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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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54 **Introduction**

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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 morality 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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Materials & Methods

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Collection and maintenance of experimental animals

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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.

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Experimental set up

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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± 0.17ºC, 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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161 **Functional response trials**

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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.

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171 **Statistical analysis**

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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**

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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

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

Discussion

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

Reduction in habitat complexity significantly increased consumption rates by invasive juvenile largemouth bass *Micropterus salmoides* of a prey species, the female guppy *Poecilia reticulata*. We have thus demonstrated that the impact by juvenile largemouth bass, one of the "100 world's worst" invaders (ISSG 2013), may be heightened with degradation of habitat. In addition, we found that between zero to intermediate structural complexities, there was no significant difference in the numbers of prey consumed. This suggests the occurrence of a threshold in complexity between the intermediate and high-complexity experimental habitats that can reduce the efficiency of the predator (Coull and Wells 1983; Gotceitas and Colgan 1989; Manatunge et 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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308   **References**

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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

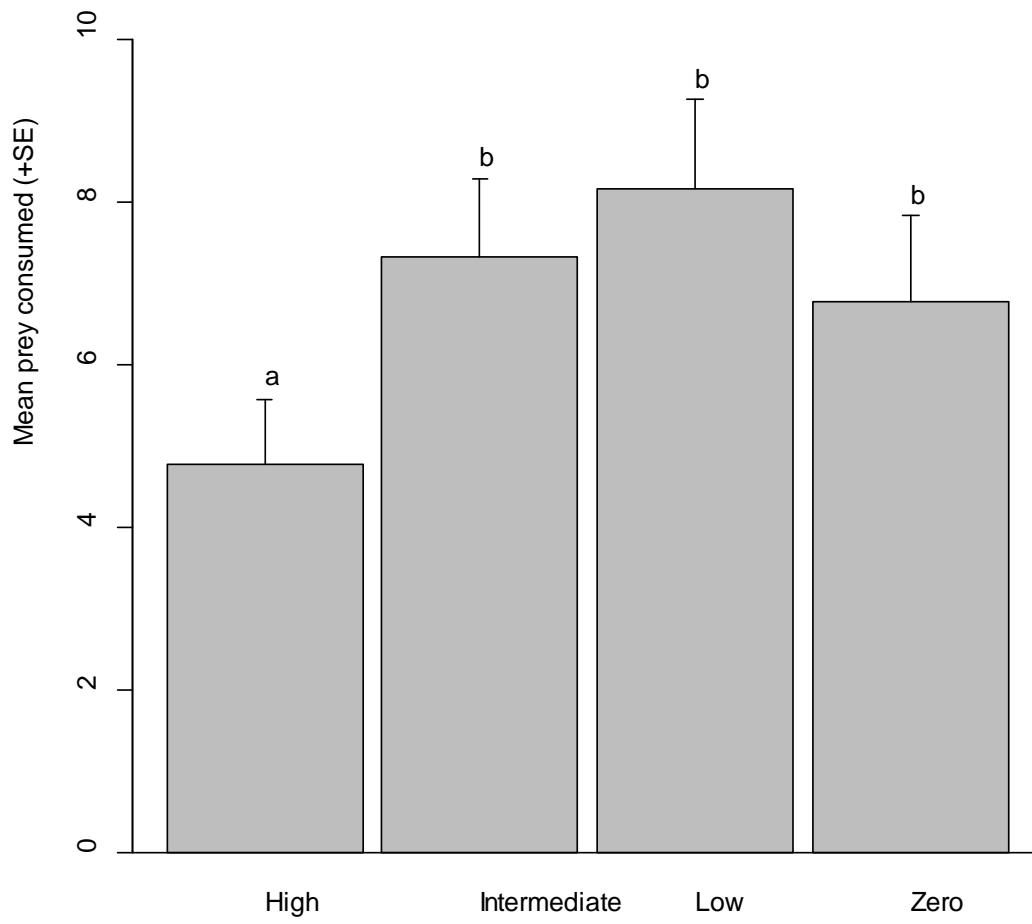509   number of prey consumed at each density $\pm$ SE.

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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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a) High complexity

