A rapid spread of the Stony Coral Tissue Loss Disease outbreak in the Mexican Caribbean

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Caribbean reef corals have experienced unprecedented declines from climate change, anthropogenic stressors and infectious diseases in recent decades. Since 2014, a highly lethal, new disease, called stony coral tissue loss disease (SCTLD), has impacted many reef-coral species in Florida. During the summer of 2018, we noticed an anomalously high disease prevalence affecting different coral species in the northern portion of the Mexican Caribbean. We assessed the severity of this outbreak in 2018/2019 using the AGRRA coral protocol to survey 82 reef sites across the Mexican Caribbean. Then, using a subset of 14 sites, we detailed information from before the outbreak (2016/2017) to explore the consequences of the disease on the condition and composition of coral communities. Our findings show that the disease outbreak has already spread across the entire region by affecting similar species (with similar disease patterns) to those previously described for Florida. However, we observed a great variability in prevalence and tissue mortality that was not attributable to any geographical gradient. Using long-term data, we determined that there is no evidence of such high coral disease prevalence anywhere in the region before 2018, which suggests that the entire Mexican Caribbean was afflicted by the disease within a few months. The analysis of sites that contained pre-outbreak information showed that this event considerably increased coral mortality and severely changed the structure of coral communities in the region. Given the high prevalence and lethality of this disease, and the high number of susceptible species, we encourage reef researchers, managers and stakeholders across the Western Atlantic to accord it the highest priority for the near future.

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18 Abstract

19 Caribbean reef corals have experienced unprecedented declines from climate change,
20 anthropogenic stressors and infectious diseases in recent decades. Since 2014, a highly lethal,
21 new disease, called stony coral tissue loss disease (SCTLD), has impacted many reef-coral
22 species in Florida. During the summer of 2018, we noticed an anomalously high disease
23 prevalence affecting different coral species in the northern portion of the Mexican Caribbean.
24 We assessed the severity of this outbreak in 2018/2019 using the AGRRA coral protocol to
25 survey 82 reef sites across the Mexican Caribbean. Then, using a subset of 14 sites, we detailed
26 information from before the outbreak (2016/2017) to explore the consequences of the disease on
27 the condition and composition of coral communities. Our findings show that the disease outbreak
28 has already spread across the entire region by affecting similar species (with similar disease
29 patterns) to those previously described for Florida. However, we observed a great variability in
30 prevalence and tissue mortality that was not attributable to any geographical gradient. Using
31 long-term data, we determined that there is no evidence of such high coral disease prevalence
32 anywhere in the region before 2018, which suggests that the entire Mexican Caribbean was
33 afflicted by the disease within a few months. The analysis of sites that contained pre-outbreak
34 information showed that this event considerably increased coral mortality and severely changed
35 the structure of coral communities in the region. Given the high prevalence and lethality of this
36 disease, and the high number of susceptible species, we encourage reef researchers, managers
37 and stakeholders across the Western Atlantic to accord it the highest priority for the near future.

38

39 **Keywords**: White plague; White syndrome; SCTLD; Coral mortality; Disease prevalence;
40 Reef monitoring; Long-term data, Reef functioning
41
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43 Association of Marine Laboratories of the Caribbean (AMLC).
44
45 **Introduction**
46
47 Over the past four decades, coral reefs have experienced declines in their condition and function,
48 which has been attributed to coral disease, overfishing and herbivore loss, eutrophication,
49 sedimentation, and climate change (Jackson et al., 2014; Hughes et al., 2017; Lapointe et al.,
50 2019). For the Caribbean in particular, diseases have caused devastating declines in living coral
51 cover of more than 50% to 80% within a few decades (Aronson & Precht, 2001; Jackson et al.,
52 2014). Furthermore, diseases have also impacted populations of other key components of
53 Caribbean ecosystems, such as the decimation of *Diadema antillarum* populations due to a non-
54 identified pathogen during the 1980s (Lessios et al., 1984). The region-wide outbreak of the
55 white-band disease in the late 1970s led to a substantial loss of the major reef-building corals
56 *Acropora palmata* and *Acropora cervicornis* (Gladfelter, 1982; Aronson & Precht, 2001). It is
57 estimated that nearly 80% of the population was lost during this event (Gladfelter, 1982;
58 Aronson & Precht, 1997). In the late 1990s, the white-pox disease, apparently caused by a
59 human-related pathogen, further decimated the populations of *A. palmata* (Patterson et al., 2002).
60 In addition, the increase in the incidence of the yellow-band disease during the 1990s affected
61 the populations of *Orbicella* spp., which are important reef-building species that tend to
62 dominate many fore-reef zones (Cervino et al., 2001; Gil-Agudelo et al., 2004). Multiple events
63 of white-plague disease outbreaks during the last decades have also substantially decimated the
64 populations of a range of coral species (Weil, 2004; Harvell, 2007; Precht et al., 2016). It has
65 been suggested for some sites that white-plague disease may have a greater impact on the
66 Caribbean than other diseases (Cróquer et al., 2005). Due to the fact that the most severely
67 impacted coral species are also major reef-building corals, disease outbreaks in the Caribbean
68 have largely contributed to the substantial changes in spatial heterogeneity and ecological
69 functionality of Caribbean reefs, along with their capacity to provide important ecosystem
70 services to humans (Alvarez-Filip et al., 2009; Aronson & Precht, 2001; Weil, 2004).
71
72 Although Caribbean reef-related diseases were first reported in the early 1970s, our knowledge
73 of their pathology, etiology, and epizootiology (i.e. what are the main drivers that potentially
74 trigger a disease outbreaks) of most coral reef diseases is still limited. However, it is likely that
75 increasing pressures in the form of climate change and coastal development will increase disease
76 prevalence and the negative effects of diseases on coral communities. For instance, coral
77 diseases are likely to be exacerbated in a context of rapidly increasing sea surface temperatures,
78 as thermal stress has been linked to coral disease outbreaks (Bruno et al., 2007; Randall et al.,

79   2014; van Woesik & McCaffrey 2017). In addition, coral diseases have also been related to
80   stressors such as excess nutrients from sewage or high levels of sedimentation (e.g. Sutherland et
81   al., 2010, Bruno et al., 2003).
82
83   In 2014, a new emergent coral disease, the Stony Coral Tissue Loss Disease (SCTLD), was first
84   reported off the coast of Miami-Dade County, Florida in September 2014, just after an intense
85   bleaching event during the summer of the same year (Precht et al., 2016; Precht, 2019; FDEP,
86   2019). Since then, the SCTLD has gradually spread across the Florida Reef Tract (FDEP, 2019)
87   and began to reach other regions in the Caribbean (AGRRA, 2019). In Florida, regional declines
88   in coral density approached 30% loss and live tissue loss was upward of 60% as a result of the
89   disease outbreak (Walton et al., 2018). The cause of the disease is still unknown but it is
90   affecting more than 20 species of corals (FDEP, 2019), with highly-susceptible species showing
91   initial signs of infection, followed by intermediate-susceptible species (FDEP, 2019). The most
92   evident symptom is the display of multiple lesions that provoke rapid tissue loss, leading to the
93   exposure of bright white skeletons that are rapidly covered by turf, macroalgae or sediment.
94   Highly susceptible species include *Pseudodiploria strigosa*, *Dendrogyra cylindrus, Meandrina*
95   *meandrites, Dichocoenia stokesii, Montastraea cavernosa* and *Eusmilia fastigiata*, among others
96   (Precht et al. 2016; Precht, 2019; FDEP, 2019). According to early reports, the SCTLD has not
97   shown seasonal patterns linked to warming or cooling ocean temperatures, contrary to previous
98   white plague diseases that have subsided in winter months as temperatures cooled (Harding et al
99   2008; Miller et al 2009; FDEP, 2019).
100
101   On July 2018, following alerting reports issued by local divers, and in collaboration with the
102   authorities of the Parque Nacional Arrecife de Puerto Morelos, we found a reef near Puerto
103   Morelos, in the northern Mexican Caribbean that had a severe outbreak of a coral disease
104   affecting similar species and exhibiting similar patterns as those previously reported in Florida
105   (Fig. 1). Since then, we set out to survey other reefs in the Mexican Caribbean and found that the
106   disease outbreak spread quickly across the region. Here we document the impact of the SCTLD
107   on coral communities in the Mexican Caribbean by (i) quantifying the disease prevalence at 82
108   sites, and (ii) describing how this disease has modified the condition and composition of coral
109   communities at 14 sites by using detailed information from before the onset of the outbreak.
110

