

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

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24

25 **Abstract**

26 Recently, a body of literature has indicated the utility of comparisons among introduced  
27 and native species of their functional responses, that is, the relationship between  
28 resource use (e.g. predator consumption rate) and resource availability (e.g. prey  
29 density) to predict their impact. However, a key feature of this methodology, that has  
30 not yet been examined, is the degree to which the functional response curves of an  
31 introduced species differ within and between its native and introduced geographical  
32 ranges. Information on the variation in functional responses is key to make robust  
33 assessments on the ecological impact and to assess possible differences between native  
34 and invasive species. Here, we examine the predatory functional responses in multiple  
35 native and introduced populations of a globally high impact alien invasive fish, the  
36 topmouth gudgeon (*Pseudorasbora parva*). In standardised aquaria and with two prey  
37 species, significant differences in the functional responses among and between different  
38 populations occurring in the native and the invaded range were found. Among  
39 populations in the native range, the functional response indicated little variation, and  
40 fish always showed a Type II response, irrespective of the type of prey used. In the  
41 introduced range, populations showed a Type II response when fed chironomid larvae  
42 as prey, while a Type III response was observed when feeding *Daphnia magna*.  
43 Populations in the invaded range consumed overall more prey when fed *D. magna*  
44 compared to the populations in the native range. When feeding chironomid larvae, no  
45 consistent trend was observed. Context dependencies as well as species-specific traits  
46 and fish density most likely play an important role when comparing the functional  
47 response between populations occurring in their native and invaded ranges.

48

49 Keywords: topmouth gudgeon, alien species, *Pseudorasbora parva*, impact assessment,  
50 functional response

## 51 **Introduction**

52

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

71

72 Recently, assessing the “functional responses” of different species (the relationship  
73 between resource uptake rate and resource availability) has shown great promise as a  
74 robust method to understand and predict the ecological impacts of invasive species  
75 (Bollache et al. 2008; Dick et al. 2013; Alexander et al. 2014; Dick et al. 2014, 2017). The  
76 functional response quantifies the strength of trophic interactions and, in particular,  
77 gives insight into predator behaviour and effects on prey populations (Holling 1959;  
78 Dick et al. 2014, 2017). The shape and magnitude (asymptote) of the functional  
79 response can inform whether the consumer (e.g. introduced predator) will likely  
80 regulate, stabilise or de-stabilise the resource (e.g. prey) populations, with implications  
81 for population viability. With Type III functional responses, prey experience a low  
82 density refuge with a reduction in risk of mortality as prey densities fall below a  
83 threshold level, thus potentially imparting stability to predator–prey dynamics and  
84 facilitating prey persistence (Murdoch and Oaten 1975). This is in contrast to the

85 potentially population destabilising Type II functional response where most, if not all  
86 prey are consumed at low prey densities, potentially leading to prey extinction at a  
87 range of spatial and temporal scales (Hassell 1978). Further, the maximum feeding rate,  
88 as determined by the reciprocal of the handling time, can indicate the prey “offtake rate”  
89 (product of functional and numerical responses) and hence impact on prey populations  
90 (Dick et al. 2014, 2017).

91

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

99

100 The aim of this study was, therefore, to examine the functional response of an alien  
101 invasive species across its native and introduced range. At one extreme, the functional  
102 response of a species could be highly conserved across populations throughout its  
103 native and introduced range. On the other hand, due to bottlenecks and non-random  
104 introduction of phenotypes and genotypes or other factors (e.g. prey naiveté,  
105 plasticity,...), the functional response of a species could be highly variable, especially in  
106 the invaded range where such processes are likely. Thus, for example, the functional  
107 response could be lower in the native range compared to the invaded range and  
108 populations with a long history of invasion could have a lower impact and thus a lower  
109 functional response compared to recently introduced populations (see Iacarella et al.  
110 2015). Overall, if the functional response of a species tracks its ecological impacts and  
111 the above processes, this would add to the utility of using functional responses in a  
112 predictive capacity.

