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Habitat simplification increases the impact of a freshwater invasive fish

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1 **Habitat simplification increases the impact of a freshwater invasive fish**

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31 **Abstract**

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33 Biodiversity continues to decline at a range of spatial scales and there is an urgent requirement to understand
34 how multiple drivers interact in causing such declines. Further, we require methodologies that can facilitate
35 predictions of the effects of such drivers in the future. Habitat degradation and biological invasions are two of
36 the most important threats to biodiversity and here we investigate their combined effects, both in terms of
37 understanding and predicting impacts on native species. The predatory largemouth bass *Micropterus salmoides*
38 is one of the World's Worst Invaders, causing declines in native prey species, and its introduction often
39 coincides with habitat simplification. We investigated the predatory functional response, as a measure of
40 ecological impact, of juvenile largemouth bass in artificial vegetation over a range of habitat complexities (high,
41 intermediate, low and zero). Prey, the guppy *Poecilia reticulata*, were representative of native fish. As habitats
42 became less complex, significantly more prey were consumed, since, even although attack rates declined,
43 reduced handling times resulted in higher maximum feeding rates by bass. At all levels of habitat complexity,
44 bass exhibited potentially population de-stabilising Type II functional responses, with no emergence of more
45 stabilising Type III functional responses as often occurs in predator-prey relationships in complex habitats.
46 Thus, habitat degradation and simplification potentially exacerbate the impact of this invasive species, but even
47 highly complex habitats may ultimately not protect native species. The utilisation of functional responses under
48 varying environmental contexts provides a method for the understanding and prediction of invasive species
49 impacts.

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51 **Keywords:** Habitat complexity; invasive species; functional response; impact; global change; freshwater fish

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53

54 **Introduction**

55

56 Biodiversity at global, regional and local scales is declining and the conservation of natural resources is
57 under threat from a number of drivers of global change (Sala et al. 2000; Thomas et al. 2004; Mokany et al.
58 2012). Such processes are of particular concern in freshwater systems, with drivers such as habitat alteration and
59 invasions by non-native species identified as significant stressors (Saunders et al. 2002; Dudgeon et al. 2006).
60 The modification of freshwater habitats results from a range of human-mediated processes including changes to

61 flow regimens (Bunn and Arthington 2002), dam construction (Nilsson and Berggen 2000), and destruction of
62 vegetation (Radomski and Goeman 2001). Similarly, biological invasions are increasing due to a wide range of
63 human-mediated vectors and pathways (Levine and D'Antonio 2003). In freshwaters, invasive species modify
64 ecosystems through a range of processes including competitive exclusion (Rowles and O'Dowd 2006) and
65 predation (Griffen and Delaney 2007), which may result in dramatic changes to native communities (Crooks
66 1998).

67 One of the main challenges in ecology is the ability to predict how drivers of global change, such as
68 biological invasions, may impact ecosystems (Parker et al. 1999;; Ricciardi et al. 2013; Dick et al. 2014. These
69 drivers are commonly considered as independent, single entities (Fazey et al. 2005), however, there is an
70 emerging realisation that biodiversity loss will be better understood and predicted when the relative roles of the
71 major drivers are considered in combination (Facon et al. 2006). It is also recognised that drivers may act
72 synergistically through a variety of pathways (Didham et al. 2007). For example, changes in the traits of an
73 invasive species with habitat alterations, such as predatory efficiency, might result in changes in *per capita*
74 effects with potential wide-ranging consequences for native species population dynamics (Parker et al. 1999).

75 In aquatic systems, the role of habitat structure, such as that provided by algae and macrophytic plants,
76 is well documented in inter- and intraspecific interactions from a wide range of taxa (Boström et al. 1999; Saha
77 et al. 2009; Gosnell et al. 2012). For a number of fish species in particular, habitat structure has been shown to
78 mediate impacts of fish predation by, for example, providing refuge space for prey (Persson and Eklöv 1995;
79 Beukers and Jones 1997; Anderson 2001; Almany 2004a). Therefore the loss of structural complexity resulting
80 from habitat degradation may reduce prey survival due to increased predation vulnerability (Nelson and
81 Bonsdorff 1990). Mediatory effects may also occur in such interactions due to the physical barrier to predator
82 movement provided by habitat (Savino and Stein 1982). Conversely, however, predators that adopt a sit-and-
83 wait strategy of prey capture may perform less efficiently, with degradation of habitat reducing predation
84 success (Flynn and Ritz 1999).