Materials & Methods

112
113   Data for this region-wide assessment was produced by the Healthy Reefs Initiative (HRI), the
114   Comisión Nacional de Áreas Naturales Protegidas (Mexican Commission for Protected Areas;
115   CONANP) and the Biodiversity and Reef Conservation Laboratory, UNAM. Sites were defined
116   according to ongoing monitoring programs and research projects, therefore it was not possible to
117   design a survey protocol to systematically represent reef gradients or zonation. A total of 82 sites
118   were surveyed over the period July 2018 - April 2019 (Table S1). Seventy-seven sites are fore-

119   reefs (7-15 m deep) and five are back-reefs (1-3 m deep). All sites were surveyed using the
120   AGRRA coral protocol (Lang et al. 2012).
121
122   At each site, coral communities were surveyed by replicating 2 to 16 (mean = 4.3; SD = 3.7) belt
123   transects of 10x1 m (Table S1). Although two transects is the minimum recommended by the
124   AGRRA coral protocol (Lang et al. 2012), we aimed for more transects when possible in order to
125   have a better representation of the coral community and disease prevalence. The following data
126   were recorded for each coral colony within the transect: species name, colony size (maximum
127   diameter, diameter perpendicular to the maximum and height), percentage of bleaching,
128   percentage of mortality (new, transition and old) and the presence of SCTLD and other diseases
129   (Lang et al., 2012). We then calculated the SCTLD prevalence at each site and for all coral
130   species. For this study, we also recorded colonies with 100% mortality for which death could be
131   attributable to the SCTLD (i.e., recent or transient mortality was still evident; see Fig. 1). To
132   provide a clearer picture of the magnitude of the problem, we focused on exploring geographical
133   and temporal trends for the 11 most 'highly susceptible species', which we defined as those that
134   presented more than 10% of SCTLD prevalence across all surveyed sites (Fig. 2; Table S2).
135
136   To identify whether the SCTLD outbreak may have started earlier than the summer of 2018, a
137   variety of published and unpublished sources were used to provide a yearly estimate of disease
138   prevalence at a regional level. Datasets were obtained from AGRRA, the HRI, CONANP
139   monitoring protocols and scientific sources (publications and researchers), and are being
140   systematized in the Coral Reef Information System of the Biodiversity and Reef Conservation
141   Laboratory, UNAM (Table S1). Since the main intention of this exercise was to provide a
142   regional perspective of disease prevalence, we only used years for which enough geographical
143   representation exists. In other words, we included years with information from at least 17 sites
144   distributed in at least three of the main sub-regions identified for the Mexican Caribbean
145   (Northern Quintana Roo, Central Quintana Roo, Southern Quintana Roo, Cozumel and
146   Chinchorro Bank; Rioja-Nieto & Álvarez-Filip, 2019). In total, we present data for 7 time
147   periods: 2005/2006, 2009, 2011/2012, 2014, 2016, 2017, and 2018/2019. Some years were
148   combined into one period, as they were part of the same monitoring campaign (i.e. sites were
149   surveyed only once within each period).
150
151   In 2016 and 2017 we conducted an extensive effort to survey coral reefs systems across the
152   Mexican Caribbean (e.g. Suchley & Alvarez-Filip, 2018; Perry et al., 2018). Although surveying
153   the condition of coral communities was not part of the objectives of those campaigns, we
154   assessed coral communities in 14 of those sites using the AGRRA methodology (see above). In
155   2018 and 2019 we revisited these 14 sites to compare how coral condition and coral community
156   composition changed from before the SCTLD outbreak to after the onset of the outbreak (in
157   2018/2019). These sites are distributed in the northern portion of the Mexican Caribbean: from
158   Punta Allen to Puerto Morelos in the mainland, and in the windward and leeward coasts of

159   Cozumel (Fig. 3). Eleven sites are fore reefs and three are back-reefs. To describe patterns of
160   coral mortality between periods, we first calculated the proportion of healthy, afflicted and dead
161   colonies for each period (2016/2017 and 2018/2019). As described above, for this analysis we
162   only considered the 11 most 'highly susceptible species'.
163
164   The variation in the overall coral community composition (including all recorded species)
165   between 2016/2017 and 2018/2019 was investigated with non-metric multidimensional scaling
166   (nMDS) based on Bray-Curtis similarities of square root transformed coral cover species data in
167   Primer v6 (Clarke & Gorley., 2006). The matrix was created using the relative abundance of
168   each healthy, afflicted, and dead colony for each coral species for each period. The relative
169   abundance of each coral species was used as the variable, the sites as the samples. We used the
170   before and after periods, and the reef zones as factors. A two-way Analysis of Similarities
171   (ANOSIM) was used to test the significance of these groupings (9999 permutations).
172
173   We then used the convex hull (polygon delineated by the exterior points of each period in the
174   nMDS) to represent the variability of the coral community for each time period (2016-2017 vs
175   2018-2019), and the standard ellipse area (SEA) to quantitatively explore the overlap between
176   the two periods. Briefly, the standard ellipse is to bivariate data as standard deviation is to
177   univariate data. The standard ellipse of a set of bivariate data is calculated from the variance and
178   covariance of the two axes and contains approximately 40% of the data (Jackson et al., 2012). To
179   compare the total area for each time period, we used the Bayesian standard ellipse area corrected
180   for the sample size (SEAc) estimated, and plotted it using the SIBER routine for the SIAR
181   package in R (Parnell et al., 2015). The overlap of the time period was calculated as the
182   overlapping proportion of the SEAc (Jackson et al., 2011).
183

Results & Discussion

185
186   Here we describe how the SCTLD affected 82 reef sites distributed along the Mexican Caribbean
187   coast. More than 40% of the sites had a SCTLD prevalence of 10% or more, and nearly a quarter
188   of the sites had a disease prevalence of more than 30% (Fig. 3). Our results should be taken as a
189   conservative value, since many sites were surveyed when the SCTLD outbreak was only starting
190   (i.e., only a few colonies of a few species were afflicted by the disease; Fig. 3). We observed
191   great variability in prevalence that was not attributable to any geographical gradient or
192   seasonality (Fig. 3). For example, the SCTLD was first observed in Cozumel's windward coast
193   in November 2018 (as in most of the surveyed sites in the mainland); however, it was not until
194   December 2018 that the disease reached the reefs in the leeward side of Cozumel, followed by
195   rapid spreading during the winter. Overall, the presence of the SCTLD in the Mexican Caribbean
196   during 2018/2019 was well above the 5% disease prevalence, that has been identified as habitual
197   for Caribbean reefs (Weil, 2004; Ruiz-Moreno et al., 2012), and just slightly lower than what has
198   been reported for Florida a few years after the start of the SCTLD outbreak (Walton et al., 2018).

