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1 **Shifting interaction strength between estuarine mysid species across a temperature**  
2 **gradient**

3

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5

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16

17

18 **Abstract**

19

20 In many coastal regions, mean coastal atmospheric and water temperatures are projected to shift  
21 as climate change ensues. Interaction strengths between organisms are likely to change along  
22 with environmental changes, given interspecific heterogeneity in responses to physico-chemical  
23 variables. Biological interaction outcomes have the potential to alter food web production and  
24 trophic level biomass distribution. This is particularly pertinent for key species that are either  
25 abundant or play disproportionately large roles in ecosystem processes. Using a functional  
26 response approach, we quantified the effects of shifting temperatures on interactions between  
27 key mysid species- sympatric in their distribution across a biogeographic transition zone along  
28 the east coast of South Africa. The *Rhopalophthalmus terranatalis* functional response type  
29 toward *Mesopodopsis wooldridgei* prey was independent of temperature, with all treatments  
30 producing Type II functional responses. Temperature effects on predator-prey dynamics were,  
31 however, evident as interaction strength was greatest at 21°C, as measured by maximum feeding  
32 rates. Unlike maximum feeding rate, attack rates increased linearly with increasing temperature  
33 across the experimental treatments. Our findings suggest that interaction strength between the  
34 mysid shrimp species is likely to vary spatially along the current length of their sympatric  
35 distribution and temporally in certain regions where temperatures are projected to change. Such  
36 experimental interaction investigations are becoming increasingly important given our relatively  
37 poor understanding of the consequences of environmental change for effects on interactions  
38 among species and their wider ecosystem implications.

39

40 **Keywords:** Biogeographic zones; climate change; functional response; predator-prey;

41 *Mesopodopsis wooldridgei*; *Rhopalophthalmus terranatalis*.

42

43

## 44 **Introduction**

45           The greatest uncertainty when predicting consequences of environmental change on  
46 ecosystems is determining their effects on interactions among species (Daufresne et al., 2009;  
47 Gilbert et al., 2014). Mean coastal atmospheric and water temperatures are predicted to be  
48 affected as climate change ensues (Mead et al., 2103). Given inter-specific differences in thermal  
49 optima, tolerance and performance, temperature changes can have implications for predator-prey  
50 interactions between species (Englund et al., 2011). Variable interaction outcomes have the  
51 potential to further alter food web production and biomass distribution across different trophic  
52 levels in marine ecosystems (O'Connor et al., 2009; Le Quesne and Pinnegar, 2011). Compiling  
53 experimental datasets across a range of taxa is, therefore, important for understanding and  
54 predicting biotic responses to varying environmental conditions (Gilbert et al., 2014; South et al.,  
55 2018). This is particularly pertinent for key species that are either abundant or play a  
56 disproportionately important role in trophic dynamics.

57  
58           The South African coastline transitions from a sub-tropical to a cool-temperate climatic  
59 zone (Wooldridge and Deyzel, 2012). Many species of the region are widespread, spanning a  
60 broad range of nearshore habitats characterized by different thermal conditions (Montoya-Maya  
61 and Strydom, 2009; Wooldridge and Deyzel, 2012). *Rhopalophthalmus terranatalis* and  
62 *Mesopodopsis wooldridgei* are mesozooplanktonic mysid species that are abundant in estuaries  
63 along the temperate coastline of South Africa (Montoya-Maya and Strydom, 2009; Wooldridge  
64 and Deyzel, 2012) and are considered integral to estuarine food webs in the region (Wooldridge,  
65 1986). **The species are, however, sympatric from the cool-temperate south and west coasts**  
66 **(Montoya-Maya and Strydom, 2009) to the warm-temperate/sub-tropical biogeographic**

67 transition zone along the east coast of South Africa (Wooldridge and Deyzel, 2012).  
68 *Rhopalophthalmus terranatalis* distribution, however, reportedly extends further up the coastline  
69 well into warmer waters of the subtropical region (Ortega-Cisneros and Scharler, 2015). Since  
70 *M. wooldridgei* comprises an important component of the diet of *R. terranatalis* (Wooldridge  
71 and Webb, 1998), we wanted to assess how temperature mediates predator-prey interaction  
72 outcomes between these mysid species.