85 A promising methodology that not only provides an understanding of predator-prey interactions but
86 allows predictions of invasive species impact is to examine the functional response (Dick et al. 2013a; Dick et
87 al. 2013b; Alexander et al. 2014), that is, the relationship between prey density and predator consumption rate
88 (Solomon 1949; Holling 1959). Such a focus allows important density-dependent effects of predation on
89 population stability to be examined owing to the different contributions of response Types (I, II or III) to
90 population dynamics (Murdoch and Oaten 1975). In a Type I response, predator consumption increases linearly

91 with prey number until a threshold density plateau is reached. However, under certain ranges of prey density, a
92 Type II inversely density-dependent response can result in an increase in mortality risk to prey with decreasing
93 density (Hassell 1978). This is in contrast to reduction in mortality risk when prey density declines in a Type III
94 response (Hassell 1978). This is particularly important in habitat complexity studies, where changes in structure
95 can result in alterations to the functional response Type and hence prey population viability (Lipcius and Hines
96 1986; Buckel and Stoner 2000; Alexander et al. 2012). Furthermore, the application of functional responses in
97 invasion biology has been demonstrated to be effective, with higher functional responses of invasive species
98 compared to natives in laboratory studies corroborated by results from field studies (Bollache et al. 2008; Dick
99 et al. 2013). Here, we use functional responses to predict the impact that changes in habitat complexity,
100 representative of those resulting from habitat destruction, may have on the predator-prey dynamics of an
101 invasive fish predator, one of the “World’s Worst Invaders” (ISSG 2013), on a prey species that serves as a
102 proxy for endangered native prey species.

103 As a result of their popularity as an angling species, the largemouth bass *Micropterus salmoides* is one
104 of the five globally most introduced fish species (Welcomme 1992) and, where such introductions have
105 occurred, predation by this species has a major impact on fish communities (Godinho and Ferreira 2000;
106 Ellender et al. 2011; Almeida et al. 2012). In South Africa and in the Iberian Peninsula in southern Europe, for
107 example, largemouth bass are a well-established invasive species that have subsequently invaded a number of
108 headwater streams, where many native fish species are now endangered or absent (Ellender et al. 2011; Almeida
109 et al. 2012). In addition to this, such systems are also facing a double threat of habitat degradation due to
110 destruction of natural vegetation (Saunders et al. 2002). As ambush predators, largemouth bass typically use
111 structural littoral habitats including aquatic vegetation (Savino and Stein 1989a) , and juveniles in particular
112 predominantly select such environments (Olson et al. 2003). We therefore manipulated simulated habitat
113 complexity along a prey density gradient in order to ask questions regarding the density-dependence of impact
114 of this invasive predator on a prey population in the context of habitat degradation.

115 The aim of this study was thus to describe and quantify the functional responses, and hence impacts, of
116 juvenile largemouth bass on a prey species, the guppy *Poecilia reticulata*, that served as a commercially
117 available surrogate for endangered fish found in headwater systems, with respect to varying levels of habitat
118 complexity. The aims were to establish whether: (1) juvenile largemouth bass exhibit predatory functional
119 responses towards small fish prey; (2) the functional response Type is habitat dependent; and (3) varying habitat
120 complexity alters the strength of the functional response.

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122

123 **Materials & Methods**

124

125 **Collection and maintenance of experimental animals**

126

127 Juvenile largemouth bass *Micropterus salmoides* were collected in June 2013 by electrofishing from
128 Douglas Dam (33°19'16"S; 26°31'15"E) and Grey Dam (33°19'29."S; 26°31'39"E), Grahamstown, South Africa.
129 All fish were transported to the Department of Ichthyology and Fisheries Science (DIFS), Rhodes University,
130 Grahamstown and were housed in 600L tanks in a closed recirculating system. Fish were allowed to acclimate
131 for at least one week prior to use in predation trials and were maintained on a diet of earthworms. As this was
132 not the focal prey species used in the experiment, this diet ensured that no prior prey learning occurred in
133 holding tanks. Prey used were females of the guppy *Poecilia reticulata* (15-20mm total length), sourced from a
134 breeding stock at DIFS. Female guppies were selected over males owing to their inconspicuous coloration.
135 Guppies were housed in two 600L tanks and were fed daily on commercially available fish food.

