

Differential ecological impacts of invader and native predatory freshwater amphipods under environmental change are revealed by comparative functional responses

Ciaran Lavery · Jaimie T. A. Dick ·
Mhairi E. Alexander · Frances E. Lucy

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Abstract Predicting the ecological impacts of damaging invasive species under relevant environmental contexts is a major challenge, for which comparative functional responses (the relationship between resource availability and consumer uptake rate) have great potential. Here, the functional responses of *Gammarus pulex*, an ecologically damaging invader in freshwaters in Ireland and other islands, were compared with those of a native trophic equivalent *Gammarus duebeni celticus*. Experiments were conducted at two dissolved oxygen concentrations (80 and 50 % saturation), representative of anthropogenic water quality changes, using two larval prey, blackfly

(Simuliidae spp.) and mayfly (*Baetis rhodani*). Overall, *G. pulex* had higher Type II functional responses and hence predatory impacts than *G. d. celticus* and the functional responses of both predators were reduced by lowered oxygen concentration. However, this reduction was of lower magnitude for the invader as compared to the native. Further, the invader functional response at low oxygen was comparable to that of the native at high oxygen. Attack rates of the two predators were similar, with low oxygen reducing these attack rates, but this effect occurred more strongly for blackfly than mayfly prey. Handling times were significantly lower for the invader compared with the native, and significantly higher at low oxygen, however, the effect of lowered oxygen on handling times was minimal for the invader and pronounced for the native. Maximum feeding rates were significantly greater for the invader compared with the native, and significantly reduced at low oxygen, with this effect again lesser for the invader as compared to the native. The greater functional responses of the invader corroborate with its impacts on recipient macroinvertebrate communities when it replaces the native. Further, our experiments predict that the impact of the invader will be less affected than the native under altered oxygen regimes driven by anthropogenic influences.

C. Lavery (✉) · J. T. A. Dick
School of Biological Sciences, Institute for Global Food Security, Queen's University Belfast, 97 Lisburn Road, Belfast BT9 7BL, Ireland
e-mail: clavery14@qub.ac.uk

M. E. Alexander
Department of Botany and Zoology, Centre for Invasion Biology, Stellenbosch University,
Private Bag X1, Matieland 7602, South Africa

F. E. Lucy
Department of Environmental Science, Centre for Environmental Research Innovation and Sustainability, Institute of Technology, Sligo, Ireland

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Introduction

Invasive species have well-documented negative impacts on native biodiversity that are often severe and contribute an increasing global threat to both the environment and economy (Simberloff et al. 2013). Introduced predators in particular, such as the Eastern and Japanese oyster drills on the west coast of the USA (Carlton 1979) and the Brown tree snake on Guam (Savidge 1987; Rodda et al. 1992) have had devastating effects, although such impacts are often understood only in hindsight of the invasion event (see Savidge 1987; Ricciardi 2003). There is therefore a pressing requirement for methodologies that enable future prediction of invasive species impacts in recipient communities before they occur (Ricciardi 2003; Dick et al. 2013, 2014). Furthermore, invader impacts may be strongly context-dependent (MacNeil et al. 2009; Ricciardi et al. 2013), with abiotic and biotic factors potentially influencing the degree of impact both spatially and temporally (Ricciardi et al. 2013; Paterson et al. 2014). Indeed, many of the major hypotheses in invasion biology, such as those of biotic resistance and enemy release, make no consideration of environmental context as a factor in the damage caused to native communities by invaders; incorporation of such factors into invasion studies would improve predictive capability (Ricciardi et al. 2013; Dick et al. 2014). Here, however, we present the application of an emerging methodology, comparative functional responses (Dick et al. 2014), to assess and predict the impact of an invasive freshwater predator under a common environmental context, that of reduced oxygen levels driven by climate change and water pollution.

