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1 **Muddy waters: efficacious predation of container-breeding mosquitoes by**
2 **a newly-described calanoid copepod across differential water clarities**

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21

22 **Abstract**

23 Mosquito-borne diseases induce unrivalled morbidity and mortality in human
24 populations. In recent times, greater urbanisation has facilitated vector population expansion,
25 particularly of those which proliferate in container-style habitats. To combat increased
26 associated disease risk, we urgently require innovative and efficacious control mechanisms to
27 be identified and implemented. Predatory biological control of vectorially-important
28 mosquitoes can be effective. Despite their high prevalence in freshwater ecosystems,
29 predatory calanoid copepods have yet to be examined comprehensively for mosquito control.
30 Moreover, environmental context-dependencies can cause substantial variations in natural
31 enemy impacts on target populations. Accordingly, improved understanding of the effects of
32 context-dependencies upon predatory biocontrol is needed. Here, we use functional responses
33 (FRs) to examine the predatory impact of a newly-described species of calanoid copepod,
34 *Lovenula raynerae*, upon larval *Culex pipiens* prey across variations in prey supply and water
35 clarity. Using outdoor field trials, we assess the viability of *L. raynerae* in reducing mosquito
36 survival in container-style habitats. *Lovenula raynerae* displayed destabilising Type II FRs
37 towards larval mosquito prey across all water clarities tested, with overall predation rates
38 remaining largely unaffected across all clarity treatments. In the outdoor experiment, *L.*
39 *raynerae* applications resulted in substantial reductions in larval *C. pipiens* populations, with
40 close to total eradication achieved following the experimental period under higher predator
41 densities. These results demonstrate that environmental context such as water clarity may
42 have little effect on vector control by calanoid copepods, which suggests a predatory reliance
43 on hydromechanical signalling. Further, for the first time, we demonstrate the applicability of
44 calanoid copepods to artificial container-style habitats where mosquitoes proliferate.
45 Therefore, our results indicate that further examination into the applicability of this species
46 group to aid vector biocontrol strategies is warranted.

47 **Keywords**

48 biological control; predator-prey; functional response; turbidity; *Culex pipiens*; *Lovenula*
49 *raynerae*

50

51 **1. Introduction**

52 The effective control of mosquito-borne diseases and their vectors is of substantial
53 public health importance (Mehlhorn, 2012; Beneli and Mehlhorn, 2016; WHO, 2017).
54 Currently, a variety of chemical, physical, genetic and biological approaches are used to
55 control mosquitoes (see Becker et al. 2010). However, many population management
56 approaches are associated with drawbacks which impede their sustainability (e.g.
57 Baldacchino et al. 2015). For instance, commonly-used insecticidal chemicals have caused
58 environmental pollution, and emergent effects of insecticide resistance have presented major
59 challenges to mosquito control strategies (e.g. Scholte et al. 2004; Ranson et al. 2016; Main
60 et al. 2018). Mosquitoes which exploit artificial container-style habitats are of particular
61 public health importance due to an association with urban areas and thus high potential for
62 contact with human populations, wherein urban ‘heat islands’ can result in higher disease
63 vector mosquito abundances (Townroe and Callaghan, 2014). Indeed, exploitation of human
64 environments has facilitated invasive mosquito species to radically extend their geographic
65 range (e.g. Lambrechts et al. 2010).

66 Biological control (hereafter biocontrol) provides a relatively environmentally-
67 friendly and economical option in vector control (Rodríguez-Pérez et al. 2012). Natural
68 enemies can efficaciously suppress vectorially-important mosquito populations (Marten,
69 1990; Marten and Reid, 2007; Baldacchino et al. 2017; Cuthbert et al. 2018a, b; but see
70 Thomas, 2018), and have successfully induced community-wide disease extirpations (Kay