136

137 **Experimental set up**

138

139 Functional response experiments were conducted in 15 square 300L fibreglass tanks that were part of
140 the same flow-through system as the holding tanks described above (water flow 1 L/min⁻¹; 23.01± 0.17°C, mean
141 temperature ± SE). In the centre of each tank there was an outlet for water overflow that was covered with mesh
142 and secured with cable ties to prevent predators and/or prey escaping. To reduce potential stress on the fish,
143 each tank was half covered with a dark screen to provide a darkened refuge. An airline provided further aeration
144 of water in the tank in addition to the aerated inflowing water from the recirculating system during predation
145 trials.

146 To simulate habitat structure, strips of green polyethylene (40cm long and 1.5cm wide) were tied in a
147 uniform arrangement to green plastic mesh, cut to fit the bottom of the aquarium. The mesh was then weighted
148 to the bottom of the tanks. This allowed the artificial vegetation to float upwards and occupy the entire water
149 column in the same way that natural vegetation occurs in freshwater systems (personal observation). A plant
150 mimic was used here to allow for standardisation of cover. Densities of vegetation represented high (2700

151 blades m⁻²), medium (1800 blades m⁻²), low (900 blades m⁻²) and zero habitat complexities. To control for the
152 presence of mesh contributing a further element of habitat complexity, mesh without artificial plants was added
153 in zero complexity.

154 Bass (n=18) were selected from a common size class to reduce the influence of size-related differences
155 in prey consumption (86.86 ± 2.49mm, mean total length ± SE; 14.0 ± 0.38mm, mean gape height ± SE), and
156 were reused in the four habitat treatments (detailed below). We ensured, however, that each individual predator
157 was used a maximum of four times and only once within each prey density in each habitat complexity. At least
158 two days recovery time was allowed between uses.

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160

161 **Functional response trials**

162

163 Bass were randomly selected from their holding tanks 24 hours prior to a trial and transferred to an
164 experimental tank, where they were held without food to allow for acclimatisation and standardisation of hunger
165 levels. Individual fish were then presented with guppies at six prey densities (2, 4, 8, 16, 32, 64), with at least
166 three replicates per density. Feeding trials were initiated at 10:00h and prey consumption was examined after 4
167 hours. Controls were three replicates of each prey density in the absence of predators at each of the habitat
168 complexities.

169

170

171 **Statistical analysis**

172

173 All analysis was carried out in R v. 2.15.1 (R Development Core Team 2012). Differences in overall
174 prey consumption among habitat complexities and prey densities were assessed using a generalised linear model
175 (GLM) with binomial error distribution. As no interaction was found between habitat complexity and prey
176 density, the interaction term was removed to identify the minimum adequate model (Crawley 2007). Significant
177 effects in the model were analysed with Tukey's contrast *post hoc* tests, performed using the package Multcomp
178 1.2-8 (Hothorn et al. 2008).

179 In the assessment of a predator's functional response, there is a range of models and choice is based on
180 whether a particular study takes a mechanistic or phenomenological approach (Jeschke et al. 2002). Although

181 mechanistic application of parameters such as attack rate and handling time should be supported with empirical
182 measurements of such estimates (Caldow and Furness 2001; Jeschke and Hohberg 2008), the phenomenological
183 use of these parameters provides a tool to examine differences in functional response Types and magnitudes in
184 comparative experiments, as is the approach taken here (Alexander et al. 2013; Dick et al. 2013a; MacNeil et al.
185 2013; Dick et al. 2013b).

