



## Depth distribution of benthic dinoflagellates in the Caribbean Sea

Aurélie Boisnoir, Pierre Yves Pascal, Sébastien Cordonnier, Rodolophe Lemée

### ► To cite this version:

Aurélie Boisnoir, Pierre Yves Pascal, Sébastien Cordonnier, Rodolophe Lemée. Depth distribution of benthic dinoflagellates in the Caribbean Sea. *Journal of Sea Research (JSR)*, 2018, 135, pp.74-83. 10.1016/j.seares.2018.02.001 . hal-01968144

HAL Id: hal-01968144

<https://hal.univ-antilles.fr/hal-01968144>

Submitted on 2 Jan 2019

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1                   **DEPTH DISTRIBUTION OF BENTHIC DINOFLAGELLATES**

2                   **IN THE CARIBBEAN SEA**

3                   **Aurélie Boisnoir<sup>a,b,\*</sup>**

4                   **Pierre-Yves Pascal<sup>a</sup>**

5                   **Sébastien Cordonnier<sup>a</sup>**

6                   **Rodolophe Lemée<sup>b</sup>**

7                   <sup>a</sup> UMR 7138 Evolution Paris-Seine, Equipe biologie de la mangrove, Université des Antilles, BP 592, 97159

8                   Pointe-à-Pitre, Guadeloupe, France

9                   <sup>b</sup> Sorbonne Universités, UPMC Univ Paris 6, INSU-CNRS, Laboratoire d’Océanographie de Villefranche,  
10                   Villefranche-sur-Mer, France

11                  \*Corresponding author: aurelie.boisnoir@gmail.com

12                  Key Words: *Halophila stipulacea*, *Gambierdiscus*, *Ostreopsis*, *Prorocentrum*

13                  Running Head: Depth distribution of benthic dinoflagellates

14

15        **Abstract**

16        Monitoring of benthic dinoflagellates is usually conducted between sub-surface and  
17        5 m depth, where these organisms are supposed to be in highest abundances. However,  
18        only few studies have focused on the small-scale depth distribution of benthic  
19        dinoflagellates. In the present study, abundances of dinoflagellates were evaluated on an  
20        invasive macrophyte *Halophila stipulacea* in two coastal sites in Guadeloupe along a depth  
21        gradient from sub-surface to 3 m at Gosier and until 20 m at Rivière Sens during the  
22        tropical wet and dry seasons. Depth did not influence total dinoflagellate abundance but  
23        several genera showed particular depth-distribution preferences. The highest abundances  
24        of *Ostreopsis* and *Gambierdiscus* species were estimated preferentially in surface waters  
25        whereas *Coolia* spp. was found comparatively at depth. *H. stipulacea* biomass was  
26        positively correlated with *Ostreopsis* spp. abundance. Our study suggests that sampling of  
27        benthic dinoflagellates should be conducted at different water depths taking into account  
28        the presence of the macroalgal substrate as well. In the Caribbean area, special attention  
29        should be addressed to the presence of *H. stipulacea* which tends to homogenize the  
30        marine landscape and constitutes a substrate favourable for dinoflagellates growth.

31

32        **Introduction**

33        Toxic harmful algal bloom occurrence is becoming more frequent and can cause  
34        more problems on ecosystems and human health at global scale (Hallegraeff, 1993; Cloern  
35        et al., 2005; Glibert et al., 2005; Hallegraeff, 2010). Several species of planktonic and  
36        benthic dinoflagellates can produce ecological damages to the environment and human  
37        health when they bloom in excess. Decreased levels of oxygen in the water column when  
38        the blooms decay and/or production of toxins, can lead to mass mortalities of marine

39 organisms (Shears and Ross, 2009) and/or to intoxication when toxins are transferred and  
40 bioaccumulated in the food web (Yasumoto et al., 1987; Holmes and Teo, 2002). Those  
41 toxins are accumulated within the food chain (Yasumoto et al., 1977; Adachi and Fukuyo,  
42 1979; Lewis and Holmes, 1993; Gleibs and Mebs, 1999; Aligizaki et al., 2011).  
43 Phycotoxins potentially generate human intoxications through consumption of marine  
44 fishery products contaminated with bio-accumulated toxins (Valdiglesias et al., 2013).  
45 There are several poisoning syndromes caused by benthic dinoflagellates including,  
46 gastrointestinal (nausea, vomiting, diarrhoea) and/or neurological (tingling, headaches,  
47 dizziness, hallucinations, seizures) consequences (Ajani et al., 2017). These poisoning  
48 syndromes are mainly due to the presence of *Ostreopsis* spp., *Prorocentrum* spp. and  
49 *Gambierdiscus* spp. *Ostreopsis* spp. synthesize potent palytoxin and derivatives (Onuma et  
50 al., 1999; Lenoir et al., 2004) probably responsible for clupeotoxin fish poisoning (Onuma  
51 et al., 1999; Randall, 2005; Aligizaki et al., 2011) and palytoxicosis (Alcalá et al., 1988) in  
52 tropical areas. In temperate regions, blooms of *Ostreopsis* spp. are the causal agent of skin  
53 and eye irritations (Ciminiello et al., 2006; Tichadou et al., 2010) and respiratory  
54 syndromes due to exposure of aerosolized toxins or cells (Ciminiello et al., 2014).  
55 *Prorocentrum* spp. produce okadaic acid and dinophysistoxins (Kumagai et al., 1986;  
56 Yasumoto et al., 1987; Faust and Gullidge, 2002; Nascimento et al., 2016; Luo et al.,  
57 2017) causing diarrheic shellfish poisoning for seafood consumers (Landsberg et al.,  
58 2005). Ciguatoxins produced by *Gambierdiscus* spp. are responsible of ciguatera fish  
59 poisoning (Chinain et al., 2010; Berdalet et al., 2017). This poisoning is the most common  
60 non-bacterial food-borne illness (Tester, 1994; Tester et al., 2009) associated with  
61 consumption of several fish species (Bagnis, 1981; Tester et al., 2009; Dickey and Plakas,  
62 2010). Ciguatera can lead to death in the most severe cases (Friedman et al., 2008). *Coolia*  
63 spp. and *Amphidinium* spp., synthesize toxins that can affect marine life but the

64 bioaccumulation of these toxins through marine food chain and human poisoning have not  
65 been proven (Holmes et al., 1995; Botana, 2014; Ben-Gharbia et al., 2016). To our  
66 knowledge, effects of *Sinophysis* spp. on human health have not been documented yet.

67 Blooms of benthic toxic dinoflagellates generates also economic problems for  
68 fishermen and aquaculture (Bagnis, 1981; Shumway, 1990; Bauder et al., 2001; Heredia-  
69 Tapia et al., 2002; Berdalet et al., 2015) whose consequences are difficult to quantify  
70 (Ahmed, 1991). For instance in Australia and French Polynesia the strategy to protect  
71 human health consisted, among other actions, on a decree banning the fishing and selling  
72 of several fish species (Bagnis, 1981; Lehane and Lewis, 2000) as their contamination  
73 cannot be easily measured (Ahmed, 1991). In Guadeloupe Archipelago selling of several  
74 fish species, known to cause sanitary problems, is prohibited. It is presently suspected that  
75 new fish species could be potential poisoning vectors representing a supplementary  
76 shortfall for Caribbean fisherman. For environmental, sanitary and economic reasons it is  
77 important to set up long time-scale monitoring of benthic dinoflagellates considering  
78 physicochemical parameters to know precisely the ecological niches of each species and to  
79 allow an efficient risk management due to toxic dinoflagellates.

80 *Ostreopsis*, *Prorocentrum*, *Gambierdiscus*, *Coolia*, *Amphidinium*, *Sinophysis*  
81 species are present in the Caribbean Sea (Ballantine et al., 1988; Morton and Faust, 1997;  
82 Faust, 2009; Chomérat, 2016). Usually, samplings are restricted to shallow depths, from  
83 the surface to 5 m depth (Chang et al., 2000; Okolodkov et al., 2007; Parsons and Preskitt,  
84 2007; Mangialajo et al., 2008; Shears and Ross, 2009; Rahman Sha et al., 2014) where  
85 benthic dinoflagellates are supposed to be in highest abundances because they are  
86 considered to be mainly photosynthetic (Taylor, 1985; Faust, 1997; Ten-Hage et al., 2000;  
87 Fraga et al., 2008; Fraga and Rodríguez, 2014). However, these organisms are not  
88 necessarily restricted to the sub-surface as they can complement their autotrophic

89 behaviour with the uptake of organic matter (Burkholder et al., 2008; Pistocchi et al., 2011;  
90 Jauzein et al., 2017).

