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ORIGINAL PAPER

Intra- and intercontinental variation in the functional responses of a high impact alien invasive fish

Pieter Boets · Ciaran Laverty · Shinji Fukuda · Hugo Verreycken · Kyle Green · Robert J. Britton · Joe Caffrey · Peter L. M. Goethals · Josephine Pegg · Vincent Médoc · Jaimie T. A. Dick

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Abstract Recently, a body of literature has indicated the utility of comparisons among introduced and native species of their functional responses, that is, the relationship between resource use (e.g. predator consumption rate) and resource availability (e.g. prey density) to predict their impact. However, a key feature of this methodology, that has not yet been examined, is the degree to which the functional response curves of an introduced species differ within and between its native and introduced geographical ranges. Information on the variation in functional responses is key to make robust assessments on the ecological impact and to assess possible differences between native and invasive species. Here, we examine the predatory functional responses in multiple native and introduced populations of a globally high impact alien invasive fish, the topmouth gudgeon (*Pseudorasbora parva*). In standardised aquaria and with two prey species, significant differences in the functional responses among and between different populations occurring in the native and the invaded range were found. Among populations in the native range, the functional response indicated little variation, and fish always showed a Type II response, irrespective of the type of prey used. In the introduced range, populations showed a Type II response when fed chironomid larvae as prey, while a Type III response was observed when feeding *Daphnia magna*.

P. Boets (✉) · P. L. M. Goethals
Laboratory of Environmental Toxicology and Aquatic Ecology, Ghent University, Coupure Links 653, 9000 Ghent, Belgium
e-mail: pieter.boets@oost-vlaanderen.be

P. Boets
Provincial Centre of Environmental Research, Godshuizenlaan 95, 9000 Ghent, Belgium

C. Laverty · K. Green · J. T. A. Dick
Institute for Global Food Security, School of Biological Sciences, Medical and Biological Centre, Queen's University Belfast, 97 Lisburn Road, Belfast, Northern Ireland BT9 7BL, UK

S. Fukuda
Institute of Agriculture, Tokyo University of Agriculture and Technology, Fuchu, Japan

H. Verreycken
Team Monitoring and Restoration of Aquatic Fauna, Research Institute for Nature and Forest (INBO), Havenlaan 88 bus 73, 1000 Brussels, Belgium

R. J. Britton · J. Pegg
Department of Life and Environmental Sciences, Bournemouth University, Poole, Dorset BH12 5BB, UK

J. Caffrey
INVAS Biosecurity, 6 Lower Ballymount Rd. Walkinstown, Dublin 12, Ireland

V. Médoc
Equipe Neuro-Ethologie Sensorielle, ENES/Neuro-PSI, CNRS UMR 9197, Université de Lyon/Saint-Etienne, 23 rue Michelon, 42023 Saint-Etienne Cedex 2, France

Populations in the invaded range consumed overall more prey when fed *D. magna* compared to the populations in the native range. When feeding chironomid larvae, no consistent trend was observed. Context dependencies as well as species-specific traits and fish density most likely play an important role when comparing the functional response between populations occurring in their native and invaded ranges.

Keywords Topmouth gudgeon · Alien species · *Pseudorasbora parva* · Impact assessment · Functional response

Introduction

A key challenge in invasion ecology is to predict the future success and ecological impacts of alien invasive species (Kolar and Lodge 2001; van Kleunen et al. 2010; Dick et al. 2014, 2017). Major achievements have been made in predicting the distribution of invasive species based on species distribution modelling (Guisan and Thuiller 2005; Gallardo and Aldridge 2013; Boets et al. 2013). Further, comparing the behaviour and physiological tolerances of invasive with native species, or invasive with non-invasive species, has seen some success in determining the characteristics of successful invaders (e.g. Vila-Gispert et al. 2005; Statzner et al. 2008; van Kleunen et al. 2010; Kumschick et al. 2015) and why invasive species can have severe impacts in their introduced, but not in their native ranges (Hierro et al. 2005). Several mechanisms, such as a lack of natural enemies (Torchin et al. 2003), lower biotic resistance (Levine et al. 2004) or species-traits (e.g. higher reproduction; Azzurro et al. 2014) may partially explain the success and impacts of the introduced species, but these tend to be species specific and without general applicability (van Kleunen et al. 2010; Dick et al. 2014, 2017). There is thus still a pressing need for an ubiquitous method that can reliably explain the ecological impacts of existing invaders and predict impacts of emerging and future invaders under changing environmental conditions (Ricciardi and Rasmussen 1998; Vilà et al. 2011; Dick et al. 2014, 2017).

