

1 **Accepted for publication in *Ecology of Freshwater Fish*, 03/06/16**

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3 **Comparative functional responses of native and high impacting invasive fishes:**  
4 **impact predictions for native prey populations**

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17 Running headline: Functional responses of invaders

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23

24 **Abstract**

25

26 Comparative functional responses (FRs) can predict impacts of invasive species,  
27 including piscivorous fishes, via quantifying their depletion of native food resources  
28 as a function of prey density. The utility of FRs for predicting impacts on prey  
29 populations by invasive fishes of different trophic guilds was tested here by  
30 comparing the FRs of the invaders *Cyprinus carpio* and *Carassius auratus*, with three  
31 native, trophically analogous fishes, *Barbus barbus*, *Squalius cephalus* and *Tinca*  
32 *tinca*. Chironomid larvae and *Gammarus pulex* were used as prey items. Predictions,  
33 developed from studies on the foraging of *C. carpio* and *C. auratus* in the literature,  
34 were that the invaders would have significantly higher consumption rates for  
35 chironomids than the native fishes, but not for *G. pulex*. Mean consumption rates for  
36 chironomids were significantly lower for both invaders than *B. barbus* and *S.*  
37 *cephalus*, but were similar to *T. tinca*. *Barbus barbus* had a significantly lower  
38 consumption rate of *G. pulex* than both invaders, but there were no significant  
39 differences between *S. cephalus*, *T. tinca* and the invaders. All FRs were type II, with  
40 functional response curves for the invaders preying upon chironomids never being  
41 significantly higher than the native fishes, contrary to predictions. For *G. pulex*, some  
42 significant differences were apparent between the invaders and native fishes, but  
43 again were contrary to predictions. These results indicated that when predation  
44 impacts of invasive fishes could also be a function of their population density and  
45 body sizes, these parameters should be incorporated into FR models to improve  
46 impact predictions.

47 **Key words:** Invasion; *Cyprinus carpio*; *Carassius auratus*; consumption rate; type II  
48 functional response.

49

50 **Introduction**

51

52 Predicting impacts of invasive species is an integral aspect of their management,  
53 providing the basis for prioritising management interventions according to the  
54 ecological risk of different species (Kumschick et al. 2012; Leung et al. 2012).

55 Approaches for making rapid assessments of impacts on native communities,  
56 especially those relating to changes in competitive and predation pressures, are  
57 particularly important, as they highlight the potential severity of the ecological  
58 consequences (Iacarella et al. 2015a,b). When allied with horizon scanning and  
59 surveillance exercises, resources can be rapidly directed to preventing invasions by  
60 targeting high-risk species before they have established (Simberloff et al. 2013;  
61 Lampert et al. 2014; Roy et al. 2014).

62

63 A major issue in predicting impacts of invasive species is that assessments can be  
64 speculative and variable between contexts, making it challenging to make robust  
65 predictions (Alexander et al. 2014; Dick et al. 2014). Recent work has demonstrated  
66 that impact prediction can utilise comparative functional responses between invasive  
67 and native species, as many invaders have rapid and efficient resource exploitation  
68 that can provide advantages over native competitors (Alexander et al. 2014; Dick et  
69 al. 2014; Iacarella et al. 2015b). As these functional responses describe resource  
70 uptake rate as a function of resource density, they also have potentially high utility in  
71 predicting the consequences of invasions on native prey communities (Dick et al.  
72 2014). Three major function response types have been described, Type I, II and III  
73 (Hassell et al. 1977). Type I describes a linear increase in feeding rate with prey  
74 density until it reaches a constant value at saturation (Jeschke et al. 2004). Type II

75 responses describe a feeding rate that increases at a decreasing rate with prey density  
76 until it reaches its maximum value (Holling 1959; Murray et al. 2013, 2015). Type III  
77 responses describe a sigmoidal, density-dependent relationship, where an initial  
78 increasing risk of prey mortality switches to a decreasing risk of mortality as the prey  
79 density increases above a threshold level (Morgan & Brown, 1996). Type II responses  
80 are prevalent in many fish species (Murray et al. 2013, 2015).