Comparing the functional responses of invaders and trophically analogous natives as a methodology for impact prediction has been proposed and verified across a number of taxa (Dick et al. 2013, 2014; Alexander et al. 2014). The functional response is the relationship between resource availability (e.g. prey density) and resource uptake rate by a consumer (e.g. predator) (Holling 1959). This relationship produces three types of curve: an increasing linear relationship between prey densities and consumption (Type I); an inversely density-dependent response with a decelerating rate of consumption where most if not all prey at low densities are consumed, before reaching an asymptote at higher prey densities (Type II); and a

positive density-dependent response where few prey are consumed at low densities before once again reaching an asymptote at higher densities (Type III) (Hassell 1978). The form of a predator functional response (i.e. Type I, II or III) may lead to different impacts on prey populations, since Type II functional responses are likely to lead to prey elimination at low densities, whereas Type III responses are likely to create low density refugia for prey (Murdoch and Oaten 1975; Hassell 1978; Colton 1987). In biological invasions, the magnitude of difference in the functional responses of invaders and natives can inform and predict the degree of invader impact on different prey species (Dick et al. 2013, 2014). For example, large and small differences in the functional responses of the invasive shrimp *Hemimysis anomala* and native shrimp *Mysis salemaai* were found to reflect large and small impacts of these mysids on native zooplankton species in the field (Dick et al. 2013). In addition, this predictive methodology has shown promise when considering context-dependencies in invasive species impact, as relevant abiotic (Iacarella et al. in press) and biotic (Barrios-O'Neill et al. 2014) factors can be incorporated into experiments. This allows the impact of an invader to be predicted under conditions that are likely to change or fluctuate, providing more realistic and robust impact forecasting.

The omnivorous freshwater amphipod crustacean *Gammarus pulex* was introduced deliberately to islands, primarily Ireland and the Isle of Man, in the 1950s from England (Strange and Glass 1979). *Gammarus pulex* impacts in a number of ways, replacing the native trophic equivalent *Gammarus duebeni celticus* via intraguild predation (Dick et al. 1990) and causing declines in macroinvertebrate species richness and diversity (Kelly et al. 2003, 2006). Environmental factors have a large influence upon the distribution of these two *Gammarus* species (Dennert 1974; Dick et al. 1990; Jazdzewski et al. 2004; MacNeil et al. 2009) and on the structure of macroinvertebrate communities (Allan 2004). Disentangling the individual and interactive roles of species interactions and environmental factors in determining the impact of invasive species is thus very difficult (Kelly et al. 2003). In particular, the distributions and abundances of *G. pulex*, *G. d. celticus* and associated macroinvertebrates are influenced by dissolved oxygen concentration, which typically fluctuate inversely with the level of organic pollution present (MacNeil

et al. 2001, 2004; Kelly et al. 2006; MacNeil et al. 2009). These fluctuations are also affected by natural diurnal and seasonal cycles and by reduced water levels, with low dissolved oxygen levels most prevalent before dawn on summer nights (Francis-Floyd 2003). Naturally low dissolved oxygen levels are often further reduced by organic pollution loads (Francis-Floyd 2003). The rise in average global temperatures is also increasing both natural and anthropogenic fluctuations in dissolved oxygen concentration in streams and rivers and subsequently increasing biological oxygen demand (Ozaki et al. 2003). It is therefore imperative to investigate how such fluctuations in oxygen concentration in the environment may influence species interactions with regards to predator–prey dynamics and in particular the impacts of invasive species (Walther et al. 2009). Previous studies focusing on the impact of hypoxia on predation have indicated that reduced oxygen can impact in a number of ways; reducing the mobility of prey and increasing their vulnerability to predation indicated by increased prey consumption by predators (Shoji et al. 2005), or reducing the ability of predators to capture and consume prey resulting in higher prey survival than at higher oxygen concentrations (Neslerode and Diaz 1998; Sandberg 1997). However, no study has examined the context-dependency of oxygen level in predicting the impacts of invasive species.

