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Coral-Excavating Sponge *Cliona delitrix*: Current Trends of Space Occupation on High Latitude Coral Reefs

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1 **Title:** Coral-excavating sponge *Cliona delitrix*: current trends of space occupation on
2 **high latitude coral reefs**

3

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21

22

23

24 **Abstract**

25

26 The recent increase in abundance of coral-excavating sponges is a threat to the health of
27 coral reefs. However, the distribution and growth of these sponges is poorly documented
28 on high latitude reefs where corals live in marginal environmental conditions. In this study,
29 we characterize the current trends of space occupation of *Cliona delitrix* on high latitude
30 reefs (N 26°) in southeast Florida. *C. delitrix* densities were significantly higher on the
31 deepest habitat of this reef tract (the outer reef) in response to a higher availability of coral
32 substratum. Sponge growth rates increased with depth, and in relation to presence of
33 tunicates and absence of macroalgae living in the sponge-coral interaction band.
34 Conversely, coral tissue loss was similar between habitats, regardless of the fouling
35 organisms present in the band between sponge and coral. On high latitude reefs, *C. delitrix*
36 preferred massive scleractinian coral species as substratum, similar to tropical reefs; but
37 its' inclination for specific coral species varied. The outer reef sites (deepest habitat) are
38 most vulnerable to *C. delitrix* colonization. Reef habitats with higher coral densities and
39 more available dead coral may continue to suffer the greatest levels of sponge bioerosion.

40

41 **Keywords:** growth, substratum preferences, competition, invertebrate, Florida

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44

45

46 **Introduction**

47

48 Coral-excavating sponge abundance and cover are increasing on coral reefs around the
49 world. This is due to higher levels of nutrients and coral mortality (Holmes 1997; Ward-
50 Paige et al. 2005; Schönberg and Ortiz 2008; Carballo et al. 2013). While excess nutrients
51 are used as food by sponges, they can be detrimental to corals (Ward-Paige et al. 2005).
52 Coral mortality due to bleaching, diseases or predation increases recruitment and growth
53 of coral-excavating sponges (Carballo et al. 2013; Chaves-Fonnegra 2014). Other factors
54 controlling coral-excavating sponges' abundance and distribution include higher water
55 temperatures, exposure to currents, severe storms, light levels, and the availability of
56 suitable substratum (Alvarez et al. 1990; Sammarco and Risk 1990; Schmahl 1991; Rützler
57 2002; Schönberg 2003; López-Victoria and Zea 2004; Chaves-Fonnegra 2014). Growth of
58 excavating sponges is predominantly affected by the density and morphology of the coral
59 skeleton, and by levels of fouling or grazing by other organisms (Schönberg 2003; López-
60 Victoria et al. 2006; Chaves-Fonnegra and Zea 2011).

61

62 Bioerosion caused by coral-excavating sponges is predicted to increase with elevated water
63 temperature and ocean acidification (Schönberg 2008; Wisshak et al. 2012; Duckworth and
64 Peterson 2013; Stubler et al. 2014; Wisshak et al. 2014; Enochs et al. 2015). Therefore with
65 climate change, coral-excavating sponges are becoming a threat to the health of coral reefs
66 (Schönberg and Ortiz 2008; Carballo et al. 2013; Duckworth and Peterson 2013; Stubler et
67 al. 2014; Wisshak et al. 2014).

68 The clionaid species *Cliona delitrix* Pang, 1973 lacks photosynthetic symbionts and can
69 excavate deeply (~10 cm) into the coral skeleton, bioeroding entire coral colonies (Pang

70 1973; Chaves-Fonnegra and Zea 2011). *C. delitrix* is commonly distributed in the
71 Caribbean and western Atlantic, and to the north reaches high latitude reefs of Florida and
72 the Bahamas (Ward-Paige et al. 2005; Zilberberg et al. 2006; Banks et al. 2008; Gilliam
73 2012; van Soest 2013). On tropical reefs this species prefers to colonize massive corals and
74 grows faster on recently dead coral with clean calices (Chiappone et al. 2007; Chaves-
75 Fonnegra and Zea 2011). Monitoring efforts indicate that this species is abundant and
76 disperses along the entire Florida Keys and northern extent of the Florida Reef Tract
77 (Ward-Paige et al. 2005; Banks et al. 2008; Gilliam et al. 2013; Chaves-Fonnegra et al.
78 2015).