113

114 The topmouth gudgeon (*Pseudorasbora parva*) is a renowned invasive fish (see Gozlan  
115 et al. 2010), which is native to Japan, China, Korea and the River Amur basin (Pinder et  
116 al. 2005; Hardouin et al. 2018), but now widespread and locally abundant within most  
117 European countries (Britton et al. 2007; Verreycken et al. 2007). The species has

118 significant negative impacts on ecosystem structure and functioning in its invaded range  
 119 through interspecific competition with native species (Britton et al. 2010) and predation  
 120 on broods and eggs of native fish species (Xie et al. 2000). Although the species has been  
 121 extensively investigated in its introduced range, little is known on its impact in the  
 122 native range (but see e.g. Konishi et al. 2003). Thus, this invader is an excellent model to  
 123 examine variation in the functional response of a species across intra- and  
 124 intercontinental populations. We thus derived functional responses of populations in  
 125 two geographic locations in the invaded range in western Europe; Belgium (three  
 126 populations) and the United Kingdom (two populations) and in its native range, Japan  
 127 (two populations) to investigate differences in functional response among and between  
 128 populations in the native and invaded ranges.

## 129 **Materials and Methods**

### 130 *Fish sampling and maintenance in the laboratory*

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

140

141 Table 1: Populations of the topmouth gudgeon sampled in different geographic locations throughout its  
 142 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	1996
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	—

143

144 Each population contained around 50 individuals that were not mixed and kept in one  
145 100 l holding tank (50x30x40cm) in closed re-circulating systems filled with carbon-  
146 filtered water and aerated constantly. The light regime and air temperature were kept  
147 constant at 16h light and 8h dark and  $20(\pm 1)^{\circ}\text{C}$ . Fish were acclimatised one week prior  
148 to experiments and fed commercially available fish food (TetraMin®) three times a  
149 week, thus avoiding prior learning to the prey used in the experiments.

