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## Short Communication

### Using functional responses to quantify notonectid predatory impacts across increasingly complex environments

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**24 Abstract**

25 Predation is a key biotic interaction that influences both the structure and functioning of  
26 ecosystems, and is relevant in the biological control context. Levels of habitat complexity in  
27 aquatic ecosystems are highly variable and can profoundly affect predator-prey interactions  
28 through the presence of prey refugia, which can in turn reduce predatory efficacy. Here, we  
29 use functional responses (FRs, resource use under different resource densities) to quantify the  
30 predatory impact of the notonectid *Anisops debilis* towards larvae of the mosquito *Culex*  
31 *pipiens* under a habitat complexity gradient. *Anisops debilis* displayed a potentially  
32 population-destabilising Type II FR towards larval *C. pipiens* prey across the habitat  
33 complexity gradient. Attack rates were highest in simple environments, however handling  
34 times were not significantly affected by habitat complexity. Maximum feeding rates of *A.*  
35 *debilis* towards *C. pipiens* larvae were thus robust to habitat complexity variations. Our  
36 results demonstrate the substantial predatory impacts of notonectids towards larval mosquito  
37 prey irrespective of habitat complexities, which may assist in the biological control of pests  
38 and vectors in aquatic systems.

**39 Keywords**

40 predator-prey; biological control; functional response; habitat complexity; *Anisops debilis*;  
41 *Culex pipiens*

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## 47 **1. Introduction**

48           Biotic interactions such as predation play a central role in ecosystem structuring and  
49 functioning (Brooks and Dodson 1965; Carpenter et al. 1975; Wasserman and Froneman  
50 2013). Regulatory impacts of natural enemies towards pests, vectors and invasive species are  
51 in turn reliant on processes such as predation (Solomon 1949; O’Neil 1990; Golding et al.  
52 2015). As environmental context-dependencies can have a significant influence on predatory  
53 impacts (e.g. South et al. 2017), considering predator-prey interaction strengths across these  
54 contexts is important for robust impact quantifications towards target prey (e.g. Cuthbert et  
55 al. 2018a, b, c). Functional responses have been central to the development of consumer-  
56 resource (e.g. predator-prey) theories (Solomon 1949; Holling 1959), and have been regularly  
57 applied in examining environmental context-dependencies of biotic interaction strengths (e.g.  
58 Wasserman et al. 2016; Cuthbert et al. 2018a, b, c). Three FR forms have been broadly  
59 described: a linear Type I, hyperbolic Type II and sigmoidal Type III (Holling 1959), with  
60 each pertaining to different consumer-resource interaction outcomes. For instance, Type II  
61 FRs are considered to be destabilising to populations under certain conditions due to high  
62 resource (e.g. prey) acquisition at low prey densities by predators (Dick et al. 2014). Thus, in  
63 the context of biological control, such destabilising FRs can elicit eradications of target  
64 species.

65           Mosquitoes comprise an important trophic stage in many ecosystems, and biotic  
66 interactions strengths towards their larvae by predators are known to affect overall mosquito  
67 species distributions (Golding et al. 2015). Indeed, mosquitoes colonise a vast range of  
68 natural and artificial aquatic environments, including within urban areas (Townroe and  
69 Callaghan 2014). The physical structure of these habitats is inherently varied, with features  
70 such as submerged plants often constituting the main components of habitat complexity in  
71 aquatic environments (Tokeshi and Arakaki 2012). Such complexity can modulate the

72 interaction strengths between mosquitoes and their predators (e.g. Cuthbert et al. 2018b),  
73 which in turn could result in the emergence of reduced predatory success due to physical  
74 refugia of prey (e.g. Alexander et al. 2013), and thus has implications for vector population  
75 control.