91 Only few studies focused on depth distribution of benthic toxic dinoflagellates. A  
92 first approach is to consider several sites with different depths (Taylor, 1985; Richlen and  
93 Lobel, 2011) but observed differences can be due to local environmental conditions rather  
94 than depth effects. A way to limit this potential bias is to collect samples at different depths  
95 in a single area. The comparison at two different depths of the abundance of  
96 *Gambierdiscus* revealed a decrease in the first 10 m (Xu et al., 2014) and stability between  
97 depths of 10 and 20 m (Loeffler et al., 2015). A better way to evaluate the depth effect is to  
98 set up transects of sampling along a depth gradient. The study by Totti *et al.* (2010) was  
99 the only one considering a single substrate with this approach. As macrophytes are not  
100 often homogeneously distributed along this gradient, several macrophytes species are  
101 usually collected (Delgado et al., 2006; Cohu and Lemée, 2012; Cohu et al., 2013). When  
102 dinoflagellate abundances are coming from different macrophytes, dinoflagellates  
103 abundance comparisons are difficult because normalizing cell counts to the weight of the  
104 macroalgal host introduces a significant source of error due to different surface area to  
105 mass ratios of each host algal species (Richlen and Lobel, 2011). Previous studies have  
106 suggested a host preference of dinoflagellates depending on the macrophyte morphology  
107 (Parsons and Preskitt, 2007; Totti et al., 2010), taxonomic group (Morton and Faust, 1997;  
108 Delgado et al., 2005; Monti et al., 2007; Parsons et al., 2017) or species (Ballantine et al.,  
109 1985; Delgado et al., 2005). Furthermore, such macroalgae could produce molecules  
110 stimulating or inhibiting growth of benthic dinoflagellates (Grzebyk et al., 1994; Morton  
111 and Faust, 1997; Accoroni et al., 2015). Such allelopathic interactions between macroalgae  
112 and benthic dinoflagellates can induce bias in abundances comparisons. Several methods  
113 were recently set up to minimize bias due to host preferences and avoid macrophyte

114 destruction. Artificial substrates need 24h of incubation to have a comparable colonization  
115 between them and macrophytes at the same sampling locations (Tester et al., 2014; Jauzein  
116 et al., 2016). However, this method is collecting resuspended dinoflagellates without direct  
117 contact with the benthic stock of microalgal population (Jauzein et al., 2016) but a positive  
118 correlation was found between planktonic and benthic abundances in several studies  
119 (Aligizaki and Nikolaidis, 2006; Mangialajo et al., 2011). Benthic dinoflagellates  
120 integrator called “BEDI” (Mangialajo et al., 2017) and syringe (Abbate et al., 2012)  
121 methods are faster than artificial substrates but they would be difficult to adapt to low  
122 abundances of dinoflagellates in tropical regions.

123 The aim of the present study is to describe the natural depth distribution of harmful  
124 benthic dinoflagellates at genus level, in the Caribbean Sea. To avoid variations due to  
125 spatial ecosystem heterogeneity and variations linked to biotic substrates, a single  
126 macrophyte species, *Halophila stipulacea* Fosskal, was regularly sampled along a depth  
127 gradient in two sites in Guadeloupe. *H. stipulacea* is an invasive seagrass noticed for the  
128 first time in 2002 in Grenada (Ruiz and Ballantine, 2004), now established in the Eastern  
129 Caribbean (Willette et al., 2014) and presenting large mono-specific meadows (Willette  
130 and Ambrose, 2012). This seagrass is native from the Red Sea and Persian Gulf (den  
131 Hartog, 1970). Rapid lateral bed expansion combined with its tolerance for a wide  
132 spectrum of environmental conditions allows *H. stipulacea* to exclude dominant seagrasses  
133 in the Caribbean (Willette and Ambrose, 2012). To our knowledge enumerations of  
134 benthic dinoflagellates have never been done on *Halophila stipulacea*.

135

136        **Material and method**

137            Sampling of *H. stipulacea* was conducted in the morning by scuba diving during the  
138            wet season on September 21<sup>st</sup> and 22<sup>nd</sup> 2015 and during the dry season on February 1<sup>st</sup> and  
139            2<sup>nd</sup> respectively at Gosier (16°13'25.1"N, 61°31'50"W) and Rivière Sens (15°58'51.8"N,  
140            61°42'59.2"W) in Guadeloupe (French West Indies) (Fig. 1). Sampling was conducted  
141            according to the distribution and availability of *H. stipulacea* in each site. In the shallow  
142            site (Gosier), samples were collected every 0.5 m from 0 m depth to 3 m depth as *H.*  
143            *stipulacea* was absent deeper. In the deep site (Rivière Sens), samples were collected every  
144            0.5 m from 4 m to 10 m depth then every 5 m until 20 m depth as *H. stipulacea* was absent  
145            from the surface to 4 m depth. Samples were taken in triplicate (n=3) at each sampled  
146            depth. In Guadeloupe, tides are semidiurnal with a mean tidal amplitude of 30 cm (tide  
147            gauge of Pointe-à-Pitre, REFMAR®).

148            *Abundance of benthic toxic dinoflagellates*

149            For each depth, triplicate samples of *Halophila stipulacea* with their surrounding  
150            water were taken carefully in 250 mL plastic flasks avoiding microalgae resuspension from  
151            the macroalgae. Acidic Lugol at 1 % (vol/vol) was added in all samples to fix microalgae  
152            and 10 seconds agitation allowed to dislodge benthic dinoflagellates present on  
153            macrophyte. Samples were passed through a 500 µm mesh to separate the macrophyte  
154            from water containing dinoflagellates. To recover a maximum of dinoflagellates, *H.*  
155            *stipulacea* was rinsed twice for 10 seconds with 100 mL of filtered seawater and then  
156            weighted. Total seawater volume was measured. Samples were stocked in the dark at 4 °C.  
157            Benthic dinoflagellates present in 1 mL were counted with a Sedgewick Rafter © counting  
158            cell using a standard light microscope less than one week after the sampling. This  
159            abundance and macrophyte's fresh weight allowed calculation of the number of benthic

160 toxic dinoflagellates per gram of fresh weight of *H. stipulacea* (cells.gFW<sup>-1</sup>). An average  
161 cellular abundance was estimated per depth, for all species of benthic toxic dinoflagellates  
162 (*n* = 3).

163

164 *Density of benthic dinoflagellates and leaf surface of H. stipulacea*

165 All *H. stipulacea* present in 20 x 20 cm square surface were sampled in triplicate at  
166 each depth and kept in the dark at -4°C. *H. stipulacea* content of each square was weighed  
167 after defrosting, rinsing and drying with absorbent paper and an average biomass of  
168 macrophyte per square meter was calculated for each depth. Measurement of *H. stipulacea*  
169 weight was used to estimate the density of benthic dinoflagellates per square meter of sea  
170 bottom (cells.m<sup>-2</sup>).

$$\text{cells. m}^{-2} = \frac{10\,000 \ (\textit{H. stipulacea} \text{ biomass})}{400} \times \text{cells. gFW}^{-1}$$

171

172 Thirty entire limbs of *H. stipulacea* of each triplicate were measured (length and width)  
173 with a calliper. Measurement of leaf length and width was used to estimate leaf surface  
174 considering rectangular geometric shape of each leaf.

175 *Measurement of ecological factors*

176 A sample of 250 ml of seawater surrounding *H. stipulacea* was used to measure  
177 environmental factors at every depths. Temperature was measured immediately with a  
178 Checktemps 4 HANNA thermometer and salinity was determined in the laboratory with a  
179 Master-S/MilliM ATAGO ® manual refractometer. A SCUBAPRO Aladin Tec 3G dive  
180 computer was used to measure depth of sea bottom.

181        *Data analysis*

182        Non-parametric tests were used as variances of *H. stipulacea* biomasses and benthic  
183        dinoflagellates abundances were not normally distributed. Kruskal-Wallis tests were  
184        utilised to assess *H. stipulacea* biomass and benthic dinoflagellates abundances related to  
185        depth. Dunn test is a multiple comparison method permitting to compare the mean of the  
186        rank of each treatment after a Kruskal-Wallis test. The normal distribution is used as the  
187        asymptotic distribution of the standardized difference of the mean of the ranks. Mann  
188        Whitney test was performed to assess (i) differences in temperature and salinity between  
189        the wet and the dry seasons, (ii) variations of *H. stipulacea* biomass between both seasons  
190        and (iii) to determine influence of seasons on abundances of dinoflagellates. Spearman  
191        correlation tests were applied to determine potential relationships between environmental  
192        parameters and dinoflagellate abundances. All descriptive analyses are presented as mean  
193         $\pm$  standard deviation (SD).

194

195        **Results**

196        *Ecological parameters at Gosier and Rivi re Sens*

197        At Gosier, average temperature of water column during the wet and dry seasons  
198        varied from  $30.9 \pm 0.5^{\circ}\text{C}$  to  $27.3 \pm 0.3^{\circ}\text{C}$  and salinity fluctuated from  $30 \pm 1$  to  $35 \pm 0$   
199        (Figure 2). At Rivi re Sens, seawater temperature varied from  $29.4 \pm 0.1^{\circ}\text{C}$  to  $26.5 \pm 0.4^{\circ}\text{C}$   
200        and salinity from  $31 \pm 1$  to  $36 \pm 0$  during the two sampled seasons. At both sites,  
201        temperatures were warmer during the wet than the dry season ( $p < 0.01$ ) and salinity was on  
202        average higher during the dry than the wet season ( $p < 0.003$ ).

