal system as quantified by functional responses. *Oikos*, **122**, 1521–1531.

Aljetlawi A.A., Sparrevik E. & Leonardsson K. (2004) Prey-predator size-dependent functional response: derivation and rescaling to the real world. *Journal of Animal Ecology*, **73**, 239–252.

Angerbjorn A., Tannerfeldt M. & Erlinge S. (1999) Predator-prey relationships: arctic foxes and lemmings. *Journal of Animal Ecology*, **68**, 34–49.

Barrios-O'Neill D., Dick J.T.A., Emmerson M.C., Ricciardi A., MacIsaac H.J., Alexander M.E. et al. (2014) Fortune favours the bold: a higher predator reduces the impact of a native but not an invasive intermediate predator. *The Journal of Animal Ecology*, **83**, 693–701.

Bolker B.M. (2010) bbmle: tools for general maximum likelihood estimation. R Package.

Boscarino B.T., Halpin K.E., Rudstam L.G., Walsh M.G. & Lantry B.F. (2012) Age-specific light preferences and vertical migration patterns of a Great Lakes invasive invertebrate, *Hemimysis anomala*. *Journal of Great Lakes Research*, **38**, 37–44.

Byers J.E. & Noonburg E.G. (2003) Scale dependent effects of biotic resistance to biological invasion. *Ecology*, **84**, 1428–1433.

Dick J.T.A., Alexander M.E., Jeschke J.M., Ricciardi A., MacIsaac H.J., Robinson T.B. et al. (2014) Advancing impact prediction and hypothesis testing in invasion ecology using a comparative functional response approach. *Biological Invasions*, **16**, 735–753.

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.

Dodd J.A., Dick J.T.A., Alexander M.E., MacNeil C., Dunn A.M. & Aldridge D.C. (2014) 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*. *Freshwater Biology*, **59**, 337–352.

Gilpin M. (1990) Ecological prediction. *Science*, **248**, 88–89.

Goldman C.R., Morgan M.D., Threlkeld S.T. & Angeli N. (1979) A population dynamics analysis of the cladoceran disappearance from Lake Tahoe, California-Nevada. *Limnology and Oceanography*, **24**, 289–297.

Grosholz E.D. & Ruiz G.M. (1996) Predicting the impact of introduced marine species: lessons from the multiple invasions of the European green crab *Carcinus maenas*. *Biological Conservation*, **76**, 59–66.

Gross J.E., Shipley L.A., Hobbs N.T., Spalinger D.E., Bruce A. & Wunder B.A. (1993) Functional response of herbivores in food-concentrated patches : tests of a mechanistic model. *Ecology*, **74**, 778–791.

Hays G.C. (2003) A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia*, **503**, 163–170.

Hulme P.E., Pyšek P., Jarošík V., Pergl J., Schaffner U. & Vilà M. (2013) Bias and error in understanding plant invasion impacts. *Trends in Ecology & Evolution*, **28**, 212–218.

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

Kalinkat G., Schneider F.D., Digel C., Guill C., Rall B.C. & Brose U. (2013) Body masses, functional responses and predator-prey stability. *Ecology Letters*, **16**, 1126–1134.

Kestrup Å.M., Dick J. & Ricciardi A. (2010) Interactions between invasive and native crustaceans: differential functional responses of intraguild predators towards juvenile hetero-specifics. *Biological Invasions*, **13**, 731–737.

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.

Kulhanek S.A., Ricciardi A. & Leung B. (2011) Is invasion history a useful tool for predicting the impacts of the world's worst aquatic invasive species? *Ecological Applications*, **21**, 189–202.

Leahy S.M., Mccormick M.I., Mitchell M.D. & Ferrari M.C.O. (2011) To fear or to feed: the effects of turbidity on perception of risk by a marine fish. *Biology Letters*, **7**, 811–813.