186 We first determined the functional response Type using logistic regression, testing for a negative linear
187 coefficient (fitted using maximum likelihood) in the relationship between the proportion of prey eaten and prey
188 density that indicates a Type II response (Trexler et al. 1988; Juliano 2001). Further, we estimated values of ‘ a ’
189 (attack rate), ‘ h ’ (handling time) and maximum feeding rate ($1/hT$, where T = experimental period) using the
190 ‘random predator equation’ (Rogers 1972), which is appropriate where prey are not replaced as they are
191 consumed (Juliano 2001);

192

$$193 N_e = N_0 \{1 - \exp [a(N_e h - T)]\}$$

194 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
195 time and T is the experimental period. Due to the implicit nature of the random predator equation, the Lambert
196 W function was implemented to fit the model to the data (Bolker 2008). Bootstrapping was used to generate
197 multiple estimates ($n = 30$) of the response parameters of attack rate a , handling time h and maximum feeding
198 rate ($1/hT$), which were then compared between habitat complexities in a GLM with Tukey’s contrast *post hoc*
199 tests.

200

201 **Results**

202

203 In control groups with no predators, prey survival was always >98% in each of the habitat treatments.
204 Experimental deaths were therefore attributed to predation by juvenile largemouth bass. As habitat became less
205 complex, significantly more prey were eaten ($F_{3, 68} = 8.41, p < 0.001$; Figure 1), and bass in the highest habitat
206 complexity consumed significantly less prey compared to all other complexities (Tukey’s contrasts, $p < 0.01$;
207 Figure 1). There were no differences in prey consumed between intermediate, low and zero habitat complexities.
208 Significantly more prey were consumed at higher as compared to lower densities ($F_{5, 68} = 76.88, p < 0.001$).

209 Logistic regression indicated that, in each of the habitat complexities, largemouth bass exhibited a

210 Type II functional response towards prey, as revealed by significantly negative linear coefficients (Table 1;
211 Figure 2a-d). As habitat became less complex, attack rate a significantly declined ($F_{3, 116} = 26.28, p < 0.001$;
212 Figure 3a). In comparison to low and intermediate habitats, which did not differ from each other, attack rate was
213 significantly reduced in zero habitat treatments, and significantly greater in high complexity treatments (Tukeys
214 contrasts, all $p < 0.01$; Figure 3a). Again as habitat became less complex, handling time h declined ($F_{3, 116} =$
215 $151.12, p < 0.001$), and was greatest in high complexity in comparison to the other treatments (Tukeys contrasts,
216 all $p < 0.01$; Figure 3b). This was also reflected in an increase in maximum feeding rate ($F_{3, 116} = 99.09, p <$
217 0.001), that was greatest for zero and low habitat complexities, and lowest in high complexity treatments
218 (Tukeys contrasts, all $p < 0.01$; Figure 3c).

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220

221

222 Discussion

223

224 Freshwater systems are threatened by a number of drivers of global change (Sala et al. 2000; Buisson et
225 al. 2013) and, around the world, formerly pristine headwater stream environments are impacted by both habitat
226 destruction and biological invasions by non-native species (Impson et al. 2002; Ellender et al. 2011). Such
227 drivers have important consequences when considered individually, however, they may also act in combination
228 to result in greater, synergistic impacts to native populations (Didham et al. 2007). Furthermore, there is a
229 pressing requirement to predict such impacts of both established and emerging invasive species under a range of
230 environmental conditions such that appropriate mitigation and control measures may be implemented (Byers et
231 al. 2002; Dick et al. 2013a; Simberloff et al. 2013).

232 Reduction in habitat complexity significantly increased consumption rates by invasive juvenile
233 largemouth bass *Micropterus salmoides* of a prey species, the female guppy *Poecilia reticulata*. We have thus
234 demonstrated that the impact by juvenile largemouth bass, one of the “100 world’s worst” invaders (ISSG
235 2013), may be heightened with degradation of habitat. In addition, we found that between zero to intermediate
236 structural complexities, there was no significant difference in the numbers of prey consumed. This suggests the
237 occurrence of a threshold in complexity between the intermediate and high-complexity experimental habitats
238 that can reduce the efficiency of the predator (Coull and Wells 1983; Gotceitas and Colgan 1989; Manatunge et
239 al. 2000). This may in turn have important consequences for predatory behaviours in instances where predators

240 alter their foraging modes in response to changes in their surrounding environment (Scharf et al. 2006). There
241 may also be additional consequences for predator-prey dynamics due to effects on predator-predator
242 interactions, potentially influencing facilitation or interference outcomes (Sih et al. 1998; Warfe and Barmuta
243 2004).