199 During the past 13 years, disease prevalence in the Mexican Caribbean was below 10%, and it
200 reached its lowest point during 2016-2017, just one year before the SCTLD outbreak in this
201 region, with only 1% prevalence (Fig. 4). Similarly throughout the Florida Reef Tract, the
202 prevalence of disease before the first SCTLD reports was below 2%, but this prevalence doubled
203 after the region-wide outbreak (Walton et al., 2018). For this study, we present the temporal
204 trend of disease prevalence to provide context to the SCTLD outbreak. However, we
205 acknowledge that the information presented in Fig. 4 should be taken conservatively, since
206 prevalence values are usually driven by few (sometimes different) afflicted species and are
207 dependent on coral mortality from previous years.
208 For Florida, it has been shown that the 2014 SCTLD disease outbreak was linked to a severe
209 thermal stress resulting from warm winter and spring temperatures followed by an anomalously
210 warm summer (Gintert et al., 2019; van Woesik & McCaffrey, 2017; Walton et al., 2018). For
211 the Mexican Caribbean, we did not find evidence of intense thermal stress during this study (July
212 2018 - April 2019). Coral bleaching was very low and unrelated to the disease prevalence in all
213 our surveyed sites (Fig. S1). However, and although sea-surface temperatures rarely exceeded
214 the bleaching threshold, temperature anomalies during the winter were relatively high (Cerdeira-
215 Estrada et al., 2019; Fig. S1). The above-normal temperatures during the winter might have
216 contributed to the rapid spread of the disease observed in Cozumel's leeward coast during this
217 season, since coral diseases are likely to be exacerbated by thermal stress (Bruno et al., 2007;
218 Randall et al., 2014; van Woesik & McCaffrey 2017). During this study, there were no other
219 severe natural events, such as tropical storms or extraordinary rainfall that affected our study
220 sites.
221
222 The SCTLD has a very high host range Our field surveys revealed that 24 out of 46 recorded
223 species presented symptoms of SCTLD with a high disease prevalence: *Dendrogyra cylindrus*
224 (71%, 5 out of 7 colonies), *Pseudodiploria strigosa* (40%), *Meandrina meandrites* (38%),
225 *Eusmilia fastigiata* (33%), *Siderastrea siderea* (26%), *Diploria labyrinthiformis* (25%), among
226 others (Fig. 2, Table S2). As in Florida, we have also observed that some of the most susceptible
227 species have disappeared from long-term monitoring sites. Potentially, this emergent disease has
228 even driven local-extinction events of species such as *M. meandrites and D. cylindrus*, since
229 these species that have vanished from several reef sites on the mainland coast of our study
230 region. In fact, a recent study suggests that *D. cylindrus*, a species that has been rare for hundreds
231 of thousands of years, has a high likelihood of becoming extinct in the coming years due to this
232 disease outbreak (Chan et al., 2019). We still recorded healthy colonies of *M. meandrites and D.*
233 *cylindrus* at Chinchorro Bank and Cozumel Island, but some of the more recent surveys (not
234 included in this study) revealed that the colonies from these two species are increasingly being
235 afflicted by the SCTLD in Cozumel. Although there is the precedent of other diseases affecting
236 multiple species in the Caribbean, such as the black band disease, yellow band syndrome and
237 White Plague type II (Weil, 2004), it is possible that the SCTLD may become one of most lethal

238 diseases in the recent history of the region, given the high levels of prevalence and high mortality
239 rates on several coral species (see also FDEP, 2019; Gintert et al., 2019).
240
241   Although there are some differences between the lists (and ranking) of afflicted species
242 identified for the Mexican Caribbean (this study) and those reported for Florida (e.g. Precht et
243 al., 2016 and Walton et al., 2018), the overall pattern is similar. Many of the species that
244 remained as important reef-building corals after the declines of *Acropora* and *Orbicella,* are
245 being severely affected by the SCTLD (Gonzalez-Barrios & Alvarez-Filip, 2018; Fig. 2).
246 Complexity-contributing species that exhibited significant declines include *P. strigosa*, *D.*
247 *labyrinthiformis*, *C. natans* and *M. cavernosa* (Fig. 2). In contrast, we found very low disease
248 prevalence on non-framework building corals such as *Agaricia agaricites* and *Porites astreoides*,
249 which are species that have been previously described as intermediately-susceptible species to
250 the SCTLD (FDEP, 2019). These two species are very abundant across reef sites in the Mexican
251 Caribbean and the wider Caribbean (Table S1; Green, Edmunds & Carpenter, 2008; Gonzalez-
252 Barrios & Alvarez-Filip, 2018). Therefore, the decline in the abundance of several species due to
253 the SCTLD is likely to further increase the dominance of *A. agaricites* and *P. astreoides* in the
254 region. This may have started to become apparent already. The relative abundance of these two
255 species represented 46% of the surveyed colonies in 2016 and 2017, yet by 2018/2019 they
256 accounted for 52% of the total number of recorded coral colonies. However, this is a preliminary
257 observation and further studies should assess coral communities once the SCTLD has already
258 passed its peak in the region. Overall, these findings suggest that the ultimate consequence of the
259 SCTLD outbreak may be a further decrease on the physical persistence and ecological
260 functionality of coral reefs (Alvarez-Filip et al., 2013; Perry et al., 2015; Perry & Alvarez-Filip,
261 2019).
262
263   Transmission, or the spread of disease among individuals, is a key factor in
264 understanding the epidemiology and ecology of infectious diseases (Shore & Caldwell, 2019).
265 Although the data for this study was not collected in a way that allowed us to quantitatively
266 explore how the disease is transmitted between colonies, it is important to mention that we did
267 not observe evidence that suggests a single potential mechanism of disease transmission. For
268 example, we repeatedly observed, at different sites, individuals of the butterflyfish *Chaetodon*
269 *capistratus* feeding on the edge of the lesions and then swimming away to feed off on other
270 (healthy or afflicted) colonies (Fig 1A). This behavior of *C. capistratus* was commonly observed
271 on colonies of *P. strigosa* but very occasionally on other susceptible species such as *D.*
272 *labyrinthiformis* and *Orbicella* spp. During our field surveys it was also common to observe that
273 neighboring colonies were afflicted (e.g. Fig. 1A), but in other instances we found colonies of
274 the same species in direct contact with each other with no evidence of transmission from the
275 afflicted colony to the apparently healthy colony (e.g. Fig 1B). Thus, although it is suspected that
276 the SCTLD is infectious (transmissible from a sick coral to a healthy coral), further pathological,

277   etiological and genetic analyses are required to fully understand the sources and mechanisms of
278   transmission of this emergent threat to Caribbean reefs.
279
280   The analysis of sites that contained pre-outbreak information showed that this outbreak
281   event considerably increased coral mortality and severely changed the structure of coral
282   communities in the region. In total, we surveyed 3,059 coral colonies of the highly susceptible
283   species for both periods (2016/2017 and 2018/2019). During the pre-outbreak period, 99.5% of
284   the coral colonies were healthy, yet during 2018-2019 the disease prevalence reached 25.9%,
285   while another 12.9% of the colonies were already dead; probably as a consequence of the
286   SCTLD (Fig. 5). All the colonies exhibited similar symptoms to those colonies from Florida,
287   with rapid tissue loss occurring within a period of just a few weeks in the most extreme cases,
288   leaving the white skeletons exposed, which were either colonized by macroalgae or covered by
289   sediment shortly after. Additionally, our percentage of afflicted colonies by the SCTLD is
290   similar to what was observed in Florida during 2014-2015, where they registered a 30%
291   proportion of afflicted colonies (Precht et al., 2016). The coral community composition of those
292   14 sites changed considerably between the pre-outbreak surveys and 2018/2019 (Fig. 6). The
293   two-way ANOSIM showed significant differences between sampling periods (R= 0.561, p =
294   0.001) and reef zones (R = 0.44, p = 0.004).The analysis revealed that the period of 2018/2019
295   had no overlap with the period of 2017/2019, which means that this corresponds to
296   compositional changes in the coral reef communities. This is particularly explained by the
297   sudden increase of afflicted colonies and of the number of dead colonies, especially from the
298   species *M. meandrites*, *P. strigosa*, *D. labyrinthiformis* and *E. fastigiata*. This massive disease-
299   outbreak is a clear example of how coral diseases are drivers of change for coral communities
300   (Harvell et al., 2007).
301
302   The SCTLD outbreak reached the north of the Mesoamerican Reef System in 2018,
303   which affected most of the coral reefs throughout the 400 linear km of the Mexican Caribbean
304   coast in less than a year with a non-recognizable geographical pattern. This pattern contrasts the
305   gradual spread observed across the Florida Reef Tract between 2014 and 2019 (FDEP, 2019).
306   The extremely rapid geographical progression of the SCTLD across the Mexican Caribbean
307   could be explained, at least in part, by the rapidly decreasing quality of sea water in the region.
308   The Mexican Caribbean coast has experienced dramatic coastal development over the last
309   decades. Over 10 million tourists visit the region annually and the local population has grown
310   exponentially (Suchley & Alvarez-Filip, 2018). Consequently, the coastal waters of the region
311   have experienced eutrophication and increased sedimentation levels (Murray, 2007; Baker et al.,
312   2013; Hernández-Terrones et al., 2015). Eutrophication resulting from inadequate wastewater
313   treatment has been previously identified as a major driver of declining reef condition in the
314   region (e.g. Suchley & Alvarez-Filip, 2018). In addition and more recently, the Mexican
315   Caribbean coast has regularly experienced a massive influx of drifting *Sargassum* that
316   accumulates on the shores and rapidly decomposes, resulting in near-shore, murky-brown waters