The aim of this study was thus to utilise comparative functional responses to investigate the influence of variation in dissolved oxygen concentration on the potential ecological impact of the invasive *G. pulex* as compared to the trophically analogous *G. d. celticus*; we did this with two common prey species that are readily consumed by both *Gammarus* spp and which are not highly pollution sensitive, as indicated by the BMWP system (Biological Monitoring Working Party 1978). Specifically, we investigated the functional responses of each gammarid species towards blackfly larvae (Simuliidae spp.) and mayfly larvae (*Baetis rhodani*) under high and low dissolved oxygen. Our aims were to: (1) establish the magnitude and form of the functional responses of *G. pulex* and *G. d. celticus*; (2) test whether the functional responses of *G. pulex* and *G. d. celticus* were statistically significantly different, and; (3) investigate whether changes in the oxygen concentration influence the comparative functional responses of *G. pulex* and *G. d. celticus*.

Methods

Experimental methods

Between 10/7/13 and 5/8/13 in Northern Ireland, blackfly larvae (Simuliidae spp; 0.5–0.6 cm body length) were collected from Colin Glen River (N54.568 W6.014), mayfly larvae (*Baetis rhodani*; 0.7–0.8 cm body length) and *Gammarus pulex* from Minnowburn River (N54.548 W5.952) and *Gammarus duebeni celticus* from the Upper Colin River at Divis mountain National Trust site (N54.601 W6.032). Gammarids selected for experiments were unparasitised size-matched (1.5–2 cm body length) males, to standardize the predator type as much as possible: as females are at various stages of egg/embryo development, are generally smaller, and often in precopula with males, we chose to reduce any variability this would add to the data. Each species was transported to the laboratory in its own source water, then transferred and maintained separately in 3 l of continuously aerated Minnowburn river water with food (stream fauna and flora) available ad libitum at 12 °C and on a 12:12 h light and dark regime. Gammarids were starved for 24 h prior to experimental trials in cylindrical arenas of 8 cm in diameter without substrate with 150 ml of Minnowburn River water filtered through qualitative filter paper. Prey were allowed to settle in identical arenas for 2 h and then individual gammarid predators were introduced. The blackfly and mayfly were presented separately at densities of 2, 4, 6, 8, 10, 20, 40 ($n = 3$ per experimental group). The experiment was run at 12 °C with ‘high’ and ‘low’ oxygen concentrations, which were 80 and 50 % oxygen saturation (8.6 and 5.4 mg/l respectively), monitored using an YSI model 550A dissolved oxygen meter. High and low oxygen replicates had air or nitrogen, respectively, bubbled into the water for around 5 s before experiments, giving the desired oxygen concentration (± 4 % saturation). Trials were initiated with the addition of a predator and the number of prey killed was recorded after 24 h; any predator that moulted during a trial was excluded and the replicate repeated. Controls were three replicates of each prey species at the seven prey densities, at high and low oxygen concentrations, in the absence of predators.

Statistical methods

Data were analysed using the statistical programme R, version 2.15.3 (R core team 2013). Mean prey consumption was compared using generalised linear models (GLMs) assuming a poisson error structure with respect to four factors, ‘predator species’, ‘oxygen concentration’, ‘prey density’ and ‘prey species’. A step-deletion process was used until the most parsimonious model was found that excluded all non-significant terms and interactions. Logistic regression of the proportion of prey killed as a function of prey density was used to distinguish functional response types. These are considered to be Type II when there is a significant negative first order linear coefficient and Type III if there is a significant positive first order linear coefficient followed by a significant negative second order coefficient (Trexler et al. 1988; Juliano 2001). Values for ‘ a ’ (attack rate), ‘ h ’ (handling time) and $1/hT$ (maximum feeding rate, T = experimental period) were estimated using Rogers’ equation for prey depletion and non-replacement (Juliano 2001):

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

where N_e is the number of prey eaten, N_o is the initial density of prey, a is the attack constant, h is the handling time and T is the total experimental period, in this case 24 h. Model fitting used the Lambert W function (Bolker 2008) in R due to the implicit nature of the random predator equation. Bootstrapping of data ($n = 30$) allowed calculation of multiple estimates of attack rate, handling time and maximum feeding rate. These parameters were compared with respect to three factors, ‘predator species’, ‘oxygen concentration’, and ‘prey species’ using a GLM assuming a quasipoisson error structure, to account for the overdispersion in the model.