81

82 The comparative functional response approach also enables testing of hypotheses  
83 developed from empirical data on the impact of specific invaders (Alexander et al.  
84 2014; Dick et al. 2014). For example, empirical data often indicate that prey  
85 populations are depleted by invaders through direct predation pressure, such as the  
86 impacts detected for small native prey fishes following peacock bass *Cichla* spp.  
87 invasions in Southern Brazil (e.g. Pelicice and Agostinho 2009; Menezes et al. 2012),  
88 and the reduction in macro-invertebrate communities, including Chironomid larvae,  
89 following pumpkinseed *Lepomis gibbosus* invasions (e.g. van Kleef et al., 2008). In  
90 these situations, it would be predicted that the functional responses of the invaders on  
91 these prey species would be higher than functionally-analogous native species (Dick  
92 et al. 2014). Conversely, where the functional response parameters for a particular  
93 prey species are similar between an invasive and native species, it would be predicted  
94 that the consumers have similar effects on that prey population (Dick et al. 2014).  
95 Recent studies have, for example, indicated that existing and emerging invasive  
96 piscivorous fishes in South Africa have significantly higher functional responses than  
97 native fishes with similar functional traits, facilitating their invasion and increasing  
98 the predation pressure on prey populations (Alexander et al. 2014).

99

100 Here, the utility of comparative functional responses to predict invasion impacts was  
101 tested using two globally invasive fishes, common carp *Cyprinus carpio* and goldfish  
102 *Carassius auratus*, on prey populations of Chironomid larvae and *Gammarus pulex*.  
103 *Cyprinus carpio* is listed on the world's worst 100 invaders (IUCN 2013) and is  
104 highly invasive at the global scale (Koehn 2004; Britton et al. 2007; Oyugi et al.  
105 2011). *Carassius auratus* is recognised as a high impacting invasive species in  
106 countries as diverse as Australia and Tibet (Haynes et al. 2012; Liu et al. 2015). In  
107 Europe, *C. carpio* has a wide distribution over lentic and lotic habitats, including  
108 major river catchments, whereas *C. auratus* tends to be restricted to lentic situations  
109 (Britton et al. 2010a). Invasion risk assessments also suggest these species are among  
110 the most ecologically-damaging, non-native species in the region (Britton et al.  
111 2010a). Both fishes consume Chironomid larvae (e.g. Richardson et al. 1995; Garcia-  
112 Berthou 2001; Khan 2003), with studies including Anderson et al. (1964) and Frie et  
113 al. (2007) suggesting *C. carpio* can cause significant reductions in their population  
114 densities. Gupta and Banerjee (2009) suggested *C. auratus* have high potential as a  
115 control agent for biting insects via their predation on larval stages. By contrast, there  
116 is minimal evidence for their widespread predation and impact on amphipod species  
117 such as *G. pulex*.

118

119 Consequently, the impact assessment tested the functional responses of these two  
120 invaders on these prey populations against three native, functionally analogous fishes:  
121 tench *Tinca tinca* (lentic), chub *Squalius cephalus* (lotic) and barbel *Barbus barbus*  
122 (lotic), all of the Cyprinidae family and present across North West Europe. The  
123 prediction was that the functional response parameters would indicate significantly

124 higher consumption rates of Chironomid larvae for both invaders compared with the  
125 functionally analogous native fishes, but with no significant differences for *G. pulex*.

126

## 127 **Materials and Methods**

128

### 129 **Experimental design**

130 All experimental fish were sourced from aquaculture sites in Southern England and  
131 transferred to Bournemouth University where they were acclimatised in tank aquaria  
132 of 40 L for 28 days at 20 °C. Water filtration was provided via flow-through systems.

133 All fish were of lengths 68 to 80 mm, age 1+ years, and were fed pelletized fish-meal  
134 to standardize prior experience. Live *Gammarus pulex* was sourced locally, with  
135 individuals only used that were not infected with *Pomphorhynchus laevis*, as this  
136 could have altered their response to predation risk (Bauer et al., 2000). Frozen  
137 chironomid larvae were used in order to standardise their quality and size, and were  
138 defrosted before use.

139

140 Individual fish were randomly selected 24 h prior to use and allocated to 10 L  
141 experimental tanks at 20 °C supplied with oxygen to provide constant conditions.  
142 They were without food in this period to standardize hunger levels. Individual fish  
143 were then presented with prey at six densities (2, 4, 8, 16, 32 and 64), using a  
144 minimum of three replicates per density; 128 was also used when analyses revealed  
145 that the asymptote of the functional responses had not been reached. Exposure to prey  
146 was for one hour, with the fish then removed and the number of remaining prey  
147 counted to enable calculation of the consumption rate (number consumed per hour).