73  
74 As a measure predatory interaction strength, a functional response (FR) approach was  
75 employed. The FR of a predator is the relationship between prey density and consumption  
76 (Holling, 1959) and is routinely used by ecologists to gain insight into predation dynamics  
77 (Holling, 1959; Rall et al., 2012; Wasserman et al., 2016; Dick et al., 2017 and references  
78 therein). Three forms of the FR are typically considered (Hassell, 1978; Alexander et al., 2013).  
79 Type I FRs are usually associated with filter feeders whereby there is a density independent  
80 response characterized by the presence of an abrupt plateau in consumption as a result of  
81 handling constraints (Hassell, 1978; Jeschke et al., 2004; Alexander et al., 2013). Type II FRs  
82 are, however, inversely density-dependent with prey consumed in high proportion at low  
83 densities while at high densities consumption occurs at a decelerated rate until an asymptote is  
84 reached (Alexander et al., 2013). The Type III FR is a density dependent sigmoidal response  
85 with low prey consumption at low prey densities (Hassell, 1978; Alexander et al., 2013). Each  
86 FR Type is, therefore, thought to have different implications for prey population stability with  
87 Type II FR's considered more de-stabilizing for prey populations than the Type III FRs (Hassell,  
88 1978).

89

90 Ricciardi et al. (2013) posit that individual performance will decline as differences  
91 between ambient conditions and physiological optimum increase (environmental matching  
92 hypothesis). This is pertinent in predator-prey systems given that the performances of both are  
93 integral in interaction outcomes, and the level of environmental matching may differ between  
94 predator and prey. Predator functional responses are, therefore, sensitive to changes in  
95 environmental conditions. Temperature, for example, has been shown to have implications for  
96 functional response type and magnitude, with implications for prey population dynamics (e.g.  
97 Cuthbert et al., 2018; South et al., 2018). As such, in the present study we specifically wanted to  
98 test whether (1) the predator functional response type of *R. terranatalis* toward *Mesopodopsis*  
99 *wooldridgei* is dependent on temperature, and (2) varying temperature alters the strength of the  
100 functional response. Such information would be useful for understanding how *R. terranatalis*-*M.*  
101 *wooldridgei* predator-prey dynamics vary spatially, along the length of their current sympatric  
102 distribution. It would also add insight into how interaction strength may vary per region as  
103 climate change ensues, since localized ocean temperatures are projected to increase or decrease,  
104 depending on the region and oceanographic features (Mead et al. 2013).

105

## 106 **Methods**

107 Mysids were collected from the middle reach of the permanently open Kariega Estuary  
108 (33.630640°S; 26.639894°E) in the Eastern Cape, South Africa. At the time of collection the  
109 salinity and temperature recorded was 35ppt and 19 °C, respectively. Animals were collected  
110 from a boat by towing a zooplankton net (57 cm diameter, 200 µm mesh) horizontally along the  
111 axial length of the estuary, at ~10 cm beneath the water surface. Zooplankton was preliminarily  
112 sorted on the boat through a series of size fractionated filtration whereby all larger components

113 of the zooplankton (including the large predatory *R. terranatalis*) were separated from  
114 intermediary-sized organisms (*M. wooldridgei*), while all small organisms were discarded on  
115 site.

116

117 In the laboratory, *R. terranatalis* and *M. wooldridgei* were separated into aerated glass  
118 aquaria (46 × 23 × 60 cm) in temperature controlled environmental rooms at a 12:12h  
119 (light:dark) photoperiod cycle. Aquaria contained estuarine water from the collection site filtered  
120 through 0.7 µm mesh sieve. All mysids were kept at a salinity and temperature of 35 ppt and 19  
121 °C, respectively, for 24 h after collection prior to acclimation regimes. Animals were then  
122 acclimated to one of four treatment temperatures; 13 ± 0.5 °C, 17 ± 0.5 °C, 21 ± 0.5 °C or 25 ±  
123 0.5 °C, for 5 days during which time they were fed daily on crushed commercial fish flakes  
124 (TetraMin® tropical flakes).