317 that rapidly increases nutrient concentration in the water column and reduces light, oxygen and
318 pH levels (van Tussenbroek et al., 2017). These sargassum-brown-tides have been proven to
319 have drastic consequences on near-shore seagrass meadows and coral communities (van
320 Tussenbroek et al., 2017). Given the large amount of *Sargassum* reaching the coast, these
321 negative effects are likely to disseminate further offshore reaching coral reefs (usually located
322 0.5-3 km from the coast). Further research is needed to fully comprehend the relationship
323 between rapidly changing water quality in the Mexican Caribbean and the susceptibility of reef
324 corals to diseases; however, chronic nutrient enrichment has already been related to coral
325 diseases and bleaching under experimental conditions (Vega Thurber et al., 2013).
326
327

328 ## Conclusion
329
330 The Caribbean region is a well-known 'disease hot-spot' because of the fast emergence, high
331 prevalence, and virulence of coral-reef diseases and syndromes (Weil, 2004). These events have
332 deeply marked the community composition of Caribbean reefs by decimating populations of
333 important reef-building coral species such as *A. palmata*, which has not fully recovered from
334 these events (e.g. Rodríguez-Martínez et al., 2014). However, the SCTLD is likely to become the
335 most lethal coral disease ever recorded because of its high prevalence, the high number of
336 susceptible species, its transmissibility, and the high levels of mortality exhibited by affected
337 corals (Precht et al., 2016; Precht et al., 2018; Gintert et al., 2019). A total of 29 species,
338 including rare and important reef-building coral species, have been reported to be affected by the
339 SCTLD (this study; Precht et al., 2016; Walton et al., 2018; FDEP, 2019), but even more
340 concerning is the fact that this disease is covering a wide geographic range and it is expanding
341 rapidly. Recent, reports of the SCTLD have also been issued for Jamaica, St. Maarten, the
342 Dominican Republic and St. Thomas in the U.S. Virgin Islands (AGRRA, 2019). The ultimate
343 consequences for the wider Caribbean are yet to be seen, however, our findings suggest that this
344 event has the potential to further decrease physical persistence and ecological functionality of
345 coral reefs at a regional scale (Perry & Alvarez-Filip 2019). Amelioration or eradication
346 intervention have only partially succeeded in impeding the spread of the SCTLD disease across
347 Florida and Mexico, in part because the disease is spreading more rapidly (weeks) than our
348 capacity (scientists, managers, stakeholders) to respond to these types of events (e.g. Precht,
349 2019). Given the high prevalence and lethality of this disease, and the high number of
350 susceptible species, we encourage reef researchers, managers and stakeholders across the
351 Caribbean to accord it the highest priority for the near future.
352

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360 historical background to this disease outbreak. The Comisión Nacional de Áreas Protegidas is
361 currently coordinating the Disease Response Plan for the Mexican Caribbean, this initiative
362 allowed us to present and discuss with a broader group of scientists, managers and NGOs our
363 preliminary observations. The Atlantic and Gulf Rapid Reef Assessment program provided
364 support to L.A.-F. to attend and present an earlier version of this study in the 39th meeting of the
365 Association of Marine Laboratories of the Caribbean in Punta Cana, Dominican Republic. We
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367

References

369 AGRRA 2019. Coral Disease Outbreak, Stony coral tissue loss disease
370   http://www.agrra.org/coral-disease-outbreak/

371 Alvarez-Filip L, Carricart-Ganivet JP, Horta-Puga G, Iglesias-Prieto R. 2013. Shifts in coral-
372   assemblage composition do not ensure persistence of reef functionality. *Scientific Reports*.
373   DOI: 10.1038/srep03486.

374 Alvarez-Filip L, Dulvy NK, Gill JA, Côté IM, Watkinson AR. 2009. Flattening of Caribbean
375   coral reefs: Region-wide declines in architectural complexity. *Proceedings of the Royal*
376   *Society B: Biological Sciences* 276:3019–3025. DOI: 10.1098/rspb.2009.0339.

377 Aronson RB, Precht WF. 2001. White-band disease and the changing face of Caribbean coral
378   reefs. In: Porter JW ed. *The Ecology and Etiology of Newly Emerging Marine Diseases*.
379   Dordrecht: Springer Netherlands, 25–38. DOI: 10.1007/978-94-017-3284-0_2.

380 Aronson RB, Precht WF. 1997. Stasis, biological disturbance, and community structure of a
381   Holocene coral reef. *Paleobiology* 23:326–346. DOI: 10.1017/S0094837300019710.

382 Baker DM, Rodríguez-Martínez RE, Fogel ML. 2013. Tourism's nitrogen footprint on a
383   Mesoamerican coral reef. Coral Reefs. DOI: 10.1007/s00338-013-1040-2.

384 Bruno JF, Petes LE, Harvell CD, Hettinger A. 2003. Nutrient enrichment can increase the
385   severity of coral diseases. *Ecology Letters*. DOI: 10.1046/j.1461-0248.2003.00544.x.

386 Bruno JF, Selig ER, Casey KS, Page CA, Willis BL, Harvell CD, Sweatman H, Melendy AM.
387   2007. Thermal stress and coral cover as drivers of coral disease outbreaks. *PLoS Biology*.
388   DOI: 10.1371/journal.pbio.0050124.

389 Cerdeira-Estrada, S., R. Martell-Dubois, J. Valdéz, R. Ressl. 2019. Monthly night time Sea
390   Surface Temperature (M-NSST) at 1-km. Satellite-based ocean monitoring system
391   (SATMO). Marine-Coastal Information and Analysis System (SIMAR). CONABIO.
392   México. Dataset accessed [2018-05-10] at simar.conabio.gob.mx.

393 Cervino, J., Goreau, T. J., Nagelkerken, I., Smith, G. W., & Hayes, R. 2001. Yellow band and
394   dark spot syndromes in Caribbean corals: distribution, rate of spread, cytology, and effects
395   on abundance and division rate of zooxanthellae. In: The Ecology and Etiology of Newly
396   Emerging Marine Diseases.

397 Chan AN, Lewis CL, Neely KL, Baums IB. 2019. Fallen Pillars: The past, present, and future
398   population dynamics of a rare, specialist coral-algal symbiosis. Frontiers in Marine Science
399   6:1–18. DOI: 10.3389/fmars.2019.00218.

400 Clarke KR, Gorley RN. 2006. *PRIMER v6:*

401 Cróquer A, Weil E, Zubillaga AL, Pauls SM. 2005. Impact of a white plague-II outbreak on a
402   coral reef in the archipelago Los Roques National Park, Venezuela. *Caribbean Journal of*
403   *Science.*

404 FDEP (Florida Department Environmental Protection), 2019. Florida Reef Tract Coral Disease
405   Outbreak (2014 – Present). https://floridadep.gov/fco/coral/content/florida-reef-tract-coral-
406   disease-outbreak

407 Gil-Agudelo DL, Smith GW, Garzón-Ferreira J, Weil E, Petersen D. 2004. Dark Spots Disease
408   and Yellow Band Disease, Two Poorly Known Coral Diseases with High Incidence in
409   Caribbean Reefs. In: *Coral Health and Disease.* DOI: 10.1007/978-3-662-06414-6_19.

410 Gladfelter WB. 1982. White-band disease in Acropora palmata: implications for the structure
411   and growth of shallow reefs. *Bull Mar Sci.*

412 Gintert BE, Precht WF, Fura R, Rogers K, Rice M, Precht LL, D'Alessandro M, Croop J, Vilmar
413   C, Robbart ML. 2019. Regional coral disease outbreak overwhelms impacts from local
414   dredge project. Environmental Monitoring and Assessment 191

415 González-Barrios FJ, Álvarez-Filip L. 2018. A framework for measuring coral species-specific
416   contribution to reef functioning in the Caribbean. *Ecological Indicators* 95:877–886. DOI:
417   10.1016/j.ecolind.2018.08.038.

418 Harding S, van Bochove JW, Day O, Gibson K, Raines P. 2008. Continued degradation of
419   Tobago's coral reefs linked to the prevalence of coral disease following the 2005 mass coral
420   bleaching event. *Proceedings of the 11th International Coral reef symposium*:738–741.

421 Harvell D, Jordán-Dahlgren E, Merkel S, Rosenberg E, Raymundo L, Smith G, Weil E, Willis B.
422   2007. Coral Disease, Environmental Drivers, and the Balance Between Coral and Microbial
423   Associates. *Oceanography.* DOI: 10.5670/oceanog.2007.91.

