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BIODIVERSITY RESEARCH

A spatio-temporal contrast of the predatory impact of an invasive freshwater crustacean

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ABSTRACT

Aim Impacts of invasive species may vary across invasion gradients, owing to trait-based sorting of individuals through dispersal: those aggregating at invasion fronts may be more aggressive and voracious. We examine, in the field and laboratory, variation in the predatory impacts of an invasive Ponto-Caspian crustacean *Hemimysis anomala* G.O. Sars, 1907 at two sites along a spatio-temporal gradient of invasion.

Location Republic of Ireland.

Methods We used reciprocal transplant field-deployed mesocosms to compare predation rates of invasion front and well-established *H. anomala* on natural zooplankton assemblages. In the laboratory, we measured the functional response (relationship between predation rate and prey supply) of *H. anomala* from both sites, for a per capita mechanistic comparison of predation efficiency. We also assessed prey selectivity of *H. anomala* in the mesocosm experiments to further compare feeding behaviour. Finally, we used a correlative approach to assess the community impact of *H. anomala* across sites, including a nearby uninvaded site, by comparing zooplankton diversities and densities.

Results Invasion front *H. anomala* had higher predation rates than well-established *H. anomala* at high *in situ* zooplankton densities. Invasion front *H. anomala* also had higher functional responses – in particular showing higher 'attack rates' – indicating a heightened ability to locate and capture prey. Prey selectivity was consistent across the spatio-temporal contrast, with positive selection for cladocerans. Zooplankton diversity and density declined with time since *H. anomala* invasion, both being maximal at the uninvaded site.

Main conclusions Our study, for the first time, (1) reveals differences in predatory per capita effects and associated behavioural traits between two sites along a spatio-temporal invasion gradient and (2) shows a negative community-level impact of the invasive *H. anomala* in natural water bodies. Further spatio-temporal comparisons of predatory per capita effects of invaders are needed to assess the generality of these results.

Keywords

Functional response, impact, invasion front, invasive species, per capita effect, zooplankton.

INTRODUCTION

The impacts of invasive species can vary greatly over their invaded ranges, such that they may reduce – or even extirpate – native species at some locations, but coexist with them elsewhere (Mack *et al.*, 2000; Strayer *et al.*, 2006; Ricciardi *et al.*, 2013). Invader ecological impact is a function of the per capita effect (i.e. resource consumption rates of individuals), abundance and range of the species (Parker *et al.*, 1999; Dick *et al.*, 2014). Per capita effects may vary in part owing to non-random sorting and segregation of individuals during the dispersal process (Burton *et al.*, 2010; Phillips *et al.*, 2010a). As an invasive species spreads, those individuals that have a higher physical ability (Llewellyn *et al.*, 2010;

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Phillips *et al.*, 2010a) and behavioural tendency for dispersal (Cote *et al.*, 2010a,b) move to the invasion front (Crooks, 2005; Phillips *et al.*, 2010a; Chapple *et al.*, 2012). Assortative mating leads to adaptation towards increased dispersal abilities, while propagating positively or neutrally linked behavioural traits (Burton *et al.*, 2010; Phillips *et al.*, 2010a), such as heightened movement (Alford *et al.*, 2009), aggression (Duckworth & Badyaev, 2007) and reduced sociability (Cote *et al.*, 2010b). Such differences in physical and behavioural traits may alter the per capita effects – and hence the ecological impacts (Dick *et al.*, 2014) – of invasive species along their invaded ranges (see Table 1 for results from other studies comparing traits of invasive animals along temporal gradients).

Few studies have examined variation in consumptive per capita effects of invasive species in general or, in particular, along spatio-temporal invasion gradients; in animal studies comparing traits across such gradients, 85% focus on dispersal traits, whereas none directly measure foraging traits (Lopez *et al.*, 2012). Faster growth rate (Phillips, 2009; Brown *et al.*, 2013), higher gut fullness (Raby *et al.*, 2010; Lopez *et al.*, 2012) and larger body size (Brandner *et al.*, 2013; J.C.I. pers. obs.) have been observed in individuals at invasion fronts, but an unresolved issue is whether these traits stem from differences in resource quality/availability or from differences in the invader created by the dispersal process (Raby *et al.*, 2010; Lopez *et al.*, 2012; Brandner *et al.*, 2013; Brown *et al.*, 2013). Comparisons of consumptive per capita effects between invasive and native species have shown that invasive species exhibit increased foraging activity compared to native species (Rehage *et al.*, 2005; Dodd *et al.*, 2014; Alexander *et al.*, 2014), and newly invading populations display increased foraging innovation compared to separate, well-established populations (Martin & Fitzgerald, 2005). However, these studies do not consider the adaptive effects of dispersal within a population by comparing individuals along a single gradient of invasion (Phillips *et al.*, 2010a). The dispersal process may lead to differences in foraging behaviour that could increase impact on native communities at invasion fronts. Therefore, quantifying differences in per capita effects along invaded ranges may enhance our predictive understanding of how impacts vary with time since invasion.

