

A peer-reviewed version of this preprint was published in PeerJ on 5 January 2017.

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Andradi-Brown DA, Head CEI, Exton DA, Hunt CL, Hendrix A, Gress E, Rogers AD. (2017) Identifying zooplankton community changes between shallow and upper-mesophotic reefs on the Mesoamerican Barrier Reef, Caribbean. PeerJ 5:e2853 <https://doi.org/10.7717/peerj.2853>

1 Article Title:

2 **Identifying zooplankton community changes between shallow and upper-**
3 **mesophotic reefs on the Mesoamerican Barrier Reef, Caribbean**

4

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16 **Abstract**

17

18 Mesophotic coral ecosystems (MCEs, reefs 30 -150m) are understudied, yet the
19 limited research conducted has been biased towards large sessile taxa, such as
20 scleractinian corals and sponges, or mobile taxa such as fish. Here we investigate
21 zooplankton communities on shallow reefs and MCEs around Utila, on the southern
22 Mesoamerican Barrier Reef using planktonic light traps. Zooplankton samples were
23 sorted into broad taxonomic groups. Our results indicate similar taxonomic
24 zooplankton richness and overall biomass between shallow reefs and MCEs, but that
25 abundance of larger bodied (>2 mm) zooplanktonic groups, including decapod crab
26 zoea, mysid shrimps and peracarid crustaceans was higher on MCEs than shallow
27 reefs. Our findings highlight the important of considering zooplankton when
28 identifying broader reef community shifts across the shallow reef to MCE depth
29 gradient.

30

31 **Introduction**

32

33 Tropical coral ecosystems are some of the most diverse ecosystems on the
34 planet (Sala and Knowlton 2006), with light-dependent reefs extending from the
35 surface down to approximately 150 m depth (Hinderstein et al. 2010). Yet most coral
36 reef research is heavily biased towards the shallows (<30 m) (Menza et al. 2008)
37 because of the difficulties associated with accessing deeper reefs. Mesophotic coral
38 ecosystems (MCEs), reefs from 30 m to 150 m, are increasingly recognized as
39 containing important components of reef diversity, both as refuge habitats for
40 shallow reefs but also as unique ecological assemblages that need protection in their
41 own right (Bongaerts et al. 2010; Bridge et al. 2013; Andradi-Brown et al. 2016a).

42 Most of the limited work on MCEs has focused on large sessile taxa, such as
43 scleractinian corals and sponges, or large mobile taxa such as fish (Kahng et al. 2010;
44 Kahng et al. 2014). It has, however, been estimated that 168,000 invertebrate
45 species have been described on coral reefs (Ruppert et al. 2003; Stella et al. 2011),
46 far greater than the approximately 5,000 fish species and 700 scleractinian coral

47 species currently recognized (Veron 2000; Bellwood et al. 2012). Most biodiversity
48 on reefs is therefore comprised of small mobile invertebrates, many of which are
49 cryptic and found associated with other sessile reef fauna or in the zooplankton
50 (Fautin et al. 2010; Plaisance et al. 2011).

51 Zooplankton is comprised of a diverse range of organisms, with different
52 components normally classified into coarse groups based on size, for example
53 mesozooplankton range from 0.2 – 20 mm and macrozooplankton from 2 – 20 cm
54 (Johnson and Allen 2012). In the Caribbean zooplankton recorded adjacent to coral
55 reefs has generally been found to be dominated by copepods, with amphipods,
56 isopods, polychaetes, shrimp larvae and crab larvae all present but at lower
57 abundances (Heidelberg et al. 2004; Heidelberg et al. 2010). Previous studies have
58 suggested major factors affecting zooplankton abundance on reefs include active
59 zooplankton avoidance behavior of reef habitats and differing exploitation patterns
60 by predators (Motro et al. 2005; Yahel et al. 2005; Heidelberg et al. 2010). Many
61 zooplankton can exhibit active swimming behavior to avoid predation or areas with
62 higher risk of predation (Haury et al. 1980; Ohman 1988). Approximately 20% of reef
63 invertebrates are crustaceans, making them one of the largest and most speciose
64 groups on coral reefs (Kramer et al. 2014) and so an important component of reef
65 fish diets (Randall 1967). Planktivorous fish predation pressure is thought to lead to
66 depleted plankton abundance over reefs, though because planktivorous fish tend to
67 feed <1.5 m over the reef, this effect is limited to close to the reef surface (Motro et
68 al. 2005).