424 Hernández-Terrones LM, Null KA, Ortega-Camacho D, Paytan A. 2015. Water quality
425   assessment in the Mexican Caribbean : Impacts on the coastal ecosystem. Continental Shelf

426   Research 102:62–72. DOI: 10.1016/j.csr.2015.04.015

427   Hughes TP, Barnes ML, Bellwood DR, Cinner JE, Cumming GS, Jackson JBC, Kleypas J, Van
428   De Leemput IA, Lough JM, Morrison TH, Palumbi SR, Van Nes EH, Scheffer M. 2017.
429   Coral reefs in the Anthropocene. *Nature* 546:82–90. DOI: 10.1038/nature22901.

430   Jackson MC, Donohue I, Jackson AL, Britton JR, Harper DM, Grey J. 2012. Population-level
431   metrics of trophic structure based on stable isotopes and their application to invasion
432   ecology. *PLoS ONE*. DOI: 10.1371/journal.pone.0031757.

433   Jackson AL, Inger R, Parnell AC, Bearhop S. 2011. Comparing isotopic niche widths among and
434   within communities: SIBER - Stable Isotope Bayesian Ellipses in R. *Journal of Animal*
435   *Ecology* 80:595–602. DOI: 10.1111/j.1365-2656.2011.01806.x.

436   Jackson JBC, Donovan MK, Cramer KL LV. 2014. 1891-Status and Trends of Caribbean Coral
437   Reefs- 1970-2012-2014 Caribbean Coral Reefs - Status Report 1970-2012 (1). *Global Coral*
438   *Reef Monitoring Network, IUCN, Gland, Switzerland*.

439   Lang JC, Marks KW, Kramer PR, Kramer PA. 2012. Protocolos AGRRA 5.5. :1–44.

440   Lapointe, B.E., Brewton, R.A., Herren, L.W., Porter, J.W., Hu, C., 2019. Nitrogen enrichment,
441   altered stoichiometry, and coral reef decline at Looe Key, Florida Keys, USA: a 3-decade
442   study. Marine Biology, 166(8), 108

443   Lessios HA, Robertson DR, Cubit JD. 1984. Spread of Diadema mass mortality through the
444   Caribbean. *Science* 226:335–337. DOI: 10.1126/science.226.4672.335.

445   Miller J, Muller E, Rogers C, Waara R, Atkinson A, Whelan KRT, Patterson M, Witcher B.
446   2009. Coral disease following massive bleaching in 2005 causes 60% decline in coral cover
447   on reefs in the US Virgin Islands. *Coral Reefs* 28:925–937. DOI: 10.1007/s00338-009-
448   0531-7.Murray G. 2007. Constructing paradise: The impacts of big tourism in the Mexican
449   coastal zone. *Coastal Management*. DOI: 10.1080/08920750601169600.

450   Parnell A, Jackson A. 2015. Package 'siar': Stable Isotope Analysis in R. *R Found. Stat.*
451   *Comput., Vienna*:34. DOI: 10.1063/1.4919278.

452   Patterson KL, Porter JW, Ritchie KB, Polson SW, Mueller E, Peters EC, Santavy DL, Smith
453   GW. 2002. The etiology of white pox, a lethal disease of the Caribbean elkhorn coral,
454   Acropora palmata. *Proceedings of the National Academy of Sciences*. DOI:
455   10.1073/pnas.092260099.

456   Perry CT, Steneck RS, Murphy GN, Kench PS, Edinger EN, Smithers SG, Mumby PJ. 2015.
457   Regional-scale dominance of non-framework building corals on Caribbean reefs affects

458   carbonate production and future reef growth. *Global Change Biology*. DOI:
459   10.1111/gcb.12792.

460   Perry CT, Alvarez-Filip L, Graham NAJ, Mumby PJ, Wilson SK, Kench PS, Manzello DP,
461   Morgan KM, Slangen ABA, Thomson DP, Januchowski-Hartley F, Smithers SG, Steneck
462   RS, Carlton R, Edinger EN, Enochs IC, Estrada-Saldívar N, Haywood MDE, Kolodziej G,
463   Murphy GN, Pérez-Cervantes E, Suchley A, Valentino L, Boenish R, Wilson M,
464   MacDonald C. 2018. Loss of coral reef growth capacity to track future increases in sea
465   level. *Nature* 558:396–400. DOI: 10.1038/s41586-018-0194-z.

466   Perry CT, Alvarez-Filip L. 2019. Changing geo-ecological functions of coral reefs in the
467   Anthropocene. Functional Ecology. DOI: 10.1111/1365-2435.13247.Precht WF, Gintert
468   BE, Robbart ML, Fura R, Van Woesik R. 2016. Unprecedented Disease-Related Coral
469   Mortality in Southeastern Florida. *Scientific Reports*. DOI: 10.1038/srep31374.

470   Precht WF, Gintert BE, Robbart ML, Fura R, van Woesik R. 2016. Unprecedented Disease-
471   Related Coral Mortality in Southeastern Florida. Scientific Reports 6:1–11. DOI:
472   10.1038/srep31374.

473   Precht, W., Gintert,B., Fura, R., Precht, W.,Rogers,K., & Robbart, M. (2018). Coral disease
474   ravages reef-building corals throughout Southeast Florida. Inside Ecology (April 5, 2018)
475   https://insideecology.com/2018/04/05/coral-disease-ravages- reef-building-corals-
476   throughoutsoutheast-florida/.

477   Precht WF. 2019. Failure to respond to a coral disease outbreak: Potential costs and
478   consequences. PeerJ Preprints 7:e27860v2 https://doi.org/10.7287/peerj.preprints.27860v2

479   Randall CJ, Jordan-Garza AG, Muller EM, Van Woesik R. 2014. Relationships between the
480   history of thermal stress and the relative risk of diseases of Caribbean corals. *Ecology*. DOI:
481   10.1890/13-0774.1.

482   Rioja-Nieto R, Álvarez-Filip L. 2019. Coral reef systems of the Mexican Caribbean: Status,
483   recent trends and conservation. *Marine Pollution Bulletin*. DOI:
484   10.1016/j.marpolbul.2018.07.005.

485   Rodríguez-Martínez RE, Banaszak AT, McField MD, Beltrán-Torres AU, Álvarez-Filip L. 2014.
486   Assessment of Acropora palmata in the mesoamerican reef system. *PLoS ONE*. DOI:
487   10.1371/journal.pone.0096140.

488   Ruiz-Moreno D, Willis BL, Page AC, Weil E, Cróquer A, Vargas-Angel B, Jordan-Garza AG,
489   Jordán-Dahlgren E, Raymundo L, Harvell CD. 2012. Global coral disease prevalence
490   associated with sea temperature anomalies and local factors. *Diseases of Aquatic*
491   *Organisms*. DOI: 10.3354/dao02488.

492 Shore A, Caldwell JM. 2019. Modes of coral disease transmission: how do diseases spread
493   between individuals and among populations? Marine Biology 166:1–14. DOI:
494   10.1007/s00227-019-3490-8.

495 Suchley A, Alvarez-Filip L. 2018. Local human activities limit marine protection efficacy on
496   Caribbean coral reefs. *Conservation Letters* 11:1–9. DOI: 10.1111/conl.12571.

497 Sutherland KP, Porter JW, Turner JW, Thomas BJ, Looney EE, Luna TP, Meyers MK, Futch JC,
498   Lipp EK. 2010. Human sewage identified as likely source of white pox disease of the
499   threatened Caribbean elkhorn coral, Acropora palmata. *Environmental Microbiology*. DOI:
500   10.1111/j.1462-2920.2010.02152.x.

501 van Tussenbroek BI, Hernández Arana HA, Rodríguez-Martínez RE, Espinoza-Avalos J,
502   Canizales-Flores HM, González-Godoy CE, Barba-Santos MG, Vega-Zepeda A, Collado-
503   Vides L. 2017. Severe impacts of brown tides caused by Sargassum spp. on near-shore
504   Caribbean seagrass communities. Marine Pollution Bulletin 122:272–281. DOI:
505   10.1016/j.marpolbul.2017.06.057.

506 van Woesik R, McCaffrey KR. 2017. Repeated Thermal Stress, Shading, and Directional
507   Selection in the Florida Reef Tract. *Frontiers in Marine Science*. DOI:
508   10.3389/fmars.2017.00182.

