Microphytoplankton variations during coral spawning at Los Roques, southern-Caribbean

Francoise Cavada-Blanco, Ainhoa L Zubillaga, Carolina Bastidas

Phytoplankton drives primary productivity in marine pelagic systems. This is also true for the oligotrophic waters in coral reefs, where natural and anthropogenic sources of nutrients can alter pelagic trophic webs. In this study, microphytoplankton assemblages were characterized for the first time in relation to expected coral spawning dates in the Caribbean. A hierarchical experimental design was used to examine these assemblages in Los Roques archipelago, Venezuela, at various temporal and spatial scales for spawning events in both 2007 and 2008. At four reefs, superficial water samples were taken daily for 9 days after the full moon of August, including days before, during and after the expected days of coral spawning. Microphytoplankton assemblages comprised 100 microalgae taxa at up to 50 cells per mL (mean ± 8 SD) and showed temporal and spatial variations related to the coral spawning only in 2007. However, chlorophyll *a* concentrations increased during and after the spawning events in both years, and this was better matched with analyses of higher taxonomical groups (diatoms, cyanophytes and dinoflagellates), that also varied in relation to spawning times in 2007 and 2008, but asynchronously among reefs. Heterotrophic and mixotrophic dinoflagellates increased in abundance, correlating with a decrease of the diatom *Cerataulina pelagica* and an increase of the diatom *Rhizosolenia imbricata*. These variations occurred during and after the coral spawning event for some reefs in 2007. For the first time, a fresh-water cyanobacteria species of *Anabaena* was ephemerally found (only 3 days) in the archipelago, at reefs closest to human settlements. Variability among reefs in relation to spawning times indicated that reef-specific processes such as water residence time, re-mineralization rates, and benthic-pelagic coupling can be relevant to the observed patterns. These results suggest an important role of microheterotrophic grazers in re-mineralization of organic matter in coral reef waters and highlight the importance of assessing compositional changes of larger size fractions of the phytoplankton when evaluating primary productivity and nutrient fluxes.

1   **Microphytoplankton variations during coral spawning at Los Roques, southern-**

2   **Caribbean**

3   Francoise Cavada-Blanco[1]*, Ainhoa L. Zubillaga[2], Carolina Bastidas[2,3]

4   [1]Laboratorio Conservación Marino-Costera, Departamento de Estudios Ambientales,

5   Universidad Simón Bolívar, Caracas, Venezuela

6   [2]Laboratorio de Ecotoxicología y Comunidades Marinas, Departamento de Biología de

7   Organismos, Universidad Simón Bolívar, Caracas, Venezuela

8   [3]Current address: MIT Sea Grant College Program, Cambridge MA, USA

9   **Correspondence:**

10   Msc.   Francoise   Cavada-Blanco,   Laboratorio   de   Conservación   Marino-Costera,

11   Departamento de Estudios Ambientales, Universidad Simón Bolívar, PA4-013, Carretera El

12   Placer-Hoyo de La Puerta, Baruta, Edo. Miranda 9800, Venezuela.

13   fcavada@usb.ve

14   **Abstract**

15   Phytoplankton drives primary productivity in marine pelagic systems. This is also true for

16   the oligotrophic waters in coral reefs, where natural and anthropogenic sources of

17   nutrients can alter pelagic trophic webs. In this study, microphytoplankton assemblages

18   were characterized for the first time in relation to expected coral spawning dates in the

19   Caribbean. A hierarchical experimental design was used to examine these assemblages in

20   Los Roques archipelago, Venezuela, at various temporal and spatial scales for spawning

21   events in both 2007 and 2008. At four reefs, superficial water samples were taken daily for

22   9 days after the full moon of August, including days before, during and after the expected

23   days of coral spawning. Microphytoplankton assemblages comprised 100 microalgae taxa

24   at up to 50 cells per mL (mean ± 8 SD) and showed temporal and spatial variations related

25   to the coral spawning only in 2007. However, chlorophyll *a* concentrations increased

26   during and after the spawning events in both years, and this was better matched with

27   analyses of higher taxonomical groups (diatoms, cyanophytes and dinoflagellates), that also

28 varied in relation to spawning times in 2007 and 2008, but asynchronously among reefs.

29 Heterotrophic and mixotrophic dinoflagellates increased in abundance, correlating with a

30 decrease of the diatom *Cerataulina pelagica* and an increase of the diatom *Rhizosolenia*

31 *imbricata*. These variations occurred during and after the coral spawning event for some

32 reefs in 2007. For the first time, a fresh-water cyanobacteria species of *Anabaena* was

33 ephemerally found (only 3 days) in the archipelago, at reefs closest to human settlements.

34 Variability among reefs in relation to spawning times indicated that reef-specific processes

35 such as water residence time, re-mineralization rates, and benthic-pelagic coupling can be

36 relevant to the observed patterns. These results suggest an important role of

37 microheterotrophic grazers in re-mineralization of organic matter in coral reef waters and

38 highlight the importance of assessing compositional changes of larger size fractions of the

39 phytoplankton when evaluating primary productivity and nutrient fluxes.

40 **1.   Introduction**

41 Phytoplankton drives the energy flow in most marine ecosystems as they are the main

42 primary producers in environments where sufficient light allows for photosynthetic

43 fixation of carbon (C) (Reynolds, 2006). In coral reefs, this productivity appears to be

44 limited by nitrogen (N), as reef waters usually have minimal macronutrient concentrations

45 (Charpy-Roubaud 1990; Furnas et al., 1990; Dizon & Yap, 1999; Koop et al., 2001; Heil et

46 al., 2004). Nutrients and organic compounds enter the typically oligotrophic waters of coral

47 reefs constantly through different pathways, from either natural or anthropogenic sources

48 (Wild et al., 2004; Wolanski et al., 2004; Mumby et al,. 2007; Hoegh-Guldberg et al., 2007).

49 For instance, various recirculation processes in reefs drive fluxes of submarine

50 groundwater that might transfer in-land nitrogen into the reefs (Santos et al., 2010). Other

51 natural processes, such as mucus release by corals as well as massive or multi-specific coral

52 spawning events, also represent influxes of labile organic compounds, from which the

53 composition and amount of organic matter released into the water column varies greatly in

54 space and time (Coffroth 1990, 1991; Wild et al., 2004). Anthropogenic sources of nutrients

55 are often derived from land-based pollution, such as coastal development and agriculture

56 on watersheds, among other activities (Burke et al., 2011).

57 Regardless of the source, a surplus of organic or inorganic nutrients in coral reefs can alter

58 the ecosystem biogeochemistry and both the pelagic and benthic food webs (Koop et al.,

59 2001; Eyre et al., 2008). For example, dissolved inorganic nutrients seem to be rapidly

60 incorporated by the phytoplankton (Fabricius et al., 2013), but chronic inputs might lead to

61 higher oxygen demand, through phyto-, bacterio- and zooplankton overgrowth and

62 decomposition (Lapointe & Clark, 1992). Nutrient addition is a well-documented driver of

63 taxonomical and biomass changes in marine phytoplankton assemblages (Piehler et al.,

64 2004; Furnas et al., 2005; Howardth & Marino, 2006; Pirela-Ochoa et al., 2008; Strom,

65 2008; Mutshinda et al., 2013). Seasonal changes in phytoplankton composition in

66 oligotrophic ocean waters, upwelling sites and coastal waters in response to both organic

67 and inorganic nutrient inputs have been reported round the world (Casas et al., 1997; Bode

68 et al., 2001; Oguz et al., 2001; Vuorio et al., 2005; Wu et al., 2005; Harris, 2012).

69 In coral reefs, phytoplankton is dominated by small-size fractions (<2 μm) such as the

70 cyanobacteria *Synechococcus* and *Prochlorococcus* (Furnas & Mitchell 1989; Furnas et al.,

71 2005). This small-size fraction has been the focus of studies into the response of pelagic

72 primary producers to coral spawning events, as this response has been mainly evaluated

73 using biomass and pigment concentrations (Eyre et al., 2008; Glud et al., 2008; Wild et al.,

74 2008; Apprill & Rappé, 2011; Patten et al., 2011). However, species of larger sizes (i.e.

75 nano- and microphytoplankton: 2 to 200 μm), especially diatoms, also increase their

76 primary production with nutrient inputs in coral reefs (Furnas, 1991; Crosbie & Furnas,

77 2001). As a result of nutrient input and cell division, larger sizes achieve greater

78 abundances in shallow waters than in oceanic waters (Duyl et al., 2002); suggesting that

79 these microalgae might also play an important role in nutrient uptake and pelagic trophic

80 webs in coral reefs.