203       *Biomass and leaf surface of Halophila stipulacea*

204       At Gosier, average biomass of *H. stipulacea* did not change with depth during the  
205       wet and dry seasons ( $p<0.051$ ). *H. stipulacea* biomass averaged  $803 \pm 392 \text{ g.m}^{-2}$  and was  
206       statistically not different during the two seasons ( $p=0.564$ ) (Figure 3). At Rivière Sens,  
207       average biomass of *H. stipulacea* did not change with depth during the dry season but it  
208       was higher at depth during the wet season ( $p=0.008$ ) (Fig 3). Biomass of *H. stipulacea* was  
209       higher at the dry ( $1\ 075 \pm 445 \text{ g.m}^{-2}$ ) than the wet season ( $528 \pm 329 \text{ g.m}^{-2}$ ) ( $p<0.0001$ ).

210       Leaf surface of *H. stipulacea* significantly increased with depth at both sites  
211       ( $p=0.0001$ ). At Gosier, leaf surfaces were statistically higher at 2.5 m depth ( $3.4 \pm 1.1 \text{ cm}^2$ )  
212       than these collected at 0 m and 0.5 m depth ( $2.1 \pm 0.7 \text{ cm}^2$ ). At Rivière Sens, the highest  
213       leaf areas were at 15 m and 20 m depths ( $2.9 \pm 1.3 \text{ cm}^2$ ) and smallest between 4 m and 7  
214       m, and at 10 m depths ( $1.5 \pm 0.5 \text{ cm}^2$ ) (Figure 3).

215       *Abundances of benthic dinoflagellates and depth distribution*

216       *Ostreopsis* spp., *Prorocentrum* spp., *Coolia* spp., *Amphidinium* spp. and *Sinophysis*  
217       were found during this survey. *Ostreopsis* spp. and *Prorocentrum* spp. were found in  
218       higher abundances than the other genera.

219       At Gosier, abundances of benthic dinoflagellates decreased with depth during the wet  
220       season ( $p=0.008$ ). The highest average abundances of benthic dinoflagellates were  
221       observed at 0 m depth ( $2079 \pm 831 \text{ cells.gFW}^{-1}$ ) while no cells were found at 3 m depth  
222       (Figure 4). *Ostreopsis* was the dominant genus reaching  $1\ 669 \pm 1\ 027 \text{ cells.gFW}^{-1}$  at 0 m  
223       depth and  $120 \pm 17 \text{ cells.gFW}^{-1}$  at 1 m depth. For similar depths, abundances of  
224       *Prorocentrum* were respectively  $262 \pm 110$  and  $77 \pm 52 \text{ cells.gFW}^{-1}$ . Abundances of  
225       *Gambierdiscus* spp. decreased from  $113 \pm 104 \text{ cells.gFW}^{-1}$  at 0 m depth to  $79 \pm 43$   
226       cells.gFW $^{-1}$  at 2.5 m depth. Maximum abundances were observed at 0 m depth for  
227       *Amphidinium* spp. ( $18 \pm 16 \text{ cells.gFW}^{-1}$ ), at 1 m depth for *Coolia* spp. ( $22 \pm 21 \text{ cells.gFW}^{-1}$ )

228  $^1$ ) and at 1.5 m depth for *Sinophysis* spp. ( $9 \pm 16$  cells.gFW $^{-1}$ ). Abundances of benthic  
229 dinoflagellates changed also with depth during the dry season ( $p=0.026$ ). The highest  
230 abundances were found at 1.5 m depth while no cell was found at 2.5 m. *Prorocentrum*  
231 spp. dominated other genera of benthic dinoflagellates (Figure 4). The highest average  
232 abundances of *Ostreopsis* spp and *Prorocentrum* spp. were respectively at 0.5 m depth (75  
233  $\pm 62$  cells.gFW $^{-1}$ ) and 1.5 m depth ( $939 \pm 718$  cells.gFW $^{-1}$ ) . Abundances of  
234 *Gambierdiscus*, *Coolia*, *Amphidinium* and *Sinophysis* genera were constant during both  
235 seasons. They never exceeded an average abundance of 30 cells.gFW $^{-1}$ . Abundances of  
236 benthic dinoflagellates did not differ between the wet and the dry seasons ( $p=0.150$ ).

237 At Rivière Sens, abundances of benthic dinoflagellates changed with depth during  
238 wet season ( $p=0.036$ ). The highest abundances were observed at 7 and 8 m depths ( $753 \pm$   
239 238 cells. gFW $^{-1}$ ) and lowest at 20 m depth ( $149 \pm 82$  cells.gFW $^{-1}$ ) (Figure 5).  
240 *Prorocentrum* spp. dominated the benthic dinoflagellate assemblage. The highest mean  
241 abundances were observed during the sampled period at depth of 4 m for *Ostreopsis* spp.  
242 ( $30 \pm 51$  cells. gFW $^{-1}$ ), 5 m for *Sinophysis* spp. ( $28 \pm 30$  cells.gFW $^{-1}$ ), 7 m for *Sinophysis*  
243 spp. ( $28 \pm 30$  cells. gFW $^{-1}$ ), 8 m for *Prorocentrum* spp. ( $676 \pm 254$  cells.gFW $^{-1}$ ), 8 - 9 m  
244 for *Coolia* spp. ( $60 \pm 42$  cells.gFW $^{-1}$ ) and 15 m for *Amphidinium* spp. ( $31 \pm 31$  cells. gFW $^{-1}$ ).  
245 Abundances of benthic dinoflagellates varied with depth also during the dry season  
246 ( $p=0.003$ ). The highest abundance was at 4 m ( $1850 \pm 656$  cells.gFW $^{-1}$ ) and lowest was at  
247 20 m depth ( $26 \pm 45$  cells.gFW $^{-1}$ ) (Fig 5). *Ostreopsis* spp dominated the community of  
248 benthic dinoflagellates overall. From 4 to 6 m *Ostreopsis* spp. dominated *Prorocentrum*  
249 spp. with respective abundances of  $930 \pm 433$  cells gFW $^{-1}$  and  $619 \pm 282$  cells.gFW $^{-1}$   
250 whereas from 7 to 9 m *Prorocentrum* spp. dominated *Ostreopsis* spp. with respective  
251 abundances of  $307 \pm 143$  cells gFW $^{-1}$  and  $181 \pm 91$ cells.gFW $^{-1}$ . The highest abundances  
252 were observed at depth of 6 m for *Coolia* spp. ( $59 \pm 67$ ), 7 m for *Sinophysis* spp. ( $21 \pm 36$ ),

253 8 m for *Gambierdiscus* spp. ( $16 \pm 14$ ) and 9 m for *Amphidinium* spp. ( $20 \pm 22$ ). The  
254 abundances for these genera were low.

255 Abundances of benthic dinoflagellates were similar during the wet and the dry season  
256 ( $p=0.387$ ).

257 Preferential depth of *Ostreopsis* spp. and *Prorocentrum* spp. changed according to  
258 the dominant genus. *Prorocentrum* spp. present a peak of abundance deeper than  
259 *Ostreopsis* spp. when *Prorocentrum* spp. dominated the benthic dinoflagellates community  
260 (Gosier during the dry season and Rivière Sens during the wet season). Furthermore, peak  
261 abundances of *Prorocentrum* spp. and *Ostreopsis* spp. occurred at the same depth when  
262 *Ostreopsis* spp. were dominant in the microalgae community (Gosier during the wet season  
263 and Rivière Sens during the dry season). Concerning *Coolia* spp., *Amphidinium* spp. and  
264 *Sinophysis* spp., the depth of the peak abundances changed between the seasons at Riviere  
265 Sens. Peak abundances of *Coolia* spp. and *Amphidinium* spp. were deeper during the wet  
266 season than the dry season at Rivière Sens. The highest abundances of *Coolia* spp. and  
267 *Amphidinium* spp. were found respectively at 8-9 m depths and 15 m respectively during the  
268 wet season while highest abundances of these genera where at 6 m depth and 8 m depth  
269 respectively. However, the depth of peak abundance of *Sinophysis* spp. was shallowest  
270 during the wet season (5 m depth) than the dry season (8 m depth). *Coolia* spp.,  
271 *Amphidinium* spp. and *Sinophysis* spp. have not been found during the dry season at  
272 Gosier.

273

274 *Temperature, salinity and benthic dinoflagellates*

275 Highest *Ostreopsis* spp. abundances occurred for the wet season at Gosier with an  
276 optimal salinity of  $31.3^{\circ}\text{C}$  and  $31.4^{\circ}\text{C}$  while the highest abundance of *Ostreopsis* spp. was  
277 observed at  $26.8^{\circ}\text{C}$  for the wet season at Rivière Sens. *Ostreopsis* spp. abundances

278 occurred in maximal abundance during the dry season when evaporation was maximal and  
279 with a water salinity of 36. Highest abundances of *Prorocentrum* spp. were observed  
280 during the dry season with a temperature of 27.4°C and a salinity of 35. The highest  
281 abundance of *Gambierdiscus* spp. were found at the shallow site (Gosier) during the wet  
282 season when seawater temperature was the warmest above 30°C and when salinity was of  
283 30.

284 The highest abundances of *Coolia* spp. were found during the warmest season (the wet  
285 season), when temperature was included between 29.4°C and 31°C with a salinity of  
286 seawater of 30. Highest abundances of *Amphidinium* spp. were found at Gosier and at  
287 Rivière Sens during the wet season when temperature and salinity were above 29°C and 30  
288 respectively. Highest abundances of *Sinophysis* spp; were found at Riviere Sens, the  
289 deepest site when temperature was comprised between 26.8°C and 29.8°C and salinity  
290 included 30-36.