69 On Caribbean MCEs zooplankton is particularly important as a food source,
70 with zooplanktivorous and mobile-invertebrate feeding widely observed as the
71 dominant fish trophic groups (Garcia-Sais 2010; Bejarano et al. 2014; Andradi-Brown
72 et al. 2016b) and studies suggesting approximately 60% of MCE reef fish feed on
73 zooplankton and mobile-invertebrates on the Mesoamerican Barrier Reef, Caribbean
74 (Andradi-Brown et al. 2016b). Shallow-reef corals also feed on zooplankton,
75 providing an important additional energy source to that provided by their symbionts
76 (Ferrier-Pagès et al. 2003). On MCEs however, because of low light availability, corals
77 are believed to increase heterotrophic feeding, likely making them more dependent
78 on zooplankton than their shallow counterparts (Lesser et al. 2010). In addition,

79 invertebrate groups such as decapods have important functional roles in maintaining
80 fish health. For example, cleaning fish of parasites, e.g. cleaner shrimp (Becker and
81 Grutter 2004), and defending coral colonies from predators and clearing excess
82 sediment thus preventing smothering of coral polyps, e.g. *Trapezia* crabs (McKeon
83 and Moore 2014).

84 Despite the important roles zooplankton are likely to have on MCEs, few
85 studies have documented MCE zooplankton communities and how they differ from
86 those on shallow reefs. Here we investigate the mesozooplankton and
87 macrozooplankton community on shallow reefs and upper-MCEs on the
88 Mesoamerican Barrier Reef, Caribbean, to identify differences in abundance,
89 biomass and community structure across the depth gradient.