Recently, assessing the "functional responses" of different species (the relationship between resource uptake rate and resource availability) has shown great promise as a robust method to understand and predict the ecological impacts of invasive species (Bollache et al. 2008; Dick et al. 2013, 2014, 2017; Alexander et al. 2014). The functional response quantifies the strength of trophic interactions and, in particular, gives insight into predator behaviour and effects on prey populations (Holling 1959; Dick et al. 2014, 2017). The shape and magnitude (asymptote) of the functional response can inform whether the consumer (e.g. introduced predator) will likely regulate, stabilise or de-stabilise the resource (e.g. prey) populations, with implications for population viability. With Type III functional responses, prey experience a low density refuge with a reduction in risk of mortality as prey densities fall below a threshold level, thus potentially imparting stability to predator–prey dynamics and facilitating prey persistence (Murdoch and Oaten 1975). This is in contrast to the potentially population destabilising Type II functional response where most, if not all prey are consumed at low prey densities, potentially leading to prey extinction at a range of spatial and temporal scales (Hassell 1978). Further, the maximum feeding rate, as determined by the reciprocal of the handling time, can indicate the prey "offtake rate" (product of functional and numerical responses) and hence impact on prey populations (Dick et al. 2014, 2017).

Functional response experiments have shown that ecologically damaging invasive species mostly have a higher functional response (i.e. higher asymptote or estimated maximum feeding rate), allowing them to more rapidly and efficiently consume resources compared to native species (Dick et al. 2013; Alexander et al. 2014). However, the usefulness of the method requires an understanding of the consistency, or otherwise, of the functional response of a species across populations in both the native and introduced ranges, an aspect that is, as yet, unexplored (Dick et al. 2014).

The aim of this study was, therefore, to examine the functional response of an alien invasive species across its native and introduced range. At one extreme, the functional response of a species could be highly conserved across populations throughout its native and introduced range. On the other hand, due to bottlenecks and non-random introduction of phenotypes and genotypes or other factors (e.g. prey naivety, plasticity,…), the functional response of a species could be

highly variable, especially in the invaded range where such processes are likely. Thus, for example, the functional response could be lower in the native range compared to the invaded range and populations with a long history of invasion could have a lower impact and thus a lower functional response compared to recently introduced populations (see Iacarella et al. 2015). Overall, if the functional response of a species tracks its ecological impacts and the above processes, this would add to the utility of using functional responses in a predictive capacity.

The topmouth gudgeon (*Pseudorasbora parva*) is a renowned invasive fish (see Gozlan et al. 2010), which is native to Japan, China, Korea and the River Amur basin (Pinder et al. 2005; Hardouin et al. 2018), but now widespread and locally abundant within most European countries (Britton et al. 2007; Verreycken et al. 2007). The species has significant negative impacts on ecosystem structure and functioning in its invaded range through interspecific competition with native species (Britton et al. 2010) and predation on broods and eggs of native fish species (Xie et al. 2000). Although the species has been extensively investigated in its introduced range, little is known on its impact in the native range (but see e.g. Konishi et al. 2003). Thus, this invader is an excellent model to examine variation in the functional response of a species across intra- and intercontinental populations. We thus derived functional responses of populations in two geographic locations in the invaded range in western Europe; Belgium (three populations) and the United Kingdom (two populations) and in its native range, Japan (two populations) to investigate differences in functional response among and between populations in the native and invaded ranges.

Materials and methods

Fish sampling and maintenance in the laboratory

Topmouth gudgeon were collected in the field by electrofishing or via baited traps at a total of seven locations throughout its invaded range (Europe, 5 locations) and native range (Japan, 2 locations) between June and December 2014 (five populations of the invaded range and two populations of the native range Table 1). Only fish showing no pathologies (visually observed) were transported to the laboratory and used for experiments. Each population contained at least 50 individuals but no more than 60. We use the term "population" for the fish sampled at a specific geographic location and sufficiently geographically distinct from each other to be considered a separate population.

Each population contained around 50 individuals that were not mixed and kept in one 100 l holding tank (50 × 30 × 40 cm) in closed re-circulating systems filled with carbon-filtered water and aerated constantly. The light regime and air temperature were kept constant at 16 h light and 8 h dark and 20(± 1) °C. Fish were acclimatised one week prior to experiments and fed commercially available fish food (TetraMin®) three times a week, thus avoiding prior learning to the prey used in the experiments.