79

80 Current trends of space occupation by coral-excavating sponges at higher latitudes ($>25^{\circ}\text{N}$)
81 are unknown, but are important to predict future changes in these reef habitats.
82 Environmental conditions at high latitudes are marginal for coral reef development, mainly
83 due to low aragonite saturation and low mean seasonal and annual temperatures (Kleypas
84 et al. 1999; Perry and Larcombe 2003). These environmental differences affect coral
85 biology by decreasing both coral calcification rates and metabolism, which in turn may
86 influence coral-excavating sponge occurrence and dispersal (Buddemeier 1997; Kleypas et
87 al. 1999; Perry and Larcombe 2003; Banks et al. 2008).

88

89 Possible community shifts from coral-dominated to excavating sponge-dominated reefs
90 appear to be linked to eutrophication and climate change (López-Victoria and Zea 2004;
91 Ward-Paige et al. 2005; Chaves-Fonnegra et al. 2007; Schönberg and Ortiz 2008; Carballo
92 et al. 2013). Therefore, it is important to evaluate how changes in the available coral

93 substratum affect sponges' distribution and growth. This study evaluates current trends of
94 space occupation by *C. delitrix* on high latitude (26° N) coral reefs at the northern extent
95 of the Florida Reef Tract. The specific objectives were to 1) determine if differences in
96 coral substratum (density and cover) affect *C. delitrix* distribution among reef habitats, 2)
97 evaluate *C. delitrix* substratum preferences in a high latitude reef environment, and 3)
98 determine if the lateral growth rate of *C. delitrix* varies with depth.

99

100 **Methods**

101

102 *Study Area*

103 This study was conducted offshore of southeast Florida in Broward County at the northern
104 extent of the Florida Reef Tract, between 26°00.26' N and 26°20.80' N. In this region, the
105 reef tract consists of three well-defined linear reefs that run parallel to shore: the inner (3-
106 7 m depth), middle (6-8 m depth), and outer (15-21 m) reefs (Banks et al. 2008). Colonized
107 pavement habitats and nearshore hardbottom ridges are located inshore of the inner reef
108 (Moyer et al. 2003; Banks et al. 2008; Walker et al. 2008). These reef communities are
109 impacted by various sources of land-based pollution including nutrient runoff, treated
110 waste discharges, and shipping port effluent (Finkl and Charlier 2003; Banks et al. 2008;
111 Finkl and Makowski 2013).

112

113

114 *Habitat Distribution*

115 To determine *C. delitrix* distribution, sampling was conducted at 21 reef monitoring sites
116 in four habitats: nearshore ridge complex (NR), inner reef (IR), middle reef (MR), and
117 the outer reef (OR). At each of these 21 sites, three 20 m x 1.5 m (30 m²) belt transects
118 were used to obtain quantitative data on stony coral density and cover, and *C. delitrix*
119 density. Within each transect, all stony coral colonies (≥ 4 cm) were identified to species,
120 colony diameter was measured, and the percentage of dead coral was estimated. Coral
121 cover (cm²) per transect was calculated as the total sum of areas for each colony. The
122 percentage of dead coral per colony was used to calculate how much of the total coral
123 area corresponded to dead and live cover. For each coral colony the presence/absence of
124 *C. delitrix* was noted. To avoid overestimating sponge density, multiple ramets of *C.*
125 *delitrix* on the surface of an individual coral colony were considered to be a single sponge
126 (Chaves-Fonnegra et al. 2007).

127

128 *Substratum Preferences*

129 Substratum preferences of *C. delitrix* were determined using two indices, Ivlev's Index of
130 Electivity (Chiappone et al. 2007; Manly et al. 2007) and the occupation/availability ratio
131 (Lopez-Victoria and Zea 2005). Both have been previously used to determine *C. delitrix*
132 substratum preferences in lower latitude environments (Chiappone et al. 2007; Chaves-
133 Fonnegra and Zea 2011). Ivlev's Index compares the actual pattern of stony coral
134 colonization to the expected coral colonization pattern based on relative abundance of each
135 coral species. All coral colonies and sponge individuals were pooled across 63 transects at
136 21 sites. Ivlev's index calculates an electivity value, (*e*), and states that:

137

$$e = \frac{r_i - P_i}{r_i + P_i},$$

138

where i represents the individual coral species, r_i is the proportion of that coral species

139

colonized by *C. delitrix*, and P_i is the available proportion of coral species i . This index

140

then ranks coral species from -1 to +1, where -1 indicates a rejection of preferential *C.*

141

delitrix colonization of the species, 0 indicates the species is colonized in proportion to its

142

abundance, and +1 indicates a *C. delitrix* preference for that particular coral species.