Here, we assessed, in the field and laboratory, the per capita effects of a known invasive predator (the bloody red mysid shrimp *Hemimysis anomala* G.O. Sars, 1907) from two sites that delineate a spatio-temporal gradient of invasion. Native to the freshwater margins of the Black Sea basin, *H. anomala* has invaded western Europe (including Ireland) and North America within the past decade. Adult *H. anomala* are voracious consumers of zooplankton, especially cladocerans (Gallagher *et al.*, 2011). Indeed, comparisons of pre- and post-invasion observations of aquatic communities in a Dutch reservoir implicate *H. anomala* as the cause of

Table 1 Tests of traits of invasive animals along temporal invasion gradients showing physical and behavioural differences that may lead to higher per capita effects of invasion front individuals (IF) compared with well-established individuals (WE). Results that support this hypothesis are in bold.

Taxa	Site	Traits compared	Result	Reference
African Jewelfish, *Hemichromis letourneuxi*	Everglades National Park, United States	Body size	**IF > WE**	Lopez *et al.* (2012)
		Body condition	**IF > WE**	
		Reproductive investment	**IF > WE**	
		Boldness	IF = WE	
		Dispersal tendency	IF = WE	
Cane toad, *Rhinella marinus*	Queensland & Northern Territory, Australia	Dispersal tendency	**IF > WE**	Alford *et al.* (2009)
		Dispersal rate	**IF > WE**	
		Movement endurance	**IF > WE**	Llewellyn *et al.* (2010)
		Movement speed	IF = WE	
		Dispersal distance	**IF > WE**	Phillips *et al.* (2010b)
	Northern Territory, Australia	Body size	**IF > WE**	Brown *et al.* (2013)
		Body condition	**IF > WE**	
		Growth rate	**IF > WE**	
Round Goby, *Neogobius melanostomus*	Lake Ontario region, Canada	Body size	IF < WE	Ray & Corkum (2001)
	Lake Erie region, Canada	Gut fullness	**IF > WE**	Raby *et al.* (2010)
		Body size	**IF > WE**	Gutowsky & Fox (2011)
		Body size	IF < WE	Brownscombe & Fox (2012)
	Danube River, Austria & Germany	Body size	**IF > WE**	Brandner *et al.* (2013)
		Body condition	**IF > WE**	
		Trophic level	**IF > WE**	
		Reproductive investment	IF < WE	
Western bluebird, *Sialia mexicana*	Montana, United States	Aggression	**IF > WE**	Duckworth & Badyaev (2007)

severe declines in zooplankton (Ketelaars *et al.*, 1999) – a common impact of freshwater mysid introductions (Ricciardi *et al.*, 2012). Ireland has a native mysid (*Mysis salemaai* Audzijonyte & Vainola, 2005) that is closely related to *H. anomala*, although the invader is a more efficient predator (Dick *et al.*, 2013). As such, the ongoing invasion of *H. anomala* in Ireland has generated concern over potential disruptions to aquatic food webs and fisheries in natural water bodies (Dick *et al.*, 2013).

Using *in situ* field mesocosms and laboratory functional response experiments, we tested the hypothesis that invasion front *H. anomala* have a higher predatory impact owing to greater per capita effects. Functional response – the relationship between predation rate and prey supply – provides a mechanistic measurement of differences in predation efficiency. Relative functional response comparisons can be used to predict the magnitude of impact in the field (Dick *et al.*, 2014) through analyses of invasive species and trophically similar natives (Haddaway *et al.*, 2012; Barrios-O'Neill *et al.*, 2014a,b; Alexander *et al.*, 2014), and of invaders in different environmental contexts (Alexander *et al.*, 2012; Iacarella *et al.*, 2015). We also tested for variation in prey selectivity of *H. anomala* in the mesocosm experiments, given that plastic feeding behaviours may be characteristic of individuals at invasion fronts (Sol & Lefebvre, 2000; Sol *et al.*, 2002; Martin & Fitzgerald, 2005). Finally, we assessed the community-level impact of *H. anomala* by comparing zooplankton diversities and densities between three sites of differing invasion history (one uninvaded, one recently invaded and one where *H. anomala* is well established). This study is a first attempt at understanding how per capita consumptive effects vary along spatio-temporal gradients of invasion. Although we contrasted sites from a single invasion gradient, we provide two lines of evidence – from mesocosm and functional response experiments, respectively – to comprehensively assess predatory differences between invasion front and well-established *H. anomala.* In addition, our reciprocal transplant design controls for local environmental effects on predatory behaviour to reveal inherent differences in the per capita effects of invasion front and well-established individuals.