Experimental design

Functional response experiments were conducted in separate plastic aquaria of 12 l filled with 10 l of aerated and carbon-filtered water. The same light regime and temperature were used as for the holding tanks. No flow-through system was used and aquaria

Table 1 Populations of the topmouth gudgeon sampled in different geographic locations throughout its introduced and native range, with indication of the year of introduction

Country	Status	Location	Coordinates	Year of introduction
Belgium	Introduced	Zonhoven	50°58′06″N; 5°20′58″E	1992
Belgium	Introduced	Sint-Pieters-Leeuw	50°47′01″N; 4°14′27″E	1992
Belgium	Introduced	Kastel	51°03′05″N; 4°11′23″E	1992
United Kingdom	Introduced	Crampmoor	50°59′54″N; 1°27′26″W	1985
United Kingdom	Introduced	Upper Lliedi Reservoir	51°43′11″N; 4°9′23″W	1996
Japan	Native	Fuchu	35°41′03″N; 139°28′55″E	–
Japan	Native	Kunitachi	35°40′48″N; 139°25′32″E	–

were wrapped in aluminium foil to avoid visual contact between individual fish and to reduce the possible disturbance caused by research personnel. No habitat enrichment or aeration was provided during the experiments. Water quality variables were measured at the start and end of the experiment with mean temperature of 19.8 ± 0.0.2 °C, mean pH of 7.3 ± 0.1 and mean oxygen saturation of 89 ± 5%.

Two types of prey were used, separately, in experiments: juvenile *Daphnia magna,* which were fed alive (1 ± 0.2 mm) and frozen chironomid larvae, which were provided as dead organisms (10 ± 3 mm). The selection of prey was based on a previous study conducted by Declerck et al. (2002) investigating the diet and gut content of *Pseudorasbora parva* in its introduced range. Scientific studies on the food sources of the species in its native range are lacking. The study of Declerck et al. (2002) indicated that the gut content of small fish mainly consisted of cladocerans, while the gut content of larger fish (> 50 mm standard length) was filled 75% with chironomid larvae. Fish were not fed in the holding tanks during 48 h prior to the functional response experiments to standardize hunger levels (Alexander et al. 2014). Fish were randomly selected from the holding tanks (containing on average 50 individuals per population) and transferred to the individual aquaria one hour prior to the introduction of the prey. All fish (18 individuals per population and per prey species, see Fig. 1) were selected from a relatively uniform size class (50–60 mm standard length) to reduce the influence of size-related differences in prey consumption. Functional response experiments were run per prey species at six different prey densities (4, 8, 16, 32, 64, 128), with three replicates per density. Per experiment, 18 aquaria filled with one individual of *P. parva* from one of the populations and the aforementioned prey densities per prey species were set up. In total, 252 individual fish were used in the experiments of which 108 (3 populations with 36 fish) originating from Belgium, and 72 fish from the UK and 72 fish from Japan (2 populations with 36 fish). Pilot experiments were run to determine the prey densities at which a functional response asymptote appeared (128 individuals of *D.* magna and 64 individuals of chironomid larvae). Fish were removed and prey consumption was examined 60 min after the experiments were initiated. Individuals of *P. parva* were re-used at random in the two different prey experiments. At least three days recovery time was allowed for fish between two experimental runs.

Statistical analyses

The functional response was determined based on logistic regression analyses modelling the proportion of the available prey consumed (initial prey density/number of prey consumed) using the following equation:

$$P(Y_i) = \alpha + \beta_1 X_1 + \beta_2 X_2 + \cdots \beta_i X_i + \varepsilon \quad (1)$$

where Y_i denotes the response variable Y (prey consumed) at the ith term, X_i denotes the explanatory variable X (prey density) at the ith term, β_i denotes the regression coefficient β at the ith term, α denotes a constant and ε denotes the prediction error between the observed value of the dependent variable for a given observation and the value of the dependent variable predicted for that observation from the linear model. Based on the values of β_1 and β_2 it was possible to determine the Type (Type II or Type III) of functional response. In case of a significant negative β_1 coefficient (first order term), a Type II response was determined. In case of a significantly positive β_1 coefficient in the first section of the line (first order term) and the second order term being significantly negative (β_2), this indicated a Type III response. In case of a Type II response, we used Rogers' Random Predator equation as the number of prey was decreasing over time (i.e. prey were not replaced as they were consumed; see Alexander et al. 2012) which is denoted by:

$$N_e = N_0(1 - \exp(a(N_e h - T))) \quad (2)$$

where N_e is the number of prey eaten, N_0 is the initial density of prey, a is the attack constant, h is the handling time and T is the total experimental period.