125

126 Individual *R. terranatalis* (total length ± SD; 14 ± 0.5 mm) were each presented with *M.*  
127 *wooldridgei* (7 ± 0.5 mm) at 1 of 8 prey densities (2, 4, 6, 8, 10, 20, 30 or 40 individuals,  $n = 4$   
128 per prey density) for each temperature treatment. Experiments were carried out in circular  
129 polyethylene containers (60 mm deep, 110 mm diameter) filled with 500 mL aerated, filtered  
130 estuarine water (35 ppt salinity) from the collection site. The experimental containers were  
131 placed in temperature regulated water baths set to the same temperature as the environmental  
132 rooms. *Mesopodopsis wooldridgei* prey were stocked into containers 2 h prior to the introduction  
133 of the predator. Upon predator transferral, containers were covered with 500µm nylon mesh to  
134 prevent mysid escape, and left undisturbed for 12 h under dark conditions. Controls were also  
135 run at the same temperatures and prey densities ( $n = 4$ ) for the same length of time, but with no



136 predators. At the end of each trial, samples were collected in a 60  $\mu\text{m}$  mesh sieve and the prey  
137 counted.

138  
139 Overall prey consumption was analysed with respect to ‘temperature’ and ‘prey supply’  
140 and their interactions using generalised linear models (GLMs) assuming Poisson error  
141 distribution as residuals were not overdispersed in relation to degrees of freedom. Non-  
142 significant terms and interactions were removed stepwise to satisfy the minimum adequate model  
143 (Crawley, 2007), with  $\chi^2$  used to compare residual deviance between models and report the  
144 relevance of factors to the dependent variable. We employed the ‘multcomp’ package in R  
145 (Hothorn et al., 2008) to undertake post-hoc comparisons of significant effects in the resulting  
146 model using Tukey’s comparisons. Functional responses (FRs) were analysed using the ‘frair’  
147 package in R (Pritchard et al., 2017). Logistic regression was used to infer FR types, whereby a  
148 significantly negative first order term is indicative of a Type II FR (Juliano, 2001). As prey were  
149 not replaced as they were consumed, we fit Rogers’ random predator equation (Juliano, 2001) to  
150 account for prey depletion:

151  
152 
$$N_e = N_0(1 - \exp(a(N_e h - T)))$$
 Eqn. 1.

153  
154 where  $N_e$  is the number of prey eaten,  $N_0$  is the initial density of prey,  $a$  is the attack constant,  $h$   
155 is the handling time and  $T$  is the total experimental period. We applied the Lambert W function  
156 in R due to the implicit nature of the random predator equation (Bolker, 2008). Functional  
157 responses were non-parametrically bootstrapped ( $n = 2000$ ) to construct 95% confidence  
158 intervals (CIs) around FR curves. This procedure enables data to be considered at the population-

159 level as opposed to the sample-level, with a lack of overlap in CIs sufficient to ascribe  
160 differences between FRs (see Barrios-O'Neill et al., 2014). All statistical analyses were  
161 undertaken in R v3.4.2 (R Core Team, 2017).

162

## 163 **Results and Discussion**

164 Survival in control treatments exceeded 98.5% at all temperatures, and so experimental  
165 deaths were attributed to predation by mysids, which was also directly observed. Overall  
166 consumption was significantly affected by temperature ( $\chi^2 = 10.590$ ,  $df = 3$ ,  $p = 0.014$ ), an effect  
167 driven by significantly greater predation at 21 °C than at 13 °C ( $z = 2.607$ ,  $p = 0.045$ ). Overall  
168 consumption increased under greater prey density ( $\chi^2 = 79.948$ ,  $df = 7$ ,  $p < 0.001$ ) and there was  
169 no significant 'temperature  $\times$  prey density' interaction effect ( $\chi^2 = 8.46$ ,  $df = 21$ ,  $p = 0.993$ ). Type  
170 II FRs were detected irrespective of temperature (Table 1). Overall, *R. terranatalis* exhibited the  
171 highest magnitude FR at 21 °C (Fig. 1). Attack rates increased concurrently with temperature  
172 (Table 1), and were significantly greater at 25 °C compared to 13 °C and 17 °C as CIs did not  
173 overlap at low-intermediate prey densities. Functional responses were indifferent between 13 °C  
174 and 17 °C as CIs overlapped at all prey supplies here. Functional response CIs at 21 °C did not  
175 overlap with those at 13 °C, and diverged from CIs at 17 °C at intermediate-high densities,  
176 indicating significantly lower handling times at 21 °C and, inversely, greater maximum feeding  
177 rates at this temperature regime.