81 For example, a nutrient input after a typhoon that occurred in a reef in French Polynesia,

82 was followed by an increase in phytoplankton biomass and primary productivity, and by a

83 change in taxonomic composition of the microphytoplankton (Delesalle et al., 1993). Also,

84 Glud et al. (2008) reported a dinoflagellate bloom in a reef flat after a coral spawning in the

85 Great Barrier Reef; and Horne (2011) detected an increased abundance of the

86 dinoflagellate *Ceratium* spp. 2 days after a spawning event in the Gulf of Mexico. As coral

87   spawning events constitute an input of nutrients in coral reefs (Wild et al., 2004b; Eyre et
88   al., 2008; Glud et al., 2008; Wild et al., 2008; Patten et al., 2011), and growth of various
89   microphytoplankton groups is nitrogen limited (Hauss et al., 2012), it would be expected
90   that this input of nutrients affects the abundance and composition of larger size fraction.
91   Coral spawning events have been used as large natural experiments to understand the
92   effects of an episodic organic matter input on phytoplankton primary productivity and
93   biomass in coral reef systems (Wild et al., 2001, 2004b, 2008; Eyre et al., 2008; Glud et al.,
94   2008; Patten et al., 2011; Apprill & Rappé 2011). After coral spawning, Wild et al. (2004)
95   reported an increase in sediment oxygen demand and Glud et al. (2008) found an increased
96   pelagic and benthic primary production. Similarly, Eyre et al. (2008) showed a post-
97   spawning peak in phytoplankton biomass coinciding with the removal of dissolved
98   inorganic nutrients and changes in nitrogen cycling on the top layer of the sediment.
99   Nutrient additions through mass coral spawning events are thus expected to drive changes
100   in the nitrogen and phosphorous concentrations, and consequently have effects on
101   autotrophic and heterotrophic communities on reefs.
102   Reproductive timing of most common coral species in the Caribbean is well known
103   (Szmant, 1986; Bak & Engle, 1979; Fadlallah, 1983; deGraaf et al., 1999; Budd, 1990;
104   Bassim et al., 2002; Carlon, 2002, Brooke & Young, 2003; Beaver et al., 2004; Bastidas et al.,
105   2005; Severance & Karl, 2006); however, the effects of this event on the reef´s pelagic
106   trophic web have not yet been documented in the region. To contribute to this knowledge,
107   herein we describe changes on the composition and abundance of the microphytoplankton
108   assemblages at various spatial and temporal scales at Los Roques, Venezuela during 2007
109   and 2008 coral spawning events. As Los Roques is an oceanic archipelago with a marginal
110   and local source of anthropogenic nutrients, expected coral spawning dates are a good
111   opportunity to assess the effects of a natural source of organic nutrients on the
112   composition and abundance of microphytoplankton separately from those of human
113   sources.

114   **2.   Materials and Methods**
115   **2.1.   Study Site**

116 Los Roques National Park is the most important reef complex in Venezuela, as well as in the
117 Southern Caribbean (Casanova et al., 2007). Los Roques is located 160 km north of the
118 coast (66.55-66.95 W 11.65-11.98 N; Fig. 1), and the archipelago encompasses more than
119 50 coralline cays that are protected from wave exposure by two barrier reefs: the eastern
120 barrier and the southern barrier, which are 20 km and 30 km long, respectively (Méndez-
121 Baamonde, 1978). Los Roques was the first marine area in Venezuela to be protected under
122 the category of National Park and is part of the southern corridor, one of the most
123 important areas in the Caribbean region in terms of biodiversity and extension (Rodríguez-
124 Ramírez, 2008). The human population at Los Roques (approximately 2,000) is
125 concentrated in the Northeast, specifically on Gran Roque. In the Southwest there is no
126 permanent settlement and it is relatively less affected by recreational and fishing activities;
127 thus, anthropogenic nutrient sources in the archipelago are marginal when compared with
128 coastal reefs. Studies on biological and physicochemical oceanography are scarce and
129 limited at Los Roques, however there have been studies describing temporal variability in
130 zooplankton and phytoplankton composition and abundance at one or two reefs (González,
131 1989; Spiniello, 1996, Madera & Furderer, 1997), and a seasonal variation has been found
132 in relation to the drought (November-July) and rain (May-October) regimes.

133 **2.2.   Sample Collection**

134 To assess variations in microphytoplankton assemblages in relation to coral spawning at
135 Los Roques, a hierarchical design was employed considering the following factors: 1)
136 Locality (fixed, crossed with two levels: Northeast (NE) and Southwest (SW); 2) Reef
137 (random, nested in locality with two levels: Gran Roque (GR) and Madrizquí (MD) on the
138 NE and Dos Mosquises (DMS) and Cayo de Agua (CYA) on the SW); and 3) Period (fixed,
139 crossed with three levels: before, during and after the expected spawning dates). The
140 samples were taken from a motor boat by gently submerging a sterile 1,000 mL plastic
141 bottle in the water down to ~0.5 to 1 m depth until filled. Samples were taken by two
142 different teams at approximately the same hour (9:00-10:00 a.m.) in the NE and SW reefs,
143 while samples were collected less than one hour apart between reefs of the same locality.
144 The samples were then fixed with 10% formalin, stabilized with sodium tetraborate and
145 closed with a sealed cap. Samples were transported to the laboratory and stored in a cold
146 dark place until analysis. Four replicate samples were taken daily for 9 consecutive days

147   after the full moon of August 2007 and 2008 on the basis of the expected dates of

148   spawning. Expected dates for the first coral species that start spawning in these multi-

149   specific events (i.e., 2 to 4 days after the full moon of August and September, Szmant, 1986)

150   marked the end of the "Before" and the start of the "During" sampling period. These dates

151   are specified for each period and year in Table 1 and were chosen based on extensive

152   observations of coral spawning dates in the Caribbean (e.g. Van Veghel, 1994, Szmant et al.,

153   1997; Sánchez et al., 1999; Mendes & Woodly, 2002) and in our study site (Bastidas et al.,

154   2005).

155   The presence of *Acropora palmata* larvae in the water during the sampling period of this

156   study was further corroborated through specific antibody signals (Zubillaga, 2010). Briefly,

157   the procedure consisted of three steps: (1) inoculation of an *Acropora palmata* larvae into

158   rabbits; these larvae were harvested in the laboratory from bundles collected from *A.*

159   *palmata* colonies in the field during a spawning event in 2006; (2) extraction of antibodies

160   from rabbit´s blood samples and (3) immunological assays based on ELISA (Enzyme Linked

161   Inmunoabsorbent Assay) to test for specificity and accuracy of the antibodies (Zubillaga

162   2010). The presence of larvae in water samples was detected using a spectrophotometer

163   that measured the colorimetric product of the enzymatic reaction between the antibodies

164   and the coral larvae (Zubillaga 2010). This method was preferred over direct counts due to

165   the superior overall accuracy it has for identifying coral larval species (Carlon & Olson,

166   1993; Coffroth & Mulawka, 1995; Garland et al., 2002).

167   **TABLE 1.** Sampling dates for the Before, During and After periods of coral spawning at Los
168   Roques, according to the expected dates for the first coral species (*Acropora palmata* and *A.*
169   *cervicornis*) that start spawning in these multi-specific events

2007		2008	
Period	**Date**	**Period**	**Date**
Before	August 28th-30th	Before	August 16th-18th
During	August 31st-September 2nd	During	August 19th-21st
After	September 3rd-5th	After	August 22nd-24th

170

171   **2.3.   Environmental variables**

172   Surface Sea Water Temperature (SST) and chlorophyll *a* (Chl*a*) concentration (mg/m^3)

173   were obtained for the sampling dates by satellite image analysis (MODIS SCAR; Klein &

174   Castillo, 2010). For this, centroids of the image cells (1 Km x 1 Km spatial resolution) that

175   contained the sampling sites were used to download historical data. No neighbour pixels

176   were used to obtain values of both environmental variables. Due to the proximity between

177   MD and GR, these sampling sites in the northeast fell within the same pixel and thus, SST

178   and Chl*a* had the same values for these reefs.

179   **2.4. Sample Processing and Data Analysis**

180   Microalgae from the water column were identified to the lowest possible taxonomic level

181   using a Leika D MIL inverted contrast microscope. Samples were analyzed after 48 h of

182   sedimentation in a 100 mL settling chamber. The settlement periods were used according

183   with the Utermöhl method for oceanic/oligotrophic samples referred to in Hasle (1978).

184   Phase contrast was used on the same sample to enhance cell detection. Magnification

185   power used for microalgae detection (all fields were viewed) was 200x; however, 400x and

186   1000x magnifications were used for identification. The abundance of microalgae species

187   was calculated using the same protocol, based on the volume of the sample taken.

188   Identification to the lowest possible taxonomic level was performed using Peragallo &

189   Peragallo (1897-1908), Cupp (1943), Saunders y Glenn (1969), Ferguson (1968), Marshall

190   (1986), La Barbera (1984, 1993), Sournia (1973, 1986), Sánchez-Suárez (1992, a,b), Tomas

191   (1997), Berárd-Therriault et al. (1999), Díaz-Ramos (2000) and Krayesky et al. (2009).

192   Microalgae species were grouped into diatoms, dinoflagellates, chlorophytes, cyanophytes

193   and coccolithophores and, based on previous work (Jeong, 1994; Jeong & Latz, 1994; Jeong

194   et al.. 2004, 2005a, 2005b, 2005c, 2007, 2008, 2010, Du Yoo et al., 2009; Seong et al., 2010),

195   dinoflagellate species were further classified according to trophic functional groups into

196   obligate autotrophic, mixotrophic and heterotrophic species.