Results

Survival of prey in controls was >95 % in all cases, therefore experimental deaths were attributed to predation by the gammarids. *G. pulex* consumed significantly more prey overall than did *G. d. celticus* ($z = 2.510$, $P < 0.05$, Fig. 1a, b). Overall, prey consumption was significantly reduced at the low as compared to the high oxygen concentration ($z = 5.839$, $P < 0.001$, Fig. 1a, b) and was

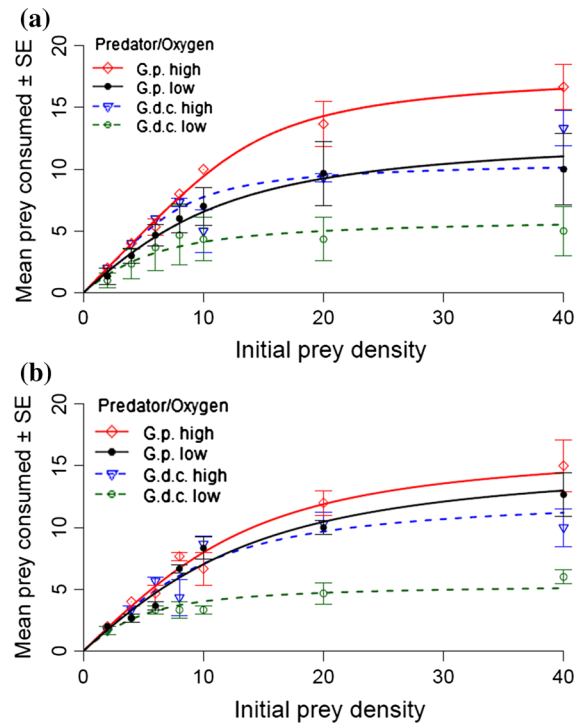


Fig. 1 Functional responses of the invader *Gammarus pulex* (G.p.) and the native *Gammarus d. celticus* (G.d.c.) at high and low oxygen concentrations. Prey species are (a) blackfly larvae maximum density = 40 and (b) mayfly larvae maximum density = 40 at time period = 24 h. Means are \pm SE

significantly greater at higher prey densities ($z = 11.145$, $P < 0.001$, Fig. 1a, b). There was no overall significant difference in consumption of the two prey species ($z = 0.301$, $P = \text{NS}$, Fig. 1a, b). *G. pulex* predation was less affected at the low oxygen concentration than was *G. d. celticus* predation as indicated by the significant ‘predator species \times oxygen concentration’ interaction effect ($z = 2.680$, $P < 0.01$, Fig. 1a, b). For both blackfly and mayfly, *G. pulex* consumption at the low oxygen concentration was not significantly different than *G. d. celticus* consumption at the high oxygen concentration (blackfly, $z = 0.327$, $P = \text{NS}$, Fig. 1a; mayfly, $z = 0.953$, $P = \text{NS}$, Fig. 1b).

Type II functional responses were observed in each combination of predator, oxygen and prey (Table 1). Overall, attack rates were not significantly different between predator species ($F_{1,239} = 0.04$, $P = \text{NS}$, Fig. 2a), but were significantly lower at the low oxygen concentration ($F_{1,237} = 130.71$, $P < 0.001$, Fig. 2a) and lower towards mayfly larvae

Table 1 First order linear coefficient results (lc) from logistic regressions for predator, prey and oxygen combinations