71 and Nam, 2005; Nam et al. 2012). However, many candidate biocontrol agents remain
72 entirely unexplored, or underexploited in the context of container-style aquatic habitats where
73 vectorially-efficient mosquitoes can proliferate *en masse* (e.g. Townroe and Callaghan,
74 2014). Biological control of larval mosquito populations by deliberate application of
75 predatory copepod species has proven to be highly efficacious (reviewed by Marten and Reid,
76 2007). Presently, however, only those present within the cyclopoid order have been examined
77 and utilised for control. Yet, copepods represent a vastly extensive group of crustaceans,
78 comprising a broad range of orders adapted to both ephemeral and perennial hydrologic
79 ecosystems (Dussart and Defaye, 2001). Despite previous erroneous categorisation as
80 herbivorous, considered unable to prey upon mosquito larvae (Marten and Reid, 2007),
81 predatory calanoid copepods exist and can exert profound trophic impacts in aquatic
82 environments (Wasserman et al. 2016a; Dalu et al. 2016a; Cuthbert et al. 2018d). Moreover,
83 certain calanoid copepod species can be atypically large in size (e.g. Suárez-Morales et al.
84 2015), and can therefore handle larval mosquito stages throughout their ontogeny (Cuthbert
85 et al. 2018d). This contrasts to cyclopoid copepods which impart a size-refuge to larger prey
86 (Marten and Reid 2007). Therefore, examining the efficacy of calanoid copepods towards
87 container-breeding mosquitoes across ranging environmental contexts is of pertinence for the
88 applied biocontrol of mosquito-borne disease vectors.

89 Environmental context-dependencies can cause substantial variations in natural
90 enemy impacts on target populations (e.g. Cuthbert et al. 2018a), both as a result of biotic
91 (e.g. Alexander et al. 2013; Barrios-O'Neill et al. 2014; Wasserman et al. 2016c) and abiotic
92 (e.g. Wasserman et al. 2016b; Cuthbert et al. 2018a, b) factors, and is thus highly relevant to
93 biocontrol agent selection. However, the implications of these context-dependencies on the
94 efficacy of biocontrol agents often remain poorly understood. This, in turn, reduces the
95 capacity of practitioners to fully understand and quantify biocontrol agent impacts. As

96 vectorially-efficient mosquito species are adapted to breed in a highly variable range of
97 aquatic habitats (see Becker et al. 2010), understanding the implications of environmental
98 context is integral to robust quantifications of biocontrol agent impacts on target mosquito
99 species. Further, finding biocontrol agents that are also robust to environmental variability
100 would be desirable. In particular, water clarity is highly variable in hydrological
101 environments, and variations in water clarity can affect food webs through alterations of
102 predation efficacy by visual predators (e.g. van De Meutter et al. 2005; Lunt and Smee,
103 2015), manipulations of microhabitat structures and temperature regimes (e.g. Meysman et al.
104 2006; Paaajmans et al. 2017), and by directly impacting filter feeders (e.g. Rellstab and Spak,
105 2007), including larvae of many mosquito species. In addition, disease vector mosquitoes
106 have been shown to be attracted to low-clarity habitats due to perceived higher nutritional loads
107 or greater depth (Ortiz-Perea and Callaghan, 2017; Cuthbert et al. 2018b), with concurrent
108 implications for mosquito abundances (e.g. Medlock and Vaux, 2014). Therefore, identifying
109 biocontrol agents to target disease vector mosquitoes which are not impacted by turbid
110 environments is crucial for successful field applications in diverse aquatic habitats (see
111 Cuthbert et al. 2018c).

112 Functional responses (FRs), i.e. the *per capita* consumption rates of consumers with
113 changes to resource densities (Solomon, 1949; Holling, 1959; Juliano, 2001), have been
114 applied extensively to quantify the resource regulation potential of consumers (e.g. Abrams,
115 1990; Dick et al. 2014), and can be applied to concurrently test environmental context-
116 dependencies of consumer impact (e.g. South et al. 2017; Cuthbert et al. 2018a, b). Given that
117 density- and context- dependencies of *per capita* impact may affect the viability of biocontrol
118 agents in regulating target organisms (O’Neil, 1990; Van Driesche and Bellows, 1996;
119 Cuthbert et al. 2018a), and the regulatory efficacy of many agents is yet to be explored, here,
120 we examine the predatory potential of *Lovenula raynerae* Suárez-Morales, Wasserman and