509 Vega Thurber RL, Burkepile DE, Fuchs C, Shantz AA, Mcminds R, Zaneveld JR. 2014. Chronic
510   nutrient enrichment increases prevalence and severity of coral disease and bleaching.
511   *Global Change Biology*. DOI: 10.1111/gcb.12450.

512 Walton CJ, Hayes NK, Gilliam DS. 2018. Impacts of a Regional, Multi-Year, Multi-Species
513   Coral Disease Outbreak in Southeast Florida. *Frontiers in Marine Science* 5. DOI:
514   10.3389/fmars.2018.00323.

515 Weil E. 2004. Coral Reef Diseases in the Wider Caribbean. In: *Coral Health and Disease*. DOI:
516   10.1007/978-3-662-06414-6_2.

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518

519 **Figure legends**

520

521 **Figure 1**. Susceptible species affected by Stony Coral Tissue Loss Disease during the outbreak.
522 A) Two colonies of *Pseudodiploria strigosa* observed the 3rd of July, 2018 at a fore-reef reef site
523 in Puerto Morelos, Mexico. One colony (front) shows the classic symptoms of the Stony Coral
524 Tissue Loss Disease, while the other one died shortly before the photo was taken (recent and
525 transient mortality). A Foureye butterflyfish (*Chaetodon capistratus*) is feeding on the edge of
526 the lesion on the colony at the front. B) Diseased colony of *Montastraea cavernosa* in direct

527   contact with an apparently healthy colony of the same species in Cozumel observed in Cozumel
528   the 3rd of July, 2019. The close-up shows the touching-boundaries between the two colonies.
529   Photo credits: Lorenzo Álvarez-Filip.
530
531   **Figure 2.** Prevalence of the Stony Coral Tissue Loss Disease for the 11 most susceptible species
532   across 82 reef sites in the Mexican Caribbean (n = number of colonies). For this figure, we
533   include coral colonies with total mortality but for which death could be attributable to the
534   SCTLD (exposed bright white skeletons; see Fig. 1).
535
536   **Figure 3.** Prevalence of the Stony Coral Tissue Loss Disease in the Mexican Caribbean. Dots
537   represent the location of the 82 surveyed reefs and the colours represent the SCTLD prevalence
538   for the 11 most afflicted species (see methods and Fig. 2). Data on this figure was collected by
539   the Healthy Reefs Initiative, the Comisión Nacional de Áreas Naturales Protegidas (Mexican
540   Commission for Protected Areas; CONANP) and the Biodiversity and Reef Conservation
541   Laboratory, UNAM. Please note that reef sites were surveyed at different times (between July
542   2018 and April 2019).
543
544   **Figure 4.** Disease prevalence of the 11 most susceptible species to the Stony Coral Tissue Loss
545   Disease (STCLD) from 2005/2006 to 2018/2019 in the Mexican Caribbean. From 2009 to 2014
546   black-band disease was the most abundant coral disease and was mainly recorded in *Siderastrea*
547   *siderea* in Cozumel.
548
549   **Figure 5.** Proportion of healthy, afflicted and dead colonies of the highly susceptible species in
550   2016/2017, before the onset of the Stony Coral Tissue Loss Disease Outbreak (SCTLD) in the
551   Mexican Caribbean, and in 2018/2019 when the SCTLD was spread across many sites in the
552   region.
553
554   **Figure 6.** Coral community composition for the study sites before and after the disease. Non-
555   metric multi-dimensional scaling (nMDS) analysis displaying degree of similarity of the
556   community composition across 14 sites in the Mexican Caribbean for the coral cover by species.
557   The blue color represent the sites before the disease (2016-2017) and the grey color represent the
558   sites after the disease (2018-2019). The circles represent the back-reef sites and the triangles the
559   fore-reef sites. Dotted lines: convex hull total area (TA). Solid lines: standard ellipse area
560   corrected for small sample sizes (SEAc).
561

Figure 1

Susceptible species affected by Stony Coral Tissue Loss Disease during the outbreak

A) Two colonies of *Pseudodiploria strigosa* observed the 3rd of July, 2018 at a fore-reef reef site in Puerto Morelos, Mexico. One colony (front) shows the classic symptoms of the Stony Coral Tissue Loss Disease, while the other one died shortly before the photo was taken (recent and transient mortality). A Foureye butterflyfish (*Chaetodon capistratus*) is feeding on the edge of the lesion on the colony at the front. B) Diseased colony of*Montastraea cavernosa*in direct contact with an apparently healthy colony of the same species in Cozumel observed in Cozumel the 3rd of July, 2019. The close-up shows the touching-boundaries between the two colonies. Photo credits: Lorenzo Álvarez-Filip.

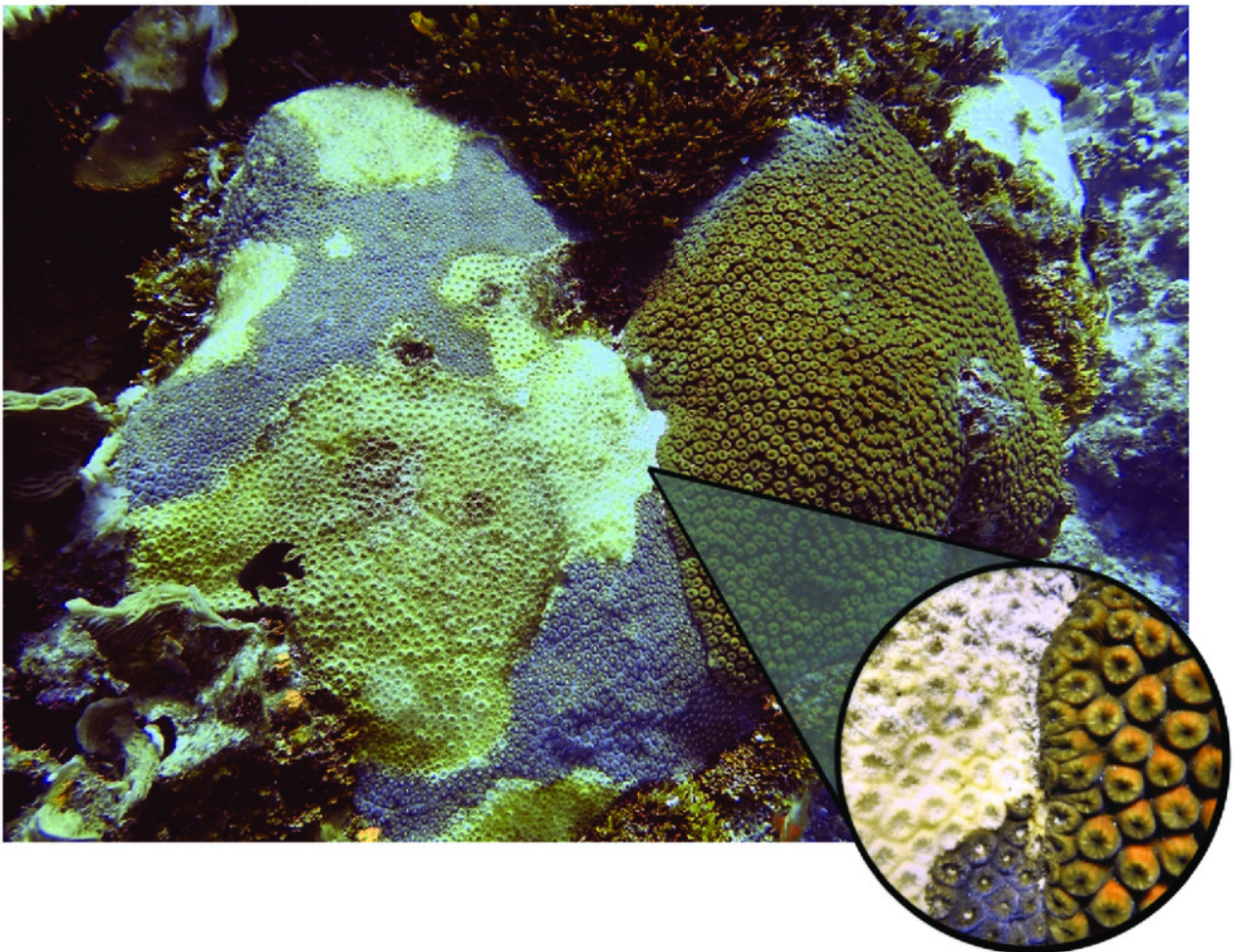



Figure 2

Prevalence of the Stony Coral Tissue Loss Disease for the 11 most susceptible species across 82 reef sites in the Mexican Caribbean (n = number of colonies).