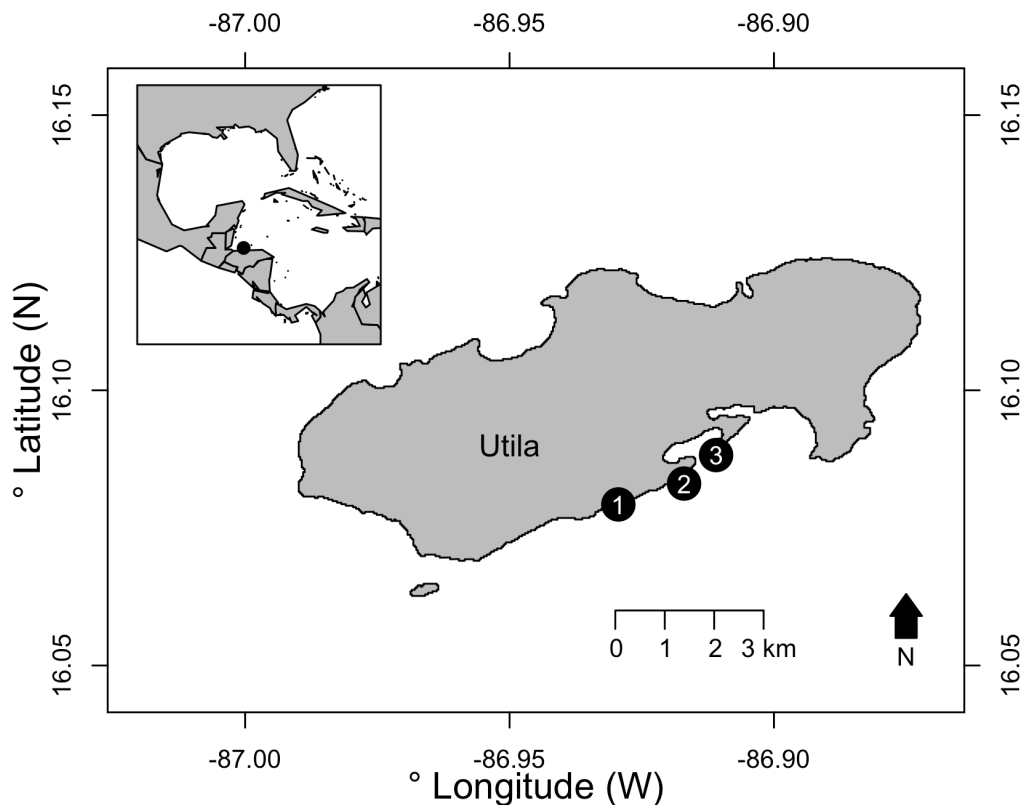
90

91 **Methods**

92

93 Surveys were conducted on the south shore of Utila, Bay Islands, Honduras. Utila is
94 located off the north shore of Honduras, with its reefs forming the southern extent
95 of the Mesoamerican Barrier Reef. Off the south shore of Utila, shallow reefs form a
96 spur and groove system, with a reef slope down to approximately 35 m, where the
97 seabed flattens and a patch reef MCE is formed. From these MCE patch reefs, the
98 south shore seabed continues to gently slope to approximately 70 - 80 m before
99 rising to the Honduran mainland. Three replicate light trap deployments were
100 conducted at 15 m (shallow) and 40 m (MCE) at three sites: Coral View, Black Coral
101 Wall and Little Bight (Figure 1, see Supplemental Table S1 for GPS locations) during
102 July - September 2015. Light traps were built following Jones (2006). Traps were
103 modified from these specifications to use twelve 12 V light-emitting diodes (LEDs)
104 powered by a 12 V, 4,800 mAh rechargeable lithium ion battery as the light source in
105 each trap. LEDs were white light emitting with each LED having a luminous intensity
106 of 12,000 – 14,000 mcd and wavelength of 5,000 – 6,500 nm. Light traps were
107 deployed by divers 0.5 m above the reef at each depth during the afternoon. They
108 were activated with a digital timer set to illuminate the trap 30 minutes before
109 sunset and remain lit until sunrise the following morning. Divers recovered the light

110 traps at 7:30 am the morning following deployment. Sites and depths were surveyed
111 over multiple nights, with no more than two traps deployed at a site in a single night.
112 All light traps were placed a minimum of 20 m distance from previous light trap
113 deployments. Research permits for this work were issued to Operation Wallacea by
114 the Instituto de Conservación Forestal (ICF), Honduras. As the focus of the work was
115 on invertebrates, and no higher vertebrates were involved, ethical review was not
116 required.
117



118
119 Figure 1. The three survey sites on the south shore of Utila, Bay Islands, Honduras.
120 Sites were: (1) Little Bight, (2) Black Coral Wall and (3) Coral View. See Supplemental
121 Table S1 for full GPS location data. Inset – The location of Utila is indicated with a
122 black circle relative to the western Caribbean and Gulf of Mexico.

123

124 Samples were sorted following groupings used in Johnson and Allen (2012)
125 into broad taxonomic and developmental groups readily identifiable in the field with
126 the use of a dissecting microscope. These groups were: (i) arrow worms, (ii) barnacle
127 larvae, (iii) cladocerans, (iv) copepods, (v) decapod crab zoea, (vi) decapod shrimp

128 zoea, (vii) decapod crab megalopae, (viii) lobster phyllosoma, (ix) mantis shrimp
129 larvae, (x) mysid shrimps, (xi) peracarid crustaceans, (xii) oligochaetes, (xiii)
130 polychaetes, (xiv) mites, (xv) urochordates and (xvi) fish larvae. All sampled
131 individuals >2 mm were counted to give abundance, and all individuals regardless of
132 size were sorted and dry weighed to record biomass.

133 Nonmetric multidimensional scaling (NMDS) and permutational multivariate
134 analysis of variance (PERMANOVA) were used to visualize and test for differences in
135 abundance and biomass between the two depths based on Bray-Curtis dissimilarities
136 on a fourth root transformed matrix (Anderson et al. 2008), while differences in
137 richness were tested using a Euclidean PERMANOVA. Transformed data were used
138 to reduce the influence of the most abundant taxonomic groups when assessing
139 community differences in the PERMANOVA (Anderson et al. 2008). When processing
140 samples, one 15 m Black Coral Wall light trap collected no taxonomic groups with
141 sufficient biomass to register on our field scales (weight <0.01g), this necessitated its
142 removal from multivariate analysis of biomass data. All PERMANOVAs were run for
143 99999 permutations and run using the 'adonis' function in vegan (Oksanen et al.
144 2013) in R (R Core Team 2013). Constrained analysis of principal coordinates (CAP)
145 was conducted for the abundance data using the 'capscale' function in vegan
146 (Oksanen et al. 2013). All taxonomic groups with a Pearson correlation coefficient
147 $|\gt;0.5|$ with either of the first two CAP axes were identified as potential drivers of
148 community difference with depth. The abundance of these taxonomic groups was
149 then individually tested using a Euclidian PERMANOVA to identify whether they
150 changed with depth.