121 Dalu 2015, a recently described and remarkably large (4 – 5 mm) calanoid copepod species,
122 towards larvae of the disease vector complex *Culex pipiens* in container-style environments.
123 *Lovenula raynerae* is a predatory ephemeral pond specialist species which hatches from
124 dormant eggs within sediment during the early stages of hydroperiod (Suárez-Morales et al.
125 2015; Wasserman et al. 2016a). Such ephemeral aquatic systems are highly varied with
126 respect to their water clarity, particularly as a result of bioturbation which can heavily impact
127 ecosystem functioning (e.g. Waterkeyn et al. 2016). Although high predatory impacts of *L.*
128 *raynerae* have recently been described upon larval mosquitoes across their ontogeny
129 (Cuthbert et al. 2018d), further research is required to elucidate additional context-
130 dependencies of their impact, alongside assessments of their use in container-style habitats
131 which foster disease vector mosquitoes (Townroe and Callaghan 2014). Therefore, the
132 present study examines the FRs of *L. raynerae* towards larvae of the mosquito *C. pipiens*
133 across a water clarity gradient, and also assesses the predation potential of the copepod in
134 outdoor artificial container-style habitats under varying modes of predator and prey density.

135 **2. Materials and methods**

136 *2.1. Animal collection and rearing*

137 Adult male and female *L. raynerae* (4 – 5 mm) were collected from an ephemeral
138 pond in the Eastern Cape, South Africa (33° 10' 04.1" S 27° 16' 10.6" E) by towing a 64 µm
139 zooplankton net through the upper water column. Copepods were transported in source water
140 to a controlled environment (CE) room at Rhodes University, Grahamstown (25 °C ± 1 °C;
141 14:10 light:dark) and housed in 25 L aquaria containing strained (200 µm) water from the
142 collection site prior to the experiments. *Culex pipiens* complex larvae originated from egg
143 rafts collected from artificial container-style aquatic habitats on the Rhodes University

144 campus, and were reared to the desired size class on a diet of crushed rabbit food pellets
145 (Agricol, Port Elizabeth).

146 2.2. Experimental protocols

147 We conducted two experiments to discern the efficacy of the calanoid copepod *L.*
148 *raynerae* in mosquito control. In experiment 1, in the CE room, we quantified the effect of a
149 water clarity gradient on the predatory impact of *L. raynerae* towards larval mosquito prey.
150 Adult male *L. raynerae* were starved for 48 h prior to experimentation. Here, males were
151 selected for experimentation to provide standardisation of predator type, given the various
152 reproductive stages of female copepods that may influence predation rates. Functional
153 responses of copepods were constrained under three water clarity treatments, conducive with
154 the variability observed in ephemeral systems (Cuthbert, pers. obs.). Water clarity was
155 defined as 0%, 50% and 100% against a predefined scale using a water clarity tube
156 (GroundTruth, Leonard) by diluting turbid water to the prescribed clarity, with each treatment
157 continuously aerated and filtered (200 µm) prior to use. *Culex pipiens* (3.3 ± 0.2 mm) larvae
158 were established at five prey densities (2, 4, 8, 16, 32; $n = 4$ per density) in 80 mL arenas of
159 5.6 cm diameter containing the appropriate clarity treatment. Once predators were added,
160 they were allowed to feed undisturbed for 6 h, after which they were removed and remaining
161 prey counted to derive those killed. Controls consisted of three replicates at each density and
162 clarity treatment without predators.

163 In experiment 2, we ascertained the efficacy of *L. raynerae* in outdoor artificial
164 container-style habitats at regulating *C. pipiens* populations. This was done in a partially
165 shaded outdoor location within the Rhodes University campus, similar to the environments
166 from which *C. pipiens* rafts were collected. *Culex pipiens* larvae ($1.89 \text{ mm} \pm 0.08$) were
167 added at two densities (50, 100), to 2 L arenas of 13.5 cm diameter, each containing 1.5 L

168 filtered (200 µm) aerated water from the copepod collection site and 0.3 g of crushed rabbit
169 food pellets. Then, three predator densities were added (0, 4, 8) in a fully randomised array.
170 We maintained copepod sex ratios of 3:1 male:female across predator treatments (i.e. 0:0,
171 3:1, 6:2) to minimise cannibalism (Lavens and Sorgeloos, 1996). After 72 h, the predators
172 were removed and remaining live mosquito prey counted to derive the number eaten. We
173 conducted at least three replicates per experimental group. Water temperatures within arenas
174 were found to be within the 16 – 20 °C range across the duration of the experiment.