178

179 The *R. terranatalis* functional response type toward *M. wooldridgei* prey was  
180 independent of temperature, with all treatments producing Type II FRs. However, temperature  
181 effects on predator-prey dynamics were clear. **The results reflect the findings of Rall et al.**

182 (2012), who showed that while attack rate may increase linearly with temperature, handling time  
183 and temperature relationships are often non-linear. In the present study, interaction strengths  
184 were greatest at 21 °C as maximum feeding rates were high at this temperature, while those of 13  
185 °C, 17 °C and 25 °C temperature treatments were similar. Unlike the maximum feeding rates,  
186 attack rates increased linearly with increasing temperature and these findings have implications  
187 for *R. terranatalis* – *M. wooldridgei* interactions since the species span different biogeographic  
188 zones in sympatry (Montoya-Maya and Strydom, 2009; Wooldridge and Deyzel, 2012).  
189 Furthermore, along the South African coastline temperatures are projected to increase in certain  
190 regions and decrease in others, due to increased upwelling events (Mead et al., 2013). The results  
191 of the present study, therefore, suggest that interaction strength between the mysid shrimp  
192 species is likely to vary spatially along the current length of their sympatric distribution and  
193 temporally in certain regions where temperatures are projected to change.

194

195 Wooldridge and Webb (1998) calculated that *R. terranatalis* predation could result in  
196 local removal of *M. wooldridgei* based on predator feeding rates (at one temperature) and estuary  
197 predator and prey numbers. The persistence of a Type II FRs across temperature treatments  
198 further highlights the potential significance of *R. terranatalis* predation towards *M. wooldridgei*  
199 in estuarine ecosystems where they commonly co-occur and interact. Unlike Type III FRs, Type  
200 II FRs are associated with prey extinction likelihood as they have a de-stabilizing effect on prey  
201 populations since proportional consumption is high even at low prey densities (Taylor and  
202 Collie, 2003; Ward et al., 2008). While overall consumption was highest at an intermediate  
203 temperature, attack rates were greatest at the highest temperature, decreasing linearly with a  
204 reduction in temperature. This suggests that at low densities *M. wooldridgei* are at increased risk

205 of predation from *R. terranatalis* under high temperature conditions relative to cooler  
206 temperatures. The results of Wooldridge and Webb (1998) and this study suggest that small  
207 populations of *M. wooldridgei* at the edge of their thermal limits may be more susceptible to  
208 biotic-driven localised extinctions.

209

210 The experimental temperature range employed spanned the temperature extremes found  
211 in estuaries in which the mysid species co-occur (Montoya-Maya and Strydom, 2009;  
212 Wooldridge and Deyzel, 2012). The effects of temperature on the mysid species interactions are  
213 evident, but the mechanisms facilitating these observations need further elucidation. The  
214 relationship between temperature and predator-prey interaction strength is inherently complex as  
215 predation differs from conventional measures of performance in that it is dependent on both the  
216 predator and the prey (Rall et al., 2012, Ohlund et al., 2014). Both interacting species are  
217 affected by environmental conditions such as temperature variability (Ziarek et al., 2011; Rall et  
218 al., 2012) and levels of environmental matching may differ between predator and prey.  
219 Environmental matching considerations are important when assessing predation effects  
220 (Ricciardi et al., 2013). Future work should, therefore, include measures of predator and prey  
221 thermal optima, and performance such as swimming, attack and escape speeds across a range of  
222 relevant temperatures. Such an approach would add insight into how inter-specific variations in  
223 performance facilitate interaction outcomes and could explain how maximum feeding rates were  
224 similar at the lower and upper end of the experimental temperature ranges. Such pairwise  
225 interaction investigations are a fundamental component of food web ecology and are central to  
226 the mechanistic understanding of predator-prey dynamics (Rall et al., 2012; Barrios-O'Neill et

227 al., 2014; Dick et al., 2017). Key trophic species are particularly important in this regard given  
228 that their interaction outcomes likely have increased community-wide implications.