METHODS

Mesocosm field experiments: data collection

Reciprocal transplant field experiments were run with natural zooplankton densities to compare predation rates of *H. anomala* from an invasion front and well-established site, while accounting for potential environmental differences between sites that may have influenced predation rates. *Hemimysis anomala* predation rates were compared at two sites along a spatio-temporal invasion gradient in August 2012 in the Shannon River basin at (1) Lough Key ('invasion front', 53°59′7.34″ N, 8°14′0.68″ W), where the invader was found in low abundances in 2009, and (2) Lough Derg ('well-established site', 52°54′18.88″ N, 8°20′43.27″ W), where *H. anomala* was discovered in Ireland in 2008 (Minchin & Holmes, 2008; Minchin & Boelens, 2010). Lough Allen (54°2′54.99″ N, 8°3′2.05″ W) was used as a comparator site, because it contains the native mysid but not the invader ('uninvaded site', Fig. 1; Gallagher *et al.*, 2011). Mesocosm experiments (and functional response experiments; see below) were run using size-matched *H. anomala* individuals from invasion front and well-established sites [lengths: 9.5 ± 0.1 mm (± 1 SE; $n = 40$) and 9.8 ± 0.2 mm, respectively] to control for the effect of body size on per capita consumption, recognizing that potential site differences may have influenced growth rates and body size. Habitat conditions measured at the start and end of each experimental trial showed that conductivities did not differ substantively between invasion front (407–430 $\mu S\ cm^{-1}$) and well-established sites (433–440 $\mu S\ cm^{-1}$), and temperature differences never exceeded 2 °C (range 15.3–17.4 °C).

Mesocosm experimental design was similar to that of Vanderploeg *et al.* (1982, 1993), whereby control mesocosms without *H. anomala* were run simultaneously to estimate starting zooplankton densities in experimental mesocosms. On two successive nights at invasion front and well-established sites, six replicates (six control containers without *H. anomala* and six experimental containers with

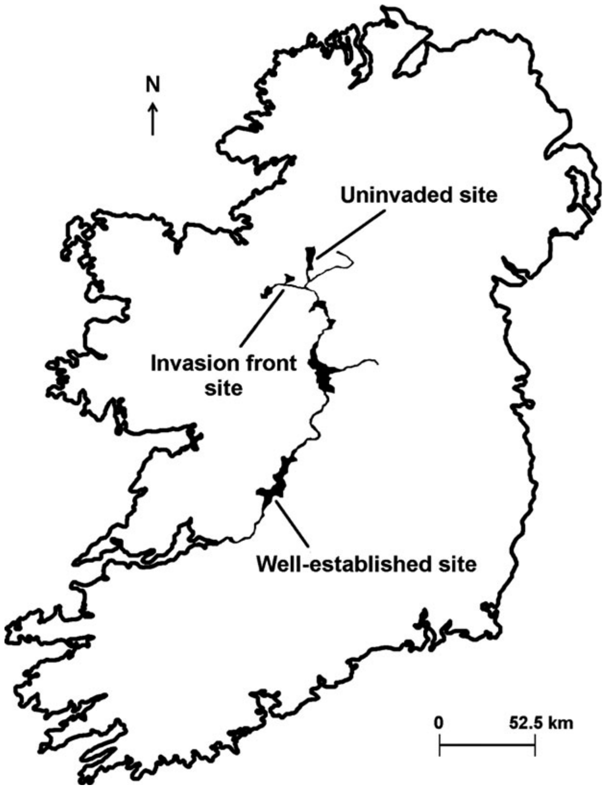

Figure 1 Sites along an invasion gradient of *Hemimysis anomala* in Ireland. Map adapted from Ezilon maps (http://ezilon.com).

H. anomala) were run with reciprocal transplants of *H. anomala* from both sites. One to two nights prior to the experiment, *H. anomala* was collected with vertical phytoplankton net tows and held in water from the site at ambient water temperatures (13.4–16.7 °C). At the uninvaded site, 12 mesocosms were run without *H. anomala* on one night. This ensured similar treatment of zooplankton across sites to enable comparisons of community diversity and density among the three sites.