244 In each of the four levels of habitat complexity, juvenile bass exhibited a Type II functional response
245 towards the fish prey. This is counter to a number of studies demonstrating how variations in environment, such
246 as habitat complexity, light levels and temperature (Eggleston 1990; Koski and Johnson 2002; Alexander et al.
247 2012), may result in changes towards Type III responses. Generally changes in responses occur when factors,
248 such as environmental conditions, affect the searching ability of a predator. These are generally most influential
249 at low prey densities (Crowder and Cooper 1982; Heck and Crowder 1991) and habitat complexity is often an
250 important determinant of such outcomes (Buckel and Stoner 2000; Kushner and Hovel 2006; Alexander et al.
251 2012). Such a change in functional response can be significant when considering population stability and
252 viability, as Type II responses can drive prey populations to local extinction if prey are unable to match predator
253 consumption rate, with, for example, reproductive output (Twardochleb et al. 2012; MacNeil et al. 2013).

254 Although Type II responses were observed in each habitat, there were differences recorded in model
255 parameters. Attack rates were greatest in the most complex habitat treatment and lowest when no habitat was
256 present. As the scaling parameter of the curve, the attack rate describes the slope of the line at the lowest prey
257 densities and therefore provides an indication of predator efficiency at these densities (Hassell and May 1973;
258 Jeschke et al. 2002). The observed attack rates thus reflect the behaviour of a species that is predominantly an
259 ambush predator that seeks out structure (Savino and Stein 1982; Savino and Stein 1989b). Juvenile bass in
260 particular may be efficient predators in dense vegetation, with smaller body size permitting comparably easier
261 access to prey than older, larger individuals (Almany 2004b). Thus, the reduction in attack parameter in less
262 complex habitats in comparison to the denser structure in the present study therefore suggests that at low
263 densities, degradation of habitat may in fact provide prey with a reduced mortality risk in comparison to more
264 complex habitats.

265 As a further reflection of the greater predatory efficiency of juvenile bass at higher prey densities,
266 differences in mean handling times, and thus maximum feeding rates, indicated greater predation at higher prey
267 densities when habitat complexity was reduced. In comparison, high complexity structure reduced maximum
268 feeding rates, suggesting that, although efficient predators at lower densities in these habitats, juvenile bass are
269 impeded overall by such structure. At zero and low habitat complexities, bass were comparably more efficient

270 as indicated by significantly greater feeding rates, therefore with reductions in habitat cover, certain densities of
271 prey are more vulnerable to predation by this species. This may result from the reduction in the physical barrier
272 the habitat complexity provides with simplification in structure (Warfe and Barmuta 2004), or indeed be a
273 consequence of reduced refuge space for prey whereby safe areas become saturated and prey are pushed out into
274 the open where they are more vulnerable to predation (Forrester and Steele 2004).

275 Type II functional responses can, under certain conditions, be de-stabilising to prey populations and
276 reduce their viability, and indeed at low prey densities in high habitat complexity areas prey populations may be
277 driven to local extinction by juvenile bass as suggested by the elevated attack rates. Prey populations under such
278 circumstances may, however, be stabilised with the presence of alternative prey whereby as one species
279 becomes rare, the predator switches to feed on another, resulting in a Type III functional response (Akre and
280 Johnson 1979; Elliott 2004) . However, field studies consistently suggest that prey populations are heavily
281 impacted by largemouth bass (Ellender et al. 2011; Weyl et al. 2013), and we therefore assume that the strength
282 of the Type II responses observed here drive lack of coexistence between bass and native prey as is congruent
283 with other functional response studies that link experimental findings with observed field patterns (Bollache et
284 al. 2008; MacNeil et al. 2013; Dick et al. 2013b).