150

### 151 *Experimental design*

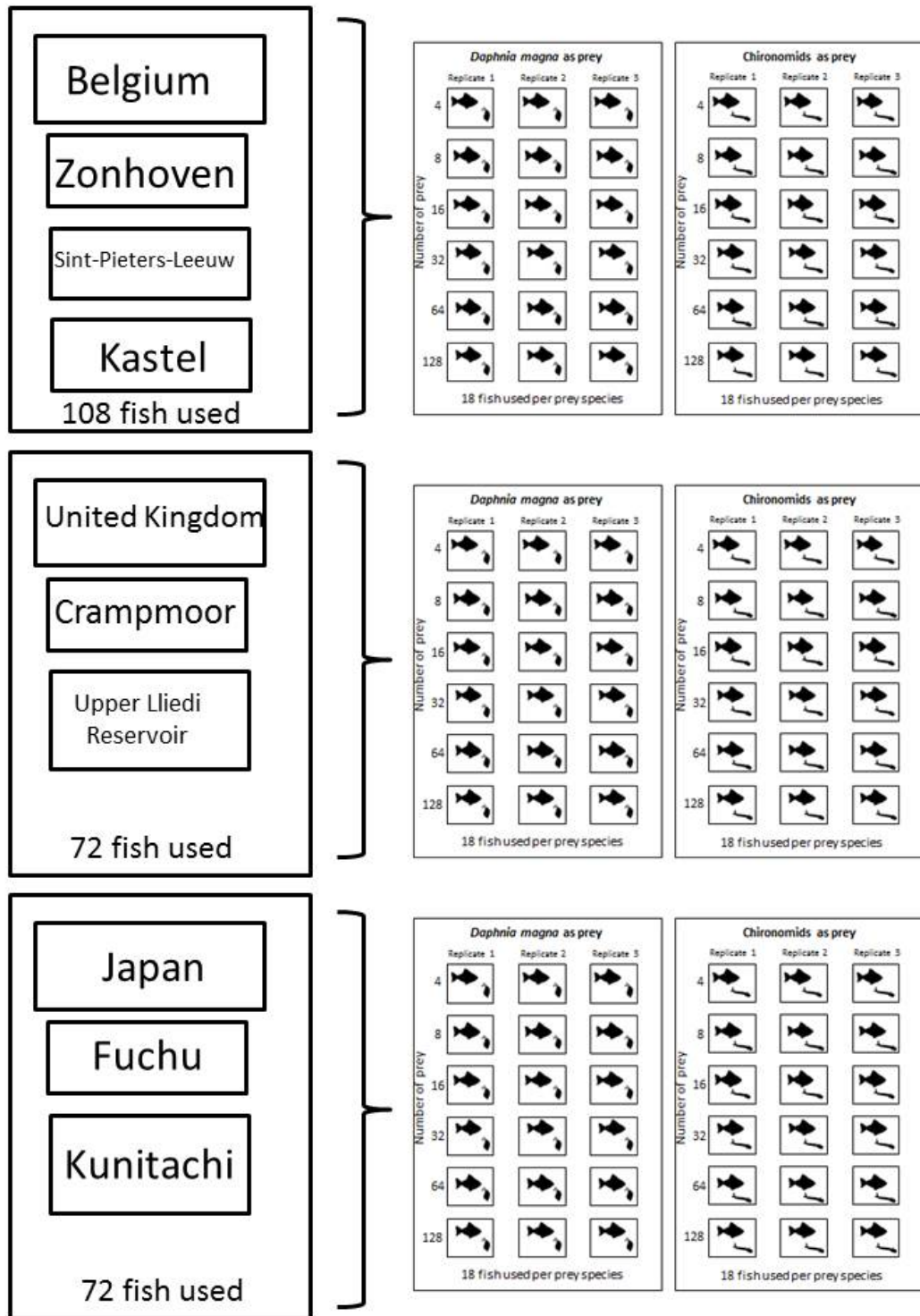
152 Functional response experiments were conducted in separate plastic aquaria of 12 l  
153 filled with 10 l of aerated and carbon-filtered water. The same light regime and  
154 temperature were used as for the holding tanks. No flow-through system was used and  
155 aquaria were wrapped in aluminium foil to avoid visual contact between individual fish  
156 and to reduce the possible disturbance caused by research personnel. No habitat  
157 enrichment or aeration was provided during the experiments. Water quality variables  
158 were measured at the start and end of the experiment with mean temperature of  
159  $19.8\pm 0.0.2^{\circ}\text{C}$ , mean pH of  $7.3\pm 0.1$  and mean oxygen saturation of  $89\pm 5\%$ .

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161 Two types of prey were used, separately, in experiments: juvenile *Daphnia magna*,  
162 which were fed alive ( $1\pm 0.2\text{mm}$ ) and frozen chironomid larvae, which were provided as  
163 dead organisms ( $10\pm 3\text{mm}$ ). The selection of prey was based on a previous study  
164 conducted by Declerck et al. (2002) investigating the diet and gut content of  
165 *Pseudorasbora parva* in its introduced range. Scientific studies on the food sources of the  
166 species in its native range are lacking. The study of Declerck et al. (2002) indicated that  
167 the gut content of small fish mainly consisted of cladocerans, while the gut content of  
168 larger fish ( $>50\text{mm}$  standard length) was filled 75% with chironomid larvae. Fish were  
169 not fed in the holding tanks during 48h prior to the functional response experiments to  
170 standardize hunger levels (Alexander et al. 2014). Fish were randomly selected from the  
171 holding tanks (containing on average 50 individuals per population) and transferred to  
172 the individual aquaria one hour prior to the introduction of the prey. All fish (18  
173 individuals per population and per prey species, see Fig. 1) were selected from a  
174 relatively uniform size class (50-60mm standard length) to reduce the influence of size-  
175 related differences in prey consumption. Functional response experiments were run per  
176 prey species at six different prey densities (4, 8, 16, 32, 64, 128), with three replicates

177 per density. Per experiment, 18 aquaria filled with one individual of *P. parva* from one of  
178 the populations and the aforementioned prey densities per prey species were set up. In  
179 total, 252 individual fish were used in the experiments of which 108 (3 populations with  
180 36 fish) originating from Belgium, and 72 from the UK and Japan (2 populations with 36  
181 fish). Pilot experiments were run to determine the prey densities at which a functional  
182 response asymptote appeared (128 individuals of *D. magna* and 64 individuals of  
183 chironomid larvae). Fish were removed and prey consumption was examined 60 min  
184 after the experiments were initiated. Individuals of *P. parva* were re-used at random in  
185 the two different prey experiments. At least three days recovery time was allowed for  
186 fish between two experimental runs.