175 2.3. Statistical analyses

176 All statistical analyses were undertaken in R v3.4.2. (R Core Team, 2017). In
177 experiment 1, generalised linear models (GLMs) assuming a Poisson error distribution were
178 used to examine the effects of ‘water clarity’ and ‘prey density’ on raw prey consumption.
179 All FR analyses were undertaken within the ‘frair’ package in R (Pritchard et al. 2017).
180 Logistic regression considering the proportion of prey consumed as a function of the ‘prey
181 density’ factor was used to infer FR types. Here, a Type II FR is determined categorically by
182 a significantly negative first order term, and a Type III FR by a significantly positive first
183 order term followed by a significantly negative second order term. We fit Rogers’ random
184 predator equation to account for non-replacement of prey during the experiment (Trexler et
185 al. 1998; Juliano, 2001):

$$186 \quad N_e = N_0(1 - \exp(a(N_e h - T)))$$

187 Eqn. 1.

188

189 where N_e is the number of prey eaten, N_0 is the initial density of prey, a is the attack constant,
190 h is the handling time and T is the total experimental period. We applied the Lambert W
191 function to fit the random predator equation (Bolker, 2008). The difference (delta) method

192 (see Juliano, 2001) was employed to compare FR attack rates and handling times between
193 treatments with respect to the ‘water clarity’ factor. We applied Bonferroni corrections to
194 account for multiplicity of comparisons (i.e. $\alpha = 0.017$). Furthermore, we employed a non-
195 parametric bootstrapping procedure ($n = 2000$) to generate 95% confidence intervals around
196 the FR curves (see Pritchard et al. 2017).

197 In experiment 2, GLMs assuming a quasibinomial error distribution, as residuals were
198 found to be over-dispersed relative to degrees of freedom, were used to model mortality rates
199 with respect to the ‘predator density’ and ‘prey density’ factors. Here, we used Tukey’s
200 comparisons *via* the ‘multcomp’ package in R (Hothorn et al. 2008). In all cases, non-
201 significant terms and interactions were removed stepwise to obtain models with maximal
202 parsimony (as per Crawley, 2007).

203 3. Results

204 In experiment 1, survival in control groups was 100% and so experimental deaths of
205 larval mosquitoes were attributed to predation by copepods, which were also observed eating
206 the larvae. Overall consumption was not significantly affected by water clarity ($\chi^2 = 1.76$, df
207 $= 2$, $p = 0.42$) but increased significantly with higher prey densities ($\chi^2 = 80.45$, $df = 4$, $p <$
208 0.001). The consumptive effect of ‘prey density’ was not dependent on the water clarity as
209 the ‘water clarity \times prey density’ effect was not significant ($\chi^2 = 7.46$, $df = 8$, $p = 0.49$). Type
210 II FRs were detected in all water clarity treatments (Table 1; Figure 1). Functional response
211 parameters (attack rate, a ; handling time, h) did not differ significantly between any water
212 clarity treatment pairs (Table 1; Figure 1; a , low – medium, $z = 0.64$, $p = 0.52$; a , medium –
213 high, $z = 0.25$, $p = 0.80$; a , low – high, $z = 0.87$, $p = 0.39$; h , low – medium, $z = 0.55$, $p =$
214 0.58 ; h , medium – high, $z = 0.79$, $p = 0.43$; h , low – high, $z = 0.32$, $p = 0.75$).