143

144

The occupation/availability ratio (Lopez-Victoria and Zea 2005) indicates the preference

145

that the sponge has towards a specific substratum (coral species), taking substratum cover

146

into consideration. If the ratio is >1 , the substratum is occupied in a proportion greater

147

than its availability; if <1 , it is occupied in a proportion lower than its availability; and if

148

the value is 1, it is occupied in the same proportion of its availability. To obtain the ratio,

149

substratum cover was obtained per transect based on the area of each coral colony

150

(estimated from the diameter). Then, the frequency of sponges in a specific substratum

151

(each coral species) was divided by the percentage cover of that substratum in each

152

transect.

153

154

Sponge lateral growth and coral tissue loss

155

To compare growth rates of *C. delitrix* and associated coral tissue loss across three reef

156

habitats, a total of 41 *Montastraea cavernosa* Linnaeus, 1766 coral-sponge pairs (colonies

157

with visible *C. delitrix* individuals) were monitored at the nearshore ridge habitat (n=11,

158

6.1 m), the middle reef (n=15, 12.2 m), and the outer reef (n=15, 18.3 m). *M. cavernosa*

159 was selected because this species was present in all habitats and a high abundance of coral
160 colonies in interactions with the sponge were available.

161

162 *M. cavernosa* colonies selected were <1 m in diameter, free of bleaching or disease, had
163 >50% live tissue, and had only one visible *C. delitrix* ramet with a narrow dead band
164 interface indicative of direct coral-sponge interaction. Following Chaves-Fonnegra and
165 Zea (2011), steel nails were driven into the coral skeleton along the dead band between the
166 sponge and surrounding live coral tissue, and were used as reference points for growth
167 measurements (minimum of 2 nails per coral). Initial measurements from each nail to the
168 nearest sponge tissue and from each nail to the nearest live coral tissue were taken for each
169 coral-sponge pair using calipers (0.1 cm accuracy). These measurements were repeated 6
170 months and 12 months following the initial measurements. The presence of macroalgae,
171 turf algae, sediment, and other fouling organisms on the dead coral band around the sponge
172 were also noted during measurements. Nails within the same coral colony served as
173 replicates, and measurements were pooled to calculate mean sponge growth and coral
174 tissue loss rates for each coral-sponge pair.

175

176 *Data analysis*

177

178 *Habitat Distribution*

179 Relationships between mean *C. delitrix* density (number of individuals \cdot m⁻²) per site and
180 reef variables depth, stony coral density, and stony coral cover (total, live, and dead) were
181 explored with a multiple regression analysis in R (Crawley 2012; R Core Team 2015). For

182 these analyses, the three 30 m² transects were pooled as one sampling area of 90 m² per
183 site (total n= 21).

184

185 *C. delitrix* density, coral density, and coral cover (total, live, and dead cover) were
186 compared independently and between three habitats using the sampling area of each
187 transect (30 m²) (NR: sites= 7, n= 21; MR: sites= 6, n= 18; OR: sites= 6, n= 18). The inner
188 reef habitat was excluded from this analysis due to its low number of sites (2) and transects
189 (n=6) comparatively. One-way ANOVA or Kruskal-Wallis analyses were used for these
190 comparisons depending on the normality and variance homogeneity of each dataset.

191

192 *Substratum Preferences*

193 To evaluate if preferences for a specific coral species were related to coral cover, the
194 Ivlev's Index of Electivity was tested for correlation with total, live, and dead coral cover
195 using Spearman's rank correlation in R 3.2.1. as data did not fit normal distribution
196 (Crawley 2012; R Core Team 2015).

197

198 *Sponge lateral growth and coral tissue loss*

199 These data were analyzed using a nested mixed-model ANOVA, where colony was nested
200 within reef site, and coral colony was treated as a random effect. In addition, fouling
201 organisms on the dead band were compared between the three habitats using a X^2 test of
202 independence in R 3.2.1 with 100,000 simulations to compute the most approximate p-
203 value.