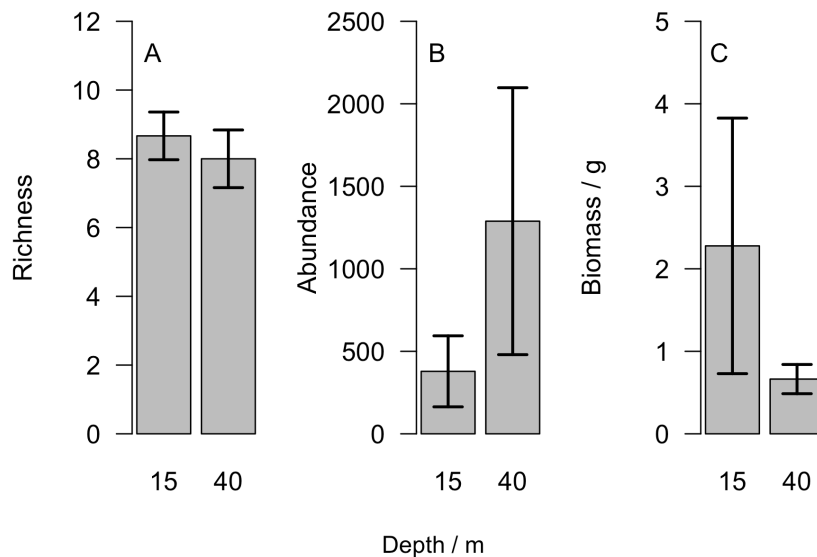
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152 Results

153

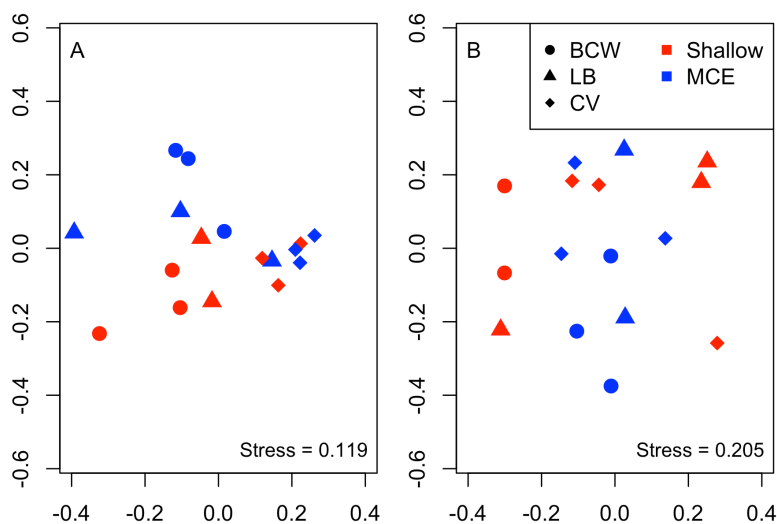
154 Overall we found similar richness of taxa groups on shallow and mesophotic
155 reefs (Figure 2A), with much variation in the overall abundance and biomass at both
156 depths (Figure 2B-C). We used an NMDS to visualise differences in the community
157 sampled by the light traps at shallow and mesophotic depths. Abundance data
158 appeared to show a difference in the community between shallow and mesophotic

159 reefs (Figure 3A), while biomass-weighted data showed no clear patterns (Figure 3B).
 160 We tested these patterns in a PERMANOVA (Table 1), finding differences in the
 161 recorded light trap community taxonomic richness abundance and biomass between
 162 survey sites. Abundance of taxonomic groups also changed between the two depths,
 163 but no pattern with depth was found for taxonomic richness or biomass.
 164



165
 166 Figure 2. (A) Number of different taxonomic groups recorded, (B) mean abundance
 167 per light trap and (C) total biomass across all taxa groups comparing reefs at 15 m
 168 and 40 m. Bars show mean \pm 1 standard error.