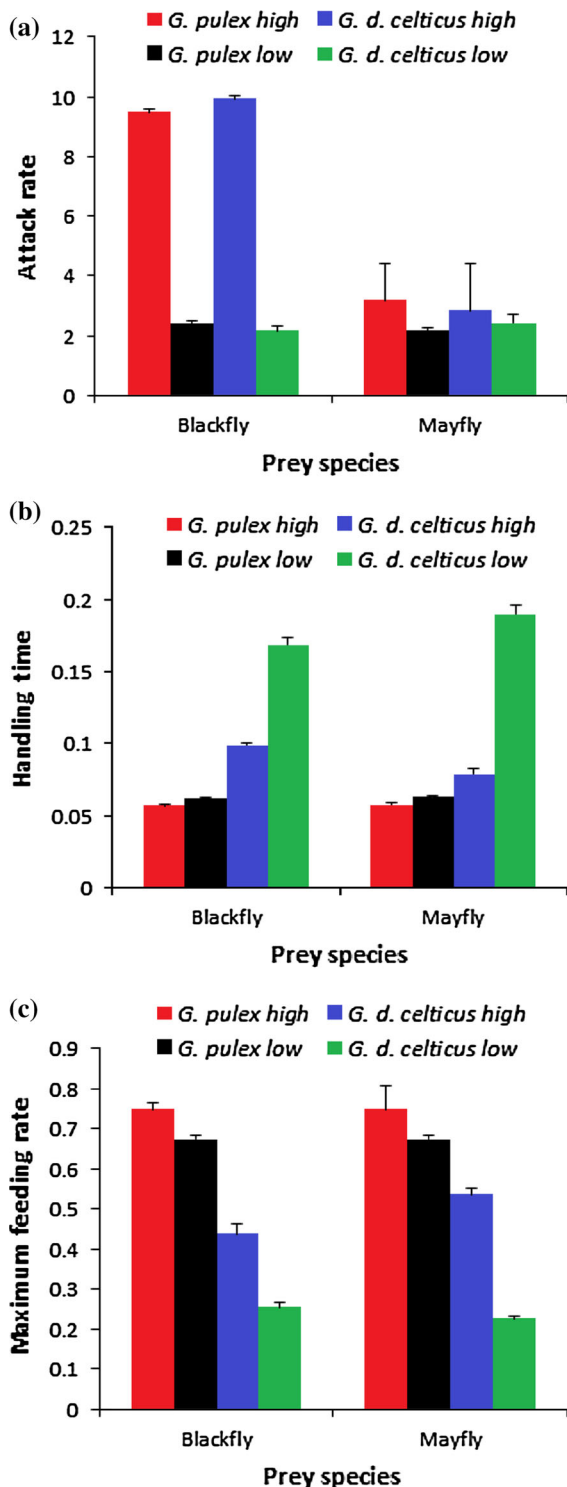
Predator species	Prey species	Oxygen concentration	Linear coefficient	P value
<i>Gammarus pulex</i>	Blackfly larvae	High	-0.091	<0.001
		Low	-0.062	<0.001
	Mayfly larvae	High	-0.031	<0.001
		Low	-0.038	<0.001
<i>Gammarus d. celticus</i>	Blackfly larvae	High	-0.063	<0.001
		Low	-0.064	<0.001
	Mayfly larvae	High	-0.039	<0.001
		Low	-0.032	<0.001