To collect zooplankton prey for the mesocosms, an 8.2 L messenger-operated water sampler was deployed at 1 m depth and emptied twice each into 12 opaque plastic, cylindrical containers to a total volume of 16.4 L of water per container. Eight *H. anomala* were then introduced to each of the six experimental containers (three containers each received *H. anomala* from the invasion front and well-established sites). No *H. anomala* were added to the six control containers. Containers were then sealed and placed in the water with weights to submerge the containers just below surface level, with the following exception: on the second night at the well-established site, experiments were kept on a rowboat to simulate the wave conditions from the night before, whereas the marina had become too rough to place the containers directly in the water. All experiments were left overnight for 8 h, from 23:00 h to 07:00 h.

Upon completion of the experiments, water from the mesocosms was poured over a 63 μm Nitex mesh filter held between two 1 mm sieves to exclude debris. *Hemimysis anomala* were taken off of the sieve and placed in a vial with 70% ethanol. The mesh with zooplankton prey was then rinsed with tap water into a small container, and zooplankton were preserved in Lugol's solution for subsequent identification. Zooplankton samples were identified and separated into cladocerans, copepod adults and copepod nauplii, while cladocerans were further identified down to family for diversity assessments (see 'Zooplankton assemblage: data analysis').

Mesocosm experiments: data analysis

Per capita predation rates [(control – experiment)/(time × number of predators)] were calculated by averaging the number of zooplankton counted in the controls from each night and subtracting the experimental zooplankton counts for the corresponding nights. By averaging control counts, we assumed that each experimental mesocosm started with the same number of zooplankton; we do not pair control and experimental mesocosms, as this would arbitrarily influence the calculated predation rates. We analysed predation rates of *H. anomala* using a two-way nested analysis of variance (ANOVA) that included the factors of *H. anomala* origin (invasion front versus well established) and control zooplankton density nested within the site of the experiment. Tukey's honest significant differences (HSDs) were used for *post hoc* analysis. Data were normally distributed (K–S test, $P = 0.2$).

Functional response experiments: data collection

There are two defining parameters of the functional response: the attack rate characterizes the ability of the predator to search for and capture its prey (indicated primarily by the initial slope of the curve), whereas the maximum feeding rate is the inverse of the time needed to handle and digest a prey item (1/handling time, indicated by the asymptote of the curve; Holling, 1959, 1966; Jeschke *et al.*, 2002). These parameters were measured in the laboratory for *H. anomala* individuals from both the invasion front and well-established sites. Experimental animals were used within 2 weeks of collection and held in their habitat water at 17 °C. *Daphnia magna* were used as prey and were size matched using 180 μm Nitex mesh and visual selection of the smallest size classes (approximately 1–2 mm). *Hemimysis anomala* individuals were starved for 24 h to standardize hunger before being placed individually into containers with 170 mL of dechlorinated tap water and *Daphnia* densities of 4, 6, 8, 10, 16, 20, 30, 40, 60, 80 and 120. Controls without *H. anomala* were run simultaneously at the highest prey density to ensure prey survival rates of at least 90%. Experiments were run in the dark for 12 h, after which *H. anomala* was removed and preserved in ethanol and surviving *Daphnia* counted. Trials with *H. anomala* that moulted during the experiments were omitted and repeated. All prey densities were repeated three times.

Functional response experiments: data analysis

We used generalized linear models with binomial distributions to assess the effect of *H. anomala* origin and prey density on the amount of prey eaten. We then determined whether the functional response was of Type II or Type III, following the methods of Alexander *et al.* (2012) and Dick *et al.* (2013). We derived functional response types using logistic regressions of the proportion of prey consumed as a function of prey density. Functional response curves were then modelled using maximum likelihood estimation (bbmle R package; Bolker, 2010) with Rogers' random predator equation (Rogers, 1972) for Type II curves with non-replacement of prey (Juliano, 2001). This provided estimates of attack rates '*a*' and handling times '*h*', the latter converted to estimated maximum feeding rates (1/*h*). Bootstrapping with replacement was then used to generate multiple curve fits ($n = 1500$) with 95% confidence intervals (CIs) around the mean curve (frair R package; Pritchard, 2014).

Zooplankton assemblage: data analysis

Prey selectivity on cladocerans, copepod adults and copepod nauplii in the field mesocosm experiments was estimated separately for each combination of *H. anomala* origin and experimental site, by calculating Pearre's selectivity index with Yates' correction for continuity (*C*; Pearre, 1982). A positive value of *C* indicates higher predation of a prey type than expected compared to the amount of prey available, a value of 0 represents no difference and a negative value indicates lower predation of a prey type than expected. Statistical significance was tested using χ^2 and a Bonferroni correction of $\alpha = 0.017$.