204 **Results**

205

206 *Sponge Density and Habitat Distribution*

207 Multiple regression analysis indicated that *C. delitrix* density had a strong positive
208 relationship with total coral cover, both live and dead coral cover, and with the
209 interaction of coral density and live coral cover (Multiple $r^2 = 0.8565$, Adjusted $r^2 =$
210 0.8087 , $F = 17.91$, all $p < 0.00$, Figure 1). Although the multiple regression analysis
211 showed that depth did not have a significant influence on *C. delitrix* density ($p > 0.05$),
212 the non-parametric comparison between reef habitats showed that *C. delitrix* density was
213 significantly higher on the deepest habitat, the outer reef (Kruskal Wallis = 16.741, $df =$
214 2 , p -value < 0.05 , Dunn-test $p < 0.05$). Similarly, coral density was statistically higher on
215 the outer reef compared to the middle reef and nearshore ridge (ANOVA $F = 5.61$, $df = 2$,
216 p -value = 0.006, Tukey test < 0.05). However, the total coral cover, live coral cover, and
217 dead coral cover were similar between all three habitats (Kruskal-Wallis and chi-squared
218 values for each comparison = 3.9, 3.5, and 5.2, $df = 2$, $p > 0.05$). Therefore, the trend of
219 increasing *C. delitrix* density with depth is not due to site depth, but rather to the amount
220 of available substratum (combined effect of coral density and cover), which is highest on
221 the outer reef.

222

223

224 *Substratum Preferences*

225 The Ivlev's index was positive for six coral species (*Colpophyllia natans* Houttuyn, 1772,
226 *Pseudodiploria clivosa* Ellis & Solander, 1786, *Diploria labyrinthiformis* Linnaeus,
227 1758, *Montrastraea cavernosa*, *Orbicella faveolata* Ellis & Solander, 1786, and

228 *Solenastrea bournoni* Milne Edwards & Haime, 1849) indicating that *C. delitrix*
229 preferentially occupied their skeletons (Table 1). In contrast, the occupation/availability
230 ratio distinguished *M. cavernosa*, *O. faveolata*, *Porites astreoides* Lamarck, 1816, and
231 *Siderastrea siderea* Ellis & Solander, 1786 as the species of corals that are occupied by
232 the sponge in a greater proportion than their availability at high latitudes in Florida
233 (occupation/availability ratio significantly greater than 1, Student t-test $p < 0.01$, Table
234 1). These preferred coral species tend to have higher densities on the outer reef (Figure
235 2). In addition, the Ivlev's index significantly correlated with total coral cover
236 (Spearman's rank correlation $S = 78$, $p = 0.01$, $\rho=0.72$) and dead coral cover ($S = 42$, $p =$
237 0.00 , $\rho=0.85$, Figure 3).

238

239 *Sponge lateral growth and Coral tissue loss*

240 Sponge growth was slowest on the middle reef ($n=15$, $0.058 \pm 0.12 \text{ cm}\cdot\text{yr}^{-1}$) and
241 significantly different from the fastest sponge growth measured on the outer reef ($n=15$,
242 $0.613 \pm 0.11 \text{ cm}\cdot\text{yr}^{-1}$). However, sponge growth on the nearshore ridge was similar to rates
243 on both the middle reef and outer reef ($n=11$, $0.357 \pm 0.13 \text{ cm}\cdot\text{yr}^{-1}$), ANOVA ($F(2,37) =$
244 5.52 , $p < 0.01$, Figure 4A). Corals colonized by *C. delitrix* in all three habitats had
245 statistically similar tissue loss rates (ANOVA, $F(2,37) = 0.71$, $p = 0.50$), although the
246 middle reef and outer reef showed slightly higher coral tissue loss rates (0.350 ± 0.15
247 $\text{cm}\cdot\text{yr}^{-1}$ and $0.347 \pm 0.15 \text{ cm}\cdot\text{yr}^{-1}$, respectively) than the nearshore ridge (0.098 ± 0.17).

248

249 During growth measurements, the dead coral band between the sponge and coral tissue
250 was commonly colonized by turf algae with trapped sediment, other macroalgae, and

251 tunicates; possibly *Polyandrocarpa tumida* Heller, 1878 (Figure 5). Clean coral calices or
252 coral calices scraped clean by grazers (i.e. sea urchins, parrotfish) were not observed in
253 the sponge-coral interaction band. *C. delitrix* lateral growth across *Montastraea*
254 *cavernosa* varied in relation to the organisms found in the dead coral band, as
255 significantly faster sponge growth rates occurred in presence of tunicates and turf algae
256 with sediment, compared to other conditions that included the presence of macroalgae
257 (ANOVA, $F = 4,12$, $p = 0.003$; Tukey < 0.05 , Figure 4B). However, coral tissue loss was
258 similar across habitats regardless of the organisms found in the interaction band
259 (ANOVA, $F = 0.97$, $p = 0.42$, Figure 4D). The percentage of sponge-coral interactions
260 that included tunicates and turf algae with sediment was highest on the outer reef ($X^2 =$
261 40.261 , $p = 0.00$), whereas more macroalgae interactions were recorded on the middle
262 reef (Figure 6). Coral-sponge pairs on the nearshore ridge showed interactions with turf
263 algae and macroalgae, but interactions with tunicates were absent in this habitat (Figure
264 6).