For this figure, we include coral colonies with total mortality but for which death could be attributable to the SCTLD (exposed bright white skeletons; see Fig. 1).

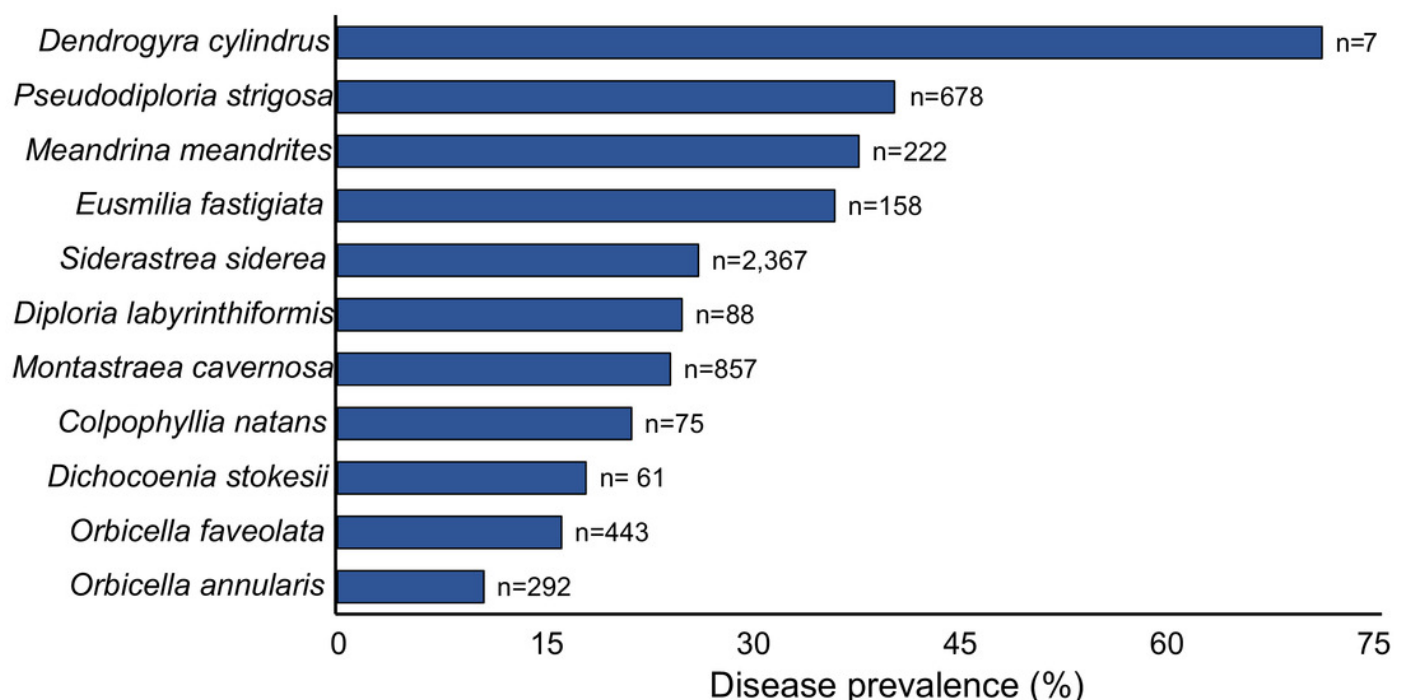
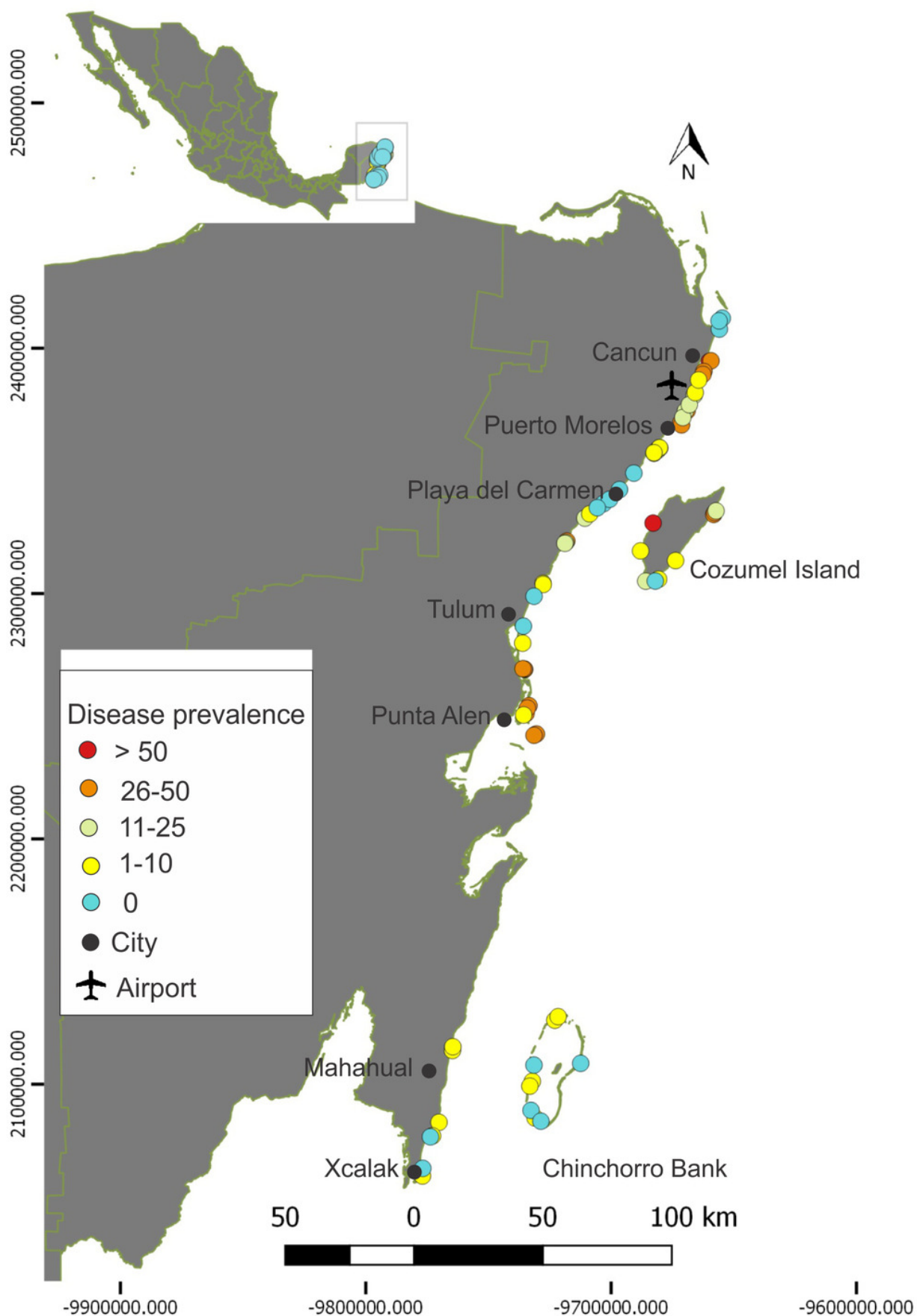



Figure 3

Prevalence of the Stony Coral Tissue Loss Disease in the Mexican Caribbean.

Dots represent the location of the 82 surveyed reefs and the colours represent the SCTLD prevalence for the 11 most afflicted species (see methods and Fig. 2). Data on this figure was collected by the Healthy Reefs Initiative, the Comisión Nacional de Áreas Naturales Protegidas (Mexican Commission for Protected Areas; CONANP) and the Biodiversity and Reef Conservation Laboratory, UNAM. Please note that reef sites were surveyed at different times (between July 2018 and April 2019).