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**Figure 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.  
*Statistical analyses*



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

$$197 \quad P(Y_i) = \alpha + \beta_1 X_1 + \beta_2 X_2 + \dots + \beta_i X_i + \varepsilon \quad (1)$$

198  
199 where  $Y_i$  denotes the response variable  $Y$  (prey consumed) at the  $i$ th term,  $X_i$  denotes the  
200 explanatory variable  $X$  (prey density) at the  $i$ th term,  $\beta_i$  denotes the regression  
201 coefficient  $\beta$  at the  $i$ th term,  $\alpha$  denotes a constant and  $\varepsilon$  denotes the prediction error  
202 between the observed value of the dependent variable for a given observation and the  
203 value of the dependent variable predicted for that observation from the linear model.  
204 Based on the values of  $\beta_1$  and  $\beta_2$  it was possible to determine the Type (Type II or Type  
205 III) of functional response. In case of a significant negative  $\beta_1$  coefficient (first order  
206 term), a Type II response was determined. In case of a significantly positive  $\beta_1$  coefficient  
207 in the first section of the line (first order term) and the second order term being  
208 significantly negative ( $\beta_2$ ), this indicated a Type III response. In case of a Type II  
209 response, we used Rogers' Random Predator equation as the number of prey was  
210 decreasing over time (i.e. prey were not replaced as they were consumed; see Alexander  
211 et al. 2012) which is denoted by:

$$212 \quad N_e = N_0 (1 - \exp(-a(N_e h - T))) \quad (2)$$

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

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

$$216 \quad N_e = N_0 (1 - \exp(-((d + bN_0) (T_h N_e - T) / (1 + cN_0)))) \quad (3)$$

217 where  $N_e$  is the number of prey eaten,  $N_0$  is the initial density of prey,  $a$  the attack  
218 constant is replaced with but equal to  $(d + bN_0) / (1 + cN_0)$ ,  $h$  is the handling time,  $T$  is  
219 the total experimental time,  $b$ ,  $c$  and  $d$  are constants. Raw consumption data were non-  
220 parametrically bootstrapped ( $n=1000$ ), using either equation (2) for Type II data or  
221 equation (3) for Type III data to construct 95% confidence intervals around the mean  
222 functional response curve for each experimental group (Barrios-O'Neill et al. 2014). All  
223 analyses were carried out in R using the FRAIR package (R core development team  
224 2014, Pritchard et al. 2017).

225

226

227 **Results**

228

229 *Intracontinental differences in functional response*

230 For the populations in Belgium, when fed *D. magna* or chironomid larvae, there was  
231 overlap of all three populations (95% confidence intervals) (Fig. 2, table 2). This  
232 indicates that both attack rates and handling times were not significantly different  
233 among these populations (table 2). For the populations in the UK, there was some  
234 overlap between the populations at higher prey densities (> 96 individuals) for *D.*  
235 *magna* and at lower prey densities for chironomid larvae (< 32 individuals). The  
236 population originating from the Upper Lliedi reservoir showed a higher functional  
237 response indicating that attack rates were significantly greater and handling times  
238 lower for this population (Fig. 2, table 2). For the populations in Japan, overlap was  
239 observed at prey densities above 42 individuals, whereas no overlap of the 95%  
240 confidence intervals occurred at the lower prey densities for both *D. magna* and  
241 chironomid larvae (Fig. 2, table 2).