Changes to Simpson's diversity (1/*D*) of zooplankton assemblages in uninvaded, invasion front and well-established sites were determined by comparing rarefaction curves. We used counts of cladocerans split into six families (Bosminidae, Daphniidae, Sididae, Chydoridae, Leptodoridae and Polyphemidae) and of copepod adults. Samples were randomly selected with replacement for calculations of unconditional 95% CIs. Curves were considered significantly different when CIs did not overlap at the highest abundance level of the smallest community (Magurran, 2004). We also used a one-way ANOVA and Tukey's HSDs for *post hoc* analysis to compare zooplankton density between uninvaded, invasion front and well-established sites. Rarefaction curve analysis was conducted in ESTIMATES (Colwell, 2013), and all other analyses were conducted in R (R Development Core Team, 2012).

RESULTS

Invasion front *H. anomala* had higher predation rates on *in situ* zooplankton than well-established *H. anomala* ($F_{1,16} = 4.36$, $P = 0.05$), supporting our hypothesis. Predation rates increased with zooplankton prey density ($F_{3,16} = 49.28$, $P < 0.001$). *Hemimysis anomala* origin and zooplankton density had significant interacting effects on predation rates ($F_{3,16} = 4.33$, $P = 0.02$), with invasion front *H. anomala* consuming more than well-established *H. anomala* at the highest zooplankton density ($t = 3.86$, $P = 0.02$; Fig. 2).

In functional response experiments, invasion front *H. anomala* consumed more than well-established *H. anomala* ($z = -5.74$, $P < 0.001$), and consumption increased with prey density ($z = -14.12$, $P < 0.001$), consistent with field results. Logistic regression returned significantly negative linear coefficients ($P < 0.001$), indicating that both functional responses were of Type II (Table 2, Fig. 3). Invasion front *H. anomala* had much higher attack rates '*a*', as reflected in lack of overlap of 95% CIs at low prey densities; however, maximum feeding rates converged at higher densities (Table 2, Fig. 3) – hence the significant interaction between *H. anomala* origin and prey density ($z = 5.03$, $P < 0.001$).

Prey selectivity in mesocosm experiments was similar between invasion front and well-established *H. anomala.* Both exhibited significant positive selection of cladocerans ($C > 0$, $P < 0.01$) and negative selection of copepod adults ($C < 0$, $P \leq 0.01$; Table 3). Copepod nauplii were negatively selected at the invasion front site ($P < 0.001$), with neutral selection at the well-established site ($C \approx 0$, $P > 0.10$; Table 3).

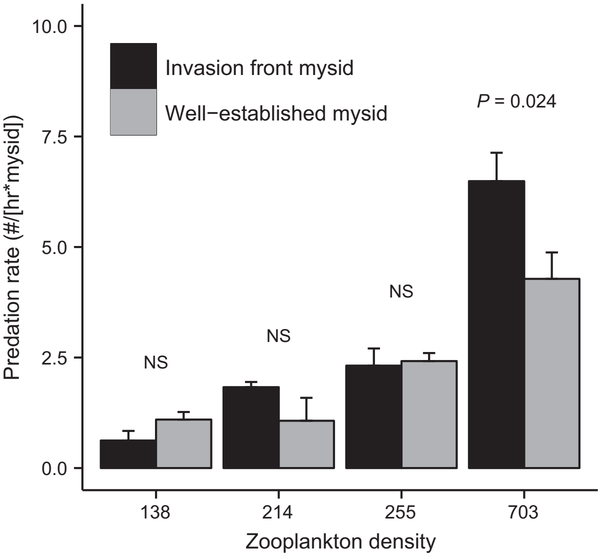

Figure 2 Predation rates of invasion front (black bars) and well-established *Hemimysis anomala* (grey bars) at zooplankton densities (prey/16.4 L) across invasion front and well-established sites and experimental nights. Error bars are ± 1 SE, and NS indicates $P > 0.05$.