b) Intermediate complexity

c) Low complexity

d) Zero complexity
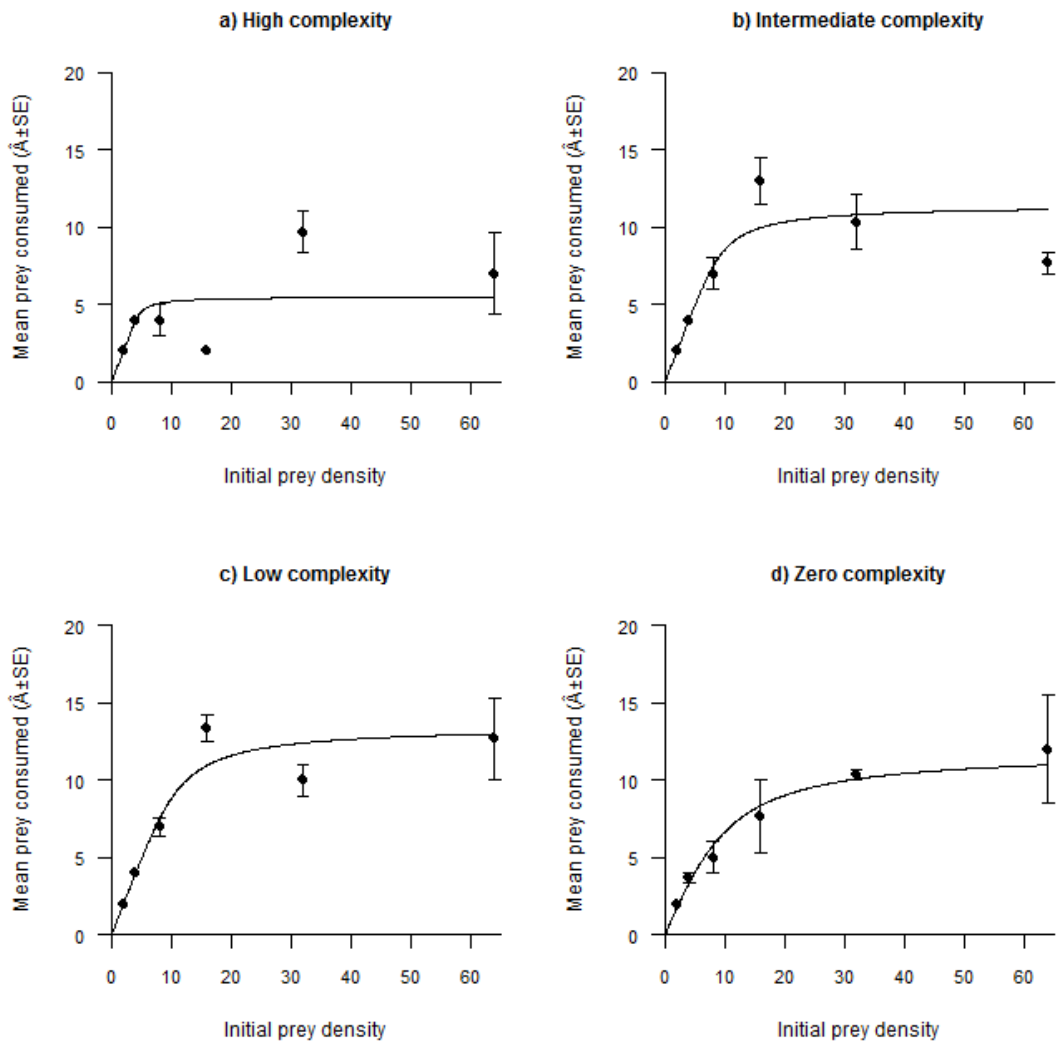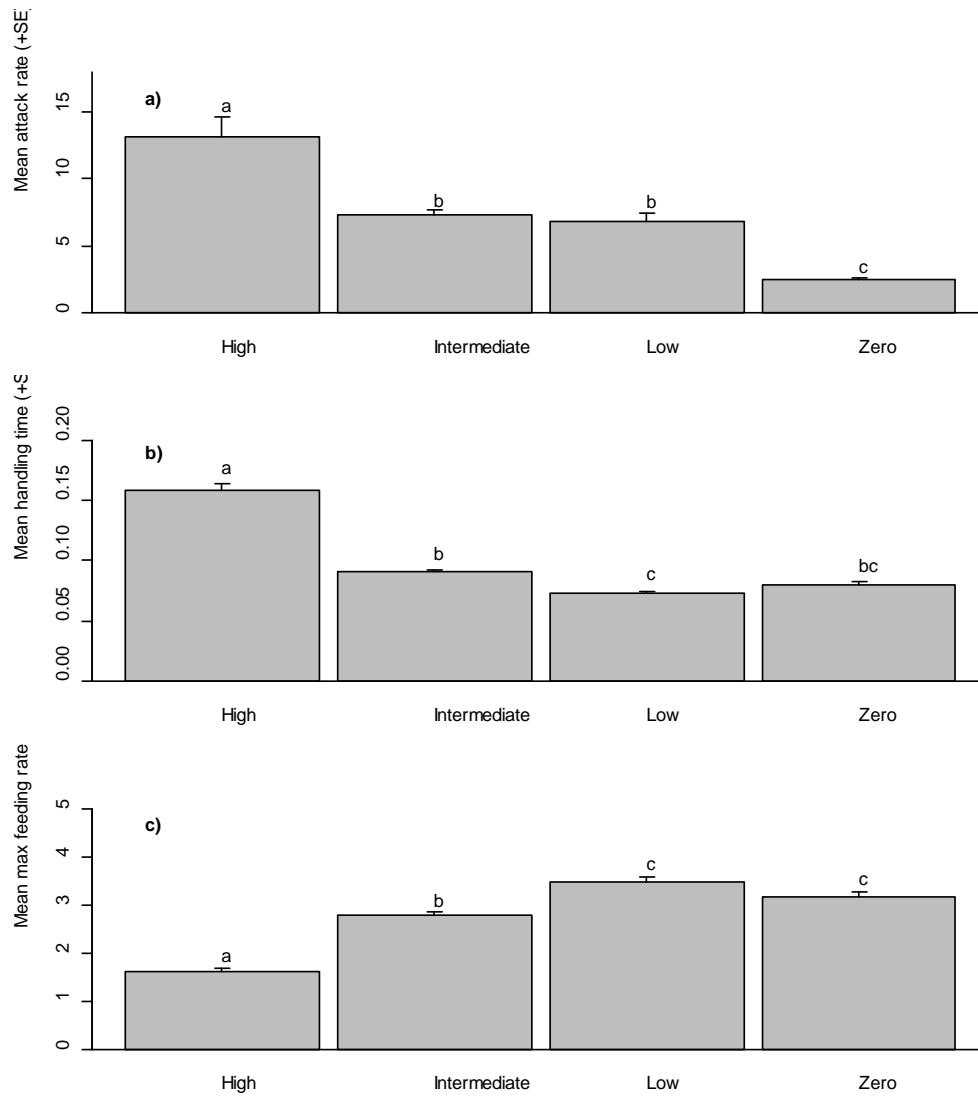
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527   **Fig. 2.**

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537   **Fig.3.**

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