242

243 *Intercontinental differences in functional response*

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

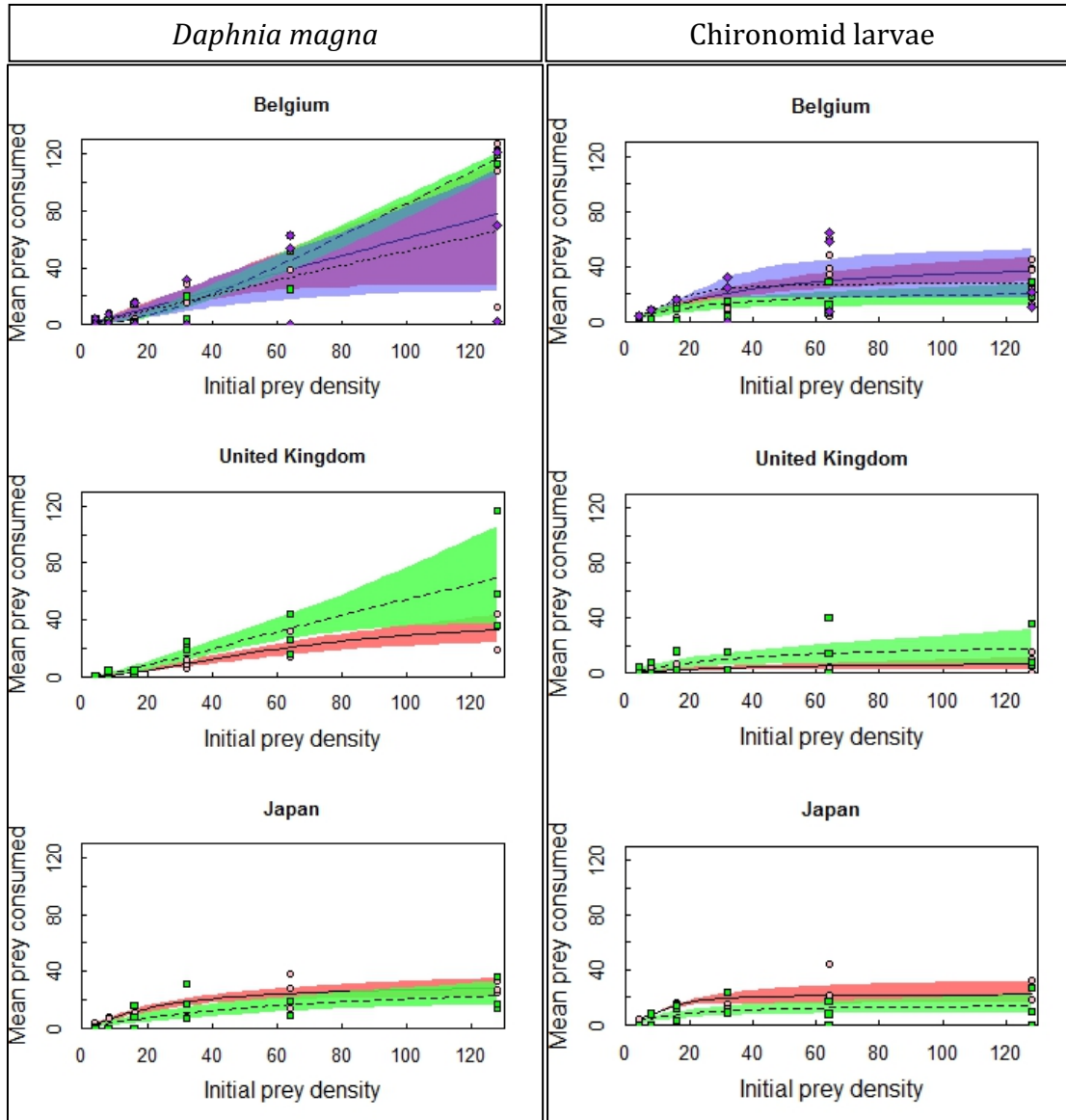
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254 Table 2: Parameters for the different functional response curves that were developed for each country, each population and for each prey type used in the  
 255 experiments. For details on the parameters we refer to the statistical analyses in materials and methods.