169



170
 171 Figure 3. Nonmetric multidimensional scaling plot for (A) abundance and (B) biomass
 172 of the invertebrate and fish larvae. Colours indicate different depths, while shapes

173 indicate different survey sites. Sites were: BCW – Black Coral Wall, LB – Little Bight
 174 and CV – Coral View.

175

176 Table 1. PERMANOVA results testing for differences in the recorded light trap
 177 community between sites and depth for abundance and biomass data.

		Richness		Abundance		Biomass	
	<i>DF</i>	<i>pseudo-F</i>	<i>P</i>	<i>pseudo-F</i>	<i>P</i>	<i>pseudo-F</i>	<i>P</i>
Survey Site	2	3.97	0.04	5.58	<0.0001	2.33	0.01
Depth	1	0.76	0.41	2.71	0.03	1.42	0.24
Residual	13						
Total	16						

178

179 We conducted Euclidian PERMANOVAs on abundance results correlating with
 180 the CAP axis to identify taxonomic groups varying with depth (Table 2). We identified
 181 decapod crab zoea, mysid shrimps, peracarid crustaceans and oligochaete
 182 abundance as increasing on MCEs compared to shallow reefs, with no oligochaetes
 183 recorded on shallow reefs. We did not detect any zooplanktivorous groups at greater
 184 abundance on shallow reefs than MCEs, nor any changes in fish larvae abundance
 185 between shallow reefs and MCEs.

186

187 Table 2. Euclidian PERMANOVA results for abundance of taxonomic groups that
 188 correlate $|\gt;0.5|$ with the first or second CAP analysis.

Taxonomic Group	Shallow (15 m)		Mesophotic (40 m)		<i>Pseudo-F</i>	<i>P</i>
	Mean	SE	Mean	SE		
<i>First axis</i>						
Decapod crab megalopae	25.00	18.92	15.78	14.13	0.47	0.24
Decapod crab zoea	17.89	17.39	69.11	56.53	2.31	<0.01

Decapod shrimp zoea	52.00	19.66	38.22	26.72	0.27	0.53
Mysid shrimps	84.11	63.12	637.44	600.61	1.52	0.04
Peracarid crustaceans	68.22	44.79	216.11	93.51	5.04	<0.01
Urochordates	29.11	29.11	83.89	74.11	1.32	0.15
<i>Second axis</i>						
Cladocerans	4.33	4.33	0.33	0.33	2.44	0.10
Oligochaetes	0.00	0.00	93.67	93.67	2.28	<0.01

189

190

191 **Discussion**

192

193 While MCEs are of increased interest because of their potential role as
 194 refuges for threatened shallow-reef taxa (Bongaerts et al. 2010), almost all existing
 195 research has focused on large sessile benthic taxa such as hard corals, macroalgae
 196 and sponges or large mobile organisms such as fishes (Kahng et al. 2010; Kahng et al.
 197 2014). Few studies have considered changes in small mobile invertebrates making up
 198 reef cryptofauna and zooplankton. We found significant differences in zooplankton
 199 richness, abundance and biomass between study sites and, interestingly, higher
 200 abundances on MCEs than on shallow reefs while biomass did not change.

201 Previous work has suggested zooplankton, in particular larger planktonic
 202 individuals such as mysids, isopods and decapod larvae are particularly important
 203 prey items for planktivorous fish (Hobson and Chess 1978). Unlike in many locations
 204 (see Kahng et al. 2010; Kahng et al. 2014), a previous study on Utila at our study sites
 205 found no difference in relative planktivorous reef fish biomass between shallow
 206 reefs and MCEs, and a decline in actual biomass of planktivorous reef fish with
 207 increased depth (Andradi-Brown et al. 2016b). This pattern is surprising as we
 208 identified greater abundance of zooplankton >2 mm size and no change in biomass
 209 of zooplankton across the depth gradient, suggesting similar or potentially greater

210 food resources for planktivorous fish on MCEs. In addition, planktivorous reef fish
211 exhibit high visual system plastic adaptive ability, and show few differences in
212 feeding ability caused by changes in light levels across depth gradients, suggesting
213 they should be able to feed efficiently at MCE depths included in this study
214 (Brokovich et al. 2010). However, the previous planktivorous fish study from Utila
215 was conducted during daylight hours (Andradi-Brown et al. 2016b), while light traps
216 in this study were deployed overnight. Therefore, as zooplankton are known to have
217 diurnal movement patterns (Angel 1985), the abundance of zooplankton we
218 recorded here may not be available to the planktivorous fish during daylight hours.
219 MCEs on the south shore of Utila exist as a gently sloping patch reef system on the
220 continental shelf that remains within mesophotic depths before rising to become the
221 mainland of Honduras. Therefore, unlike other MCEs adjacent to deep-sea habitats,
222 at the sites we surveyed there is unlikely to be a large diurnal migration of
223 zooplankton from deeper water at night.