The Hassel's equation was used in case of a Type III response which is denoted by:

$$N_e = N_0(1 - \exp((d + bN_0)(T_h N_e - T)/(1 + cN_0)) \quad (3)$$

where *Ne* is the number of prey eaten, N_o is the initial density of prey, a the attack constant is replaced with but equal to $(d + bN_0)/(1 + cN_0)$, h is the handling time, T is the total experimental time, b, c and d are constants. Raw consumption data were non-

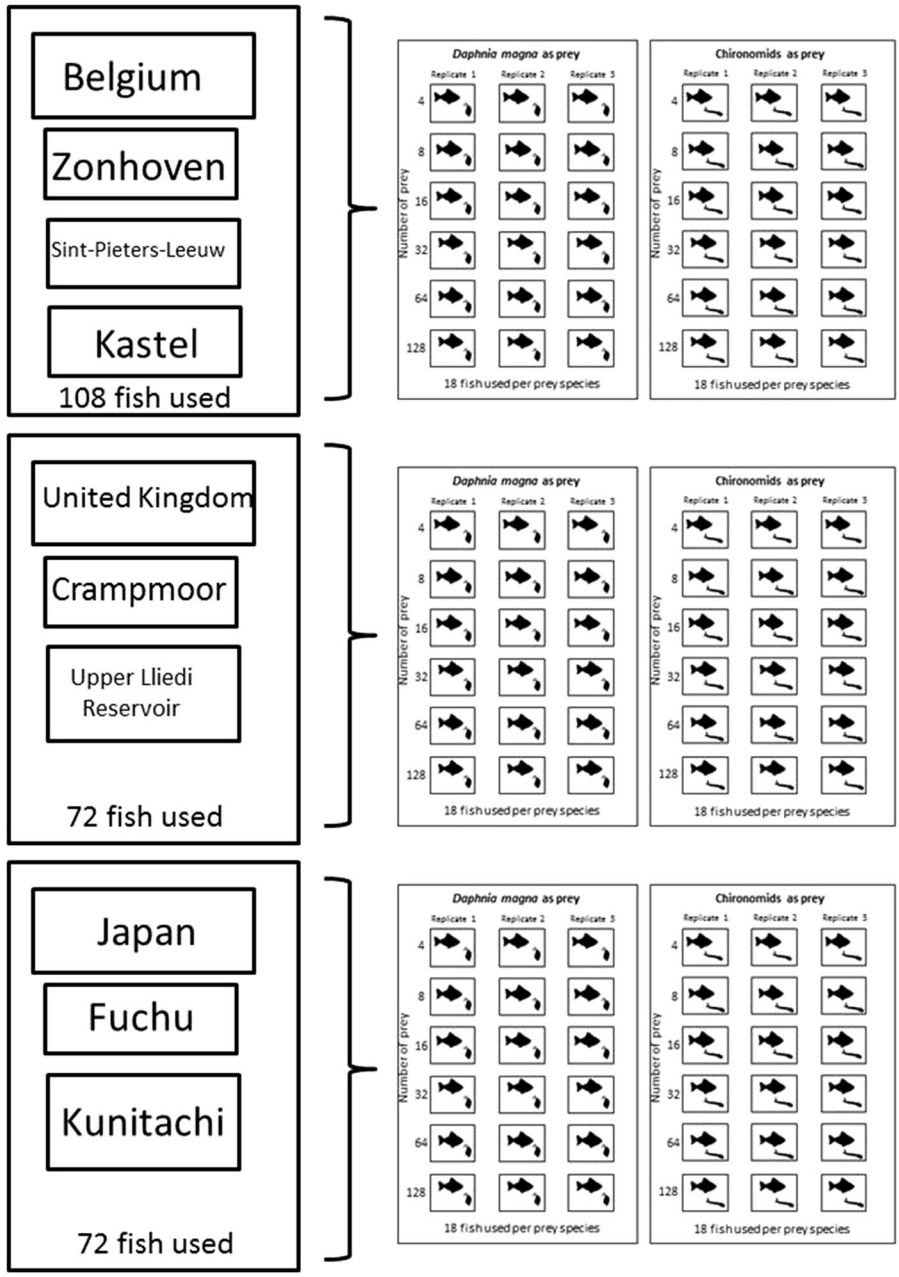

Fig. 1 Overview of the experimental set up. Three, two and two populations (see Table 1) with each individual population containing 36 individuals from respectively Belgium, the United Kingdom and Japan were used to run the experiments. For each population two prey species were tested: *Daphnia magna* and chironomid larvae. Three replicates per prey density (4, 8, 16, 32, 64 and 128 prey) were run

parametrically bootstrapped (n = 1000), using either Eq. (2) for Type II data or Eq. (3) for Type III data to construct 95% confidence intervals around the mean functional response curve for each experimental group (Barrios-O'Neill et al. 2014). All analyses were carried out in R using the FRAIR package (R core development team 2014; Pritchard et al. 2017).