Zooplankton community diversity was higher at the uninvaded site than at the invasion front site of *H. anomala*, whereas the well-established site tended to have the lowest diversity (Fig. 4). The high amount of variation at the well-established site may be attributable to stormy conditions on the second night. The uninvaded site contained counts of all six of the identified cladoceran families, whereas the invasion front site lacked one family (Leptodoridae) and the well-established site lacked two (Leptodoridae and Polyphemidae); all sites contained copepods. The density of zooplankton also differed significantly between sites ($F_{2,33} = 26.63$, $P < 0.001$); the uninvaded site tended to have a higher mean density of zooplankton (603.8 ± 14.2 prey/16.4 L) compared to both invasion front ($P = 0.11$; 1st night: 254.8 ± 25.7, 2nd night: 702.8 ± 40.1 prey/16.4 L) and well-established sites ($P < 0.001$; 1st night: 213.8 ± 10.7, 2nd night: 138.2 ± 8.4 prey/16.4 L), with the lowest density found at the well-established site ($P < 0.001$).

DISCUSSION

Reciprocal transplant mesocosm experiments on two contrasting sites delineating a spatio-temporal gradient of invasion revealed that invasion front *H. anomala* had a higher predatory per capita effect on natural zooplankton communities than well-established *H. anomala*. Furthermore, the functional response analyses demonstrated higher attack rates of invasion front *H. anomala*. Similarly, spatio-temporal studies on invasive cane toads (Phillips, 2009; Brown *et al.*, 2013) and fishes (Raby *et al.*, 2010; Lopez *et al.*, 2012; Brandner *et al.*, 2013) found indications of higher predation by invasion front individuals compared to well-established individuals, although per capita effects were not measured. These previous studies collectively offer evidence of physical and behavioural differences

Table 2 Functional responses of *Hemimysis anomala* from invasion front and well-established sites in Ireland, fitted using logistic regressions and modelled with Roger's random predator equation for non-replacement of prey. Logistic regression first-order terms, attack rates '*a*' and maximum feeding rates ('1/*h*') from the modelled curves are provided with associated *P*-values.

Site	First-order term, *P*-value	*a*	*P*-value	1/*h*	*P*-value
Invasion front	−0.043, < 0.001	9.8	< 0.001	71.4	< 0.001
Well-established	−0.025, < 0.001	4.2	< 0.001	76.9	< 0.001

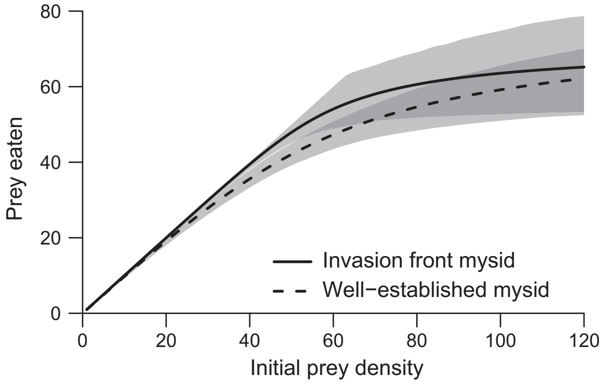

Figure 3 Type II functional responses on *Daphnia magna* (prey/170 mL) for invasion front (solid line) and well-established *Hemimysis anomala* (dashed line). Shaded areas are bootstrapped 95% confidence intervals, and darker shading indicates areas of overlap.

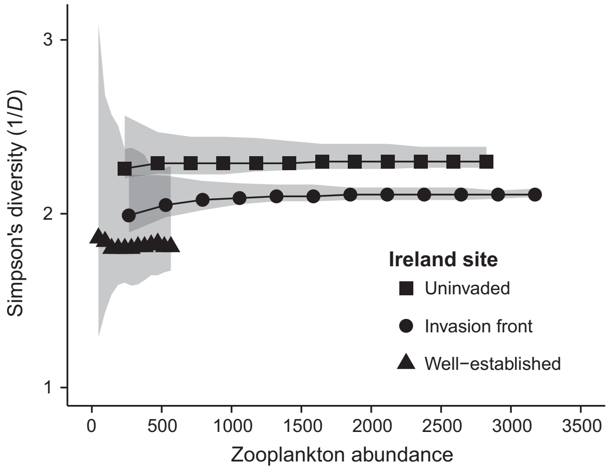

Figure 4 Rarefaction curves of Simpson's diversity index for zooplankton in Ireland. Shaded areas are bootstrapped 95% confidence intervals, and darker shading indicates areas of overlap.

Table 3 Prey selection of invasion front (IF) and well-established *Hemimysis anomala* (WE) when preying on zooplankton at both sites, estimated using Pearre's selectivity index with Yates' correction for continuity (*C*) for cladocerans, copepod adults and copepod nauplii. Significant positive selection for prey ($C > 0$) and negative selection for prey ($C < 0$) are indicated in bold ($P < 0.017$). Values close to 0 are not significant and indicate neutral selection.