country	population	Prey	parameter			
			a	b	c	h
Belgium	Kastel	<i>Daphnia magna</i>		0.562 (0.041-5.5*10 <sup>5</sup> )	0.590 (0.0-4.9*10 <sup>6</sup> )	0.0 (0.0-0.11)
Belgium	Zonhoven	<i>Daphnia magna</i>		0.019 (0.013-0.042)	0.0 (0.0-0.0)	0.0 (0.0-0.0)
Belgium	Sint-Pieters-Leeuw	<i>Daphnia magna</i>		0.205 (0.0-8.5*10 <sup>5</sup> )	0.246 (0.0-1.4*10 <sup>6</sup> )	0.002 (0.0-0.046)
United Kingdom	Upper Lliedi reservoir	<i>Daphnia magna</i>		0.014 (0.008-0.024)	0.003 (0.0-0.0172)	0.023 (0.0-0.049)
United Kingdom	Crampmoor	<i>Daphnia magna</i>		0.043 (0.023-0.148)	0.035 (0.0-0.209)	0.003 (0.0-0.0201)
Japan	Fuchu	<i>Daphnia magna</i>	2.052 (1.058-3.99)			0.031 (0.021-0.045)
Japan	Kunitachi	<i>Daphnia magna</i>	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	1.2 (0.379-3.484)			0.067 (0.035-0.131)
Belgium		<i>Daphnia magna</i>		0.068 (0.019-4.037)	0.050 (0.0-185552)	0.0 (0.0-0.018)
UK		<i>Daphnia magna</i>		0.028 (0.016-0.071)	0.023 (0.0-0.146)	0.009 (0.0-0.026)
Japan		<i>Daphnia magna</i>	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)

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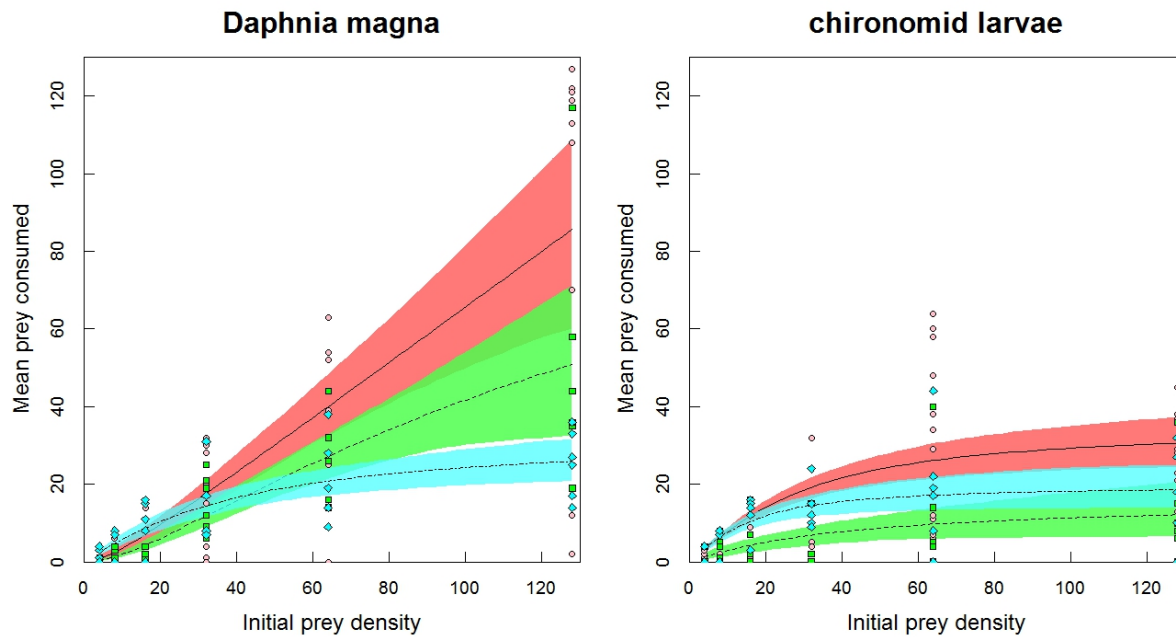


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259 **Figure 2** – Functional responses of the topmouth gudgeon when being fed as prey *Daphnia magna* (left)  
260 and chironomid larvae (right) with indication of 95% confidence intervals based on bootstrapping.  
261 Different populations were tested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