197   Shannon diversity index with natural log base were calculated for every sample to facilitate

198   comparisons among the spatial and temporal scales examined (Magurran, 2004).

199   Microphytoplankton community structure was analysed through the attributes richness

200   and abundance (based on the Bray-Curtis index), and composition (based on the Jaccard

201   index). Dissimilarity matrices for both indexes were constructed from the original

202   biological data matrices. Non-metric multidimensional ordination (nMDS) was performed

203   to aid the visualization of temporal patterns and spatial distributions of the samples in

204   terms of the microphytoplankton assemblage. When appropriate, centroids were used to

205 illustrate these patterns. Null hypotheses of no differences in the abundance and
206 composition, as well as the diversity of microphytoplankton, were tested using
207 permutational multivariate analysis of variance (PER-MANOVA, Anderson, 2001). When
208 significant differences (P(perm) <0.05) were found for certain factors or interaction terms,
209 species contributing to at least 60% of the variability between levels of the terms were
210 identified using the SIMPER routine (Clark & Warwick, 2001). Univariate ANOVAs were
211 performed on the species or taxa selected by the SIMPER routine, and *a posteriori* pair-wise
212 comparisons were performed between levels of the terms with p-values under a 0.05 alpha
213 value. These analyses were performed using PRIMER-E v6 software (Clarke & Gorley,
214 2006)

215 **3.   Results**

216 A total of 100 taxa of microalgae were identified from the water samples; 91 were
217 identified for 2007, 51 for 2008 and 42 were common to both years (Supplementary
218 Material Table 1). Taking both years into account, the most abundant group were the
219 diatoms (Bacillariophyceae), which represented 62% of the microalgae, followed by
220 dinoflagellates (Dinophyceae, 25.4%), and Cyanophytes (Cyanophyceae, 8%).
221 Coccolithophores (Haptophytes) and Chlorophytes represented less than 5% of the total
222 abundance. This two-year trend of group abundances hold true for all reefs in 2008, but in
223 2007, cyanophytes reached highest densities of 43 cells per mL at the NE reefs only (Fig. 2).
224 Most species of diatoms identified (62% of all counted diatoms) were small (6-10 and 16-
225 20 μm), oceanic taxa from the genera *Nitzschia*, *Pseudo-nitzschia*, *Paralia* and *Thalassiosira*.
226 Most taxa of dinoflagellates (48% of the counted cells) were 16-20 μm in size (Fig. 3). The
227 coccolithophores were represented only by the species *Emiliana huxleyi*.

228 Microphytoplankton abundance ranged between 0.26 ± 0.06 and 49.12 ± 8.37 cells per mL
229 (Mean ± SD) across reefs, years and spawning times. Since the variability between years
230 was high (94% of the variance explained, PERMANOVA table not shown), the
231 microphytoplankton assemblages were analyzed separately for each year to evaluate the
232 effect of the other factors examined. For both years, dissimilarity in microphytoplankton
233 abundance and composition was observed between localities (NE or solid vs. SW or empty
234 symbols in Fig. 4), however, most of the variation in assemblage structure occurred
235 between reefs, particularly in 2008 (Table 2). When considering all taxa, the

236 microphytoplankton assemblage showed little variation in structure among time periods

237 related to coral spawning (see low variation coefficients for the interaction

238 Reef(Locality)xPeriod, Table 2). Contrasting with this weak response from the

239 microphytoplankton structure, Shannon diversity indexes differed significantly among the

240 spawning times in 2007 (Pseudo-F: 2.37, p=0.042) despite, variability between replicate

241 samples being above 60% (Fig. 5). Taxa diversity differed between the spawning times in

242 NE reefs. At MD, there were differences Before and During spawning times (*a posteriori*

243 pairwise comparisons t=2.16, p=0.04) and at GR, between the During and After periods

244 (t=1.97, p=0.049). In 2008, diversity was similar among spawning times but varied

245 significantly among reefs as in 2007 (Pseudo-F: 10.18, p=0.001). In this case, diversity was

246 lowest at CYA, a SW site, compared with the other reefs (t=1.56, p=0.049, respectively; Fig.

247 5).

248 **TABLE 2.** PER-MANOVA based on the Bray–Curtis dissimilarities (no transformation) of
249 the multivariate abundance of microalgae (102 taxa); on two reefs (random, nested) in the
250 Northeast and two reefs in the Southwest ("Locality", fixed) of Los Roques, during, before
251 and after ("Period", fixed) coral spawning events in 2007 (A) and 2008 (B). The same
252 results were obtained for composition (Jaccard index based PERMANOVA) but are not
253 shown.
254 **(A)**

Source of Variation	d.f.	MS	Pseudo-F	P(perm)	VC (%)
Locality	1	20104	3.0056	0.1664	4.88
Period	2	2530.7	0.98108	0.4854	0.00
Reef (Lo)	2	6690.3	3.3611	0.0001*	3.42
LoxPE	2	2393.5	0.9279	0.5254	0.00
Re[Lo]xPE	4	2579.7	1.296	0.07	1.28
Residuals	240	1990.5			90.43
Total	251				

255 **(B)**

Source of Variation	d.f.	MS	Pseudo-F	P(perm)	VC (%)
Locality	1	9933.6	1.3887	0.336	2.78
Period	2	501.9	0.79077	0.5737	0.00

Reef(Lo)	2	7153.3	12.299	0.0001*	13.14
LoxPE	2	501.9	0.79077	0.5724	0.00
Re[Lo]xPE	4	634.7	1.0912	0.3085	0.32
Residuals	276	581.62			83.76
Total	287				

256 Lo: Locality; PE: Period of spawning times; Re: Reefs; Df: Degree of freedom; MS: Mean
257 Square; VC: Variation Coefficient; P: probability of obtaining a Pseudo-F value similar to the
258 ones calculated when actually there is no difference between the levels of the factors
259 evaluated; *: P(perm) < 0.05

260 Variations in microphytoplankton with respect to coral spawning times (Period) were
261 more evident when analyzed by higher taxonomic groups instead of all taxa. The structure
262 of diatoms, dinoflagellates and cyanophytes differed between reefs for both years, and
263 some of these assemblages differed among spawning times at specific reefs (Table 3). In
264 particular, the structure of dinoflagellates (Pseudo-F=3.93, p=0.001) and its trophic groups
265 (Pseudo-F=8.12, p= 0.001) differed significantly between spawning times (periods) for
266 some reefs in 2007 (Fig. 6). Also in 2007, the assemblage of cyanophytes differed After the
267 coral spawning at NE reefs (Pseudo-F=2.14, p=0.032), when the coccoid, filamentous and
268 the nostocal *Anabaena* sp. peaked in an episodic manner. On the other hand, the
269 oscillatorial cyanophytes *Lyngbya* and *Spyrogira* were identified only at Dos Mosquises (a
270 SW reef) on the dates of expected coral spawning. While variations in dinoflagellates and
271 cyanophytes assemblages occurred in relation to spawning times in 2007, diatoms
272 assemblage only differed spatially among reefs for both 2007 and 2008 (Pseudo-F=2.048,
273 p=0.05 and Pseudo-F=1.75, p=0.003, respectively).
274 Most of the dissimilarity in the assemblage of dinoflagellates among spawning times in
275 2007 (>70% according to the SIMPER routine) was due to variations in the presence of the
276 heterotrophic taxa *Protoperidinium* sp., *P. thorianum*, *P. minutum*, *P. excentricum*, *P.
277 conicoides*, *P. pyriforme*, and the mixotrophic species *Neoceratium lineatum* and *Scrippsiella
278 trochoidea* (Supplementary Materials Table 2). For each of these taxa, the univariate
279 PERMANOVAs showed a significant difference among spawning time periods at MD and at
280 DMS (a NE reef and a SW reef, respectively). At the SW reefs, the density of mixotrophic
281 species decreased towards the After period of the spawning times, while the heterotrophic

282 species increased (Fig. 6). At the NE reefs, the abundance of heterotrophic species also
283 increased After the spawning, whereas the mixotrophic species showed an opposite
284 pattern to the SW reefs as it increased in abundance. This pattern within locality (NE and
285 SW) was consistent for all reefs in 2007 (Fig. 6). Correlations between the abundance of
286 trophic groups were negative and low (≤ 30%), with the exception of mixotrophic and
287 obligate autotrophs dinoflagellates (64.3%), although this was not statistically significant.
288 In 2008, dinoflagellates as well as its trophic groups differed only at reefs scales (i.e. GR,
289 MD, CYA, DMS), since 95% of their abundances occurred at the NE reefs where mixotrophic
290 species peaked (Fig. 6).

291 **TABLE 3.** Statistically significant (p<0.05) results from the PER-MANOVA analysis, based
292 on the Bray–Curtis dissimilarities (no transformation) of the univariate abundance of
293 microalgae taxonomic and trophic groups; on two reefs (random, nested) in the Northeast
294 and two reef in the Southwest ("Locality", fixed) of Los Roques, during, before and after
295 ("Period", fixed) coral spawning events in 2007 and 2008.