148

149 **Data analysis and statistics**

150 The initial testing of data used generalized linear models (GLMs) with quasi-Poisson  
151 error distributions to identify differences in the overall consumption rates per species,  
152 as per Alexander et al. (2014). The dependent variable was consumption rate, species  
153 was the independent variable and food density was the covariate. For each prey item,  
154 model outputs were the estimated marginal means of consumption rate per species,  
155 their 95 % confidence intervals and the significance of differences in their estimated  
156 marginal means according to linearly independent pairwise comparisons, with  
157 Bonferroni adjustment for multiple comparisons.

158

159 The comparative functional responses for the fishes were completed across lentic and  
160 lotic contexts. Comparisons were thus between the lentic native *T. tinca* and invasive  
161 *C. carpio* and *C. auratus*, and between the lotic native *B. barbuis* and *S. cephalus*, and  
162 the invasive *C. carpio*. These combinations of species already co-exist in areas of  
163 North West Europe, such as Great Britain (Britton et al. 2010a). Note that in the  
164 experiments, lotic conditions could not be created in the systems, so the comparative  
165 data for this context were created under lentic conditions and extrapolated to lotic  
166 conditions. The comparative functional responses were then assessed as per Paterson  
167 et al. (2015), using the integrated package for functional response analysis in R (frair)  
168 (Pritchard et al. 2014). Logistic regressions of prey density versus the proportion of  
169 prey consumed were performed per fish species and prey item, with type II functional  
170 responses indicated by significant negative first-order terms (Pritchard et al. 2014).  
171 Values of the attack rate ( $a$ ) and handling time ( $h$ ) were then obtained using maximum  
172 likelihood estimation (MLE) (Bolker 2013) in the Random Predator Equation (Rogers  
173 1972), which assumes a Type II response and non-replacement of prey:

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

175

176 where  $N_e$  is the number of prey eaten,  $N_0$  is the initial density of prey,  $a$  is the attack  
177 rate,  $h$  is the handling time and  $T$  is the total time available. Finally, to visualise the  
178 uncertainty around the fitted functional responses, bootstrapping ( $n = 1500$ ) was used  
179 to construct empirical 95% confidence intervals of the fitted functional responses  
180 (Paterson et al. 2015). These bootstrapped data provided plots of the comparative  
181 functional responses between the comparator species. Where there was overlap in  
182 their 95 % confidence limits, this indicated the differences their functional response  
183 curves were not significant (Paterson et al. 2015).

184

## 185 **Results**

186

187 The GLMs testing differences in consumption rates between the species per prey item  
188 were significant (*G. pulex*: Wald  $\chi^2 = 106.9$ , d.f. = 4,  $P < 0.01$ ; Chironomid larvae:  
189 Wald  $\chi^2 = 83.7$ , d.f. = 4,  $P < 0.01$ ). The estimated marginal means indicated that for  
190 Chironomid larvae, the mean adjusted consumption rate was significantly lower for  
191 both invaders than *B. barbatus* and *S. cephalus*, but similar to *T. tinca* (Fig. 1). For *G.*  
192 *pulex*, *B. barbatus* had a significantly lower consumption rate than both invaders (Fig.  
193 1). By contrast, there were no significant differences in the consumption rates of *G.*  
194 *pulex* between *S. cephalus*, *T. tinca* and the invaders (Fig. 1).

195

196 For all species, the calculated functional responses for both prey items were always  
197 type II (Table 1; Fig. 2, 3). In the lentic comparisons, the only functional response  
198 parameter that was significantly different between *T. tinca* and the two invaders was



199 handling time of *G. pulex*, where *C. auratus* had a significantly lower value ( $P < 0.01$ ;  
200 Table 2). This lower handling time of *C. auratus* resulted in the asymptote of their  
201 functional responses being significantly higher than *T. tinca* (Fig. 2). In the lotic  
202 comparisons, significant differences were apparent in the majority of functional  
203 responses parameters between the three species ( $P < 0.05$ ; Table 2). These differences  
204 in parameters resulted in the asymptote of the functional responses being significantly  
205 higher for *S. cephalus* than the other two species (Fig. 3). For *B. barbuis* and *C.*  
206 *carpio*, differences in the asymptote of the functional response were context  
207 dependent; the species with the significantly higher asymptote was dependent upon  
208 prey type (Fig. 3).