265

266



267  
 268 **Figure 3** – Functional responses of the topmouth gudgeon when being fed *Daphnia magna* as prey (left)  
 269 and chironomid larvae (right) with indication of 95% confidence intervals based on bootstrapping. Each  
 270 colour represents a different country (green=United Kingdom, red=Belgium, and blue=Japan). Data for  
 271 these figures were based on data represented in Fig. 2. . Raw data were added for each country (green  
 272 squares, red dots and cyan rhombuses)

273  
 274 *Functional response Type*

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

282  
 283

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

Country	Status	Location	Type of functional response	
			chironomid larvae	<i>D. magna</i>
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

286

## 287 Discussion

288

### 289 *Differences in ecological impact between different populations*

290 We observed clear differences in functional responses between different populations of  
 291 the topmouth gudgeon for both prey items used. Indeed, differences were found  
 292 between populations within one country as well as between populations from the native  
 293 and introduced range. The functional response of the populations in their native range  
 294 was intermediate to the functional response derived for the populations in their invaded  
 295 range, especially when using chironomid larvae as prey. There are several possible  
 296 explanations for the difference in functional response observed between populations in  
 297 the native and invaded range such as prey naivety or species plasticity (Cuthbert et al.  
 298 2018; Hollander & Bordeau 2016). Species plasticity of predator and prey has shown to  
 299 be responsible for the observed variation in species responses caused by specific  
 300 environmental habitat conditions.

301

302 Besides the differences in functional response between different geographic areas, we  
 303 observed large variations in functional responses and thus possible ecological impact  
 304 between populations within one geographic area, especially in the invaded range.  
 305 Population differences are depending on the invasion history of the species and on the  
 306 local environmental conditions (Sakai et al. 2001). Newly introduced populations often  
 307 pass through genetic bottlenecks causing possible variations in the functional response.  
 308 Based on this, a reduction in variation of the functional response in the introduced range  
 309 could be expected, although we observed the opposite. Indeed, whereas the functional  
 310 response in the native range showed little variation there were significant differences

311 observed in functional response between the populations in the introduced range. In  
312 addition to the context dependencies (e.g. habitat complexity), these variations in  
313 populations should be taken into account when comparing the functional response  
314 between native and invasive fish species to increase the predictive power (Dick et al.  
315 2014).

316

317 Besides the functional response as calculated in this study, other aspects such as a lack  
318 of natural enemies in combination with a high reproductive capacity, should be  
319 considered when determining its ecological impact. Research carried out in the UK by  
320 Britton et al. (2010), indicated that topmouth gudgeon can reach very high densities of  
321 up to 60 individuals per square meter, a phenomenon that is not reported from its  
322 native range. In this respect, it is important to mention that the functional response  
323 examined in our study is a *per capita* effect of the alien invasive fish species (Parker et al.  
324 1999) and does not include fish density. Thus, although the functional response (per  
325 capita effect) might not be higher for populations in the invaded range (as is the case in  
326 our study for some populations), when considering its high abundance, the species  
327 might still exert a significant ecological impact on the local community. Indeed, previous  
328 research suggests that *P. parva* only has a detectable impact when being present at high  
329 densities (Britton et al. 2010; Jackson et al. 2014). In this respect, the development of the  
330 Invader Relative Impact Potential (RIP) metric by Dick et al. (2017) could provide a  
331 better understanding of the likelihood and degree of ecological impact as it considers  
332 both the functional response and the abundance. Recent research by Laverty et al.  
333 (2017) indicated that the predictive power of the functional response for topmouth  
334 gudgeon was limited, however, incorporation of their abundances relative to natives  
335 into the RIP metric gave high predictive power.