291 *Interaction between ecological parameters and benthic dinoflagellates*

292 Relation between environmental parameters measured at both sites (Rivière Sens and  
293 Gosier) and benthic dinoflagellates abundances ( $\text{cells.gFW}^{-1}$ ) has been analysed together  
294 with a Spearman correlation. None of the studied environmental parameters were  
295 significantly linked with total average abundances of benthic toxic dinoflagellates but they  
296 influenced several genera independently. The depth, salinity and biomass of *H. stipulacea*  
297 ( $\text{g.m}^{-2}$ ) were weakly correlated with abundance of benthic dinoflagellates ( $\text{cells.gFW}^{-1}$ ).  
298 The depth was negatively correlated with *Ostreopsis* spp. and *Gambierdiscus* abundances  
299 while the depth was positively correlated with *Amphidinium* spp.. The salinity was  
300 positively correlated with *Ostreopsis* spp. and negatively correlated with *Gambierdiscus*  
301 spp. abundances. The temperature was positively correlated with *Gambierdiscus* spp. only

302 (Table 1). Also, a weak positive correlation between *Ostreopsis* spp. abundances and *H.*  
303 *stipulacea* biomass was found.

304 Abudances of several genera of benthic dinflagellates were weakly correlated  
305 between them. *Ostreopsis* spp. abundances were correlated with *Prorocentrum* spp.,  
306 *Gambierdiscus* spp., and *Amphidinium* spp.. *Prorocentrum* spp. were correlated with  
307 *Coolia* spp. *Amphidinium* spp. and *Sinophysis* spp. Only weak positive correlations were  
308 found between *Coolia* spp. *Amphidinium* spp. and *Gambierdiscus* spp. and total  
309 abundances of benthic dinoflagellates while total abundances were strongly correlated with  
310 abundance of *Ostreopsis* spp. and *Prorocentrum* spp..

311 *Density of benthic dinoflagellates*

312 At Gosier the highest abundances of dinoflagellates per square meter were observed  
313 at 0 m depth ( $6.9 \cdot 10^5 \pm 2.9 \cdot 10^4$  cells.m $^{-2}$ ) during wet season and at 1.5 m depth ( $7.0 \cdot 10^5 \pm$   
314  $6.5 \cdot 10^5$  cells.m $^{-2}$ ) during the dry season (p=0.037) (Figure 6). No difference of total density  
315 of benthic dinoflagellates was found between the wet and the dry season (p=0.115).

316 At Rivière Sens the highest abundances of dinoflagellates per square meter were  
317 observed at 7 m and 8 m depths ( $3.9 \cdot 10^5 \pm 2.0 \cdot 10^5$  cells.m $^{-2}$ ) during the wet season  
318 (p=0.0024) and at 6 m ( $2.1 \cdot 10^6 \pm 9.1 \cdot 10^5$  cells.m $^{-2}$ ) during the dry season (p=0,003). Total  
319 densities of benthic dinoflagellates were similar between the wet and the dry season.  
320 (p=0.053).

321

322 **Discussion**

323 *Influence of ecological factors*

324 This study examined the depth effect on abundances of epiphytic dinoflagellates.  
325 Samples were collected on similar natural substrate at different depths in Guadeloupe at

326 Gosier and Rivière Sens. This approach was possible thanks to the presence of  
327 monospecific meadows of *H. stipulacea* along a depth gradient at both sites. However,  
328 none area presented a continuous populations of *H. stipulacea* from the surface to 25 m  
329 depth. Distribution of dinoflagellates was consequently observed in shallow depth at  
330 Gosier and deeper at Riviere Sens.

331 This is a novel study, because no dinoflagellate census has been realized in  
332 Guadeloupe so far. Only genera were determined in this study due to morphological  
333 identification difficulties leading to determination confusions. Morphogenetic analysis of  
334 benthic dinoflagellates present in Guadeloupe and Martinique are under investigation.  
335 Furthermore, to our knowledge enumerations of benthic dinoflagellates have never been  
336 done on *Halophila stipulacea*,

337 Among the studied parameters, the depth was the principal factor affecting  
338 *Ostreopsis* spp. distribution with higher abundances found at the lower depths sampled.  
339 Similar trends on depth distribution were also observed in the Pacific Ocean (Richlen and  
340 Lobel, 2011) and the Mediterranean Sea (Totti et al., 2010; Cohu et al., 2013) potentially  
341 linked with light intensity (Totti et al., 2010). However, this study did not allow to identify  
342 separately effects of light intensity and depth on *Ostreopsis* spp. distribution. *Ostreopsis*  
343 spp. occurred in maximal abundances with higher salinity in present survey. Indeed, the  
344 optimal salinity for growth of *Ostreopsis* spp. in the Caribbean area was 33 (Morton et al.,  
345 1992). Also, the temperature was not an ecological factor correlated to abundances of  
346 *Ostreopsis* spp. in this study. However, maximal abundances of *Ostreopsis* spp. were  
347 included between 26.8°C and 31.4°C in this survey while optimal growth for this genus  
348 were 25°C (Morton et al., 1992). The temperature was not found to be contributing to  
349 *Ostreopsis* spp. seasonal fluctuations in the Caribbean area (Ballantine et al., 1988;  
350 Okolodkov et al., 2007) as in temperate waters (Vila et al., 2001). However, in other

351 studies conducted in the Mediterranean Sea, the highest abundances of *Ostreopsis* spp.  
352 were found when surface seawater temperature was the highest (Aligizaki and Nikolaidis,  
353 2006; Mangialajo et al., 2008).

354 The depth is the environmental factor with the lowest influence on *Gambierdiscus* spp.  
355 abundances. According to different studies, abundances of *Gambierdiscus* were not  
356 affected by depth , increased with depth (Richlen and Lobel, 2011) or decreased with  
357 depth (Taylor, 1985; Xu et al., 2014). In the present study, abundances were higher in  
358 shallow environments. The same trend existed in Pacific Ocean where *Gambierdiscus* spp.  
359 abundance at 2–3 m depth exceeded abundances at 10–15 m depth (Xu et al., 2014).  
360 Similar distributions were observed in different islands of the Caribbean Sea (Taylor,  
361 1985) with a peak of abundance between 0.5 m and 3 m depth. It have been suggested that  
362 absence of *Gambierdiscus* spp. in surface water could be explained by decreased salinity  
363 due to rainy events (Taylor, 1985). This explanation can be excluded for this study as  
364 increased salinity during the dry season at Rivière Sens has not lead to increased  
365 abundances of *Gambierdiscus* spp.. Furthermore, highest abundances of *Gambierdiscus*  
366 spp. were found in this study during the wet season (season with the lowest seawater  
367 salinities) and at depths where the salinity was the lowest during this period suggesting  
368 seasonal salinities have more impact than salinity variations with depth. Also, the highest  
369 abundances of *Gambierdiscus* spp. were found at Gosier during the wet season and when  
370 the seawater temperature was the warmest of this study (above 30°C). Optimal growth of  
371 *Gambierdiscus* spp. from the Caribbean region was observed at conditions close to the  
372 environment conditions with temperature of 29°C and salinity of 30 (Morton et al., 1992).  
373 Abundances of *Gambierdiscus* spp. found in this study were particularly low contrary to  
374 monitoring conducted in the Caribbean area (Ballantine et al., 1988, 1985; Bomber et al.,  
375 1989). Seasonal fluctuations of *Gambiersicus* spp. are still unknown in Guadeloupe.

376 A positive correlation existed between *Coolia* spp. abundances and depth in this study. In  
377 the Mediterranean Sea this genus was observed at depths higher than 3 m (Cohu and  
378 Lemée, 2012). *Coolia* spp. distribution is often neglected in studies conducted in the  
379 tropical areas. Furthermore, among ecological study carried out in tropical areas and  
380 focusing on the depth none study has showed distribution of *Coolia* spp.. Only information  
381 about low abundances of *Coolia* spp. ( $< 1\ 000 \text{ cells.gFW}^{-1}$ ) have been found in these  
382 studies (Delgado et al., 2005; Xu et al., 2014). *Coolia* spp. present in the Caribbean area  
383 exhibited optimal growth with a salinity of 33 and a temperature of 29°C (Morton et al.,  
384 1992). The results of this ecological study corroborated partially results of this study  
385 because highest abundances of *Coolia* spp. were found during the warmest period (the wet  
386 season), when temperature was included between 29.4°C and 31°C and with a salinity of  
387 seawater of 30. *Coolia* spp. were first reported to synthesize toxins in the early work  
388 (Holmes et al., 1995) but none strains examined by Penna et al., (2005) were toxic and  
389 Rhodes et al., (2000) have found both toxic and nontoxic strains. The toxicity variation of  
390 *Coolia* spp. is difficult to interpreted and cannot be linked with a problem of identification  
391 because taxonomic problems have not been reported for this genus (Penna et al., 2005).  
392 Effects of *Coolia* spp. on human health are still unknown (Zingone et al., 2006).  
393 ~~In fact, despite some initial studies suggested that the species produced cooliatoxin.~~  
394 ~~(Holmes et al., 1995), further tests indicated that *Coolia* spp. is not toxic (Delia et al.,~~  
395 ~~2015).~~

396 Higher abundances of *Amphidinium* spp. were found in this survey with different  
397 temperature and salinity promoting optimal growth of *Amphidinium* spp. Indeed, the  
398 ecological study conducted on Caribbean benthic dinoflagellates has found an optimal  
399 growth temperature between 26°C and 28°C and a salinity of 34. This genus was found in

400 lowest abundances in Republic of Kiribati (0-12 cells.gFW<sup>-1</sup>) but distribution of  
401 *Amphidinium* spp. has not been studied according to the depth (Xu et al., 2014)  
402 *Sinophysis* spp. have been neglected by the ecological study.