209

## 210 **Discussion**

211

212 Comparative functional responses can be strong predictors of the ecological impact of  
213 high impacting and emerging invasive piscivorous fishes (Alexander et al. 2014; Dick  
214 et al. 2014; Paterson et al. 2015). Here the approach was applied to testing predictions  
215 on the consequences for prey populations of invasions by *C. carpio* and *C. auratus* in  
216 lentic and lotic situations. This was achieved by comparing the functional response  
217 parameters of these invasive fishes with a number of native fishes. The invasive and  
218 native cyprinid fishes were all benthopelagic omnivores (Noble et al. 2007a,b). Thus,  
219 any differences detected in the consumption rates and functional response parameters  
220 between these fishes should not be due to major differences in their trophic ecology  
221 and functional traits (Alexander et al. 2014). The predictions were for higher  
222 consumption rates and asymptotes of the functional response curves of both invaders  
223 compared with native fishes for Chironomid larvae. In contrast, they were predicted to

224 be similar for *G. pulex*. In the lentic context for *C. auratus*, a recognised global  
225 invader (ISSG 2016), their consumption rates and functional response curve  
226 asymptotes were significantly higher than the trophically-analogous *T. tinca*, but only  
227 for *G. pulex*. Contrary to the predictions, there were no significant differences for  
228 Chironomid larvae in the outputs of the generalized linear model and the comparative  
229 functional response parameters between *T. tinca* and both *C. auratus* and *C. carpio*.  
230 For the lotic context, both *B. barbatus* and *S. cephalus* had significantly higher  
231 consumption rates and asymptotes of the functional response curves than *C. carpio*  
232 when preying upon Chironomid larvae, with the converse for *C. carpio* and *B. barbatus*  
233 when preying upon *G. pulex*. Both results were contrary to the predictions.

234

235 From a prey population perspective, the results of the functional response experiments  
236 suggested that any deleterious impact on these populations by the invaders might be  
237 similar or even reduced compared with the native fishes. The functional responses  
238 were Type II, suggesting that where consumption rates of the fishes are high, there is  
239 an inherent risk of the prey populations becoming depleted as the consumption rates at  
240 low prey densities will remain consistent (a contrast to Type III FRs) (Dick et al.  
241 2013, 2014). However, prey species such as Chironomid larvae tend to be relatively  
242 abundant in freshwaters and thus the risk of their depletion to low abundances might  
243 be considered unlikely unless the fish populations were highly abundant (Jackson et  
244 al. 2015).

245

246 These results suggest that the comparative functional response approach provided a  
247 relatively poor prediction of impact for these invaders when compared to alternative  
248 methods and empirical evidence (Britton et al. 2010a, 2011; Vilizzi et al. 2015). For

249 example, empirical evidence suggests the ecological impacts of invasive *C. carpio*  
250 include substantial habitat disruption through macrophyte loss via their destructive  
251 foraging behaviours and ecological engineering activities that can shift lakes towards  
252 eutrophic states (e.g. Koehn 2004; Vilizzi 2012; Hickley et al. 2015). Moreover, they  
253 are also exploitative competitors that forage in shoals, with few direct interactions  
254 between conspecifics and resident fishes with similar feeding modes as they exploit  
255 the available resources non-aggressively (Britton et al. 2011; Busst and Britton 2015).  
256 By contrast, piscivorous fishes, such as those tested by Alexander et al. (2014), are  
257 often more solitary in their foraging behaviours. Salmonid fishes tend to be more  
258 territorial and antagonistic in their foraging, with some functional response  
259 parameters, such as capture rates, also differing across their body sizes and being  
260 influenced by the relative positions of the fish in the water column (Gustafsson et al.  
261 2010). These different feeding behaviours could have substantial implications for the  
262 functional response parameters of the species.

263

264 The results of these experiments contribute to a growing literature base on the  
265 application of comparative functional responses to invasion ecology (e.g. Dick et al.  
266 2013; Alexander et al. 2014; Dick et al. 2014; Iacarella et al. 2015b). The  
267 management application of these studies is their ability to inform invasion risk  
268 assessment. These risk assessments can then be used to prioritize species; those with  
269 the highest predicted severity of impacts should be highest management priorities  
270 (Kumschick et al. 2012; Leung et al. 2012). Our results indicated that the invasion  
271 impacts of species such as *C. carpio* and *C. auratus* can be variable and need to be  
272 considered in relation to the interactions and impacts of native species on their prey  
273 communities (Dick et al. 2013). These results also suggest that the stocking of native

274 species to supplement fish populations, such as for recreational angling, could result  
275 in at least similar ecological impacts to invasive fishes (Eby et al. 2006; Tran et al.  
276 2015). Consequently, the results of this study can inform risk assessment for stocking  
277 native fishes as well as for introductions of non-native and translocated fishes. When  
278 comparative functional response results are combined with other invasion impacts  
279 (Gozlan et al. 2010), this should thus ensure that freshwater ecosystems no longer  
280 receive inappropriate fish releases. In considering our results, it must also be  
281 remembered that the comparative functional responses for the lotic context were  
282 completed in a lentic context, assuming this would have minimal consequences for the  
283 fish foraging behaviours. These results should thus be interpreted cautiously, given  
284 that the assumption could not be explored further.