265

266

267 **Discussion**

268

269 We found that on high latitude reefs in the northern extent of the Florida Reef Tract, *C.*
270 *delitrix* density and growth were greatest at the deepest habitat, the outer reef. Sponge
271 density increased where both coral density and coral cover were higher, while sponge
272 growth increased with the presence of tunicates and absence of macroalgae. Coral tissue
273 loss was similar between habitats regardless of the fouling organisms present in the sponge-

274 coral interaction band. Substratum preferences of *C. delitrix* on high latitude reefs were for
275 boulder shaped stony corals as previously reported for this sponge on tropical reefs
276 (Chiappone et al. 2007; Chaves-Fonnegra and Zea 2011), predominantly for *Montastraea*
277 *cavernosa* and *Orbicella faveolata*.

278

279 *C. delitrix* densities within the high latitude reef communities of southeast Florida were
280 lower than those at lower latitudes, including the Florida Keys, Colombia, and Venezuela
281 (Table 2). Sponge density was directly related to stony coral density and cover, both of
282 which tended to increase with depth as has been suggested in the Florida Keys and Los
283 Roques - Venezuela (Alvarez et al. 1990; Chiappone et al. 2007). Thus, regardless of
284 latitude, data indicate *C. delitrix* distribution and abundance are most strongly related to
285 substratum availability (coral density and cover).

286

287

288 Within the substratum types examined, the amount of dead coral available played an
289 important role in determining *C. delitrix* substratum preferences (Ivlev's index) on high
290 latitude reefs of the Florida Reef Tract. Consequently, potential differences in recent coral
291 mortality between habitats or depths could be driving changes in the distributional patterns
292 of *C. delitrix* populations. Stressors such as higher levels of nutrients and climate change
293 can produce coral bleaching and mortality, which open new available coral substratum for
294 the sponges to attach to (Cortés et al. 1984; Holmes 1997; Williams et al. 1999; López-
295 Victoria and Zea 2004; Ward-Paige et al. 2005; Chaves-Fonnegra et al. 2007; Schönberg
296 and Ortiz 2008; Bell et al. 2013; Carballo et al. 2013; Mueller et al. 2014). Thus, areas with

297 higher coral mortality are more prone to bioerosion by excavating sponges (López-Victoria
298 and Zea 2004; Schönberg 2008; Schönberg and Ortiz 2008; Carballo et al. 2013; Wisshak
299 et al. 2014).

300

301 *C. delitrix* exhibited preferential colonization for massive, boulder-shaped coral species,
302 and avoided branching or foliose species on high latitudes reefs in southeast Florida;
303 similar to previous findings for this species and other Clionidae across the tropical W.
304 Atlantic (Lopez-Victoria and Zea 2005; Ward-Paige et al. 2005; Chiappone et al. 2007;
305 Chaves-Fonnegra and Zea 2011). However, coral species preferences varied in relation to
306 the index used in the analysis. Comparisons with a study in the Florida Keys (Chiappone
307 et al. 2007), also based on the Ivlev's index, suggest *C. delitrix* preferences at high latitude
308 in Broward County are maintained for species such as *Colpophyllia natans*, *Montrastraea*
309 *cavernosa*, *Orbicella faveolata*, *Diploria* spp., and *Solenastrea bournoni*, but not for
310 *Porites astreoides* and *Siderastrea siderea*. Comparisons with the San Andres Islands
311 (Colombia) (Chaves-Fonnegra and Zea 2011), based on the occupation/availability ratio,
312 supported *C. delitrix* preferences for *S. siderea* in both locations, but not for *M. cavernosa*,
313 *O. faveolata*, and *P. astreoides* which are only preferred at high latitude in Broward
314 County.

315 We found preferences based on the Ivlev's index were related to individual species coral
316 cover, primarily dead cover, further showing that the abundance of excavating sponges is
317 influenced by coral mortality (i.e. Carballo et al. 2013; Chaves-Fonnegra 2014). The
318 occupation/availability ratio is standardized by the cover of each substratum and estimates
319 the preference that sponge larvae have (choice, avoidance, or inability to settle), and the

320 subsequent survival after settlement (Lopez-Victoria and Zea 2005). However, this ratio
321 could be influenced by the specific abundance of each coral species in the studied habitat
322 (Chaves-Fonnegra and Zea 2011). For better estimates of substratum preferences and
323 comparisons between locations and over time, we suggest further studies to adjust the
324 electivity index or ratio and include both coral density and cover (total, live and dead) in
325 the estimation of the available substratum.