76 *Culex pipiens* complex mosquitoes are competent vectors of diseases such as West  
77 Nile Virus (WNV) (Fonseca et al. 2004) and exhibit particularly marked ecological plasticity  
78 with respect to habitat selection, colonising a range of habitats across rural-urban gradients  
79 (Townroe and Callaghan 2014). Given that these habitats are highly varied in terms of their  
80 physical structuring, understanding the implications of habitat complexity for the predatory  
81 impact of natural enemies of mosquitoes is of great importance. Notonectids are voracious,  
82 carnivorous insects, and can play a key role in the structuring of communities (e.g. Blaustein  
83 1998; Wasserman et al. 2016, 2017), including within transient, ephemeral aquatic systems  
84 where mosquitoes frequently proliferate. Indeed, notonectids have been shown to occupy the  
85 highest trophic level in ephemeral aquatic ecosystems (e.g. Dalu et al. 2016). Although  
86 notonectid predatory efficacy towards mosquito larvae has been described (e.g. Fischer et al.  
87 2013; Silberbush et al. 2014), effects of habitat complexity on these biotic interactions have  
88 not been fully constrained. Therefore, here we use a comparative, phenomenological FR  
89 approach (e.g. Dick et al. 2014; Wasserman et al. 2016; Cuthbert et al. 2018a, b, c) to  
90 decipher the effects of habitat complexity on the predatory impact of the notonectid *Anisops*  
91 *debilis* Gersaeker 1873 towards larvae of the mosquito complex *C. pipiens*.

## 92 **2. Materials and Methods**

93 Adult *A. debilis* (6.7 – 7.1 mm body length) were collected from an impounded  
94 stream in Grahamstown, Eastern Cape, South Africa (33° 19' 00.1" S 26° 31' 21.2" E) during  
95 the 2017 – 2018 austral summer by trawling a kick net through the water column.

96 Notonectids were transported in source water to a controlled environment (CE) room at  
97 Rhodes University, Grahamstown and maintained at  $25 \pm 1$  °C under a 14:10 light:dark  
98 photoperiod. The prey, larvae of the *C. pipiens* mosquito complex, originated from egg rafts  
99 sampled from artificial container-style habitats situated around the Rhodes University  
100 campus. Larvae were reared to the desired size class (see below) in the CE room on a diet of  
101 crushed rabbit food pellets (Agricol, Port Elizabeth). Notonectids were housed in  
102 continuously aerated aquaria with 25 L dechlorinated tap water for six days prior to  
103 experimentation, and fed *ad libitum* on larvae of the mosquito *C. pipiens*. Excellent  
104 survivability of notonectids (> 95 %) was observed during housing (Cuthbert pers. obs.). On  
105 the seventh day, notonectids were separately starved in glass experimental arenas of 5.6 cm  
106 diameter, containing 80 mL dechlorinated tap water from a continuously aerated source.

107         We employed a '3 × 7' experimental design with respect to 'habitat complexity' and  
108 'prey supply'. We used stalks of the bulrush *Schoenoplectus brachyceras* (4 – 6 mm  
109 diameter), collected from the notonectid sampling site, to generate three levels of habitat  
110 complexity (i.e. low, medium, high). Low complexity arenas held zero stalks, medium  
111 complexity arenas contained two stalks and high complexity arenas had four stalks, arranged  
112 in a uniform array (c. Wasserman et al. 2016), broadly representing the range of habitat  
113 complexities encountered at the notonectid collection site (Cuthbert pers. obs.). *Culex pipiens*  
114 larvae (2.4 – 3.2 mm length incl. respiratory siphon) were supplied at seven densities for each  
115 complexity level (2, 4, 6, 8, 16, 32, 64;  $n = 4$  per experimental group) in glass 80 mL  
116 experimental arenas of 5.6 cm diameter holding dechlorinated tap water from a continuously  
117 aerated source, and allowed to settle for 2 h. Individual notonectid predators were then  
118 carefully transferred to arenas containing the allocated prey supply and complexity treatment  
119 and allowed to feed for 1 h during light conditions, before being removed. Then, remaining

120 live larval mosquito prey were counted. Controls consisted of a replicate at each prey supply  
 121 and complexity level in the absence of notonectid predators.

122 Statistical analyses were conducted in R v.3.4.2 (R Core Team 2017). The present  
 123 study applies FR modelling to address the phenomenological implications of habitat  
 124 complexity variabilities for predator-prey interactions. That is, our experiment is comparative  
 125 and does not seek to offer mechanistic insights into predator behaviour (see Jeschke et al.  
 126 2002; Dick et al. 2014). Functional responses were thus modelled using the ‘frair’ package  
 127 (Pritchard et al. 2017). Functional response types were inferred through the use of logistic  
 128 regression of the proportion of prey consumed as a function of the prey density supplied,  
 129 wherein a Type II FR is characterised by a significantly negative linear coefficient (Juliano  
 130 2001). The Rogers’ random predator equation was fit as prey were not replaced as they were  
 131 consumed:

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

133 Eqn. 1.

134 where  $N_e$  is the number of prey eaten,  $N_0$  is the initial density of prey,  $a$  is the attack constant,  
 135  $h$  is the handling time and  $T$  is the total experimental period. We fit the Lambert W function  
 136 to further enable FR model fitting (Bolker, 2008). We then bootstrapped ( $n = 2000$ ) FRs to  
 137 infer 95 % confidence intervals (CIs) using original maximum likelihood estimations (MLEs)  
 138 (e.g. Wasserman et al. 2016). Overall differences in attack rate and handling time parameters  
 139 were derived using the difference method outlined in Juliano (2001). We applied Bonferroni  
 140 corrections for multiple comparisons between the three habitat complexity levels (i.e. critical  
 141  $p = 0.017$ ).

### 142 **3. Results**



143 All 396 mosquito prey survived in controls, and so prey deaths were attributed to  
144 predation by notonectids, which we also directly observed. Type II FRs were found  
145 irrespective of habitat complexity treatments, and evidenced by significantly negative first  
146 order terms (Table 1). Functional response magnitudes trended towards being highest at the  
147 low complexity treatment (Figure 1), driven by higher attack rates (initial FR slope) and  
148 marginally lower handling times (FR asymptote) (Table 1). Whilst CIs were divergent at only  
149 intermediate prey supplies between low and medium habitat treatments, CIs were divergent at  
150 all except the lowest prey supplies between low and high habitat complexities (Figure 1). On  
151 the other hand, between medium and high habitat complexities, CIs overlapped across all  
152 prey densities and thus FRs were not significantly different here. Significantly greater attack  
153 rates were found in the low compared to medium complexity treatment ( $z = 2.585, p = 0.01$ ),  
154 and in the low compared to high complexity treatment overall ( $z = 2.592, p = 0.01$ ). Attack  
155 rates did not vary significantly between the medium and high complexity treatments ( $z =$   
156  $0.102, p = 0.92$ ). However, significant differences in handling times were not detected  
157 between any levels of habitat complexity (low – medium,  $z = 0.546, p = 0.59$ ; low – high,  $z =$   
158  $1.405, p = 0.16$ ; medium – high,  $z = 0.836, p = 0.40$ ).

#### 159 **4. Discussion**

160 Our results demonstrate consistency of Type II FRs of *A. debilis* towards larvae of the  
161 disease vector *C. pipiens* irrespective of habitat complexities. Thus, destabilising predatory  
162 impacts of this notonectid are unaffected by the presence of habitat complexity, with Type II  
163 FRs characteristically associable with localised prey extinctions under certain conditions due  
164 to high resource (e.g. prey) utilisation at low prey densities (Dick et al. 2014). These results  
165 corroborate with the recorded ability of notonectids to exert marked impacts upon the biotic  
166 structure of communities within varied aquatic ecosystems (e.g. Blaustein 1998; Wasserman  
167 et al. 2016, 2017). Indeed, Type II FR forms have been previously recorded with congeners

168 of *A. debilis* (e.g. Zuhurah and Lester 2011). However, as FRs only examine *per capita*  
169 effects of consumers, further investigation of population-level responses (e.g. abundance or  
170 fecundity) would be of value in constraining comprehensive ecological impacts (see Dick et  
171 al. 2017; Cuthbert et al. 2018a).

172         As attack rates of *A. debilis* were highest under low complexities, destabilising  
173 predatory impacts at low prey densities can be deemed more profound in simplified habitats.  
174 However, as handling times were similar across habitat complexities, maximum feeding rates  
175 were relatively unaffected by the habitat complexity gradient. Thus, as maximum feeding  
176 rates have proven robust in derivations of consumer-resource impact (Dick et al. 2017), the  
177 overall predatory impact of *A. debilis* towards mosquito prey can in turn be deemed similar  
178 across habitat complexities here. Previous research has shown *A. debilis* to be tolerant to  
179 ranging environmental conditions, however predatory efficiency has been shown to be  
180 affected by salinity gradients (Silberbush et al. 2014). Furthermore, other effective predatory  
181 biological control agents of mosquitoes, such as cyclopoid copepods, have shown similar  
182 responses to habitat complexity as those demonstrated in the present study (e.g. Cuthbert et  
183 al. 2018b). Although implications of habitat complexity are constrained, biotic contexts such  
184 as alternative prey may induce further implications for predator-prey interactions through  
185 processes such as prey preferences and switching (e.g. Cuthbert et al. 2018d). Alternative  
186 prey has been shown to influence predatory impacts, and studies have shown that notonectid  
187 impacts on larval mosquito prey remain high in the presence of certain alternative prey (e.g.  
188 Saha et al. 2010; Fischer et al. 2013; Saha et al. 2014). In particular, Saha et al. (2010, 2014)  
189 demonstrate that a congeneric *Anisops* will preferentially consume mosquitoes under many  
190 circumstances, whilst generalist feeding traits are advantageous as notonectids can forage on  
191 alternative prey when mosquito abundances are low.