285 The use of functional responses in a predictive capacity, as applied here, to investigate what may be
286 expected with changes to environment when important drivers of global change interact, is a further
287 demonstration of the utilisation of this methodology (see Dick et al. 2013a). In this study, the combination of
288 habitat degradation, as simulated with reductions in the density of a plant mimic, and the *per capita* impact of
289 predation by invasive largemouth bass as determined by functional responses, indicates that impacts of the
290 invasive species may potentially be greater with reductions in habitat. Largemouth bass, however, are well
291 established in a number of systems worldwide (Welcomme 1992), and where their removal is not possible, a
292 potential mitigation measure is therefore to focus efforts on the protection of natural vegetation and riparian
293 zones. For further investigation it is suggested that other determinants of invader ecological impacts, such as the
294 numerical response to examine the reproductive and/or aggregative response to prey, are quantified; however,
295 the use of functional responses continues to be a rapid, reliable and in particular predictive assessment of the
296 potential ecological impacts of invasive species in a changing world.

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298

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307

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484 Table 1. Parameter estimates (and significance levels) from logistic regression analyses of prey consumed
485 against initial prey density, in high, intermediate, low and zero habitat complexities. Values for the intercept and
486 linear (N_0) terms are presented with p values.

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Habitat complexity	Intercept (p value)	N_0 (p value)	Functional response type
High	0.21 (p=0.39)	-0.04 (p<0.001)	II
Intermediate	2.04 (p<0.001)	-0.07 (p<0.001)	II
Low	1.73 (p<0.001)	-0.05 (p<0.001)	II
Zero	0.73 (p<0.01)	-0.04 (p<0.001)	II

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504 **Fig. 1.** Mean prey consumed (+SE) by juvenile largemouth bass in high, intermediate, low and zero complexity
505 simulated habitats. Different letters above bars indicate significant differences (Tukeys contrasts, $p < 0.01$).

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507 **Fig. 2.** Functional responses of juvenile bass towards prey in (a) high, (b) intermediate, (c) low and (d) zero
508 habitat complexity (as modelled by the Rogers random predator equation for a Type II response). Data are mean
509 number of prey consumed at each density \pm SE.

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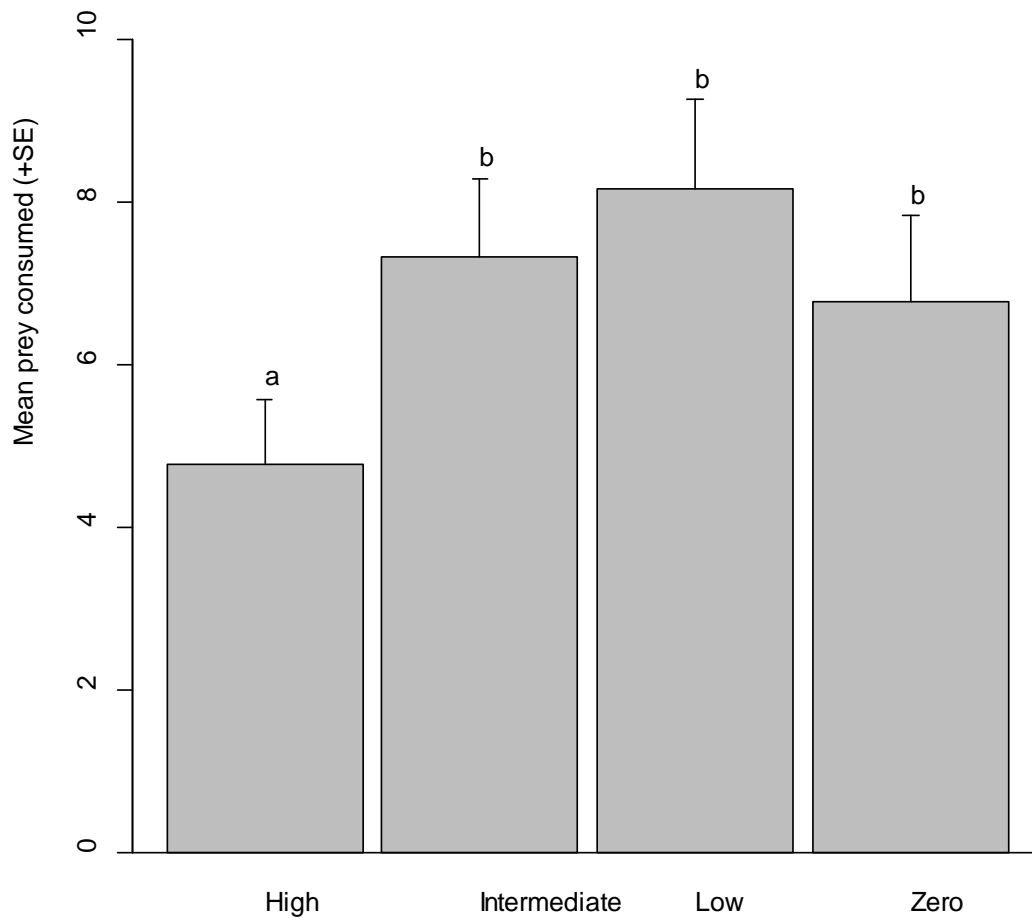
511 **Fig. 3.** Mean (+SE) (a) attack rate a , (b) handling time h and (c) maximum feeding rate $1/hT$ derived from
512 bootstrapping ($n=30$ each) of juvenile largemouth bass consuming prey in high, intermediate, low and zero
513 complexity simulated habitats. Different letters indicated significant differences (Tukeys contrasts, $p < 0.01$)