326

327 On southeast Florida reefs, the mean *C. delitrix* growth rate was fastest at the deepest site
328 and was influenced by a higher percentage of tunicates in the interaction band, while
329 slower growth rates were found at shallower sites (middle reef and nearshore ridge) in
330 response to increased macroalgae, turf algae and sediments in the interaction band.
331 Higher sedimentation rates in the middle reef and nearshore ridge habitats have been
332 reported in southeast Florida (Jordan et al. 2010) and could slow *C. delitrix* growth by
333 restricting sponge water filtration and pumping (Gerrodette and Flechsig 1979; Wilkinson
334 and Cheshire 1988). Although sponge growth was different between habitats, coral tissue
335 loss was similar. This may be due to the strong defensive abilities that *M. cavernosa* has
336 against other benthic organisms (Logan 1984), which can reduce loss of coral tissue when
337 the sponge is also interacting with algae or tunicates. Additionally, *M. cavernosa* has a
338 tendency to grow upwards and form domes when confronting neighboring sponges,
339 changing the confrontation angle and allowing stinging sweeper tentacles to be more
340 effective, therefore reducing coral tissue loss and slowing sponge advance (López-
341 Victoria et al. 2006).

342

343 The mean rate of *C. delitrix* growth in southeast Florida was slower (Table 2) than in San
344 Andres Island, Colombia (Chaves-Fonnegra and Zea 2011). This difference is probably
345 due to the coral species studied and to the organisms colonizing the band of interaction.
346 Previous studies showed faster sponge growth rates ($\sim 1 \text{ cm} \cdot \text{yr}^{-1}$) in interactions with *O.*
347 *faveolata* and *S. siderea* in which more turf algae and urchin bites were present (Chaves-
348 Fonnegra and Zea 2011). In contrast, in southeast Florida, the turf algae in the interaction
349 band contained a higher amount of trapped sediment and macroalgae than in Colombia
350 (pers. obs.), potentially contributing to reduced sponge growth. *M. cavernosa* has a higher
351 defensive ability to combat other coral species compared to both *O. faveolata* and *S.*
352 *siderea* (Logan 1984), therefore, it may be more effective at fighting off the sponge. The
353 fact that *M. cavernosa* has a thicker tissue than other coral species (Peters 1984) could also
354 play a role in lower sponge growth rates, however further research is necessary to test this
355 hypothesis.

356

357 A pattern of higher growth rates at deeper sites has also been reported for non-excavating
358 sponge species in the Florida Keys, the Bahamas, and Belize (Lesser 2006), and is
359 attributed to a higher abundance of food in the form of heterotrophic bacteria,
360 prochlorophytes, and picoplankton at depth (Leichter et al. 1998; Lesser 2006; Trussell et
361 al. 2006). At higher latitudes in southeast Florida, it is possible that the outer reef
362 experiences higher levels of nutrients due to the depth of the local inlets, location of
363 outfall sewage pipes, and summer upwelling events which increase the nutrient and
364 plankton concentrations (Smith 1982; Banks et al. 2008; Finkl and Makowski 2013).

365 However, direct nutrient, plankton, and bacteria measurements are needed in southeast
366 Florida to determine if increased food is driving this growth difference, and if it is
367 proportionally greater on the outer reef.

368 *C. delitrix* density and distribution on coral reefs varies in relation to the available
369 substratum, which relates to the combined factors of coral density and cover. Similarly,
370 other coral excavating sponges of the genus *Cliona*, such as *C. orientalis* in the Great
371 Barrier Reef, and *C. tenuis* and *C. caribbaea* in the Caribbean Sea tend to be abundant in
372 areas with more available calcium carbonate as substratum, particularly coral, although
373 their coral species preferences vary and thus their patterns (Schönberg, 2001; López-
374 Victoria and Zea, 2005). In relation to depth, *C. delitrix* distribution is not favored in
375 shallow environments with high water movement, similar to *C. caribbaea*, but
376 contrasting with *C. orientalis* and *C. tenuis*, which tend to be more abundant in shallow
377 habitats affected by intense water flow (Schönberg, 2001; López-Victoria and Zea,
378 2005).