Disease prevalence

- 🔴 > 50
- 🟠 26-50
- 🟡 11-25
- 🟡 1-10
- 🔵 0
- ⚫ City
- ✈ Airport

Cancun

Puerto Morelos

Playa del Carmen

Cozumel Island

Tulum

Punta Alen

Mahahual

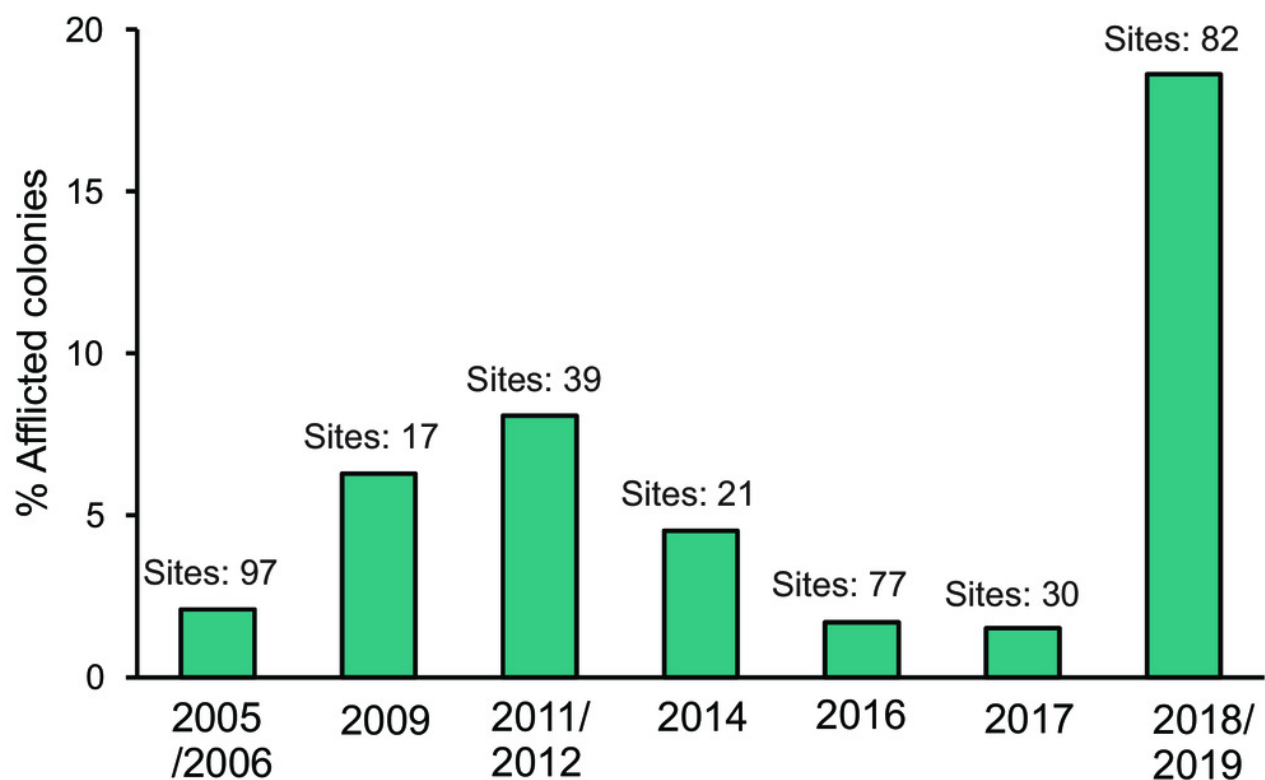
Xcalak

Chinchorro Bank

50   0   50   100 km

Figure 4

Disease prevalence of the 11 most susceptible species to the Stony Coral Tissue Loss Disease (STCLD) from 2005/2006 to 2018/2019 in the Mexican Caribbean.

From 2009 to 2014 black-band disease was the most abundant coral disease and was mainly recorded in *Siderastrea siderea* in Cozumel.

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Proportion of healthy, afflicted and dead colonies of the highly susceptible species in 2016/2017, before the onset of the Stony Coral Tissue Loss Disease Outbreak (SCTLD) in the Mexican Caribbean, and in 2018/2019 when the SCTLD was spread across many si
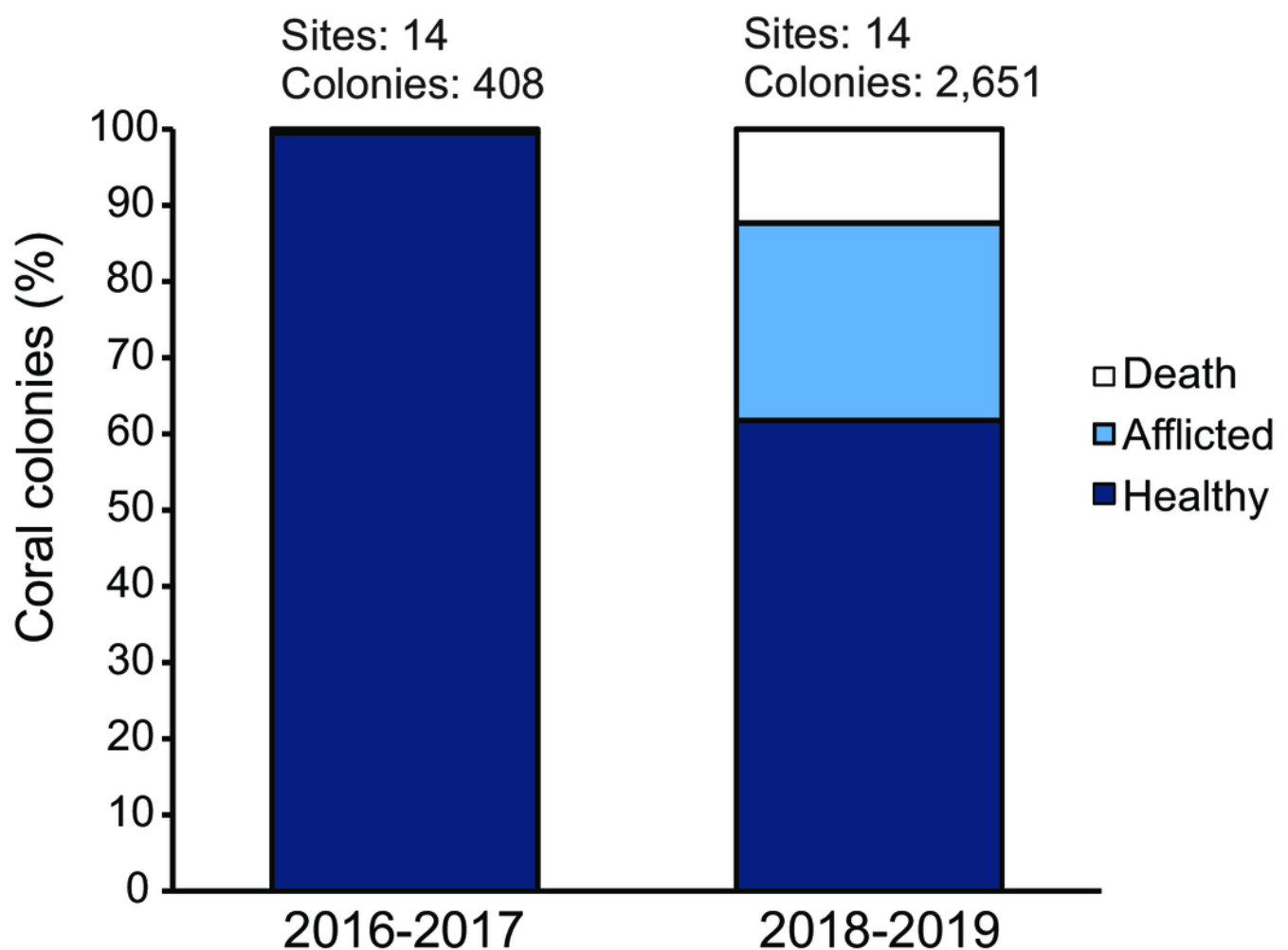
Figure 6

Coral community composition for the study sites before and after the disease.

Non-metric multi-dimensional scaling (nMDS) analysis displaying degree of similarity of the community composition across 14 sites in the Mexican Caribbean for the coral cover by species. The blue color represent the sites before the disease (2016-2017) and the grey color represent the sites after the disease (2018-2019). The circles represent the back-reef sites and the triangles the fore-reef sites. Dotted lines: convex hull total area (TA). Solid lines: standard ellipse area corrected for small sample sizes (SEAc).