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519 **Fig.1.**

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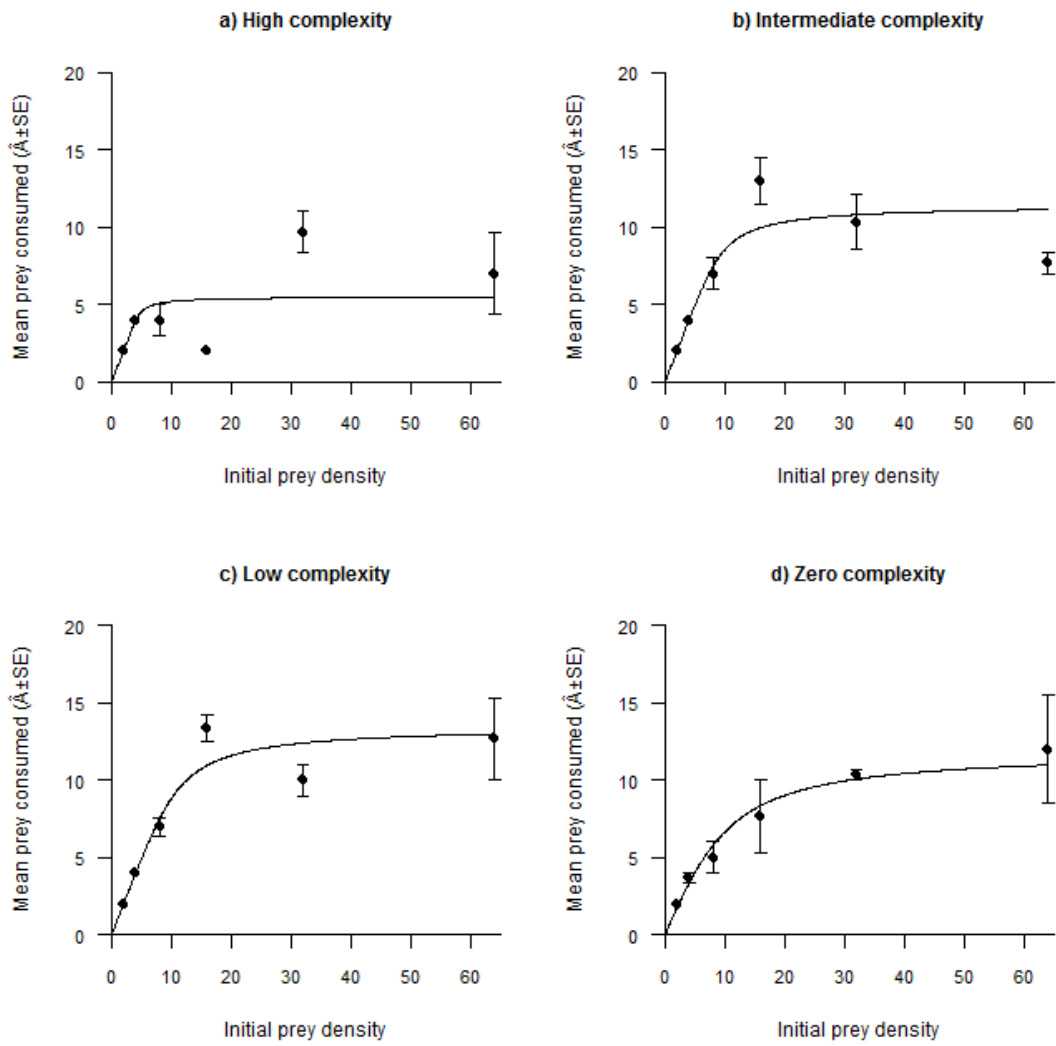
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527 Fig. 2.