285

286 Our results and interpretations also suggested that the utility of comparative functional  
287 response models to test impacts of invasion on prey populations might be strongly  
288 influenced by the foraging behaviours, body sizes and population dynamics of the  
289 species concerned. High predictive power of the models might be primarily limited to  
290 situations where the focal invasive fish is an obligate piscivore that preys on  
291 populations limited in abundance. For fishes where population density might also be  
292 important in determining their consequences for prey populations, such as the small-  
293 bodied invasive fish *Pseudorasbora parva* (Jackson et al. 2015), the approach appears  
294 a relatively poor predictor. As such, for invasive species where population density can  
295 play an important role in impact severity, including *C. carpio* and *C. auratus*, *per*  
296 *capita* effects could be developed and incorporated into models. Indeed, the classic  
297 formula for deriving impact of invaders contains terms for the abundance of the  
298 invader as well as the *per capita* effect, plus the invader's actual or predicted range

299 (Parker et al. 1999; Alexander et al. 2014). Therefore, the inclusion of population  
300 parameters can help increase the realism and complexity of the comparative  
301 functional response models. These changes would then enable population responses to  
302 be predicted that that also account for changes in the body size of the invader. This is  
303 important given the capacity of species such as *C. carpio* to attain relatively large  
304 sizes compared with many native fishes (Britton et al. 2010a,b). In doing so, this  
305 predictive impact methodology would move beyond its current constraints of  
306 individual responses, thus providing impact predictions at a higher level of ecological  
307 complexity and realism.

308

### 309 **Acknowledgements**

310

311 ZG was supported by the Erasmus Mundus programme 'TECHNO' and DS was  
312 supported by the Natural Environment Research Council (NE/J016675/1).

313

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486

Table 1. First order linear coefficient results from logistic regressions for the predator and prey combinations. All values indicate a Type II functional response. (na = native species; in = invasive species). All predator: prey relationships were significant at  $P < 0.001$ .

Predator	Prey	Linear coefficient
<i>Barbus barbatus</i> (na)	<i>Gammarus pulex</i>	-0.024
<i>Squalius cephalus</i> (na)	<i>Gammarus pulex</i>	-0.037
<i>Cyprinus carpio</i> (in)	<i>Gammarus pulex</i>	-0.050
<i>Tinca tinca</i> (na)	<i>Gammarus pulex</i>	-0.031
<i>Carassius auratus</i> (in)	<i>Gammarus pulex</i>	-0.022
<i>Barbus barbatus</i> (na)	Chironomid larvae	-0.023
<i>Squalius cephalus</i> (na)	Chironomid larvae	-0.012
<i>Cyprinus carpio</i> (in)	Chironomid larvae	-0.044
<i>Tinca tinca</i> (na)	Chironomid larvae	-0.055
<i>Carassius auratus</i> (in)	Chironomid larvae	-0.052

Table 2. Parameters of the comparative functional responses, where parameter estimates were calculated using the ‘indicator variable’ approach [10], with statistically significant differences in the parameters between species ( $\alpha = 0.05$ ) in bold. a = attack rate, h = handling time. Z and P values are statistical outputs from regression that indicate whether *a* and *h* differ significantly between the comparator species.

(a) *Gammarus pulex*

	<i>T. tinca/ C. carpio</i>	<i>T. tinca/ C. auratus</i>	<i>C. carpio/ C. auratus</i>	<i>C. carpio/ S. cephalus</i>	<i>C. carpio/ B. barbus</i>	<i>B. barbus/ S. cephalus</i>
a	2.97/ 3.62	2.97/ 2.69	3.62/ 2.69	3.62/ 2.09	3.62/ 1.18	1.18/ 2.09
Z	-0.66	0.39	1.20	-1.90	-2.77	-1.65
P	0.51	0.70	0.23	0.06	<b>&lt;0.01</b>	0.10
h	0.04/ 0.06	0.04/0.02	0.06/ 0.02	0.06/ 0.03	0.06/ 0.12	0.12/ 0.03
Z	-1.61	5.89	7.27	3.67	2.59	3.63
P	0.11	<b>&lt;0.01</b>	<b>&lt;0.01</b>	<b>&lt;0.01</b>	<b>&lt;0.01</b>	<b>&lt;0.01</b>