($F_{1,236} = 81.91$, $P < 0.001$, Fig. 2a). Attack rates towards blackfly larvae were significantly lower at the low as compared to the high oxygen concentration, but this difference was not observed for mayfly larvae, as evidenced by the significant ‘oxygen concentration x prey species’ interaction ($F_{1,233} = 36.77$, $P < 0.001$, Fig. 2a). Handling times were significantly lower for *G. pulex* compared to *G. d. celticus* ($F_{1,238} = 1,257.46$, $P < 0.001$, Fig. 2b) and handling times were significantly higher at the low as compared to the high oxygen concentration ($F_{1,237} = 518.28$, $P < 0.001$, Fig. 2b). There was no significant prey species effect ($F_{1,236} = 0.1639$, $P = \text{NS}$, Fig. 2b). Low oxygen concentration had little effect on *G. pulex* handling times, whereas *G. d. celticus* handling times were increased to a greater degree at the low oxygen concentration, as evidenced by the significant ‘predator species x oxygen concentration’ interaction. ($F_{1,235} = 157.64$, $P < 0.001$, Fig. 2b). Maximum feeding rates were significantly greater for *G. pulex* compared to *G. d. celticus* ($F_{1,238} = 1,155.72$, $P < 0.001$, Fig. 2c), and significantly lower at the low oxygen concentration as compared to the high ($F_{1,237} = 243.98$, $P < 0.001$, Fig. 2c). There was no significant prey species effect ($F_{1,236} = 2.666$, $P = \text{NS}$, Fig. 2c). *G. pulex* feeding rates were less affected at the low oxygen concentration than those of *G. d. celticus* as indicated by the significant ‘predator species x oxygen concentration’ interaction effect ($F_{1,235} = 205.89$, $P < 0.001$, Fig. 2c).

Discussion

While empirical studies are rare, the impacts of predators may be strongly context-dependent (MacNeil et al. 2009; Ricciardi et al. 2013; Dick et al. 2014;

Paterson et al. 2014), with abiotic and biotic factors potentially influencing the degree of impact both spatially and temporally (Barrios-O’Neill et al. 2014; Iacarella et al. in press; Paterson et al. 2014). This is especially true when considering the impacts of invasive species (Thomsen et al. 2011) and we thus require methods to both understand and predict the impacts of such invaders under changing environmental conditions (Walther et al. 2009; Dick et al. 2014). A major environmental context of aquatic systems is the temperature and oxygen regime, with the latter dependent on the former and also highly variable (particularly in summer months) due to organic pollution (Ansa-Asare et al. 2000; Pörtner and Knust 2007). Long term organic pollution, with consequent drops in both dissolved oxygen concentration and overall water quality, occurs due to constant loadings from diffuse or point-sources, with agriculture and municipal wastewater treatment discharges implicated as the major pollution drivers. Climate change is also predicted to increase temperature fluctuations and biological oxygen demand in water bodies (Ozaki et al. 2003; Irish EPA 2010). Thus, the assessment of invader impacts on prey populations must consider this important context dependency. In this study, variation in dissolved oxygen concentration influenced the prey consumption by both an invasive and a native amphipod, *Gammarus pulex* and *Gammarus duebeni celticus*, respectively, on two prey items, blackfly and mayfly larvae, as measured by comparative functional responses. Overall, prey consumption was significantly reduced at low (50 %) as compared to high (80 %) oxygen concentrations, demonstrating that predatory impacts may be altered under varying conditions that are likely to be met with increasing water pollution (Parkhill and Gulliver 2002) and



◀ **Fig. 2** Mean \pm SE bootstrapped ($n = 30$) functional response parameters toward blackfly and mayfly larvae at high and low oxygen concentration for both *Gammarus pulex* and *Gammarus duebeni celticus*; (a) attack rate at high and low oxygen concentrations, (b) handling time at high and low oxygen concentrations, (c) maximum feeding rate at high and low oxygen concentrations

effects on invasive as compared to native predators. That is, the functional response components of handling times and maximum feeding rates of the invader *G. pulex* were less affected by low oxygen than were those of the native *G. d. celticus*. The use of functional responses to investigate the influence of varying dissolved oxygen concentration on trophically analogous native and invasive amphipod crustaceans is a novel application of this comparative methodology.