	Source of Variation	Diatoms	Dinoflagellates	DTG	Cyanophytes
2007	Locality (Lo)				
	Period (PE)		*	*	
	Reef[Lo]	*			
	LoxPe				
	Re[Lo]xPe		*	*	*
2008	Locality (Lo)				
	Period (PE)				
	Reef[Lo]	*	*		
	LoxPe				
	Re[Lo]xPe				

296 *: P(perm)<0.05; DTG: Dinoflagellate trophic groups

297 For diatoms, more than 98% of the dissimilarity between the reefs in both years (SIMPER
298 analysis) was due to variation in the presence and abundance of *Aptinoptychus* sp.,
299 *Aulacoseria*, *Cerataulina pelagica*, *Thalassiosira subtilis*, *Rhizosolenia imbricata* and *Melosira*
300 *varians*. In 2007, significant differences on the abundance of *C. pelagica*, *T. subtilis* and *R.*

301 *imbricata* occurred between reefs and between periods for *R. imbricata* and *C. pelagica* on

302 SW reefs. *Cerataulina pelagica* was more abundant in the SW reefs, whereas *T. subtilis* was

303 only identified on NE reefs. Significant correlations between the abundance of these

304 diatoms and dinoflagellates trophic groups were found for SW reefs. Here, in 2007, *C.*

305 *pelagica* abundance was negatively and weakly correlated (r2=-0.24; p=0.055) with that of

306 the mixotrophic dinoflagellate *Scripsiella trochoidea*, and positively correlated with that of

307 heterotrophic dinoflagellates of the genus *Protoperidinium* (r2=0.77; p=0.0002; Fig. 7). On

308 the contrary, *R. imbricata* abundance decreased and was negatively correlated (r2=-0.53;

309 p=0.00056) with the abundance of the heterotrophic *Protoperidinium* species (Fig. 7). In NE

310 reefs, none of the abundances of *Thalassiosira subtilis*, *Cerataulina pelagica* or *Rhizosolenia*

311 *imbricata* were correlated to that of dinoflagellates trophic groups.

312 Chlorophyll *a* concentrations ranged between 0.35 and 1.03 mg/m^3 in 2007 and between

313 0.039 and 1.3 mg/m^3 in 2008. These concentrations increased in days corresponding to the

314 During and After spawning times, consistently for both years and for all reefs when data

315 was available (Table 4a). Also, chlorophyll concentrations were more variable in 2008 than

316 in 2007, and in the SW than in NE reefs for both years (Fig. 8). Sea surface temperatures

317 ranged between 26.45 and 29.04 ºC in 2007 and between 27.4 and 29.1 ºC in 2008 (Table

318 4b). In 2007, SST increased through the sampling period in all reefs but showing a larger

319 variability in the SW reefs (Fig. 9). In contrast, SST values were very similar among reefs in

320 2008, reaching higher temperatures During spawning time and decreasing by day 9 within

321 the After spawning time (Fig. 9).

322 **TABLE 4.** A) Chlorophyll *a* concentration (mg/m^3) and B) Seawater Surface Temperature
323 (ºC) for 9 consecutive days, "Before", "During" and "After" the expected spawning dates for
324 southern Caribbean acroporids. Data obtained from remote sensing (MODIS SCAR;
325 1kmx1km resolution).

(A)

Periods	Days	2007			Days	2008		
		NE (MD-GR)	CYA	DMS		NE (MD-GR)	CYA	DMS
Before	28-Aug	NA	NA	NA	16-Aug	0.61	0.039	NA
	29-Aug	0.631	0.387	0.903	17-Aug	0.602	0.042	0.075
	30-Aug	0.67	0.35	NA	18-Aug	NA	0.0545	0.0544

Periods	Days				Days			
During	31-Aug	0.73	0.42	NA	19-Aug	0.943	0.19	0.23
	01-Sep	NA	NA	NA	20-Aug	0.903	0.280	1.076
	02-Sep	1.03	0.58	NA	21-Aug	0.87	NA	NA
After	03-Sep	0.850	0.643	1.040	22-Aug	0.77	0.60	1.08
	04-Sep	NA	NA	NA	23-Aug	1.23	0.43	1.24
	05-Sep	0.651	0.431	0.826	24-Aug	1.30	NA	NA

(B)

		2007				2008		
Periods	Days	NE (MD-GR)	CYA	DMS	Days	NE (MD-GR)	CYA	DMS
Before	28-Aug	27.57	27.57	27.07	16-Aug	NA	NA	NA
	29-Aug	27.87	27.87	28.23	17-Aug	27.60	27.60	27.98
	30-Aug	27.72	27.72	28.09	18-Aug	27.41	27.41	27.54
During	31-Aug	27.65	27.65	26.45	19-Aug	28.91	28.91	29.15
	01-Sep	27.82	27.82	28.92	20-Aug	28.27	28.27	28.22
	02-Sep	27.94	27.94	29.04	21-Aug	29.01	29.01	28.67
After	03-Sep	28.40	28.40	29.03	22-Aug	28.13	28.13	27.96
	04-Sep	28.65	28.65	28.85	23-Aug	27.95	27.95	28.01
	05-Sep	28.90	28.90	28.93	24-Aug	NA	NA	NA

326

4. Discussion

Expected variations in microphytoplankton abundance and composition linked to the coral spawning events were mostly overridden by variations between years and spatial variations among reefs in Los Roques archipelago. However, when groups of the microphytoplankton were examined, dinoflagellate assemblages and trophic functional groups varied in relation to the spawning times. Heterotrophic dinoflagellates increased in abundance after the spawning event in 2007 for some reefs, while in 2008 this increment only occurred for mixotrophic dinoflagellates in one reef. Also, diatoms *Cerataulina pelagica* and *Rhizosolenia imbricata* varied simultaneously in abundance, suggesting that they may be responding to re-mineralization of dissolved nitrogen and grazing activity, respectively. These results suggest an important role of microheterotrophic grazers in re-mineralization of organic matter in coral reef waters. Also, our findings support the relevance of assessing compositional changes of larger size fractions of the phytoplankton when evaluating primary productivity and nutrient fluxes. A lack of direct measurements from the nutrient flux-cycling and benthic-pelagic coupling in our study, hampers an in-

342 depth discussion of the patterns observed; however, changes that occurred in a few days

343 on the composition and abundance of some taxa of the microphytoplanktonic groups

344 examined were likely related to macronutrient inputs that resulted from coral spawning, as

345 supported by concurrent increases in clorophyll *a* concentrations obtained by satellite

346 images.

347 Contrasting results among studies support that phyto- and bacterioplankton and nutrient

348 flux responses to coral spawning are variable across coral reef regions. The subtle changes

349 in microphytoplankton at the lowest taxonomic level observed at Los Roques in relation to

350 coral spawning, contrasted with studies from other regions (Wild et al., 2004; Eyre et al.,

351 2008; Glud et al., 2008; Horne, 2011). In the Great Barrier Reef (GBR), Australia and the

352 Gulf of Mexico, both planktonic and benthic microalgae blooms had been observed within

353 2-5 days following a mass coral spawning event (Wild et al., 2004; Eyre et al., 2008; Glud et

354 al., 2008; Horne, 2011). At Los Roques, chlorophyll *a* concentrations increased During and

355 After the spawning times in all reefs, however, only the abundance and composition of

356 dinoflagellates and cyanophyte assemblages varied with spawning times. Furthermore,

357 changes in cyanophytes consisted of a freshwater taxon that spiked in abundance in 2007,

358 likely due to anthropogenic influence in the NE reefs rather than to a response from spawn

359 material. Also, increased chlorophyll *a* concentrations in relation to spawning in Los

360 Roques was lower than that reported for the GBR (Glud et al., 2008). Differences in the

361 magnitude (e.g. spawned material, number of species and geographic scale) of the

362 spawning events influence the amount of organic matter released to the water column, and

363 thus affect regional differences, which support the uniqueness of the mass coral spawning

364 event at the GBR compared to that occurring in other regions (Harrison & Booth, 2007;

365 Mangubhai & Harrison, 2008). This might explain why in Los Roques and other coral reefs

366 (Apprill & Rappé, 2011), phytoplankton blooms were not detected after massive coral

367 spawning events.

368 In addition to the intensity and magnitude of spawning events across regions, other factors

369 might influence the variability in the phytoplankton response. In this study, the sampling

370 days within spawning periods (Before, During and After) were established based on

371 expected spawning dates for *Acropora palmata*, as this species marks the beginning of the

372 multi-specific coral spawning event in Caribbean shallow waters. However, variations in

373   spawning intensity and time, as reported for this coral species (unpublished data by Miller

374   & Szmant in Key Largo, Florida and La Parguera, Puerto Rico in 2000, Japp between the

375   1970s and 1980s and Miller in 2001), are likely to affect the observed response of

376   microphytoplankton assemblages between years and among spawning periods. In

377   particular, *Acropora palmata* larval abundance suggested a late start in spawning for most

378   reefs in 2008 (i.e. +5 days instead of +2-3 days, supplementary material Table 3). The

379   abundance of *Acropora palmata* larvae in the plankton at the time of this study (Zubillaga,

380   2010) strongly suggested that coral spawning at Los Roques was larger in 2008 than in

381   2007, but in 2008 it lagged with respect to our sampling periods in most of the reefs

382   (supplementary material Table 3). This would have resulted in a During period being

383   similar to a Before period, both with little spawn material; explaining the differences in

384   composition and abundance of microphytoplankton observed between 2007 and 2008 and

385   the observed increase in abundance of diatoms and chlorophyll *a* concentration at one of

386   the SW reefs only in 2008. Days and reefs with higher abundance of coral larvae (Zubillaga,

387   2010) coincided with diatoms being more abundant, a group that requires higher inorganic

388   nutrient concentrations compared to cyanophytes and dinoflagellates (Reynolds, 2006). In

389   contrast, the higher abundance of heterotrophic dinoflagellates in 2007 at various reefs,

390   and of mixotrophic dinoflagellates at the GR reef site in 2008, might indicate a subtle shift

391   in these trophic groups, favouring heterotrophy.