403

404 *Species interactions*

405 The *Prorocentrum* spp. peak of abundances was always deeper than the *Ostreopsis*  
406 spp. peak of abundance when *Prorocentrum* genus dominated the dinoflagellate  
407 community. However peaks of abundance of *Ostreopsis* and *Prorocentrum* genera  
408 occurred in surface and at the same depth when *Ostreopsis* spp. dominated the benthic  
409 dinoflagellates assemblage. Richlen and Lobel (2011) suggested habitat separation  
410 between both genera. Nevertheless, in this study abundances of *Ostreopsis* spp. and  
411 *Prorocentrum* spp. were positively correlated, suggesting common preferences and  
412 possible competition phenomena and/or allelopathic interactions. The temporal  
413 fluctuations of benthic dinoflagellates are still unknown in Guadeloupe. However,  
414 monitoring conducted in the Caribbean Sea and the Gulf of Mexico have observed a  
415 characteristic dominance of *Prorocentrum* spp. in the benthic dinoflagellate assemblage  
416 (Delgado et al., 2005; Okolodkov et al., 2014; Martinez-Cruz et al., 2015; Morton and  
417 Faust, 1997). These previous studies support the dominance of *Prorocentrum* spp. at  
418 Gosier and at Rivi re Sens during the dry and the wet season respectively in this study.  
419 Despite the dominance of *Ostreopsis* spp. seems to be unusual in the Caribbean Sea, this  
420 prevalence was found in few Caribbean monitoring however none *Prorocentrum* spp.  
421 abundance were mentioned (Ballantine et al., 1988). These results sustain dominance of  
422 *Ostreopsis* spp. found in this study at Gosier and at Rivi re Sens during the wet and the dry  
423 season respectively. Furthermore, few studies have been conducted on allelopathic  
424 interactions of benthic dinoflagellates (Richlen and Lobel, 2011). *Prorocentrum*,

425 *Ostreopsis*, *Gambierdiscus*, *Coolia*, and *Amphidinium* are known to synthetize  
426 allelochemical components inhibiting growth of microalgae (Sugg and VanDolah, 1999;  
427 Legrand et al., 2003; Graneli et al., 2008). Assimilation of nutrients and environmental  
428 factors affect toxins content of benthic dinoflagellates (Pezzolesi et al., 2012). P-nutrition  
429 has been shown to influence toxin production. A rapid P-uptake within few days was found  
430 for *Ostreopsis* spp. (Pezzolesi et al., 2014) and *Prorocentrum* spp. (Vanucci et al., 2010)  
431 suggesting *Ostreopsis* spp. and *Prorocentrm* spp. could compete. Recently, *Ostreopsis* spp.  
432 was found to favour cell attachment of *Prorocentrum* spp. with a positive dose dependent  
433 relationship while cell lysis was observed at the same time for *Gambierdiscus* spp.  
434 (García-Portela et al., 2016). All these strategies highlight complexity of allelopathic  
435 interactions used by benthic dinoflagellates and could explain different distributions of  
436 dinoflagellates along the depth

437 *Gambierdiscus* spp., *Amphidinium* spp., *Coolia* spp. and *Sinophysis* spp. were  
438 abundances dependent. They co-occurred in low abundances. Positive correlations were  
439 also found between *Coolia* spp., *Ostreopsis* spp. and *Prorocentrum* spp., as in the  
440 Mediterranean Sea (Cohu and Lemée, 2012).

441 To our knowledge enumerations of benthic dinoflagellates have never been done on  
442 *Halophila stipulacea*. In the Caribbean Sea, seagrass species are known to support lower  
443 dinoflagellate abundances than macroalgae (Taylor, 1985; Morton and Faust, 1997).  
444 However (Okolodkov et al., 2007) found the highest abundance of *Prorocentrum* spp. (31  
445 467 cells.gFW<sup>-1</sup>) on *Thalassia testudinum*, a seagrass, present in the Gulf of Mexico  
446 (Okolodkov et al., 2007). This is about 18 times more than the maximum of *Prorocentrum*  
447 spp. found in this study. At Belize (Morton and Faust, 1997) the lowest total abundance of  
448 benthic dinoflagellates was found on *T. testudinum* and was comparable with average  
449 abundances found in Guadeloupe found on *H. stipulacea*.

450 *Substratum and dinoflagellates*

451 Some previous studies have suggested a host preference of benthic *Ostreopsis* spp.  
452 depending on the macrophyte morphology with higher abundances on branched thalli  
453 (Totti et al., 2010), on Phaeophyceae and Florideophyceae (Monti et al., 2007) and on  
454 *Dictyota* sp. (Ballantine et al., 1985). However, more detailed studies on selected seagrass  
455 species are still lacking (Martinez-Cruz et al., 2015). In this study, a weak positive  
456 correlation was found between *Ostreopsis* spp. abundances (cells.gFW<sup>-1</sup>) and *H. stipulacea*  
457 biomass (g.m<sup>-2</sup>). An ecological study with enumeration of benthic dinoflagellates present  
458 on different macrophytes and *H. stipulacea* must be conducted in Guadeloupe in order to  
459 confirm a preferential association between *Ostreopsis* spp. and *H. stipulacea*.

460 At Rivière Sens, biomass and leaf surface of *H. stipulacea* increased with depth. A  
461 similar pattern was also observed for this species in the Mediterranean (Procaccini et al.,  
462 1999). However, availability of space for attachment on macrophyte does not seem to be  
463 the main limiting factor for dinoflagellates because during the wet season their maximum  
464 abundance was located at 7-8 m depths while leaf surface is maximal at 15-20 m depth. A  
465 dense vegetation cover increases available surface colonisable by benthic dinoflagellates  
466 but it also decreases light irradiance necessary for the photosynthesis of dinoflagellates  
467 limiting their growth.

468 *Halophila stipulacea* is a seagrass grazed by fish (Mariani and Alcoverro, 1999) and  
469 turtles (Becking et al., 2014). Presence of dinoflagellates at each depth on *H. stipulacea*  
470 must be considered as a risk allowing the entrance of phycotoxins in the food web via  
471 herbivorous behaviour regardless of depth. This invasive seagrass would contribute to  
472 toxic dinoflagellates growth and persistence of ciguatera fish poisoning in the Caribbean  
473 region which is the second area of the word affected by this disease (Chinain et al., 2014).  
474 Monitoring of benthic toxic dinoflagellates present on *H. stipulacea* should be set also in

475 Mediterranean Sea to assess capacity of this macrophyte to support toxic benthic  
476 dinoflagellates. Until 2007, *H. stipulacea* was too sparse to coexist under canopy of the  
477 large native seagrasses of Mediterranean Sea (Williams, 2007). Actually mono-specific  
478 meadows of *H. stipulacea* more than 2 000 m<sup>2</sup> are observed in Mediterranean Sea (Sghaier  
479 et al., 2011).

480

## 481 **Conclusion**

482 Depth was not an environmental factor influencing the total abundance of benthic  
483 dinoflagellates however it partially structured the distribution of some dinoflagellates  
484 genera suggesting interaction with other parameters. Thereby, monitoring of abundance of  
485 benthic dinoflagellates conducted at shallow depths may underestimate the risk due to  
486 presence of different benthic dinoflagellates genera. However, this common method seems  
487 to be appropriate for the Caribbean area where the main sanitary trouble is due to  
488 *Gambierdiscus* spp.. presence which is found in higher abundance at shallow depth. A  
489 temporal survey must be conducted at shallow depths in order to know population dynamic  
490 of *Gambierdiscus* spp. in Guadeloupe Island.