MacNeil C., Dick J., Alexander M., Dodd J. & Ricciardi A. (2013) Predators versus alien: differential biotic resistance to an invasive species by two resident predators. *NeoBiota*, **19**, 1–19.

Melbourne B. A, Cornell H. V, Davies K.F., Dugaw C.J., Elmendorf S., Freestone A.L. et al. (2007) Invasion in a heterogeneous world: resistance, coexistence or hostile takeover? *Ecology Letters* **10**, 77–94.

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

Murdoch W.W. (1972) The functional response of predators. *Biological Control*, **15**, 237–240.

Orrock J.L., Preisser E.L., Grabowski J.H. & Trussell G.C. (2013) The cost of safety: refuges increase the impact of predation risk in aquatic systems. *Ecology*, **94**, 573–579.

Parker I.M., Simberloff D., Lonsdale W.M., Goodell K., Wonham M., Kareiva P.M. et al. (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biological Invasions*, **1**, 3–19.

Paterson R.A., Pritchard D.W., Dick J.T.A., Alexander M.E., Hatcher M.J. & Dunn A.M. (2013) Predator cue studies reveal strong trait-mediated effects in communities despite

variation in experimental designs. *Animal Behaviour*, **86**, 1301–1313.

Penk M.R. & Minchin D. (2014) Seasonal migration of a glacial relict mysid (Crustacea) into the littoral zone and its co-occurrence with an introduced competitor in Lough Derg (Ireland). *Hydrobiologia*, **726**, 1–11.

Powers S.P. & Kittinger J.N. (2002) Hydrodynamic mediation of predator–prey interactions: differential patterns of prey susceptibility and predator success explained by variation in water flow. *Journal of Experimental Marine Biology and Ecology*, **273**, 171–187.

Pritchard D.W. (2013) frair: a package for functional response analysis in R. R Package.

Pyšek P., Jarošík V., Hulme P.E., Pergl J., Hejda M., Schaffner U. *et al.* (2012) A global assessment of invasive plant impacts on resident species, communities and ecosystems: the interaction of impact measures, invading species' traits and environment. *Global Change Biology*, **18**, 1725–1737.

R Development Core Team. (2013) R: A language and environment for statistical computing.

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.

Ricciardi A., Hoopes M.F., Marchetti M.P. & Lockwood J.L. (2013) Progress toward understanding the ecological impacts of nonnative species. *Ecological Monographs*, **83**, 263–282.

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

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.

Sinclair A.R.E., Pech R.P., Dickman C.R., Hik D., Mahon P. & Newsome A.E. (1998) Predicting effects of predation on conservation of endangered prey. *Conservation Biology*, **12**, 564–575.

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.

Strayer D.L., Eviner V.T., Jeschke J.M. & Pace M.L. (2006) Understanding the long-term effects of species invasions. *Trends in Ecology & Evolution*, **21**, 645–651.

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

Viherluoto M. & Viitasalo M. (2001) Effect of light on the feeding rates of pelagic and littoral mysid shrimps: a trade-off between feeding success and predation avoidance. *Journal of Experimental Marine Biology and Ecology*, **261**, 237–244.

Vucic-Pestic O., Rall B.C., Kalinkat G. & Brose U. (2010) Allometric functional response model: body masses constrain interaction strengths. *The Journal of Animal Ecology*, **79**, 249–256.

Wilhelm F.M., Schindler D.W. & Mcnaught A.S. (2000) The influence of experimental scale on estimating the predation rate of *Gammarus lacustris* (Crustacea: Amphipoda) on *Daphnia* in an alpine lake. *Journal of Plankton Research*, **22**, 1719–1734.

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.

Williamson M. (1999) Invasions. *Ecography*, **22**, 5–12.

Zamani A., Talebi A., Fathipour Y. & Baniameri V. (2006) Temperature-dependent functional response of two aphid parasitoids, *Aphidius colemani* and *Aphidius matricariae* (Hymenoptera: Aphidiidae), on the cotton aphid. *Journal of Pest Science*, **79**, 183–188.