192           Given the range of forms of aquatic habitats which mosquitoes colonise across rural-  
193 urban gradients, our results indicate that certain natural enemies of mosquitoes, such as *A.*  
194 *debilis*, may retain strong predatory efficacy irrespective of habitat variations. Aerial adult  
195 mosquito life-history stages ensure efficient colonisation of aquatic systems across the  
196 landscape. Unlike other aquatic mosquito predators such as copepods (Cuthbert et al. 2018a,  
197 b, c), notonectids can efficiently and naturally colonise aquatic habitats given that they too  
198 are capable of aerial dispersal (McCauley and Row 2010). Thus, encouraging the  
199 proliferation of such natural enemies may assist with population-level control of vectorially-  
200 important mosquitoes across a broad range of aquatic systems with different environmental  
201 characteristics. Further research should seek to examine the impacts of additional  
202 environmental contexts on biotic processes, particularly in terms of their effects on the  
203 efficacy of natural enemies of pests, vectors and invasive species.

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309 Tables and Figures

310 Table 1. First order terms derived from logistic regression of proportional prey consumption  
 311 as a function of prey supply across all habitat complexity levels, alongside original attack rate  
 312 and handling time parameter estimates from Rogers' random predator equation.

Habitat complexity	First order term, $p$	Attack rate, $p$	Handling time, $p$
Low	-0.036, < 0.001	2.490, < 0.001	0.040, < 0.001
Medium	-0.030, < 0.001	1.387, < 0.001	0.044, < 0.001
High	-0.028, < 0.001	1.356, < 0.001	0.052, < 0.001

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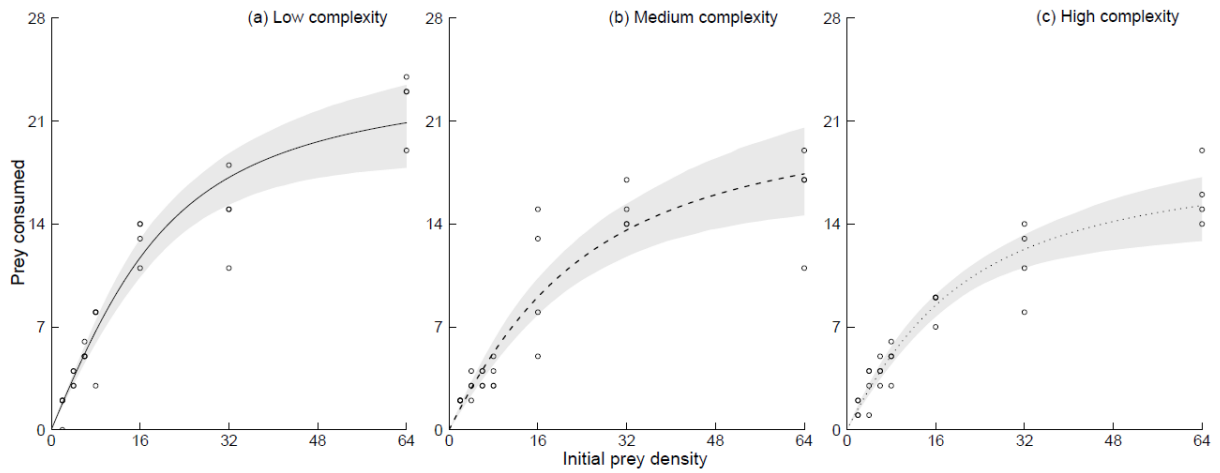
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326 Figure 1. Type II functional responses of *Anisops debilis* towards *Culex pipiens* across low (a,  
 327 solid line), medium (b, dashed line) and high (c, dotted line) habitat complexities. Shaded  
 328 areas represent bootstrapped 95% confidence intervals ( $n = 2000$ ) and open circles represent  
 329 raw residual points ( $n = 4$  replicates per density).

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