491

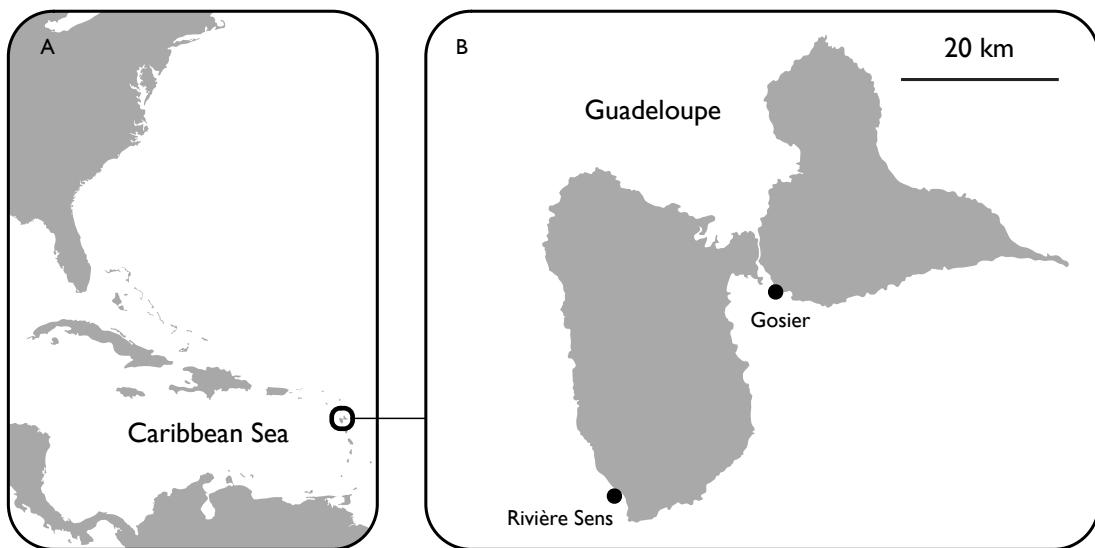
## 492 **Acknowledgements**

493 This study was made possible by the “Collectivité Territoriale de la Martinique”. This  
494 study was partly funded by the PROLITENSAN project (“Fondation de France”) and our  
495 group is part of the National French GDR PHYCOTOX (CNRS and Ifremer).

496

## Figure and table

497



498

Figure 1: A: Location of Guadeloupe archipelago in the Caribbean Sea, B: Location of  
Rivièrre Sens (deep site) and Gosier (shallow site) in Guadeloupe.

500

501

502

503

504

505

506

507

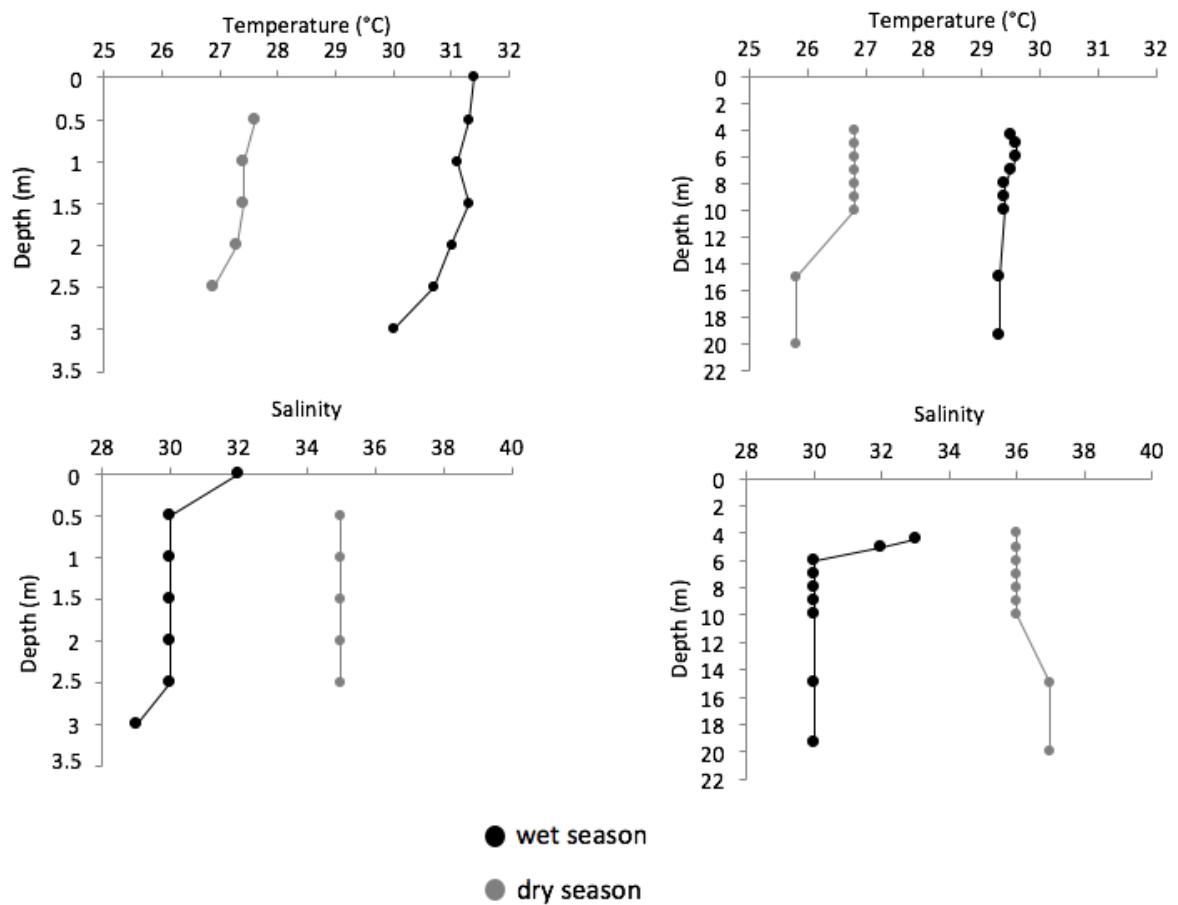
508

509

510

511

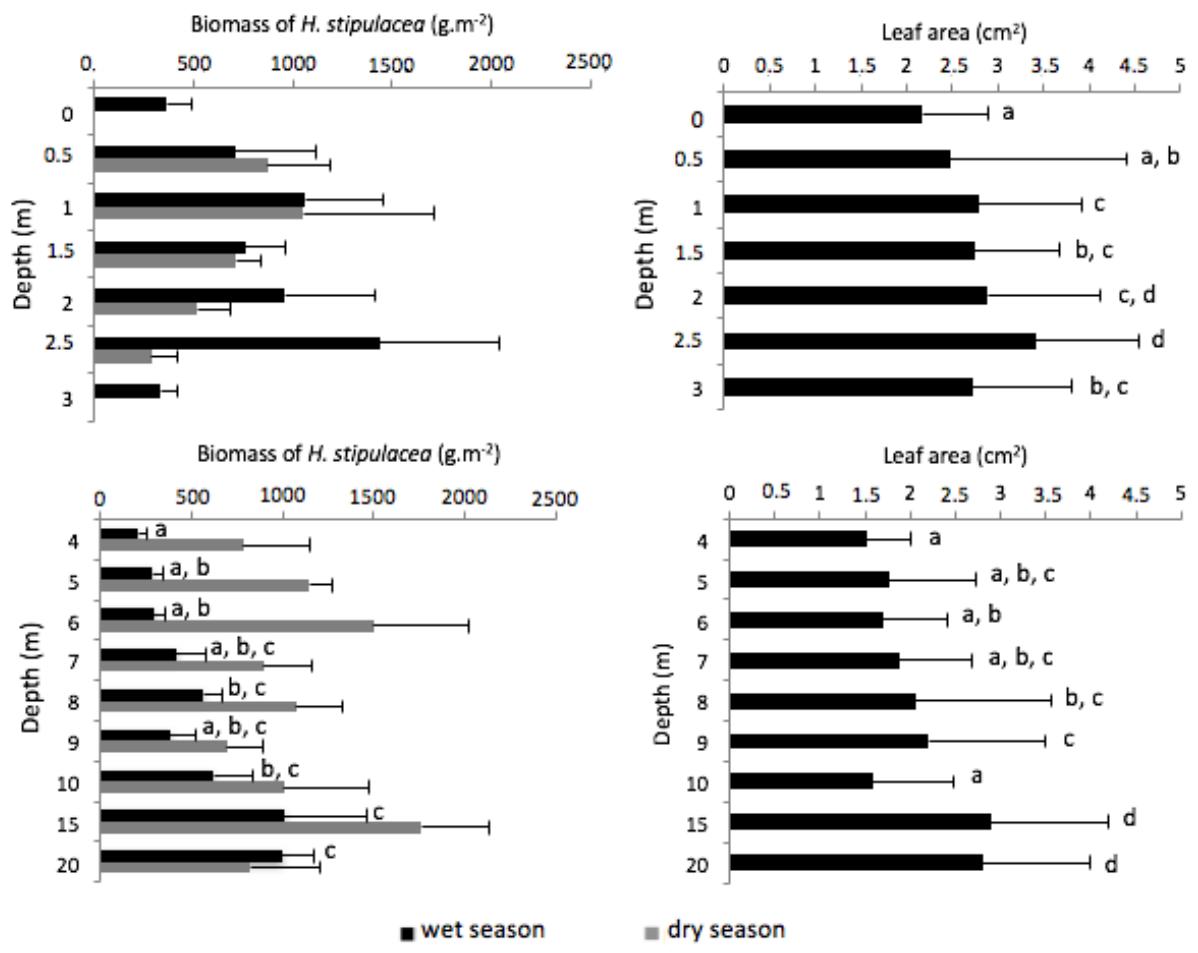
512



513

514 Figure 2. Profiles of temperature and salinity during the wet (black) and the dry (grey)  
 515 seasons at Gosier (graphs on the left) and Rivière Sens (graphs on the right).