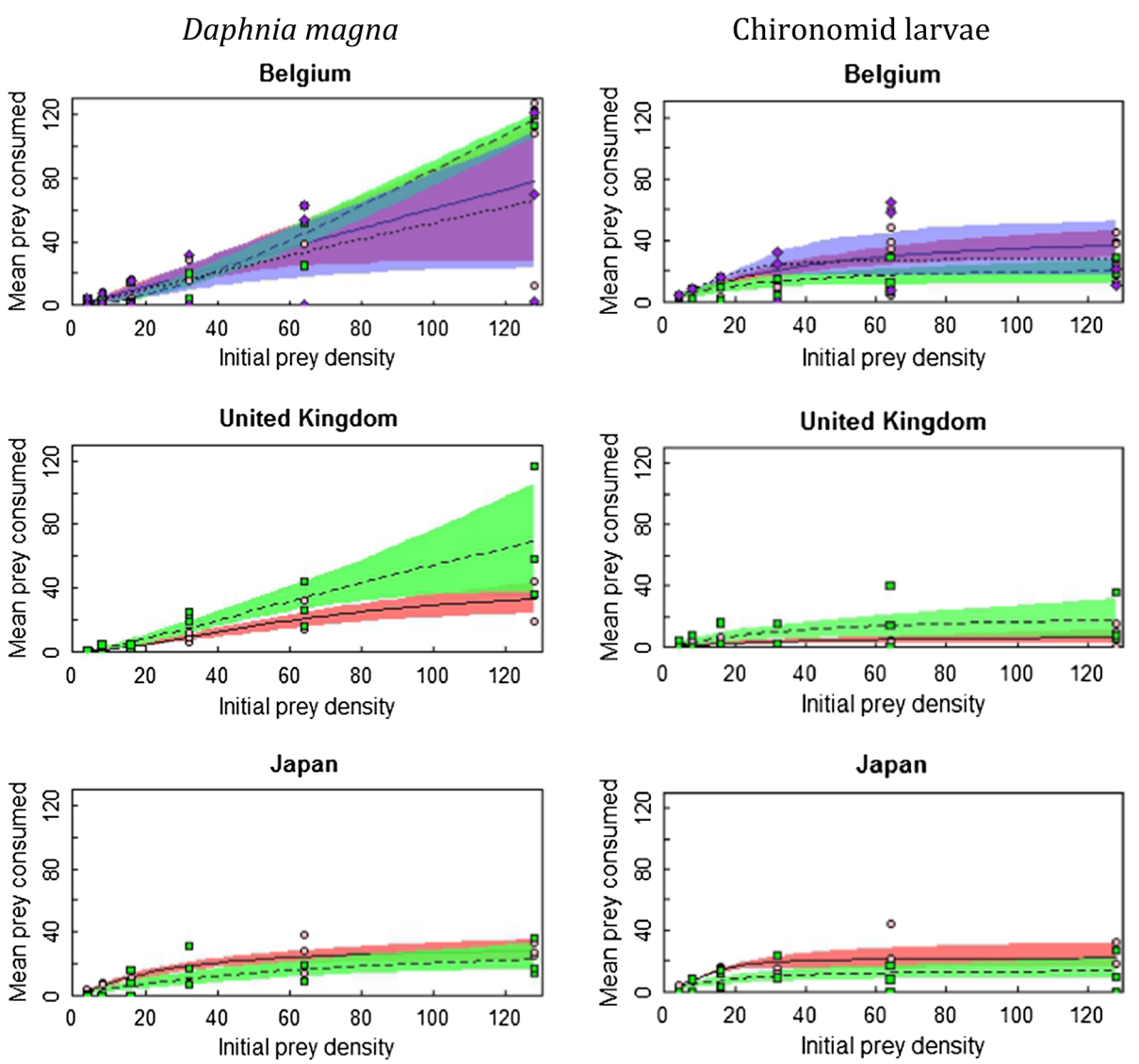

Fig. 2 Functional responses of the topmouth gudgeon when being fed as prey *Daphnia magna* (left) and chironomid larvae (right) with indication of 95% confidence intervals based on bootstrapping. Different populations were tested in Belgium (pink = Kastel, green = Zonhoven, purple = Sint-Pieters Leeuw), the United Kingdom (pink = Upper Lliedi reservoir, green = Crampmoor), and Japan (pink = Fuchu, green = Kunitachi). Each colour represents a different population in each country. Raw data were added for each population (green squares, pink dots and purple rhombuses)

Results

Intracontinental differences in functional response

For the populations in Belgium, when fed *D. magna* or chironomid larvae, there was overlap of all three populations (95% confidence intervals) (Fig. 2, Table 2). This indicates that both attack rates and handling times were not significantly different among these populations (Table 2). For the populations in the UK, there was some overlap between the populations at higher prey densities (> 96 individuals) for *D. magna* and at lower prey densities for chironomid larvae (< 32 individuals). The population originating from the Upper Lliedi reservoir showed a higher functional response indicating that attack rates were significantly greater and handling times lower for this population (Fig. 2, Table 2). For the populations in

Table 2 Parameters for the different functional response curves that were developed for each country, each population and for each prey type used in the experiments