379 In conclusion, on high latitude reefs, where both coral density and cover are lower than
380 that of tropical reefs, the density of *Cliona delitrix* is also reduced. Substratum
381 preferences of this sponge may vary by location according to coral species in the habitat,
382 frequency of coral occurrence, and availability of live and dead substratum of coral
383 species. In southeast Florida, outer reef sites (deepest habitat) with greater boulder coral
384 density are most vulnerable to *C. delitrix* colonization and may continue to suffer the
385 greatest impacts of coral bioerosion. However, predicted climate change scenarios
386 (Wisshak et al. 2014; Enochs et al. 2015) may alter coral density and the availability of

387 dead coral, thus affecting the distribution and substratum preferences of coral-excavating
388 sponges in the future.

389

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391

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399

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546 sponge *Cliona delitrix* from the Bahamas. *Coral Reefs*, **25**, 297-301.

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553 TABLES

554 **Table 1.** *Cliona delitrix* colonization (r_i) in relation to coral availability (P_i). Selectivity for
 555 coral species was calculated using the Ivlev's index (Manly et al. 2007). f_a = frequency of
 556 availability, f_c = frequency of colonization, r_i = proportion of stony corals colonized by *C.*
 557 *delitrix*, P_i = proportion of scleractinian corals available. Bold numbers indicate preference
 558 (index > than 0). The letters in parentheses next to the species name represents their most
 559 common growth morphologies in southeast Florida; B = branching, E = encrusting, P =
 560 plating, and M = massive/boulder.

561

562

Coral Species	Coral availability		<i>C. delitrix</i> colonization		Ivlev's Electivity Index	Occupation/availability ratio	
	f_a	P_i	f_c	r_i	($r_i - P_i$)/($r_i + P_i$)	(% f_c /% $cover$)	p-value (ratio)
<i>Acropora cervicornis</i> (B)	121	0.0450	0	0.0000	-1.00	0.00±0.00 (n= 5)	0.00 (<1)
<i>Agaricia agaricites</i> (E)	31	0.0115	0	0.0000	-1.00	0.00±0.00 (n= 14)	0.00 (<1)
<i>Agaricia fragilis</i> (P)	3	0.0011	0	0.0000	-1.00	*	
<i>Agaricia lamarcki</i> (P)	4	0.0015	0	0.0000	-1.00	0.00±0.00 (n= 4)	0.00 (<1)
<i>Colpophyllia natans</i> (M)	10	0.0037	1	0.0097	0.45	209.3±209 (n= 9)	0.35 (=1)
<i>Dichocoenia stokesii</i> (M)	76	0.0283	0	0.0000	-1.00	0.00±0.00 (n= 36)	0.00 (<1)
<i>Diploria clivosa</i> (E/M)	14	0.0052	1	0.0097	0.30	2.95±2.81 (n= 11)	0.53 (=1)
<i>Diploria labyrinthiformis</i> (M)	5	0.0019	1	0.0097	0.68	26.53±26.53 (n= 5)	0.39 (=1)
<i>Diploria</i> spp. (E/M)	4	0.0015	0	0.0000	-1.00	*	
<i>Diploria strigosa</i> (M)	6	0.0022	0	0.0000	-1.00	0.00±0.00 (n= 4)	0.00 (<1)
<i>Eusmilia fastigiata</i> (B)	5	0.0019	0	0.0000	-1.00	0.00±0.00 (n= 4)	0.00 (<1)
<i>Isophyllia sinuosa</i> (M)	1	0.0004	0	0.0000	-1.00	*	
<i>Madracis decactis</i> (E)	104	0.0387	4	0.0388	0.00	83.53±55.67 (n= 29)	0.15 (=1)
<i>Meandrina meandrites</i> (P/E)	93	0.0346	3	0.0291	-0.09	33.68±28.82 (n= 35)	0.27 (=1)
<i>Montastraea cavernosa</i> (M)	516	0.1920	44	0.4272	0.38	80.46±21.94 (n= 53)	0.00 (>1)
<i>Orbicella faveolata</i> (M)	52	0.0194	9	0.0874	0.64	48.44±21.93 (n= 19)	0.04 (>1)
<i>Mycetophelia aliciae</i> (P)	3	0.0011	0	0.0000	-1.00	*	
<i>Oculina diffusa</i> (B)	3	0.0011	0	0.0000	-1.00	*	
<i>Porites astreoides</i> (E,M)	498	0.1853	11	0.1068	-0.27	20.35±7.24 (n= 57)	0.01 (>1)
<i>Porites porites</i> (B)	70	0.0261	0	0.0000	-1.00	0.00±0.00 (n= 18)	0.00 (<1)
<i>Scolymia</i> spp. (P/E)	4	0.0015	0	0.0000	-1.00	*	
<i>Siderastrea siderea</i> (E/M)	604	0.2248	16	0.1553	-0.18	45.11±14.38 (n= 60)	0.00 (>1)
<i>Solenastrea bournoni</i> (M)	61	0.0227	4	0.0388	0.26	324.77±233.33 (n= 22)	0.19 (=1)