Overall, the functional response of *G. pulex* was greater than that of *G. d. celticus*. This corroborates the field impact findings reported by Kelly et al. (2003, 2006), where invaded sites with *G. pulex* exhibited reduced species richness and changes to community structure compared with sites with only *G. d. celticus* present. In the present study, at the low oxygen concentration, *G. pulex* and *G. d. celticus* had significantly reduced functional responses and consumed fewer prey in comparison to the high oxygen concentration; indeed, similar findings were reported for resource consumption by the isopod *Saduria entomon* at 35 % oxygen concentration, representative of hypoxia (Sandberg 1997). In the present study, the functional response of *G. pulex* at the low oxygen concentration was comparable with that of *G. d. celticus* at high oxygen concentration, toward both blackfly and mayfly. This finding indicates the ability of *G. pulex* to cause greater damage to native macroinvertebrate assemblages in water bodies with low dissolved oxygen concentrations compared with predation by *G. d. celticus*, further exacerbating the known impact of this invasive predator on these communities. Climate change is expected to reduce oxygen concentrations through increased biological oxygen demand in aquatic systems in the future, our findings further highlight the importance of abiotic context-dependency in investigations of invader impacts (Ozaki et al. 2003; Whitehead et al. 2009; Dick et al. 2014). Functional responses have

climate change (see Walther et al. 2009). Furthermore, variations in oxygen concentration had differential

previously been altered in shape and magnitude when predators and prey were exposed to hypoxia during experiments (Sandberg 1997; Taylor and Eggleston 2000; Long et al. 2014). However, changing functional response shape and magnitude in the lab is not always reflected in the field, as was the case with *Callinectes sapidus* feeding on *Macoma balthica* (Seitz et al. 2003; Long and Seitz 2008).

Invasion by *G. pulex* may cause selection for efficient anti-predator strategies on native prey species because of increased voracity compared to *G. d. celticus* (Abrams 2000). Invasion is a 'quantum leap' in predator impact on a system compared with the time taken by native predators to evolve novel weapons for preying upon native prey. Strong directional selection acting upon prey species imparts instability to predator-prey systems by causing stable cycles to diverge, leading to shifts in prey species relative abundances, and this may be the reason for changes in community structure documented as a product of an invasion (Abrams 2000; Kelly et al. 2006; Dick et al. 2013).

High proportions of prey were consumed at low prey densities and demonstrated the efficiency of both predators at consuming prey when it was scarce, and the resulting Type II functional responses may potentially destabilise prey populations at either of the two oxygen concentrations (Long and Whitefleet-Smith 2013). However, if a prey species has a reproductive rate that is greater than the rate of consumption of the predator, this will impart stability on the system even in the presence of a predator with a Type II functional response (Twardochleb et al. 2012; MacNeil et al. 2013). Mayfly are univoltine and blackfly may be univoltine or multivoltine depending on the species and environment (Davies and Smith 1958; Raddum and Fjellheim 1993). Therefore, both prey types are susceptible to extinction by both predators at low densities and stability may not result. Stability can occur, however, through switching by a predator to a different prey species when one prey species becomes limited, modifying a Type II functional response to become a Type III functional response (Smout et al. 2013). Switching between the prey species was not examined in our functional response experiments, but is an important consideration for future studies of *G. pulex* and *G. d. celticus* and other damaging invader and native analogues, especially in instances where changes in environmental factors result in increased predation (Murdoch 1969; Bergelson 1985; Smout

et al. 2013). Functional responses can also change from Type II to Type III if there is sufficient habitat complexity present in experimental arenas (Hossie and Murray 2010; Alexander et al. 2012). The presence of conspecifics may cause negative mutual interference or positive mutual facilitation thereby changing the functional response (Médoc et al. 2013), and this aspect requires further study. Also, as gammarids can utilise leaf and detrital material as well as prey resources, the effect of switching in such trophic roles needs investigated, although it is known that gammarids will consume both prey and leaf litter when both are present (Kelly et al. 2002).