Country	Population	Prey	Parameter			
			A	b	c	h
Belgium	Kastel	*Daphnia magna*		0.562 (0.041–5.5 × 10^5)	0.590 (0.0–4.9 × 10^6)	0.0 (0.0–0.11)
Belgium	Zonhoven	*Daphnia magna*		0.019 (0.013–0.042)	0.0 (0.0–0.0)	0.0 (0.0–0.0)
Belgium	Sint-Pieters-Leeuw	*Daphnia magna*		0.205 (0.0–8.5 × 10^5)	0.246 (0.0–1.4 × 10^6)	0.002 (0.0–0.046)
United Kingdom	Upper Lliedi reservoir	*Daphnia magna*		0.014 (0.008–0.024)	0.003 (0.0–0.0172)	0.023 (0.0–0.049)
United Kingdom	Crampmoor	*Daphnia magna*		0.043 (0.023–0.148)	0.035 (0.0–0.209)	0.003 (0.0–0.0201)
Japan	Fuchu	*Daphnia magna*	2.052 (1.058–3.99)			0.031 (0.021–0.045)
Japan	Kunitachi	*Daphnia magna*	0.599 (0.236–1.565)			0.030 (0.0–0.052)
Belgium	Kastel	Chironomid larvae	1.846 (0.991–3.03)			0.023 (0.015–0.034)
Belgium	Zonhoven	Chironomid larvae	1.247 (0.3–5.618)			0.044 (0.014–0.092)
Belgium	Sint-Pieters-Leeuw	Chironomid larvae	8.278 (1.114–183.58)			0.035 (0.015–0.065)
United Kingdom	Upper Lliedi reservoir	Chironomid larvae	0.209 (0.061–1.212)			0.115 (0–0.0441)
United Kingdom	Crampmoor	Chironomid larvae	0.675 (0.162–2972)			0.044 (0.0–0.141)
Japan	Fuchu	Chironomid larvae	6.279 (2.835–94.45)			0.044 (0.026–0.065)
Japan	Kunitachi	Chironomid larvae	1.200 (0.379–3.484)			0.067 (0.035–0.131)
Belgium		*Daphnia magna*		0.068 (0.019–4.037)	0.050 (0.0–185552)	0.0 (0.0–0.018)
UK		*Daphnia magna*		0.028 (0.016–0.071)	0.023 (0.0–0.146)	0.009 (0.0–0.026)
Japan		*Daphnia magna*	1.071 (0.603–1.947)			0.030 (0.02–0.045)
Belgium		Chironomid larvae	1.983 (1.206–2.983)			0.028 (0.02–0.038)
UK		Chironomid larvae	0.423 (1.045–1.463)			0.063 (0.0–0.156)
Japan		Chironomid larvae	2.194 (1.034–4.29)			0.050 (0.03–0.072)

For details on the parameters we refer to the statistical analyses in materials and methods