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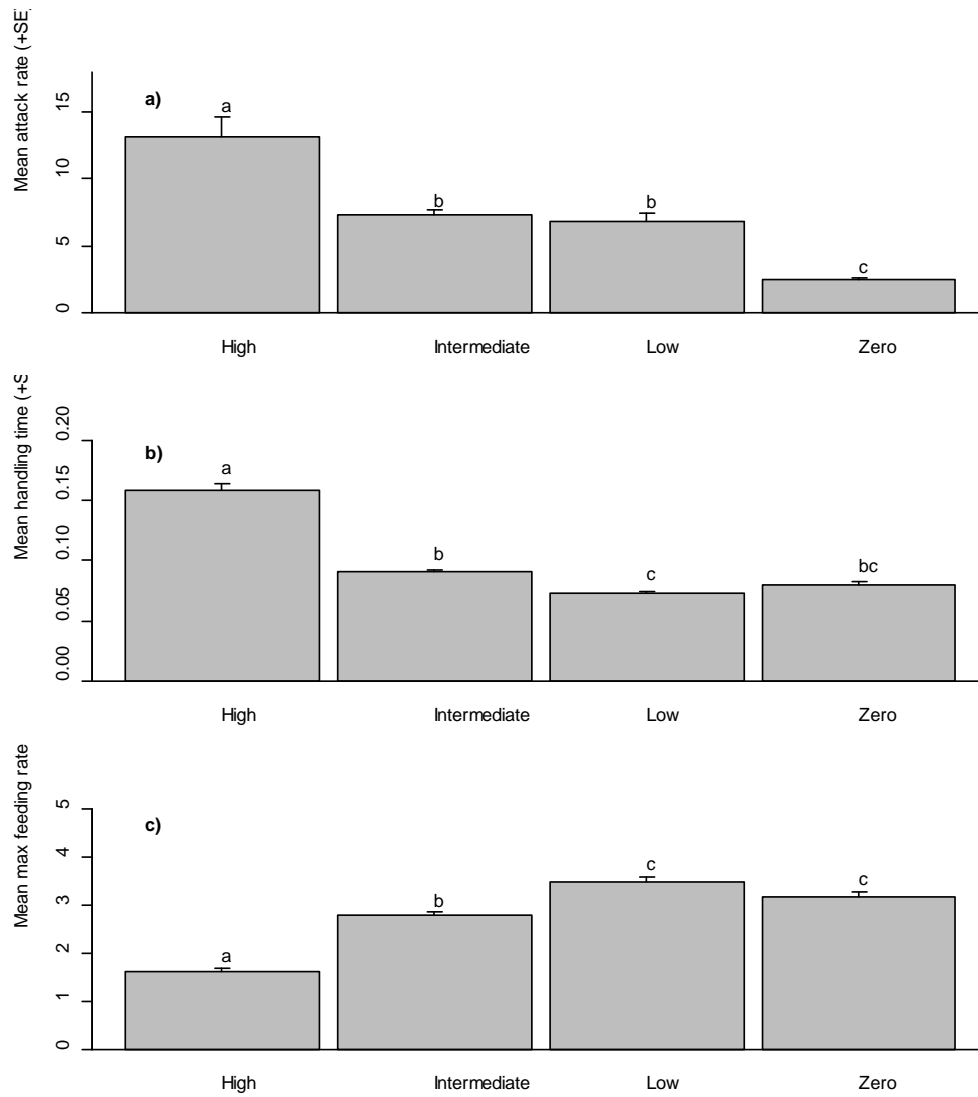
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537 **Fig.3.**

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