<i>Stephanocoenia intersepta</i> (E/M)	399	0.1485	9	0.0874	-0.26	92.80±48.32 (n= 54)	0.06 (=1)
All species	2687	1.0000	103	1.0000			

563

564 Table 2. *Cliona delitrix* densities and growth rates across the tropical W. Atlantic.

565 MCAV: *Montastraea cavernosa*, OFAV: *Orbicella faveolata*, SISID: *Siderastrea*

566 *siderea*. Data for los Roques Venezuela were calculated based on the frequency and

567 sampling area by Alvarez et al (1990).

568

Latitude	Location	<i>C. delitrix</i> Density (indv · m ⁻²)	Growth rates (cm · yr ⁻¹)	Reference
26° N	Southeast Florida, USA	0.00 – 0.16	0.34 - MCAV	Present study
24°-25° N	Florida Keys, USA	0.01 – 0.24	n.a.	Chiappone <i>et al.</i> (2007)
12° N	San Andres Island, Colombia	0.08 – 0.54	1.10 - OFAV 0.90 - SSID	Chaves-Fonnegra <i>et al.</i> (2007)
11° N	Los Roques, Venezuela	~0.33	n.a.	(Alvarez et al. 1990)

569

570

571 FIGURE LEGENDS

572

573 Figure 1. *Cliona delitrix* density (Sponge Density = individuals · m⁻²) in relation to depth

574 (m), coral density (Coral Density = colonies · m⁻²), total coral cover (Coral Cover = m² ·

575 30 m⁻²), dead coral cover (Dead Cover = m² · 30 m⁻²), and live coral cover (Live Cover =

576 m² · 30 m⁻²), and specific relationship among all variables. For each row, the variable

577 listed in that row is expressed on the y axis of each plot, and values for the other variables

578 (in the corresponding column) are on the x axis. For example, *C. delitrix* density (Sponge

579 Density) and its corresponding relationships with each variable (listed in the columns on

580 the diagonal of the figure) are shown in the bottom row of panels.

581

582

583 Figure 2. Average density \pm SE of preferred coral species (all combined: *Colpophyllia*
584 *natans*, *Diploria clivosa*, *Diploria labyrinthiformis*, *Montastraea cavernosa*, *Orbicella*
585 *faveolata*, *Porites astreoides*, *Siderastrea siderea*, and *Solenastrea bournoni*) in relation
586 to sponge density per habitat.

587

588 Figure 3. Average dead coral cover \pm SE for massive coral species. CNAT: *Colpophyllia*
589 *natans*, DCLI: *Diploria clivosa*, DLAB: *Diploria labyrinthiformis*, MCAV: *Montastraea*
590 *cavernosa*, OFAV: *Orbicella faveolata*, and SBOU: *Solenastrea bournoni*. The dotted
591 line marks a value of 0 for the Ivlev's Index of Electivity; above this line are coral
592 species preferred by *C. delitrix*, and below this line are coral species not preferred.

593

594 Figure 4. Annual mean *C. delitrix* growth rates (A, B) and coral tissue loss rates (C, D) in
595 relation to reef habitat (A, C) and the fouling organisms on the dead coral band (B, D).
596 NR: nearshore ridge (n = 11), MR: middle reef (n = 15), OR: outer reef (n = 15), TAS:
597 turf algae and sediment, MA: macroalgae, TU: tunicates. The letters **a** and **b** denote
598 statistically significant differences in A and C ($p < 0.01$), in B and D ($p < 0.05$).

599

600 Figure 5. Example of the typical condition of the sponge in interaction with *Montastraea*
601 *cavernosa* offshore southeast Florida, USA (A) and in San Andres Island, Colombia (B).

602 Notice the dead coral band of interaction between the sponge (s) and coral (c) was

603 commonly colonized by turf algae with trapped sediment, other macroalgae and tunicates
604 in southeast Florida (A), but not in San Andres Island (B).

605

606

607 Figure 6. Presence percentage of different fouling organisms in the dead coral band (band
608 of interaction between sponges and corals) at each habitat. NR: nearshore ridge, MR:
609 middle reef, OR: outer reef, TAS: turf algae and sediment, MA: macroalgae, TU:
610 tunicates.

611

612