215 In experiment 2, overall, the presence of *L. raynerae* resulted in significant larval
216 mosquito reductions given that the ‘predator density’ factor significantly affected mortality
217 rates ($F_{2, 17} = 72.59, p < 0.001$; Figure 1). Greater mortality rates were found between all
218 incremental predator density increases (0 – 4, $z = 6.69, p < 0.001$; 4 – 8: $z = 4.35, p < 0.001$; 0
219 – 8, $z = 9.90, p < 0.001$). Significantly greater mortality rates of larval mosquito prey were
220 demonstrated under the lower prey density treatments overall ($F_{1, 16} = 10.23, p = 0.006$;
221 Figure 2). There was no ‘predator density × prey density’ interaction ($F_{2, 14} = 1.37, p = 0.29$),
222 and so the efficacy of *L. raynerae* at different densities was robust to treatment variations
223 associated with prey density.

224 4. Discussion

225 Here, for the first time, we demonstrate high *per capita* predation potential of an
226 ephemeral pond specialist calanoid copepod, *L. raynerae*, towards vector mosquito prey
227 irrespective of water clarity regime. Equally, in outdoor trials, we show that this species can
228 substantially reduce larval mosquito abundances in container-style habitats which frequently
229 foster vectorially-efficient mosquito species (Townroe and Callaghan, 2014). Copepods are
230 highly efficacious predatory biocontrol agents for disease vectoring mosquitoes (Marten,
231 1984; Marten and Reid, 2007; Cuthbert et al 2018a, b). Although biocontrol examinations
232 have hitherto focused on cyclopoid copepods, other groups of copepods are also predatory
233 and thus may be of value in biocontrol strategies (Wasserman et al. 2016a; Cuthbert et al.
234 2018d).

235 Functional responses of the calanoid copepod *L. raynerae* were not significantly
236 affected by variations in water clarity, either in terms of form or magnitude. In a predation
237 context, both FR form and magnitude are powerful predictors of the interaction strengths
238 between predators and prey (Dick et al. 2014), and may be combined with predator

239 population responses to holistically assess ecological impact (Dick et al. 2017; Cuthbert et al.
240 2018a, b). Three broad forms of FR have been defined (Hassell, 1978): the linear Type I,
241 hyperbolic Type II and sigmoidal Type III. Whilst Type I FRs are mechanistically restricted
242 to filter feeders (Jeschke et al. 2004), Type II FRs are conducive to high ecological impact as
243 a result of high predation pressures at low prey densities (Dick et al. 2014). Accordingly,
244 Type II FRs are particularly desirable in biocontrol contexts as they trend towards target prey
245 eradications (Cuthbert et al. 2018a). However, Type III FRs are regarded as more stabilising,
246 wherein there is a provisioning of low-density refugia for prey, driven, empirically, by
247 processes such as prey switching (Hassell, 1978; Cuthbert et al. 2018e).

248 The present study observed Type II FRs regardless of water clarity regime. Therefore,
249 *L. raynerae* is effectively able to locate, capture and handle prey at low densities, even in
250 highly turbid conditions. These results are pertinent as ephemeral aquatic ecosystems, both
251 natural and artificial, are highly varied with respect to their water clarity regime, for instance
252 due to detritus inputs or bioturbation (Cuthbert, pers. obs.). Indeed, bioturbation associated
253 with biocontrol agents can also affect the viability of multiple management interventions in
254 aquatic habitats which target larval mosquitoes (e.g. Fry-O'Brien and Mulla, 1996).
255 Mosquitoes often exhibit predator avoidance behaviours when ovipositing (see Vonesh and
256 Blaustein, 2010), and water clarity can offset this avoidance behaviour under certain
257 conditions (Cuthbert et al. 2018b). For this reason, identifying predatory agents which are
258 unaffected by water clarity variations is imperative for effective biocontrol applications. Our
259 results suggest a reliance on hydromechanical cues by this predatory calanoid copepod when
260 detecting and capturing mosquito prey, as opposed to visual cues, which may account for the
261 lack of overall consumptive variation between water clarity treatments. Indeed, these results
262 corroborate with those demonstrating a lack of reliance on visual signals in cyclopoid

263 copepods when detecting prey across diurnal and water clarity regime shifts (e.g. Hwang and
264 Strickler, 2001; Cuthbert et al. 2018c).