224 Our finding of greater abundance of some zooplanktivorous groups on MCEs,
225 and no change in zooplankton biomass between shallow reefs and MCEs contrast
226 with previously identified zooplankton depth patterns. In Jamaica, Ohlhorst (1985)
227 studied zooplankton across a 6 – 24 m depth gradient using traps placed over the
228 reef, finding that both the abundance of zooplankton and the volume of zooplankton
229 per trap declined with depth. When looking at specific taxonomic groups, we
230 identified greater abundance of mysid shrimps and peracarid crustaceans on MCEs
231 (40 m) than shallow reefs (15 m). Whereas, no difference was identified in mysid
232 shrimp or peracarid crustacean abundance between 15 m and 24 m in Jamaica
233 (Ohlhorst 1985). In Hawaiian reef cryptofauna, brachyuran crab abundance has been
234 reported to decline across a 12 – 90 m depth gradient (Hurley et al. 2016). However
235 much of this pattern was caused by one crab genus, which when excluded led to
236 crab abundance increasing with depth. While these Hawaiian brachyuran crabs had
237 settled on the reef, we identified increased abundance of decapod crab zoea on
238 MCEs on Utila, though no difference in decapod crab megalopae with depth. In
239 addition, we found similar abundances of fish larvae between shallow reefs and
240 MCEs. However, fish larval recruitment is known to be seasonal, and previous
241 studies have identified abundance differences in fish larval recruits across 10 – 40 m

242 in the Caribbean (Luckhurst and Luckhurst 1977). These fish recruitment patterns are
243 highly species specific, with fish recruits more abundance for some species at 40 m
244 than 10 m, while the reverse is true for other species (Luckhurst and Luckhurst
245 1977).

246 In this study we found no change in taxa richness between shallow reefs and
247 MCEs, though we only classified invertebrates into broad taxonomic groups, lacking
248 the resolution needed to detect fine scale richness patterns. In Jamaica, Ohlhorst
249 (1985) reported an increase in taxonomic richness across depths from 6 – 24 m, but
250 using higher resolution taxonomic groupings. In contrast, in Hawaii Hurley et al.
251 (2016) reported the greatest brachyuran crab reef cryptofauna diversity on shallow
252 reefs, with 40% of species at 12 m and declining richness with depth to 90 m.
253 Differences in richness patterns with depth between these studies are likely caused
254 by different reef habitats, taxonomic resolution, biogeographic regions, and
255 sampling techniques. Patterns in species richness across the shallow to mesophotic
256 gradient has been a major focus of research (Kahng et al. 2010; Kahng et al. 2014),
257 potentially being used to inform conservation management and in defining MCE
258 ecology (Laverick et al. 2016).

259 This study provides a first glimpse of the patterns in zooplankton
260 communities associated with MCEs in the Caribbean. Further research is necessary
261 to determine fine-scale patterns across the depth gradient in zooplankton
262 communities to help identify depth transition zones between communities and areas
263 with unique biodiversity assemblages.

264

265 **Acknowledgements**

266

267 We thank J. Hogg and A. Price at the Department of Zoology, University of Oxford
268 workshop for light trap construction. We thank all the staff and students of
269 Operation Wallacea Utila Marine Program 2015 for help and support with deploying
270 the light traps. DAAB is funded by a Fisheries Society of the British Isles PhD
271 studentship (www.fsbi.org.uk). Operation Wallacea (www.opwall.com) provided
272 fieldwork support for DAAB, DAE, CLH, AH, EG and ADR. Operation Wallacea

273 provided financial support in the form of salaries for authors DAAB, DAE, AH and EG,
274 but did not have any additional role in the study design, data collection and analysis,
275 decision to publish, or preparation of the manuscript.

276

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