Values for the parameters 'attack rate', 'handling time' and 'maximum feeding rate' are derived from the functional responses and facilitate descriptions of predator and prey behaviour (Jeschke et al. 2002). The attack rate parameter describes the efficiency of predators when consuming prey at low densities (Hassell and May 1973; Jeschke et al. 2002). From the point of view of the *G. pulex* and *G. d. celticus* predators, generally lower attack rates at low oxygen concentrations might reflect physiological constraints on their movement due to lack of oxygen (e.g. impaired muscle and nerve function). From the point of view of the prey, heightened *G. pulex* and *G. d. celticus* attack rates toward blackfly larvae at the high oxygen concentration indicated that this prey species were more vulnerable to consumption at low densities in these treatments, with potential negative consequences for populations of blackfly larvae. Blackfly larvae filter feed by exposing the head and waving the cephalic fan (Kurtak 1978). At the high oxygen concentration blackfly larvae exposed the cephalic fan more often and for longer than at the low oxygen concentration (C. Lavery pers. obs.). This may have facilitated predator efficiency when consuming blackfly larvae in low densities at the high oxygen concentration. At the low oxygen concentration attack rates toward blackfly larvae were significantly lower than at the high oxygen concentration. This was not the case for mayfly as they are more mobile and still able to swim away from the predator species at the low oxygen concentration (C. Lavery pers. obs.). This behaviour may have allowed both predators to reduce the capture element of the handling time, as blackfly larvae are much less mobile than mayfly larvae (C. Lavery pers. obs.), therefore aiding the efficiency of consuming blackfly larvae at low densities at the high oxygen concentration.

Overall, the invasive amphipod *G. pulex* was in general able to handle prey faster in comparison to the native amphipod *G. d. celticus*. Both predator species had increased handling times at the low oxygen concentration. There was a significantly greater difference between predator species in their handling times at the low oxygen concentration, favouring *G. pulex*. This indicates a greater predatory efficiency of *G. pulex* at the low oxygen concentration compared to *G. d. celticus*. This may allow *G. pulex* impacts to propagate through the community and persist in polluted environments, while *G. d. celticus* will be have less impact. MacNeil et al. (2009) found that *G. pulex* was present and persisted in streams of lower dissolved oxygen, whereas *G. d. celticus* was present and resisted invasion in streams of higher dissolved oxygen. Our handling time and maximum feeding rate results corroborate those findings and suggest that efficiency in capturing and consuming prey is important for invasion success and native resistance.

In conclusion, previous studies show that *G. pulex* drives species richness loss and macroinvertebrate community structure changes in invaded rivers and lakes when it replaces *G. d. celticus* in Western Europe (Dick et al. 1990; Kelly et al. 2006; Piscart et al. 2007). The present study indicates, through the application of comparative functional responses in an environmental context, that such impacts of this invader will be exacerbated by climate change and pollution. The impact of the invader *G. pulex* is strongly context-dependent and this has important implications as invaders are often introduced to areas with dissimilar environmental conditions than the native range they occupy, yet many thrive and displace natives (MacNeil et al. 2009; Dick et al. 2013; Ricciardi et al. 2013). Europe is forecast to become more suitable for sub-tropical species to inhabit because temperatures are increasing, and as species migrate northward the risk of invaders establishing at northern latitudes will increase (Wittmann et al. 2013). For example, many Ponto-Caspian species are tolerant of increased temperatures and, as is the case with *Dikerogammarus villosus*, are more efficient at consuming resources than the invader considered in this study (Bollache et al. 2008; Gallardo and Aldridge 2013a, b; Dodd et al. 2014; Roy et al. 2014). Therefore, studies of relevant context dependencies are becoming increasingly important and should be incorporated into future studies on the impacts of invasive species. The

parameter values estimated from our functional response curves can provide insight into the impact of the predators on prey species and assist in resolving the reasons for damaging invader impacts. Particular attention must be given to low prey densities where it becomes evident if a prey species is in danger of local extinction, however, field functional responses may be different due to the multitude of abiotic and biotic factors that are present in the environment (Barrios-O'Neill et al. 2014; Paterson et al. 2014; Iacarella et al. in press). Further investigation of context-dependent invader impacts using comparative functional responses is needed, including the impact of switching and mutual interference and facilitation as these have been shown to modify functional responses and therefore may modify community-level impacts (Murdoch 1969; Médoc et al. 2013; Smout et al. 2013; Dick et al. 2014).

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