(b) Chironomid larvae

	<i>T. tinca/ C. carpio</i>	<i>T. tinca/ C. auratus</i>	<i>C. carpio/ C. auratus</i>	<i>C. carpio/ S. cephalus</i>	<i>C. carpio/ B. barbus</i>	<i>B. barbus/ S. cephalus</i>
a	2.63/ 14.94	2.63/ 10.60	14.94/ 10.60	14.94/ 1.37	14.94/ 3.38	1.37/ 3.38
Z	-0.74	-1.60	4.61	-0.01	-0.70	3.34
P	0.45	0.11	<b>&lt;0.01</b>	<b>&lt;0.01</b>	<b>0.49</b>	<b>&lt; 0.01</b>
h	0.11/ 0.13	0.11/ 0.09	0.13/ 0.09	0.13/ 0.01	0.13/ 0.04	0.01/ 0.04
Z	-1.56	1.00	3.88	-0.01	-7.17	7.34
P	0.11	0.32	<b>&lt;0.01</b>	<b>&lt;0.01</b>	<b>&lt;0.01</b>	<b>&lt;0.01</b>

## Figure captions

Fig. 1. Mean adjusted consumption rate (as estimated marginal means controlled for food density in generalized linear models) of each species per prey item, where cc = difference between adjusted mean of that species and the invasive *Cyprinus carpio* is significant at  $P < 0.01$  and ca = difference between adjusted mean of that species and the invasive *Carassius auratus* is significant at  $P < 0.01$ . Filled circles represent the invasive species, clear circles represent the native fishes. Error bars represent 95 % confidence limits.

Fig. 2. Type II functional response curves for invasive *Carassius auratus*, invasive *Cyprinus carpio* and native *Tinca tinca* fed (a,b) *Gammarus pulex* and (c,d) Chironomid larvae. Lines indicate mean functional response. Light grey shading represents 95% equi-tailed confidence intervals (CI) for each species, with dark grey shading representing the overlap in the CIs of the species [10]. Note differences on the x and y axes.

Fig. 3. Type II functional response curves for invasive *Cyprinus carpio*, native *Squalius cephalus* and native *Barbus barbus* fed (a,b) *Gammarus pulex* and (c,d) Chironomid larvae. Lines indicate mean functional response. Light grey shading represents 95% equi-tailed confidence intervals (CI) for each species, with dark grey shading representing the overlap in the CIs of the species [10]. Note differences on the x and y axes.