516



517

518

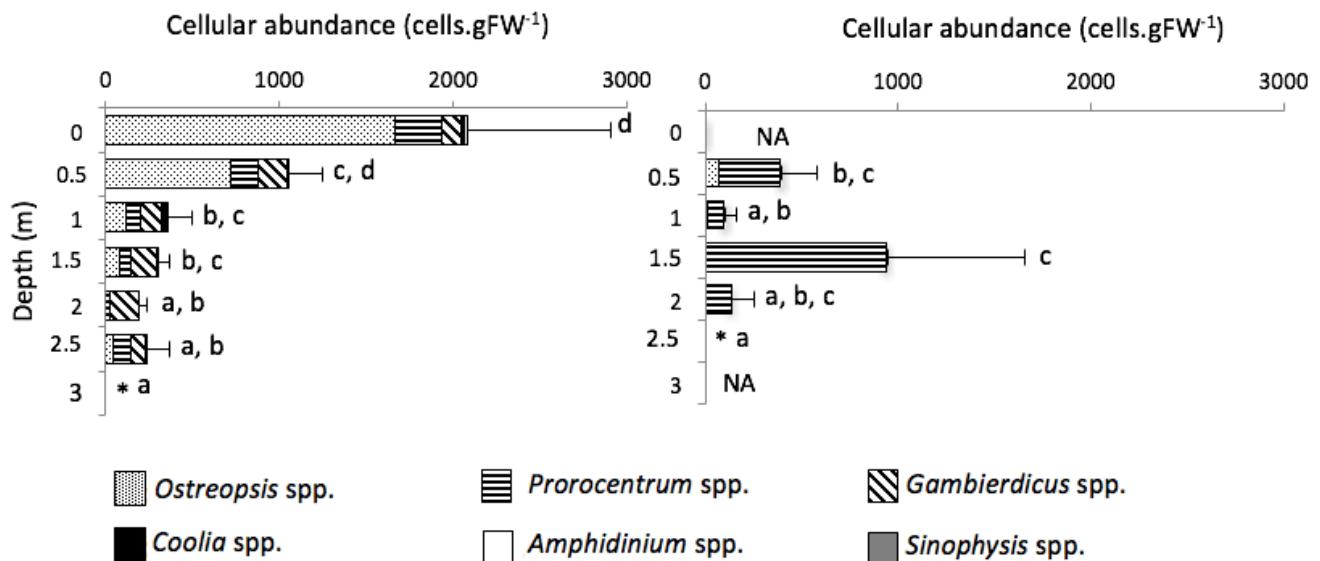
519 Figure 3: Left. Mean *Halophila stipulacea* biomass (left) and leaf surface (cm<sup>2</sup> per leaf)  
520 (right) ( $\pm$  SD, n = 3) at different depths at Gosier (above) and Rivière Sens (below) during  
521 the wet (black) and the dry seasons (grey). Significant differences between depths are  
522 indicated with letters (Kruskal Wallis test and Dunn test,  $\alpha=0,05$ ).

523 It should be noticed that, in each station, the trend of *H. stipulacea* exhibits different trends  
524 in distribution with depth in the wet than in the dry season.

525

526

527



528

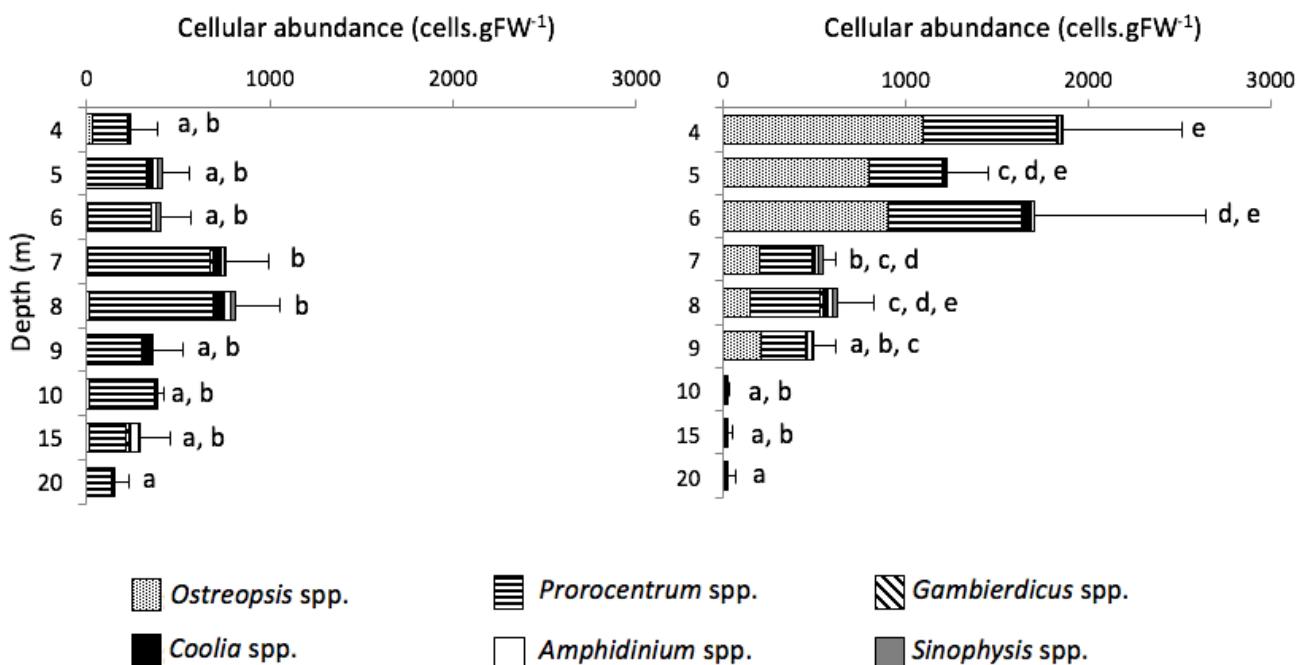
529 Figure 4: Abundance of benthic toxic dinoflagellates with depth during the wet (left) and  
 530 the dry (right) season at Gosier. “\*” indicates no cell found but depth sampled and “NA”  
 531 data no available because no macrophyte was found. Significant differences between  
 532 depths are indicated with letters (Kruskal-Wallis test and Dunn test,  $\alpha=0,05$ ).  
 533

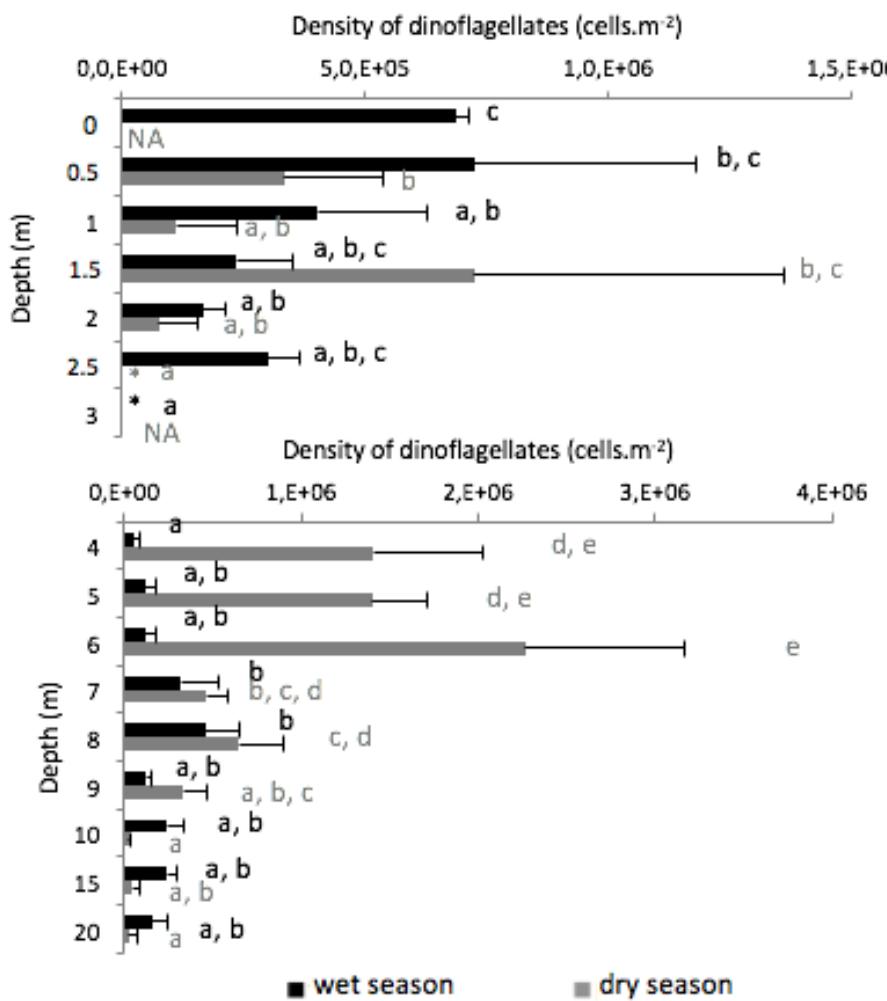
534

535

536

537





544

545 Figure 6: Mean density of benthic dinoflagellates  $\pm$  SD according to depth at Gosier  
 546 (above) and at Rivière Sens (below) for the wet (black) and the dry season (grey). “\*”  
 547 indicates no cell found but depth sampled and “NA” data no available because no  
 548 macrophyte was found. Significant differences between depths are indicated with letters  
 549 (Kruskal Wallis test and Dunn test,  $\alpha=0,05$ ).