392   A clear pattern of the role of microheterotrophy in the microphytoplankton response to

393   larvae abundance, as it has been reported for phytoplankton biomass and primary

394   productivity (Eyre et al., 2008; Glud et al., 2008), was apparently hidden by the high

395   variability observed among reefs. Previous work in which biomass, primary productivity

396   and/or respiration in sediment and water have peaked shortly after the release of spawned

397   material (Eyre et al., 2008; Glud et al., 2008) were carried out only at one site, on a reef flat.

398   Thus, an examination of these processes (i.e. phytoplankton primary production, biomass

399   and species composition in relation to nutrient re-mineralization) at larger spatial scales in

400   reefs might yield large variability as it was found in this study.

401   In addition to the amount of material spawned, other local (reef) scale-dependent

402   processes such as re-mineralization of organic matter, might be related to the variations in

403   chl*a* and microphytoplankton observed among reefs in nine days. The response of

404   photosynthetic microalgae to the input of labile organic compounds is mediated by the
405   metabolic activity of the microbial reef community, often called the microbial loop
406   (Anderson & Ducklow, 2001; Pomeroy et al., 2007; Nelson et al., 2013). This process entails
407   great variability as it may operate on time scales of hours to days (Carlson, 2002) and it
408   depends on many factors, from benthic composition to oceanographic characteristics of the
409   reefs (Nelson et al., 2011). Re-mineralization of coral spawn materials is mostly carried out
410   in reef sediments (Westneat & Resing, 1988; Haas et al., 2011, 2013), whereas the role
411   played by bacterioplankton in the process vary from immediate and significant (Wild et al.,
412   2008) to lagged and marginal (Apprill & Rappé, 2011). Thus, the temporal response of the
413   microphytoplankton community to an organic matter input might be controlled by how
414   fast the re-mineralized material is incorporated into the water column through benthic-
415   pelagic coupling (Eyre et al., 2008; Patten et al., 2008; Nelson et al., 2011; Apprill & Rappé,
416   2011). In this sense, during coral spawning events in the Gulf of Mexico, Horne (2011)
417   observed only small changes of nutrient concentrations in water, which suggests a low re-
418   mineralization activity in the water column, but he also reported an increased abundance
419   of dinoflagellates of the genus *Ceratium* spp. Thus, in our study, reef-specific differences in
420   the re-mineralization activity could have contributed towards the variability found at the
421   reef scale in the structure of diatoms assemblages.

422   In this study, functional group and species-specific patterns of microphytoplankton related
423   to the spawning period were observed at some reefs. During and After the coral spawning
424   in 2007, the increased abundance in *Protoperidinium* heterotrophic species, and the
425   concomitant decrease of the mixotrophic *Neoceratium lineatum*, may constitute a response
426   to the coral spawning via abundance of prey. The abundance of heterotrophic
427   dinoflagellates found in this study was very similar to that found by Horne (2011) in the
428   Gulf of Mexico 2 days after the coral spawning. However, at some reefs in Los Roques, the
429   abundance of mixotrophic dinoflagellates was almost double that reported by Horne
430   (2011). Some heterotrophic dinoflagellate species prey preferentially upon heterotrophic
431   bacteria and protozoans and the eggs and larvae of metazoans (Jeong, 1994, 2007, et al.,
432   2010), whereas mixotrophic species more frequently prey upon small-size microalgae like
433   haptophytes, crysophytes, picophytes, raphidophytes (not assessed on this study),
434   chlorophytes, autotrophic dinoflagellates, some diatom species and autotrophic bacteria (Li

435   et al., 2000; Jeong et al., 2005; Berge et al., 2008). The negative correlation between the
436   abundance of heterotrophic dinoflagellates and one of their grazed species, the diatom
437   *Rhizosolenia imbricata* (Willén, 1991), might indicate that preferential feeding occurred in
438   detriment of autotrophic microalgae species. Consistent with this, heterotrophic and
439   mixotrophic dinoflagellates are recognized to have important effects on plankton
440   abundance and composition as microheterotrophic grazers (Lessard & Swift, 1985). Thus,
441   despite increased Chl*a* concentrations, grazing activity by heterotrophic dinoflagellates
442   might explain the lack of a significant increase in diatom abundance in relation to spawning
443   periods at some reefs in 2007.

444   In addition to grazing, microheterotrophic phytoplankton (i.e. mixo- and heterotrophic
445   dinoflagellates among other protozoans) maintain nutrient demand through re-
446   mineralization of organic matter in oceanic waters year-round, and their contribution to
447   dissolved inorganic nutrients might be higher than that of zooplankton (Bode et al., 2005).
448   Oligotrophic coral reefs have an efficient recycling of nutrients (Szmant, 2002; Wild et al.,
449   2008) and are able to incorporate a massive coral-spawning organic matter input in less
450   than 6 days through the benthic microbial loop. Because sediment re-mineralized nitrogen
451   is not readily returned to the water column (Eyre et al., 2008), microheterotrophic re-
452   mineralization within the microphytoplankton community might be mediating the
453   response of autotrophic groups to the input of that organic matter. Although the role of
454   these grazers in the re-mineralization of spawned materials in coral reefs has not been
455   evaluated, the positive correlation between the diatom *Cerataulina pelagica* - whose
456   abundance has been related to increase on dissolved nitrate and ammonium availability in
457   the water column (Härnström et al., 2009) - and the heterotrophic dinoflagellates of the
458   genus *Protoperidinium*, might suggest an important role of the latter on the availability of
459   dissolved inorganic nutrients at the SW reefs. A similar increase in dinoflagellate
460   abundance coinciding with a decrease in that of the diatoms was found 2 days after coral
461   spawning in the Gulf of Mexico (Horne, 2011).

462   At Los Roques, high abundance of small rather than medium and large size diatoms,
463   especially in the relatively pristine SW reefs, might indicate an effective nutrient cycling as
464   cell size in microalgae has an influence on nutrient preference and uptake (Koiko et al.,
465   1985; Stolte et al., 1994), with smaller phytoplankters favoured over larger ones in systems

466   driven by regenerated nutrients and rapid cycling of organic matter (Caroppo, 2000).
467   Similarly, the peak abundance in diatoms coinciding with that of mixotrophic
468   dinoflagellates in 2008 at GR might also respond to re-mineralization of spawned materials
469   by the latter. However, the consistency of this pattern was not captured in our 2008
470   sampling probably due to lagged spawn in the other reefs. Also, sampling days for each
471   time period (i.e. Before-During-After) were relatively short (3 days each), and these
472   spawning periods were contiguous. If the response of the larger size phototrophs of the
473   phytoplankton to spawned organic matter is mediated by microheterotrophy, as suggested
474   by our results, more days between sampling periods could have been better for detecting
475   changes in the microphytoplankton assemblages. .

476   Observed microphytoplankton density, although well within previous reports for Dos
477   Mosquises in Los Roques and other oligotrophic waters (e.g. González, 1989; Spiniello,
478   1996, Madera & Furderer, 1997), revealed spatiotemporal differences of the
479   microphytoplankton community in Los Roques at scales previously unexplored.
480   Differences in plankton assemblages known to occur between the NE and SW sectors of the
481   archipelago during the dry season from November to June (González, 1989; Casanova et al.,
482   2007) also hold true for August and September during this study, a period with a weak
483   hydrodynamic influence in the area (Casanova et al., 2007). Our results also indicated a
484   strong reef-based variability within previously thought homogenous sectors (Casanova et
485   al., 2007) and a daily variability within otherwise considered constant seasons (González,
486   1989, Spiniello, 1996; Madera & Furderer, 1997). The presence of the cyanophyte
487   *Anabaena* sp. in August and September on the NE reefs in 2007 constitutes the first report
488   of this species in Los Roques, indicating episodic freshwater inputs, consistent with human
489   settlement at Gran Roque. Algae from this genus can produce toxins of public health
490   concern (Figuereido et al., 2004); however, their disappearance in samples from
491   consecutive days suggests unfavourable water conditions for these populations and/or
492   short water residence time. Toxin-producing dinoflagellate species were also identified, but
493   in low abundance.