265 Attack rates of *L. raynerae* were relatively unaffected by variations in water clarity,
266 and even trended towards being higher under lower water clarities. Attack rates correspond to
267 the initial slope steepness in FR curves, and thus high attack rates can be particularly
268 destabilising to prey populations at low prey densities. On the other hand, handling times
269 reflect the asymptote in FR curves, and can be reciprocated to infer maximum feeding rates
270 of predators (Dick et al. 2014; Cuthbert et al. 2018a). Here, although larval mosquitoes can
271 exhibit high responsiveness to predatory cues (e.g. Zuharah and Lester 2011), it is feasible
272 that low water clarity increases vulnerability to predation in larval mosquito prey, in turn
273 enhancing the capture efficiency by predators at low prey densities. Furthermore, handling
274 times were not significantly different across the water clarity gradient in the present study,
275 and so maximum feeding rates were similar between treatments. Yet, handling times trended
276 towards being lowest, and thus maximum feeding rates highest, at intermediate water
277 clarities. Hence, we present strong and sustained destabilising predatory impacts of the
278 calanoid copepod *L. raynerae* towards varying prey supplies of larval *C. pipiens* irrespective
279 of this environmental context. Importantly, although FR examinations here only considered
280 males, female *L. raynerae* are also voracious consumers of larval mosquitoes, with the
281 potential to kill over 5 first instar larvae per hour and the ability to handle late instar prey
282 (Cuthbert et al. 2018d). This intake rate is considerably higher than cyclopoid copepods
283 which are often used in biological control, and which also impart a size refuge to late instar
284 mosquito prey (Marten and Reid, 2007).

285 The study also highlights that the *L. raynerae* predation efficiency observed under
286 controlled laboratory conditions also persists in outdoor environments exposed to natural
287 conditions, where vector mosquitoes proliferate. In outdoor experiments within container-

288 style habitats, *L. raynerae* induced substantial mortality rates in larval mosquito populations.
289 As vectorially-important mosquitoes increasingly proliferate in such artificial, container-style
290 habitats (Townroe and Callaghan, 2014), exploring the suitability for biocontrol agents over
291 longer-term experiments in these environments is critical for empirical derivations of their
292 efficacy. Indeed, these aquatic habitats can often be minute and ephemeral in nature, negating
293 the use of larger larval mosquito antagonists, such as fish (see Azevedo-Santos et al. 2016).
294 Our results demonstrate that, over the experimental period, higher densities of *L. raynerae*
295 exhibited higher predation capacities relative to lower densities towards all prey supplies.
296 Thus, multiple *L. raynerae* conspecifics may be additive in their consumption of *C. pipiens*
297 larvae. Moreover, as *L. raynerae* is an ephemeral pond specialist and is capable of producing
298 dormant, drought-resistant eggs, applications of this species to ephemeral aquatic habitats
299 which foster mosquitoes may enable predator hatching *in situ* prior to, or simultaneous with,
300 colonisation by mosquitoes. Although our results are theoretically promising in this respect,
301 further research is required to test the efficacy of single applications of dormant eggs of *L.*
302 *raynerae* over recurrent hydroperiods, and thus over longer experimental times overall.
303 Furthermore, examinations of prey preferences and cannibalism in *L. raynerae* towards
304 juveniles would be of value in further discerning factors that may impede their applied
305 efficacy in biocontrol. However, it has been proposed that the most efficacious copepod
306 species in biocontrol are able to curtail overpopulation and growth stunting *via* cannibalism
307 of juveniles when the population becomes too high relative to the food supply (Marten and
308 Reid, 2007).