229

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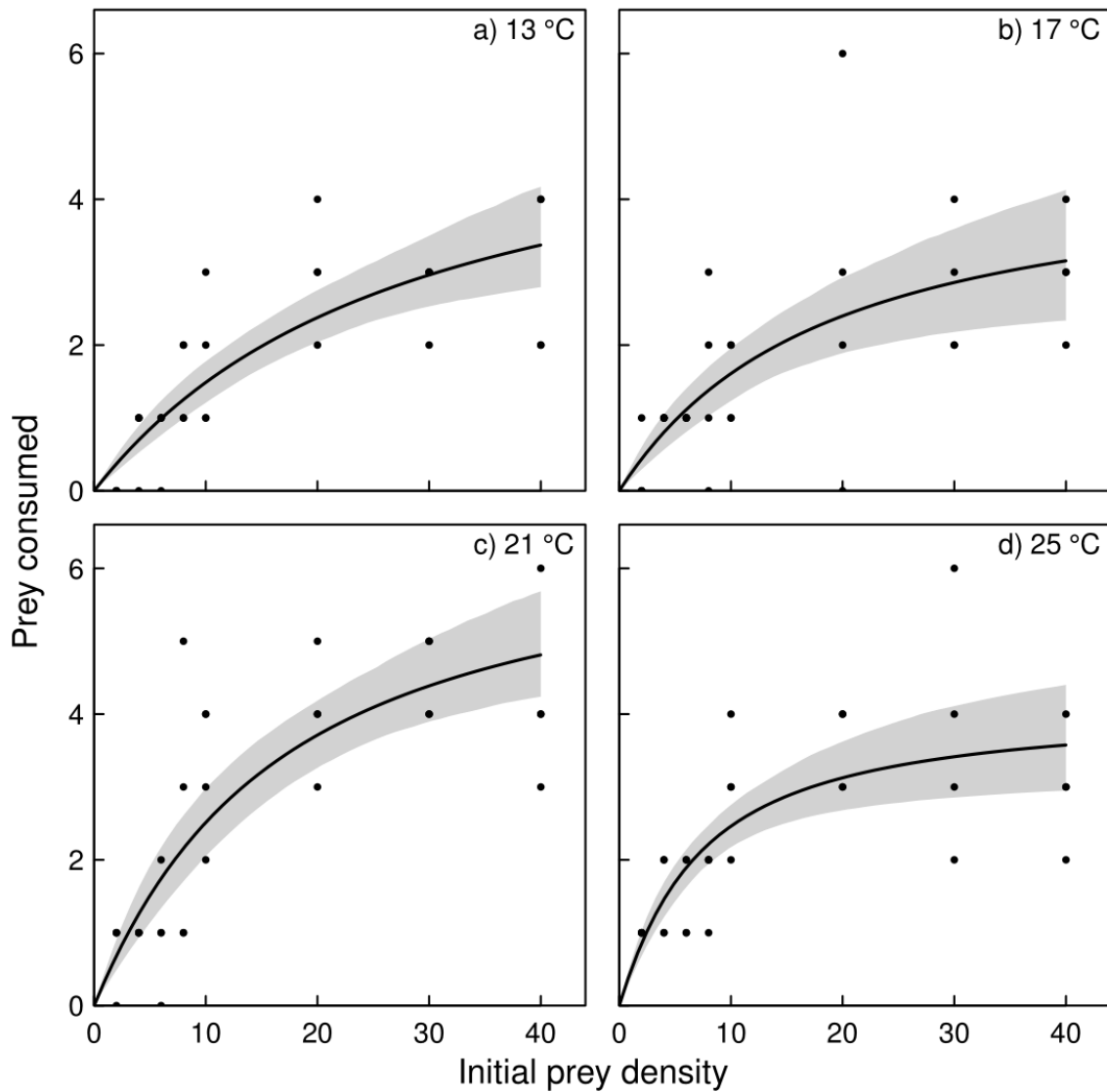
328 **Table 1.** First order terms resulting from logistic regression of proportion of prey consumed as a  
 329 function of prey supply and parameter estimates derived from Rogers' random predator equation.  
 330  $a$  = attack rate,  $h$  = handling time, \* $p < 0.05$ , \*\* $p < 0.01$ , \*\*\* $p < 0.001$

Temperature (°C)	1 <sup>st</sup> order term	$a$	$h$
13	-0.02549*	0.21864**	0.17711*
17	-0.03044**	0.27237**	0.22125**
21	-0.03540***	0.46539***	0.15053***
25	-0.04927***	0.70050**	0.24230***

331

332

333 **Fig. 1.** Functional responses of *Rhopalophthalmus terranatalis* (Mysidae) predators towards  
334 common focal *Mesopodopsis wooldridgei* prey at a) 13 °C, b) 17 °C, c) 21 °C and d) 25 °C.  
335 Shaded areas are bootstrapped ( $n = 2000$ ) 95% confidence intervals. Raw data points are  
336 overlaid.



339