494   While our study lacked of direct biomass measures through time, studies elsewhere have
495   not targeted compositional changes on microalgae assemblages. Therefore, a full picture of
496   changes in phytoplankton across regions and reefs in relation to coral spawning is still

497   lacking. Our results highlighted the importance of including taxonomical and functional

498   changes in larger size phytoplankton fractions when evaluating nutrient fluxes and primary

499   and secondary pelagic productivity in coral reefs in relation to coral spawning events, as

500   well as the importance of replication at reef spatial scales for generalizing observed

501   patterns. Manipulative experiments to establish the effect of microheterotrophic grazing

502   and nutrient re-mineralization activity by dinoflagellates on the response of the

503   phytoplankton assemblages to organic matter inputs constitute a logical next step to better

504   comprehend the role of dinoflagellates in reef waters during a nutrient input.

505   Concomitantly, specific processes related to inter-annual variability need to be assessed

506   through the sampling of non-spawning times as well in order to better discriminate

507   phytoplankton responses to coral spawning events. Similarly, large-scale operating

508   oceanographic and/or climatic processes not yet assessed on the study site may also have

509   an important role as structuring factors, as suggested by the amount of inter-annual

510   variability observed in the microphytoplankton structure and composition and the daily

511   patterns of SST and Chl*a* concentrations.

512   This study evaluated the structure of larger size fractions of the phytoplankton during coral

513   spawning for the first time in the Caribbean, showing variations in dinoflagellate

514   assemblages and its trophic groups, as well as in some diatom species. These variations

515   highlighted the potential impact of heterotrophic dinoflagellates on coral reefs primary

516   productivity and organic matter cycling. Thus, by examining the structure of

517   microphytoplankton at multiple spatiotemporal scales in Los Roques archipelago, this

518   study provides a first approximation of the effect of coral spawning on these assemblages.

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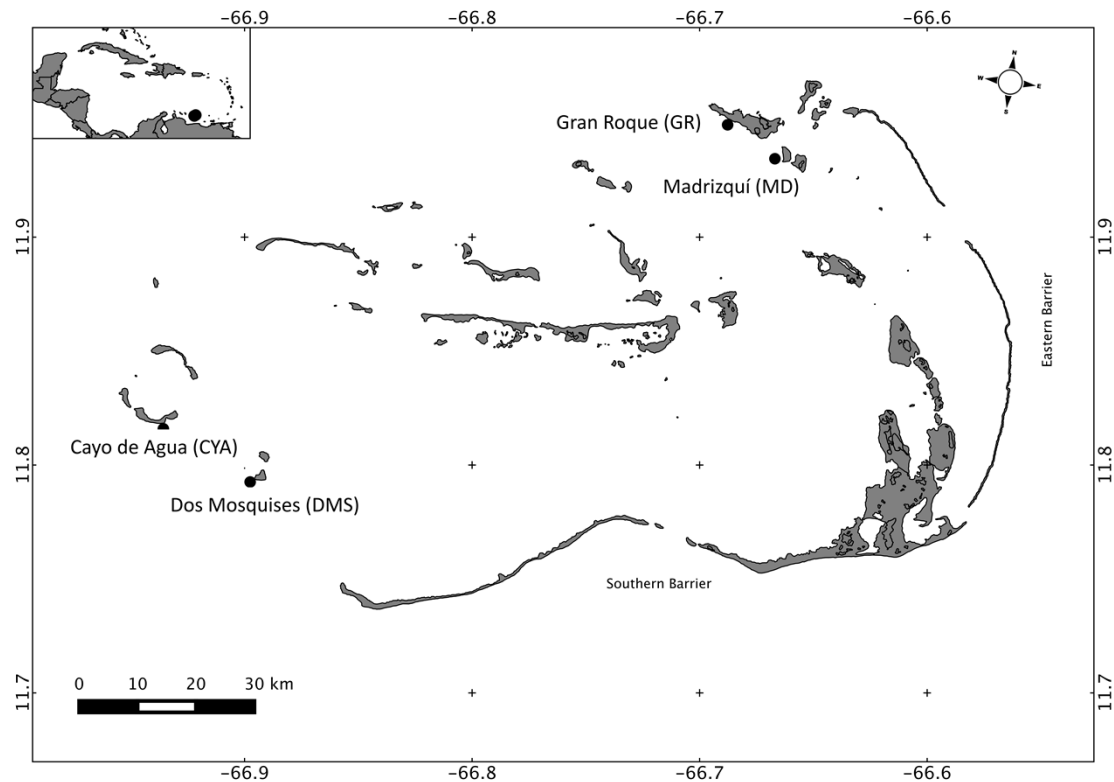825   48, 1–92.

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882   NDR4N-29121?func=full-set-set&set_number=905390&set_entry=000001&format=999.

883 **1.   Figures**
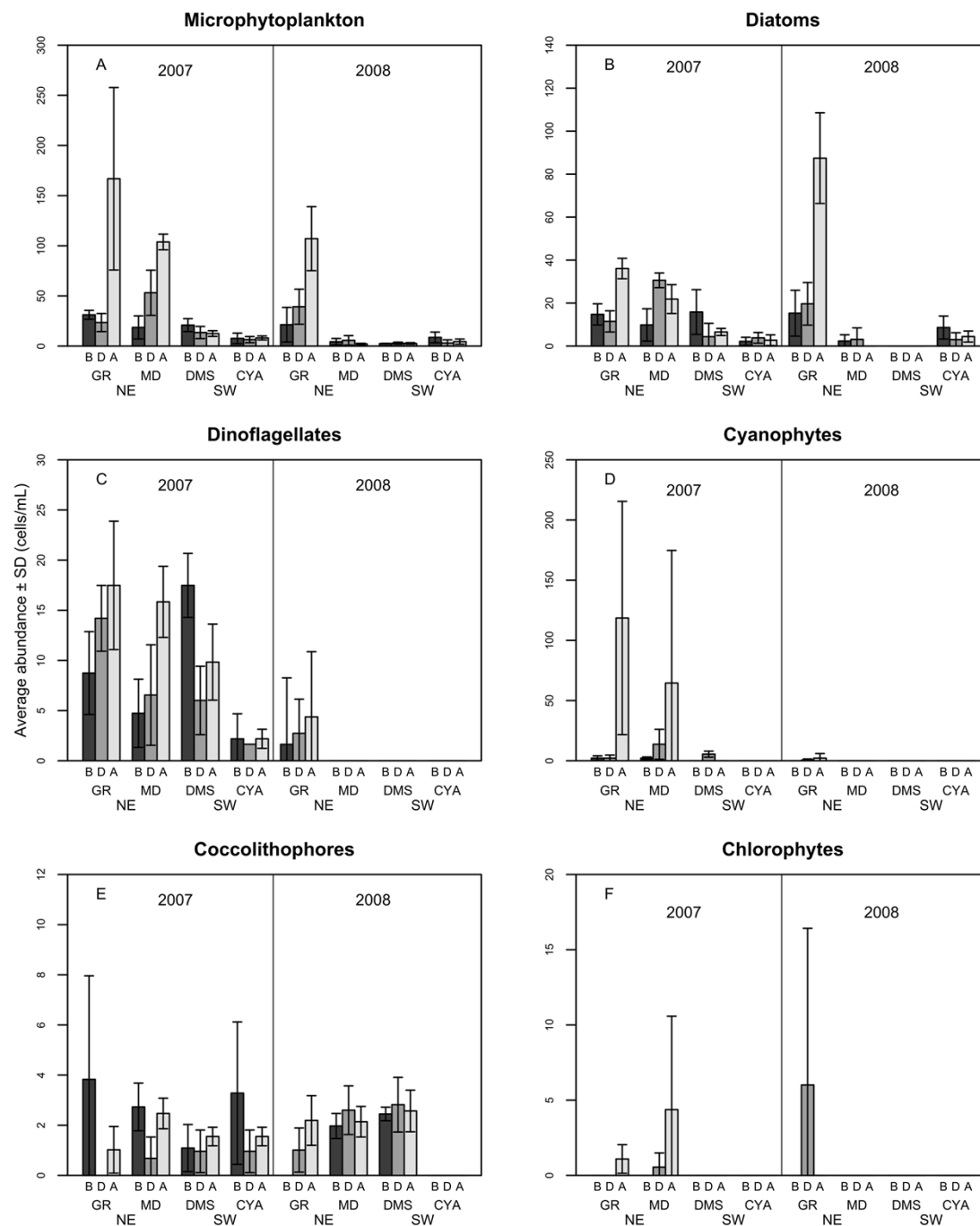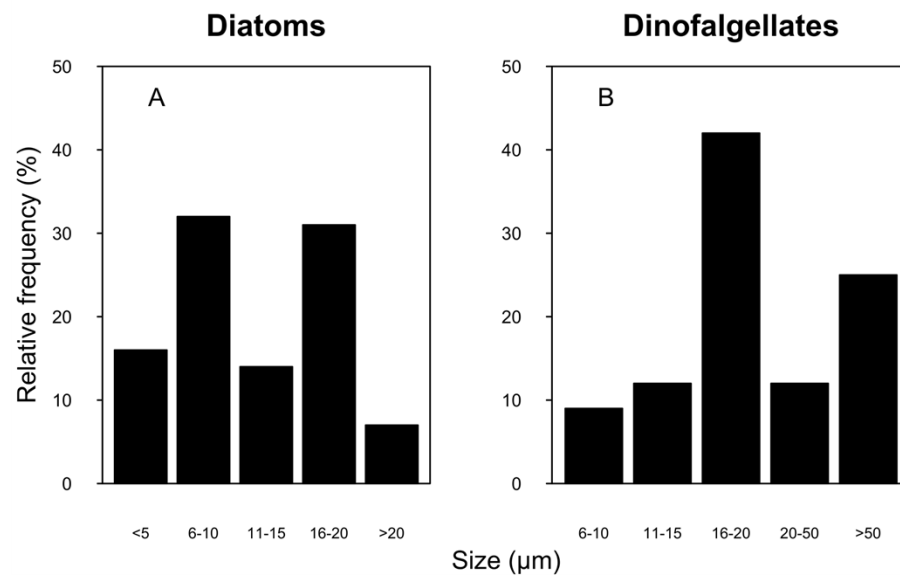
884