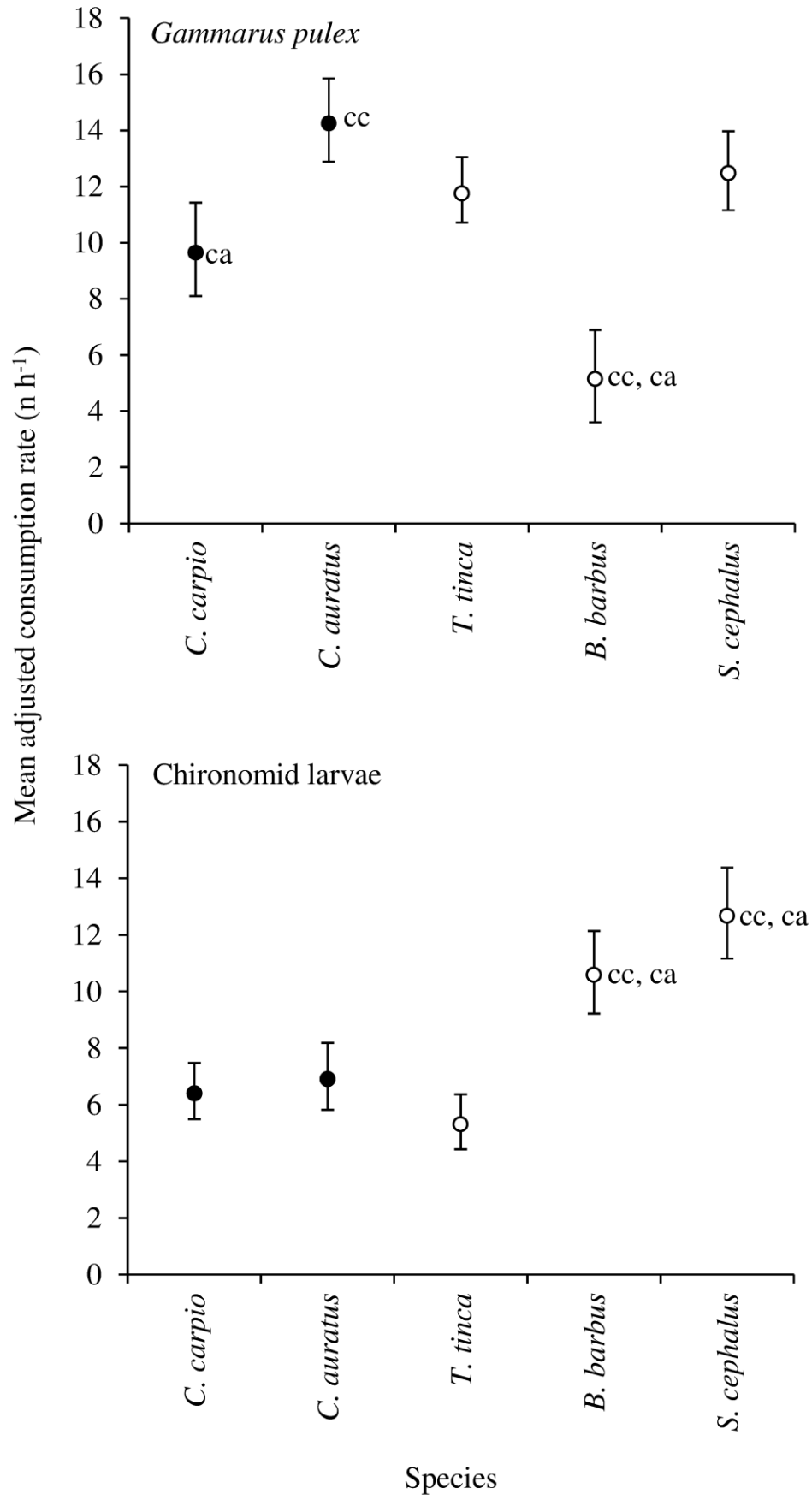


Figure 1.