	IF site		WE site	
Prey type	WE origin	IF origin	WE origin	IF origin
Cladocerans	**0.05**	**0.11**	**0.14**	**0.08**
Copepod adults	**−0.09**	**−0.06**	**−0.09**	**−0.07**
Copepod nauplii	**−0.12**	**−0.07**	0.03	0.00

across multiple invasion gradients and invasive species (i.e. Table 1), whereas our study provides a novel invasion gradient comparison that directly measures heightened consumptive per capita effects at invasion fronts.

Functional response curves revealed a mechanistic distinction in the predation efficiency of *H. anomala* across the spatio-temporal contrast. Invasion front *H. anomala* had a greater ability to locate and capture prey (as measured by attack rates) at prey densities that resembled the natural zooplankton densities used in the mesocosm experiments; the highest natural prey density (0.043 prey mL^{-1}) was equivalent to 8-prey trials (0.047 prey mL^{-1}) used in the functional response experiments. Functional responses began to diverge at the 8-prey trials, with more consistently high predation rates by invasion front *H. anomala* (8 ± 0 prey eaten out of 8) than well-established *H. anomala* (7.67 ± 0.33). We followed the prey depletion functional response design (Dick *et al.*, 2014), given the difficulty of replacing consumed *Daphnia* and to minimize disturbance during the experiments. Non-replacement of prey can lead to an underestimation of attack rates (Alexander *et al.*, 2012) and constrained our ability to observe greater differences in the slopes of the curves as invasion front and well-established *H. anomala* consumed all prey offered at lower prey densities (all prey were consumed in density trials ≤ 30, and ≤ 6, respectively). Invasion front *H. anomala* may have a more destabilizing effect on zooplankton populations than well-established *H. anomala*, as predators with Type II functional responses characterized by high attack rates can potentially lead to prey extinction (Dick *et al.*, 2014). Maximum feeding rates of invasion front and well-established *H. anomala* were more similar and reflect the physiological limitations of digestion (Jeschke *et al.*, 2002; Englund *et al.*, 2011). The functional responses and mesocosm experiments indicated that the heightened predatory per capita effect of invasion front *H. anomala* is a behavioural response rather than a physiological adaptation.

Hemimysis anomala positively selected cladocerans in our mesocosm experiments, in agreement with previous gut content analyses (Gallagher *et al.*, 2011). However, copepod adults have been found to be more abundant in gut content analyses of *H. anomala* where abundances of cladocerans are relatively low (Borcherding *et al.*, 2006). In our study, copepod adults were consistently consumed less than expected based on ambient densities, which was also observed by Ketelaars *et al.* (1999) who suggested that the dashing movements of copepods made them difficult for *H. anomala* to capture. We also observed that *H. anomala* ate fewer copepod nauplii than expected where cladoceran densities were higher (invasion front site), and they had a neutral response where the preferred prey were less available (well-established site); however, there was no observable difference in prey selection between invasion front and well-established *H. anomala.* Differences in prey selectivity may be exhibited when abundance levels of the invader are representative of the invasion front and well-established sites, allowing for potential differences in intraspecific competition. For example, Brandner *et al.* (2013) found that invasion front fish fed more selectively on preferred prey than fish at the well-established area owing to reduced intraspecific competition. The result that *H. anomala* from both sites had the same prey selectivity in the mesocosms, while provided with the same prey assemblage, supports the finding that a higher predation rate of invasion front *H. anomala* – and not different prey selectivity – led to the difference observed at the highest zooplankton density.

The mesocosm and functional response experiments measured per capita effect components of impact with controlled abundances of *H. anomala.* Impact, as influenced by abundance (Parker *et al.*, 1999), is expected to vary over spatio-temporal gradients, owing to the presence of fewer individuals at invasion fronts (Crooks, 2005; Phillips *et al.*, 2010a). *Hemimysis anomala* abundance is difficult to quantify, as a consequence of its swarming behaviour (Gallagher *et al.*, 2011), so we did not attempt to measure it here. However, the zooplankton community comparisons between uninvaded, invasion front and well-established sites provided a correlative measure of impact as a function of both per capita effect and abundance of *H. anomala*. With this approach, we found that zooplankton diversity and density declined with time since invasion. Studies of an invasive fish also found that its overall impact on native prey abundance declined from well-established sites to the invasion front (Lederer *et al.*, 2006; Brandner *et al.*, 2013), even though invasion front fish were larger and in better condition (Brandner *et al.*, 2013). Therefore, enhanced per capita effects of potentially larger, more voracious individuals at invasion fronts may not necessarily result in stronger *overall* impacts than at well-established sites, because of substantive differences in local invader abundance. Conversely, there may be a lag time (*sensu* Crooks, 2005) before detection of the full impact at the invasion front.