Figure 1. Map of Los Roques National Park, Venezuela, Southern Caribbean, showing the four

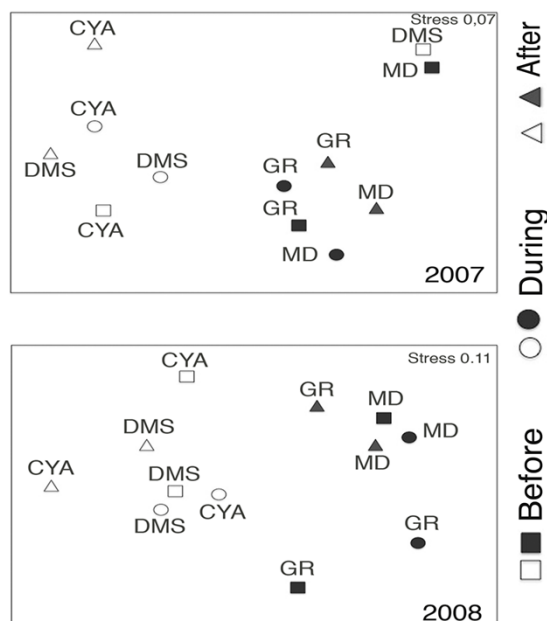reefs sampled at the Northeast (NE) and Southwest (SW) sectors.

887

Figure 2. Average density of microphytoplankton (cells per mL) of Microphytoplankton (A),

889   Diatoms (B), Dinoflagellates (C) Cyanophytes (D), Coccolithophores (E) and Chlorophytes (F)

890   in four reefs (GR, MD, DMS, CYA) located at the Northeast (NE) and Southwest (SW) localities

891   of Los Roques. B, D, A refers to Before, During and After the coral spawning events of 2007 and

892   2008. Density values are displayed with different scales for each of the taxonomic groups.

893

894   **Figure 3.** Relative frequency of the Diatoms (A) and Dinoflagellate (B) groups size classes

895   sampled in four reefs (GR, MD, DMS, CYA) located at the Northeast (NE) and Southwest (SW)

896   localities of Los Roques during 9 consecutive days in August and September 2007 and 2008.
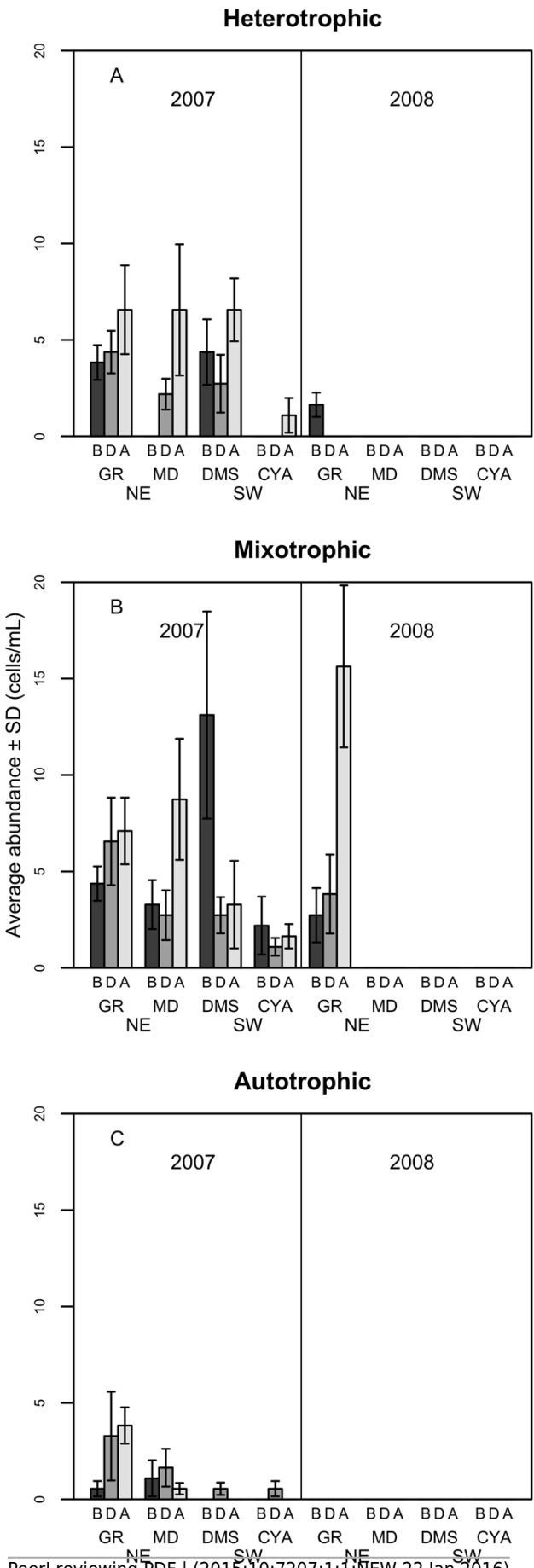

897

898   **Figure 4.** Nonmetric Multidimentional Ordination (nMDS) based on centroids for the

899   microphytoplankton assemblages in four reefs (GR, MD, DMS, CYA), located in the Northeast

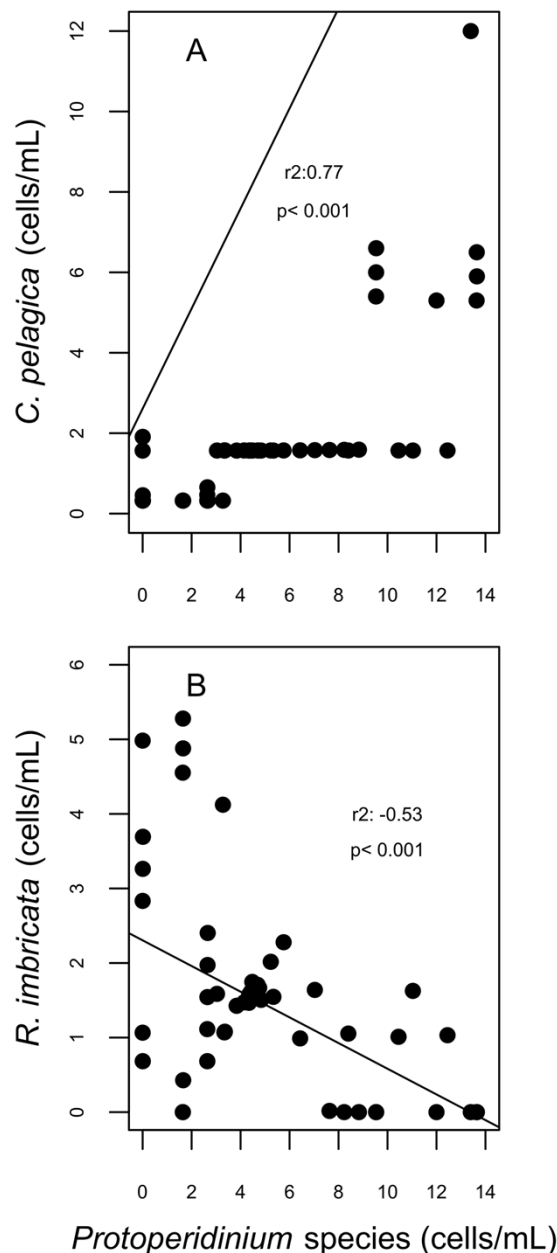900   (empty symbols) and Southwest (filled symbols) of Los Roques.