336

### 337 *Differences in the Type of functional response*

338 In its native range (Japan) topmouth gudgeon always showed a Type II functional  
339 response towards either *Daphnia magna* or chironomid larvae used as prey. A Type II  
340 functional response typically describes the foraging behaviour of a species that is  
341 capable of handling only one prey at a time and in environments of reduced complexity  
342 that do not influence factors such as capture success or learned behaviour (Abrams,  
343 1990), similar to the experiments in this study. Earlier studies on functional responses

344 have shown that this Type II response is often observed for fish (Murray et al. 2013,  
345 Alexander et al. 2014), but that with increasing habitat complexity the functional  
346 response might change to a Type III response (Alexander et al. 2015). A Type II response  
347 is likely to be destabilising with respect to prey populations (Murdoch and Oaten 1975),  
348 as prey at low densities experience increased proportional consumption, whereas prey  
349 are not consumed at low densities when predators show a Type III functional response  
350 (Juliano 2001). In any case, the shape of the functional response may not be as  
351 important as the maximum feeding rate, that is, the reciprocal of handling time “*h*”,  
352 which will determine the offtake rate of prey from the population and therefore be more  
353 indicative of ecological impact (see Dick et al. 2014).

354

355 A previous study conducted by Hanazato and Yasuno (1989) found that *P. parva* exerted  
356 a high predation pressure on *Daphnia longispina* in mesocosm experiments conducted in  
357 Japan leading to a strong reduction in abundance of the prey. Our experiments indicated  
358 that in its introduced range the topmouth gudgeon showed a Type III response when  
359 being fed *Daphnia magna* as prey. *Daphnia* typically clump together, which reduces the  
360 probability of being detected and thus their likelihood of being consumed at low fish  
361 density. Based on gut content analyses, derived from field studies, it has been shown  
362 that both *Daphnia* and chironomid larvae are being predated, but that most of the time  
363 chironomid larvae make up the largest part of the diet of *P. parva* (Gozlan et al. 2010;  
364 Yalçın-Özdilek et al. 2013). It is clear that topmouth gudgeon are limited by their  
365 handling ability, but not search efficiency with respect to chironomid larvae, and their  
366 attack rate or search efficiency but not handling ability with respect to *D. magna*.  
367 Furthermore, topmouth gudgeon are omnivorous, therefore, when prey densities are  
368 depleted their feeding mode may switch to take advantage of available algal resources,  
369 thus altering the functional response through switching (Yalçın-Özdilek et al. 2013;  
370 Médoc et al. 2017). Topmouth gudgeon are noted for the high densities they accrue in  
371 invaded ranges, thus it is unlikely that one predator would be feeding in isolation on a  
372 prey resource. Facilitative, mutualistic and antagonistic interactions between  
373 conspecifics that may alter the functional response have not been considered in this  
374 study. However, these aspects are of primary concern in future studies of topmouth  
375 gudgeon if impacts on native prey populations are to be comprehensively understood  
376 (Britton et al. 2007; Médoc et al. 2013; Barrios-O'Neill et al. 2014).



377

378 Our experiments were conducted under laboratory conditions with fixed light and  
379 temperature conditions and no substrate (low habitat complexity). As it has been shown  
380 that context dependencies (e.g. habitat complexity) are important (Alexander et al.  
381 2015), our results illustrate functional responses of adult topmouth gudgeon in a  
382 simplified habitat. As we want to compare the functional response between different  
383 populations the tests in a controlled environment can help to understand the differences  
384 in impact of a species between native and invaded regions. However, further research  
385 under different habitat and environmental conditions, different predator densities as  
386 well as the use of juvenile fish may contribute to a better understanding of the functional  
387 response of topmouth gudgeon.

388

389 In conclusion, our study shows differences in the functional responses of an invasive fish  
390 species between different populations within the native and invaded range, or when  
391 comparing populations from the native and invaded range. The topmouth gudgeon  
392 showed both a Type II and Type III functional response depending on the prey species  
393 and the population origin. Populations in the invaded range did not always show a  
394 higher functional response compared to populations in the native range. To better  
395 estimate the impact of invasive species based on the functional response, the fish  
396 density as well as habitat conditions should be taken into account. Finally, even if the  
397 functional response of this invader is highly variable, if it is still much greater than that  
398 of trophically analogous natives, the comparison of functional responses between  
399 invader and native will often be predictive of the ecological impact of the invader (see  
400 Dick et al. 2013, Alexander et al. 2014, Dick et al. 2014).

401

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409

410

411 **Conflict of Interest**

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

413

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