Correlative comparisons of invaded and uninvaded sites are the most common method of measuring impacts of invasive species; although they do not control for potential environmental differences between sites, they offer a powerful tool for impact assessment when combined with mechanistic experiments (Parker *et al.*, 1999), as performed here. Further, our study provides a baseline comparison for future impact assessments along this invasion gradient as *H. anomala* continues to expand its range. To date, community-level impacts of *H. anomala* have been previously documented only in an artificial water body in the Netherlands (Ketelaars *et al.*, 1999). Our study adds further evidence that *H. anomala* is a high-impact invader in natural water bodies (Ricciardi *et al.*, 2012; Dick *et al.*, 2013), like other freshwater mysids that are known to cause strong effects on the communities they invade (Spencer *et al.*, 1991, Ricciardi *et al.*, 2012).

Traits of invasive species that may influence impact also vary owing to local habitat conditions and thus may obscure trait differences resulting from the dispersal process. For instance, newly invading individuals have been found to have higher gut fullness than more established individuals, but it is not clear if this reflects differences in food availability across the invasion gradients or rather higher feeding rates of invasion front colonists (Raby *et al.*, 2010; Brown *et al.*, 2013). Differences in body size along spatio-temporal gradients of Round Goby invasion have revealed conflicting trends that may result from the influence of local habitat conditions that affect growth rates (Table 1; Ray & Corkum, 2001; Gutowsky & Fox, 2011; Brownscombe & Fox, 2012; Brandner *et al.*, 2013). Our use of size-matched *H. anomala* in our predation rate comparisons minimized the influence of previous growth conditions owing to any potential site differences. Furthermore, our comparisons were conservative, as well-established *H. anomala* would be expected to have higher hunger levels – and therefore potentially higher predation rates – owing to lower zooplankton density at the well-established site. To further determine trait-based impact differences created during dispersal, additional controlled comparisons should be made that reduce the influence of habitat characteristics.

Invasive species tend to have higher impacts on recipient communities in which they represent novel taxa, presumably as a consequence of the lack of evolutionary exposure by the community to functionally similar organisms (Ricciardi & Atkinson, 2004). Thus, impacts at the invasion front may also be elevated in part owing to the native community lacking sufficient time to adapt to novel predation pressure (Diamond & Case, 1986, Cox & Lima, 2006). However, in Ireland, the invaded range of *H. anomala* overlaps with a functionally similar native mysid (*M. salamaai*). Moreover, our experiment was conducted 3–4 years following invasion. Zooplankton have antipredator defenses that can be induced by predator kairomones within a single generation (Stibor, 1992; Tollrian, 1993), and some behavioural responses can be triggered within hours of predator cue introduction (Lass & Spaak, 2003). For these reasons, we consider it unlikely that prey naïveté differed between our invasion front and well-established sites.

Effective management of biological invasions requires a predictive understanding of where and when invasive species will exert strong impacts (Heger & Trepl, 2003; Ricciardi *et al.*, 2013). Our study is the first to directly compare per capita effects at sites that delineate a spatio-temporal gradient of invasion; further comparisons of per capita effects across invasion gradients will need to be made to determine the generality of our results. Higher predation rates, as shown here, and increased growth and body condition metrics of invasion front cane toads (Phillips, 2009; Brown *et al.*, 2013), fishes (Raby *et al.*, 2010; Lopez *et al.*, 2012; Brandner *et al.*, 2013) and *H. anomala* (in Quebec; J.C.I. pers. obs.) suggest that native communities at invasion fronts may be subjected to higher per capita effects of invasive species. Gene flow from individuals following the invasion front and local selection of optimal phenotypes will eventually erode spatio-temporal differences in per capita effects, while increasing abundance levels of the invasive species (Phillips *et al.*, 2010a). There is, as yet, no theoretical framework that predicts the relative importance of per capita effect and abundance to the overall impact of invasive species (Parker *et al.*, 1999). However, we hypothesize that as invasion fronts become well-established over time, maximal impacts will be temporarily reached at an optimal balance between declining per capita effects and increasing abundance of the invasive species. Spatio-temporal predictions of impact will benefit from further research on the relationship between per capita effect and abundance (Parker *et al.*, 1999; Dick *et al.*, 2014), particularly across such a transition. Furthermore, management efforts are likely to be more beneficial at the edge of an invasion front, given growing evidence that consumptive impacts are stronger there and that the cost of preventing spread is usually dwarfed by costs of controlling a well-established population (Leung *et al.*, 2002).

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