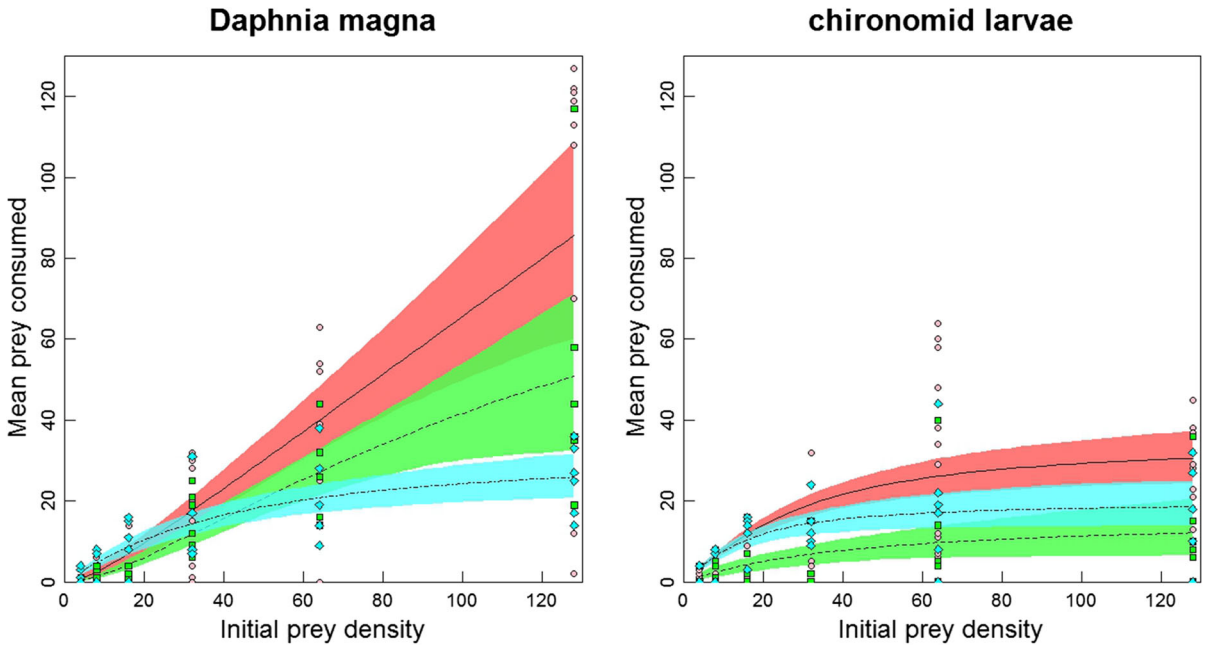

Fig. 3 Functional responses of the topmouth gudgeon when being fed *Daphnia magna* as prey (left) and chironomid larvae (right) with indication of 95% confidence intervals based on bootstrapping. Each colour represents a different country (green = United Kingdom, red = Belgium, and blue = Japan). Data for these figures were based on data represented in Fig. 2. Raw data were added for each country (green squares, red dots and cyan rhombuses)

Japan, overlap was observed at prey densities above 42 individuals, whereas no overlap of the 95% confidence intervals occurred at the lower prey densities for both *D. magna* and chironomid larvae (Fig. 2, Table 2).

Intercontinental differences in functional response

The 95% confidence intervals show that there was little overlap between Belgian and Japanese *P. parva* when consuming *D. magna* and chironomid larvae, indicating that attack rates were higher and handling times were significantly lower for Belgian than Japanese *P. parva* (Fig. 3, Table 2). The handling times of the UK topmouth gudgeon were high and the attack rates were low when fed chironomid larvae compared to the topmouth gudgeon sampled in the other countries and the 95% confidence intervals were hardly overlapping with any of the other functional response curves, indicating that the UK topmouth gudgeon consumed significantly less chironomid larvae compared to the topmouth gudgeon sampled in Belgium and Japan (Fig. 3).

Functional response type

When *Daphnia magna* were used as prey, fish populations in the invaded range always showed a Type III response, indicated by positive first order and negative second order terms derived from logistic regressions of proportions of prey eaten, whereas populations of the native range showed a Type II response (Table 3, Fig. 2). All populations of the topmouth gudgeon (invaded and native range) showed a Type II functional response towards chironomid larvae as indicated by negative first order terms derived from logistic regressions of proportions of prey eaten (Table 3, Fig. 2).

Discussion

Differences in ecological impact between different populations

We observed clear differences in functional responses between different populations of the topmouth gudgeon for both prey items used. Indeed, differences

Table 3 The Type of functional response for the different fish populations with respect to type of prey (chironomid larvae or *Daphnia magna*)

Country	Status	Location	Type of functional response	
			Chironomid larvae	*D. magna*
Belgium	Introduced	Zonhoven	Type II	Type III
Belgium	Introduced	Sint-Pieters-Leeuw	Type II	Type III
Belgium	Introduced	Kastel	Type II	Type III
United Kingdom	Introduced	Crampmoor	Type II	Type III
United Kingdom	Introduced	Upper Lliedi Reservoir	Type II	Type III
Japan	Native	Fuchu	Type II	Type II
Japan	Native	Kunitachi	Type II	Type II

were found between populations within one country as well as between populations from the native and introduced range. The functional response of the populations in their native range was intermediate to the functional response derived for the populations in their invaded range, especially when using chironomid larvae as prey. There are several possible explanations for the difference in functional response observed between populations in the native and invaded range such as prey naivety or species plasticity (Cuthbert et al. 2018; Hollander and Bordeau 2016). Species plasticity of predator and prey has shown to be responsible for the observed variation in species responses caused by specific environmental habitat conditions.

Besides the differences in functional response between different geographic areas, we observed large variations in functional responses and thus possible ecological impact between populations within one geographic area, especially in the invaded range. Population differences are depending on the invasion history of the species and on the local environmental conditions (Sakai et al. 2001). Newly introduced populations often pass through genetic bottlenecks causing possible variations in the functional response. Based on this, a reduction in variation of the functional response in the introduced range could be expected, although we observed the opposite. Indeed, whereas the functional response in the native range showed little variation there were significant differences observed in functional response between the populations in the introduced range. In addition to the context dependencies (e.g. habitat complexity), these variations in populations should be taken into account when comparing the functional response between native and invasive fish species to increase the predictive power (Dick et al. 2014).