309 In conclusion, our results suggest that calanoids and other copepod groups warrant
310 further consideration as biocontrol agents of disease vector mosquitoes. In particular,
311 ephemeral pond specialist species, such as *L. raynerae*, may be particularly promising
312 candidates, as they are often particularly large, develop rapidly, exhibit dormancy, and have

313 adapted to occupy relatively high trophic levels (Dalu et al. 2016a). Further, their especially
314 large size may make *L. raynerae* less vulnerable to higher-order predation as compared to
315 physically smaller copepod species. Generally, biotic interactions within ephemeral aquatic
316 ecosystems are often poorly studied due to spatial and temporal heterogeneity (Dalu et al.
317 2016b), and thus these systems hold much potential for biocontrol agent exploration, as
318 demonstrated in the present study. Our results show strong and destabilising predatory
319 impacts of *L. raynerae* towards larvae of *C. pipiens* across a water clarity regime, which may
320 enable consistently high impacts upon target populations under differing environmental
321 conditions. Furthermore, we show efficacious predatory potential of this species in artificial
322 container-style habitats in outdoor environments. Future research should test additional
323 environmental contexts as to their effects on biotic interaction strengths between biocontrol
324 agents and target organisms, and further explore the sustained potential of calanoid copepods
325 over longer hydroperiods within container-style habitats which harbour disease vector
326 mosquitoes.

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513 **Tables and Figure Captions**

514 Table 1. First order terms generated from logistic regression of proportional prey
515 consumption as a function of prey density alongside parameter outputs from Rogers' random
516 predator equation across water clarity regimes.

Water clarity	First order term, p	a, p	h, p
0%	-0.058620, < 0.001	1.572822, < 0.001	0.104547, < 0.001
50%	-0.044384, < 0.001	1.201939, < 0.001	0.087762, < 0.001
100%	-0.049398, < 0.001	1.082802, < 0.001	0.115452, < 0.001

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528 Figure 1. Functional responses of *Lovenula raynerae* towards larval *Culex pipiens* prey
529 across a water clarity gradient (low, 0%; medium, 50%; high, 100%). Shaded areas represent
530 bootstrapped ($n = 2000$) confidence intervals.

531 Figure 2. Mortality rate (\pm SE) of larval *Culex pipiens* at different densities in outdoor trial
532 resulting from the presence of predatory copepod *Lovenula raynerae* at three densities.

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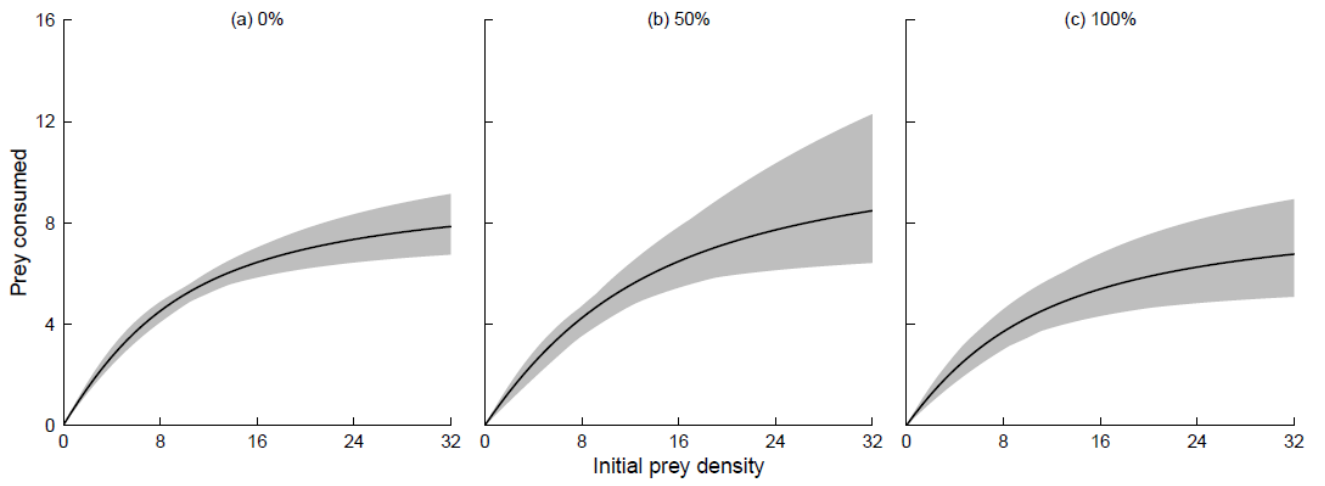
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