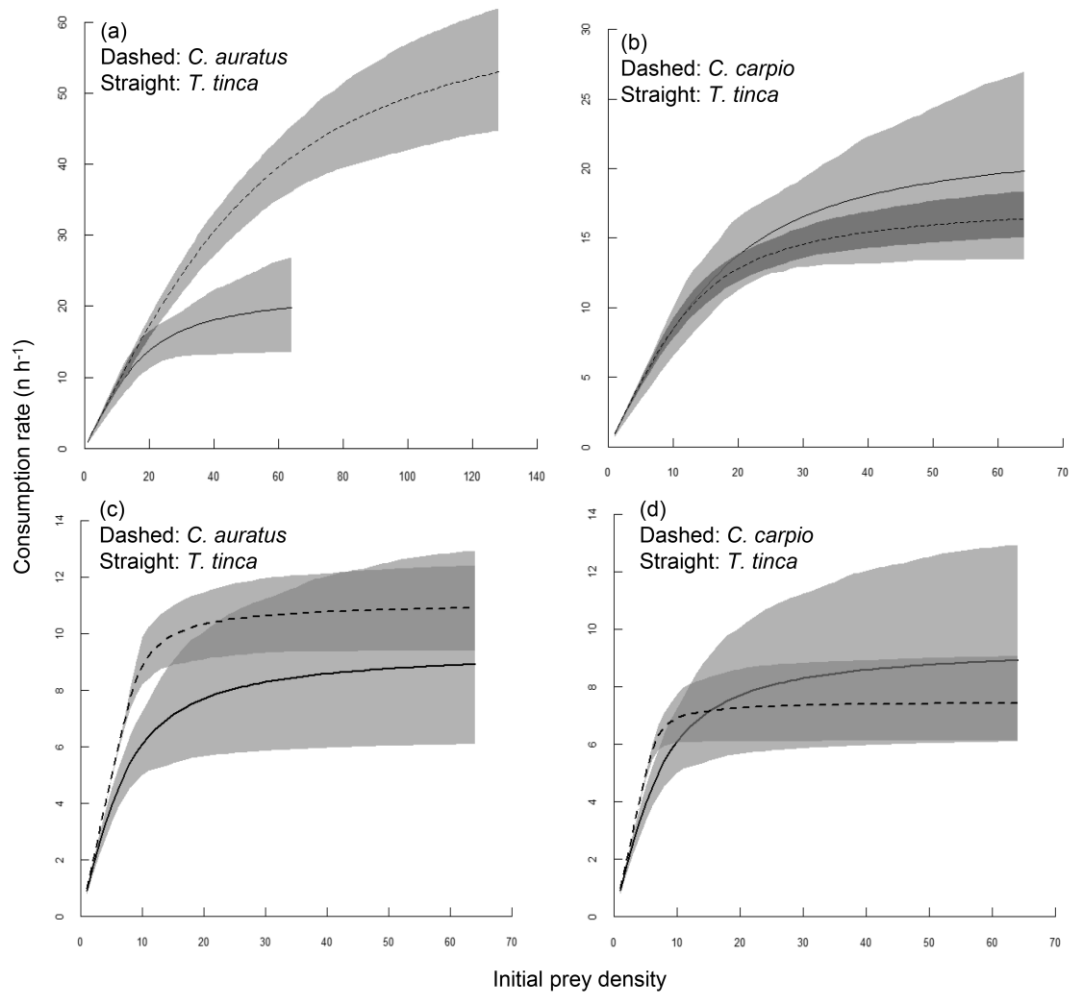


Figure 2.

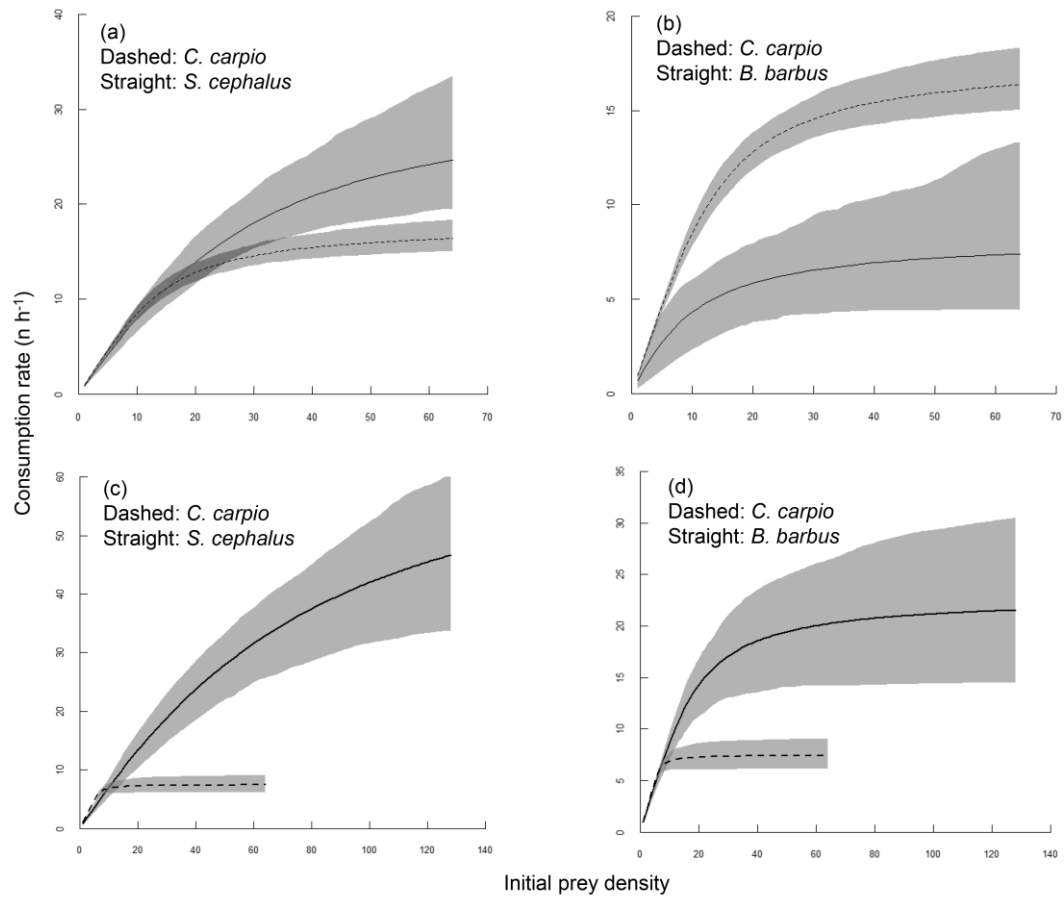


Figure 3.