Besides the functional response as calculated in this study, other aspects such as a lack of natural enemies in combination with a high reproductive capacity, should be considered when determining its ecological impact. Research carried out in the UK by Britton et al. (2010), indicated that topmouth gudgeon can reach very high densities of up to 60 individuals per square meter, a phenomenon that is not reported from its native range. In this respect, it is important to mention that the functional response examined in our study is a *per capita* effect of the alien invasive fish species (Parker et al. 1999) and does not include fish density. Thus, although the functional response (*per capita* effect) might not be higher for populations in the invaded range (as is the case in our study for some populations), when considering its high abundance, the species might still exert a significant ecological impact on the local community. Indeed, previous research suggests that *P. parva* only has a detectable impact when being present at high densities (Britton et al. 2010; Jackson et al. 2014). In this respect, the development of the invader relative impact potential (RIP) metric by Dick et al. (2017) could provide a better understanding of the likelihood and degree of ecological impact as it considers both the functional response and the abundance. Recent research by Laverty et al. (2017) indicated that the predictive power of the functional response for topmouth gudgeon was limited, however, incorporation of their abundances relative to natives into the RIP metric gave high predictive power.

Differences in the type of functional response

In its native range (Japan) topmouth gudgeon always showed a Type II functional response towards either *Daphnia magna* or chironomid larvae used as prey. A Type II functional response typically describes the foraging behaviour of a species that is capable of handling only one prey at a time and in environments of reduced complexity that do not influence factors such as capture success or learned behaviour (Abrams 1990), similar to the experiments in this study. Earlier studies on functional responses have shown that this Type II response is often observed for fish (Murray et al. 2013; Alexander et al. 2014), but that with increasing habitat complexity the functional response might change to a Type III response (Alexander et al. 2015). A Type II response is likely to be destabilising with respect to prey populations (Murdoch and Oaten 1975), as prey at low densities experience increased proportional consumption, whereas prey are not consumed at low densities when predators show a Type III functional response (Juliano 2001). In any case, the shape of the functional response may not be as important as the maximum feeding rate, that is, the reciprocal of handling time "*h*", which will determine the offtake rate of prey from the population and therefore be more indicative of ecological impact (see Dick et al. 2014).

A previous study conducted by Hanazato and Yasuno (1989) found that *P. parva* exerted a high predation pressure on *Daphnia longispina* in mesocosm experiments conducted in Japan leading to a strong reduction in abundance of the prey. Our experiments indicated that in its introduced range the topmouth gudgeon showed a Type III response when being fed *Daphnia magna* as prey. *Daphnia* typically clump together, which reduces the probability of being detected and thus their likelihood of being consumed at low fish density. Based on gut content analyses, derived from field studies, it has been shown that both *Daphnia* and chironomid larvae are being predated, but that most of the time chironomid larvae make up the largest part of the diet of *P. parva* (Gozlan et al. 2010; Yalçın-Özdilek et al. 2013). It is clear that topmouth gudgeon are limited by their handling ability, but not search efficiency with respect to chironomid larvae, and their attack rate or search efficiency but not handling ability with respect to *D. magna*. Furthermore, topmouth gudgeon are omnivorous, therefore, when prey densities are depleted their feeding mode may switch to take advantage of available algal resources, thus altering the functional response through switching (Yalçın-Özdilek et al. 2013; Médoc et al. 2018). Topmouth gudgeon are noted for the high densities they accrue in invaded ranges, thus it is unlikely that one predator would be feeding in isolation on a prey resource. Facilitative, mutualistic and antagonistic interactions between conspecifics that may alter the functional response have not been considered in this study. However, these aspects are of primary concern in future studies of topmouth gudgeon if impacts on native prey populations are to be comprehensively understood (Britton et al. 2007; Médoc et al. 2013; Barrios-O'Neill et al. 2014).

Our experiments were conducted under laboratory conditions with fixed light and temperature conditions and no substrate (low habitat complexity). As it has been shown that context dependencies (e.g. habitat complexity) are important (Alexander et al. 2015), our results illustrate functional responses of adult topmouth gudgeon in a simplified habitat. As we want to compare the functional response between different populations the tests in a controlled environment can help to understand the differences in impact of a species between native and invaded regions. However, further research under different habitat and environmental conditions, different predator densities as well as the use of juvenile fish may contribute to a better understanding of the functional response of topmouth gudgeon.

In conclusion, our study shows differences in the functional responses of an invasive fish species between different populations within the native and invaded range, or when comparing populations from the native and invaded range. The topmouth gudgeon showed both a Type II and Type III functional response depending on the prey species and the population origin. Populations in the invaded range did not always show a higher functional response compared to populations in the native range. To better estimate the impact of invasive species based on the functional response, the fish density as well as habitat conditions should be taken into account. Finally, even if the functional response of this invader is highly variable, if it is still much greater than that of trophically analogous natives, the comparison of functional responses between invader and native will

often be predictive of the ecological impact of the invader (see Dick et al. 2013, 2014; Alexander et al. 2014).

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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