901

902

903 **Figure 5.** Average Shannon Diversity index values (H´± SD) of microphytoplankton in four

904 reefs (GR, MD, DMS, CYA) located at the Northeast (NE) and Southwest (SW) localities of Los

905 Roques. B, D, A refer to Before, During and After the coral spawning events of 2007 and 2008.
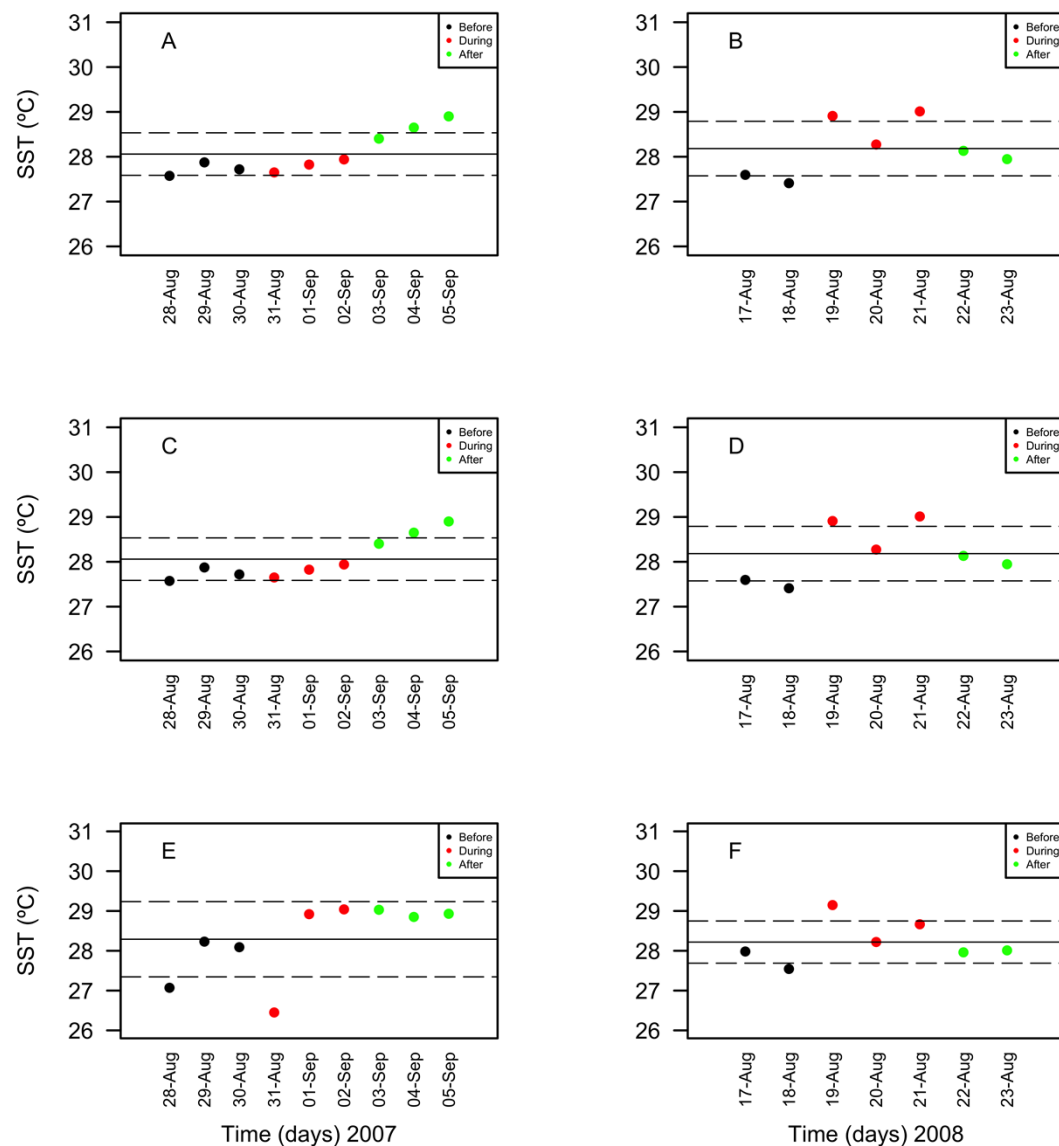
Heterotrophic

Mixotrophic

Autotrophic

907 **Figure 6.** Density of Heterotrophic (A), Mixotrophic (B) and Autotrophic (C) dinoflagellates
908 (cells per millilitre, Mean ±SD) in four reefs (GR, MD, DMS, CYA) located at the Northeast
909 (NE) and Southwest (SW) localities of Los Roques. B, D, A refers to Before, During and After
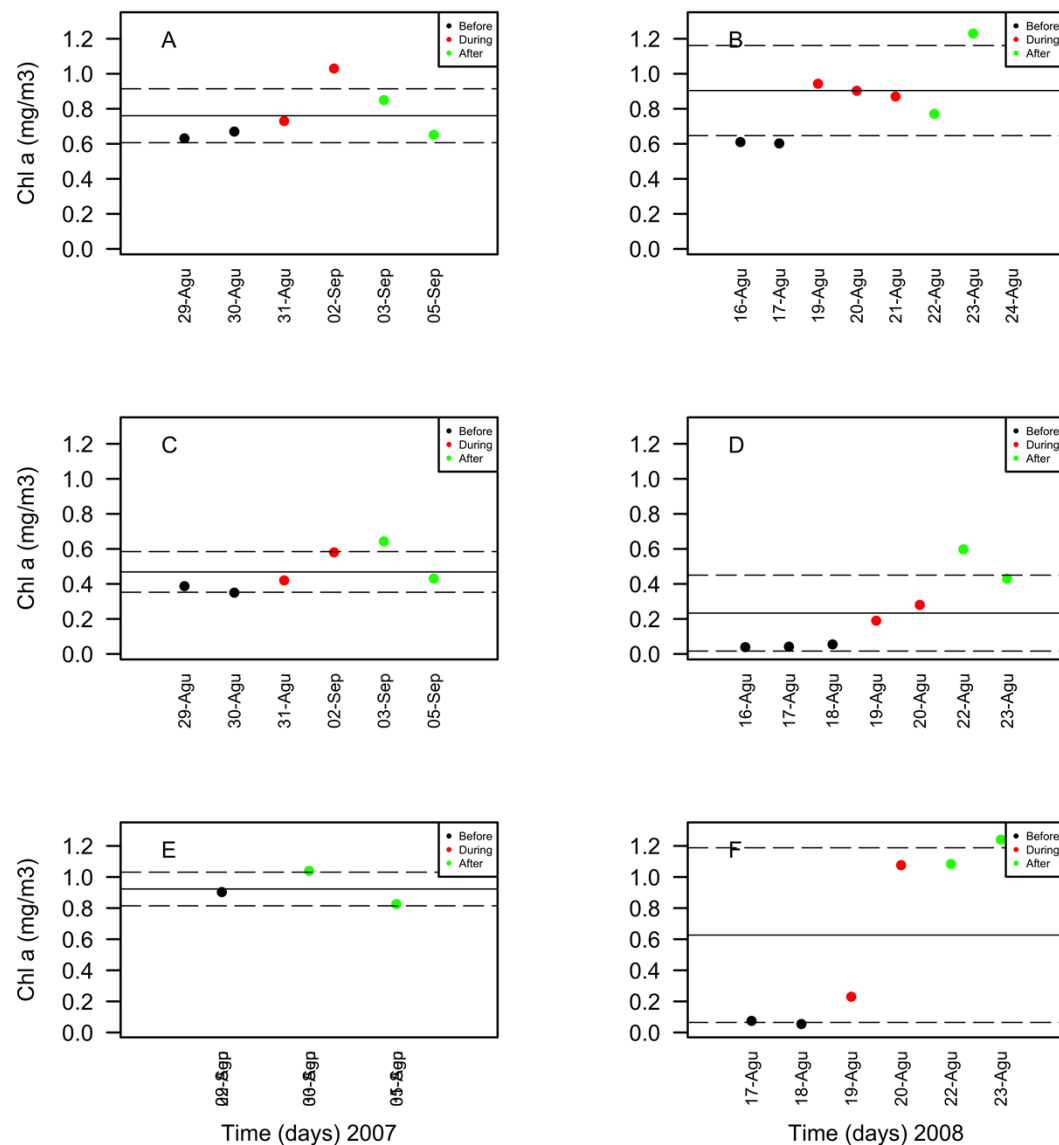910 the coral spawning event of 2007.

911

912 **Figure 7**. Correlation plots on abundances of *Cerataulina pelagica* (A) and *Rhizosolenia*
913 *imbricata* (B) and the abundance of *Protoperidinium* species; corresponding to the spawning

914 event of 2007 in two reefs (DMS, CYA) located at the Southwest (SW) sector of Los Roques.
915 Only statistically significant (p<0.05) correlations, with Spearman r^2 values are shown.
916 Abundance values in cell per millilitres are displayed with different scales for each of the
917 correlation plots.

918

919 **Figure 8**. Surface seawater temperature (SST in ºC) values obtained through remote sensing
920 (MODIS SCAR, 1km x 1Km resolution) for the nine-days sampling period corresponding to
921 Before (black), During (red) and After (green) expected coral spawning times for the study site,

922   at the Northeast (A-B) and Southwest (SW) Cayo de Agua (C-D) and Dos Mosquises (E-F) reefs

923   of Los Roques in 2007 and 2008.

924

925   **Figure 9**. Chlorophyll *a* (Chl*a* in mg/m^3) values obtained through remote sensing (MODIS

926   SCAR, 1km x 1Km resolution) for the nine-days sampling period corresponding to Before

927   (black), During (red) and After (green) expected coral spawning times for the study site, at the

928   Northeast (A-B) and Southwest (SW) Cayo de Agua (C-D) and Dos Mosquises (E-F) reefs of

929   Los Roques in 2007 and 2008.