550

551

552 Table 1: Relations between depth (m), temperature (°C), salinity, *H. stipulacea* biomass  
 553 ( $\text{g.m}^{-2}$ ), total abundances and abundances of *Ostreopsis*, *Prorocentrum*, *Gambierdiscus*,  
 554 *Coolia*, *Amphidinium* and *Sinophysis* genera (cells. $\text{gFW}^{-1}$ ). Coefficient  $r_s$  of Spearman,  
 555 bold when significant with  $p<0.05$ , bold and underlined when significant with  $p<0.01$ .

	<i>Ostreopsis</i> spp.	<i>Prorocentrum</i> spp.	<i>Gambierdiscus</i> spp.	<i>Coolia</i> spp.	<i>Amphidinium</i> spp.	<i>Sinophysis</i> spp.	Average abundance
Depth	<b>-0,299</b>	0,015	<b>-0,363</b>	<b>0,260</b>	0,090	0,152	-0,193
Temperature	0,008	-0,046	<b>0,558</b>	-0,064	0,088	0,022	0,096
Salinity	<b>0,210</b>	0,020	<b>-0,388</b>	0,060	-0,093	-0,032	0,044
<i>H.stipulacea</i> Biomass	<b>0,236</b>	-0,107	0,203	0,036	-0,021	-0,182	0,014
<i>Ostreopsis</i> spp.		<b><u>0,364</u></b>	<b>0,284</b>	0,037	<b>0,263</b>	0,120	<b>0,695</b>
<i>Prorocentrum</i> spp.			-0,139	<b>0,223</b>	<b>0,220</b>	<b>0,298</b>	<b>0,836</b>
<i>Gambierdiscus</i> spp.				-0,032	0,105	-0,007	0,164
<i>Coolia</i> spp.					0,047	0,094	<b>0,295</b>
<i>Amphidinium</i> spp.						0,248	<b>0,273</b>
<i>Sinophysis</i> spp.							<b>0,242</b>
Average abundance							

556

## **References**

- Abbate, M., Bordone, A., Cerrati, G., Festa, T.D., Melchiorre, N., Pastorelli, A.M., Peirano, A., Rosaria Petruzzelli, M., Ungaro, N., 2012. A new method for sampling potentially toxic benthic dinoflagellates. *Cryptogam. Algol.* 33, 165–170.
- Accoroni, S., Percopo, I., Cerino, F., Romagnoli, T., Pichierri, S., Perrone, C., Totti, C., 2015. Allelopathic interactions between the HAB dinoflagellate *Ostreopsis cf. ovata* and macroalgae. *Harmful Algae* 49, 147–155.
- Adachi, M., Fukuyo, Y., 1979. The thecal structure of marine toxic dinoflagellate *Gambierdiscus toxicus* gen. et sp. nov. collected in a ciguatera-endemic area. *J. Jpn. Soc. Sci. Fish.* 45, 67–71.
- Ahmed, F.E., 1991. Naturally occurring fish and shellfish poisons. *Seafood safety*, Washington, D.C.
- Ajani, P., Harwood, D.T., Murray, S.A., 2017. Recent trends in marine phycotoxins from australian coastal waters. *Mar. Drugs* 15, 1–20.
- Alcala, A.C., Alcala, L.C., Garth, J.S., Yasumura, D., Yasumoto, T., 1988. Human fatality due to ingestion of the crab *Demania reynaudii* that contained a palytoxin-like toxin. *Toxicon* 26, 105–107.
- Aligizaki, K., Katikou, P., Milandri, A., Diogène, J., 2011. Occurrence of palytoxin-group toxins in seafood and future strategies to complement the present state of the art. *Toxicon, Palytoxin-group toxins* 57, 390–399.
- Aligizaki, K., Nikolaidis, G., 2006. The presence of the potentially toxic genera *Ostreopsis* and *Coolia* (Dinophyceae) in the North Aegean Sea, Greece. *Harmful Algae* 5, 717–730.
- Bagnis, R., 1981. L'ichtyosarcotoxicisme de type ciguatera: phénomène complexe de biologie marine et humaine. *Oceanol. Acta* 4, 375–387.
- Ballantine, D.L., Bardales, A.T., Tosteson, T.R., 1985. Seasonal abundance of *Gambierdiscus toxicus* and *Ostreopsis* sp. in coastal waters of southwest Puerto Rico. Proceeding of the Fifth International Coral Reef Congress, Tahiti, pp. 417–422.
- Ballantine, D.L., Tosteson, T.R., Bardales, A.T., 1988. Population dynamics and toxicity of natural populations of benthic dinoflagellates in southwestern Puerto Rico. *J. Exp. Mar. Biol. Ecol.* 119, 201–212.
- Bauder, A.G., Cembella, A.D., Bricelj, V.M., Quilliam, M.A., 2001. Uptake and fate of diarrhetic shellfish poisoning toxins from the dinoflagellate *Argopecten irradians*, *Prorocentrum lima* in the bay scallop *Argopecten irradians*. *Mar. Ecol. Prog. Ser.* 213, 39–52.
- Becking, L.E., Bussel, T.C.J.M. van, Debrot, A.O., Christianen, M.J.A., 2014. First record of a caribbean green turtle (*Chelonia mydas*) grazing on invasive seagrass (*Halophila stipulacea*). *Caribb. J. Sci.* 48, 162–163.
- Ben-Gharbia, H., Yahia, O.K.-D., Amzil, Z., Chomérat, N., Abadie, E., Masseret, E., Sibat, M., Zmerli Triki, H., Nouri, H., Laabir, M., 2016. Toxicity and growth assessments of three thermophilic benthic dinoflagellates (*Ostreopsis cf. ovata*, *Prorocentrum lima* and *Coolia monotis*) developing in the Southern Mediterranean Basin. *Toxins* 8, 1–38.
- Berdelet, E., Fleming, L.E., Gowen, R., Davidson, K., Hess, P., Backer, L.C., Moore, S.K., Hoagland, P., Enevoldsen, H., 2015. Marine harmful algal blooms, human health

- and wellbeing: challenges and opportunities in the 21st century. *J. Mar. Biol. Assoc. U. K.* 1–31.
- Berdalet, E., Tester, P.A., Chinain, M., Fraga, S., Lemée, R., Litaker, W., Penna, A., Usup, G., Vila, M., Zingone, A., 2017. Harmful algal blooms in benthic systems: Recent progress and future research. *Oceanography* 30, 36–45.
- Bomber, J.W., Rubio, M.G., Norris, D.R., 1989. Epiphytism of dinoflagellates associated with the disease ciguatera: substrate specificity and nutrition. *Phycologia* 28, 360–368.
- Botana, L.M., 2014. *Seafood and Freshwater Toxins: Pharmacology, Physiology, and Detection*, Third Edition. CRC Press.
- Burkholder, J.M., Glibert, P.M., Skelton, H.M., 2008. Mixotrophy, a major mode of nutrition for harmful algal species in eutrophic waters. *Harmful Algae, HABs and Eutrophication* 8, 77–93. doi:10.1016/j.hal.2008.08.010
- Chang, F.H., Shimizu, Y., Hay, B., Stewart, R., Mackay, G., Tasker, R., 2000. Three recently recorded *Ostreopsis* spp. (Dinophyceae) in New Zealand: Temporal and regional distribution in the upper North Island from 1995 to 1997. *N. Z. J. Mar. Freshw. Res.* 34, 29–39.
- Chinain, M., Darius, H.T., Ung, A., Cruchet, P., Wang, Z., Ponton, D., Laurent, D., Pauillac, S., 2010. Growth and toxin production in the ciguatera-causing dinoflagellate *Gambierdiscus polynesiensis* (Dinophyceae) in culture. *Toxicon Off. J. Int. Soc. Toxicology* 56, 739–750.
- Chinain, M., Gatti, C., Roué, M., Laurent, D., Darius, H.T., 2014. Ciguatéra: aspects écologiques, biologiques et toxicologiques. *Rev. Francoph. Lab., Micro-organismes pathogènes de l'eau (2)* 2014, 27–39.
- Chomérat, N., 2016. Studies on the benthic genus *Sinophysis* (Dinophysales, Dinophyceae): I. a taxonomic investigation from Martinique Island, including two new species and elucidation of the epithecal plate pattern. *Phycologia* 55, 445–461. doi:10.2216/16-24.1
- Ciminiello, P., Dell'Aversano, C., Iacovo, E.D., Fattorusso, E., Forino, M., Tartaglione, L., Benedettini, G., Onorari, M., Serena, F., Battocchi, C., Casabianca, S., Penna, A., 2014. First finding of *Ostreopsis* cf. *ovata* toxins in marine aerosols. *Environ. Sci. Technol.* 48, 3532–3540.
- Cloern, J.E., Schraga, T.S., Lopez, C.B., Knowles, N., Grover Labiosa, R., Dugdale, R., 2005. Climate anomalies generate an exceptional dinoflagellate bloom in San Francisco Bay. *Geophys. Res. Lett.* 32, L14608.
- Cohu, S., Lemée, R., 2012. Vertical distribution of the toxic epibenthic dinoflagellates *Ostreopsis* cf. *ovata*, *Prorocentrum lima* and *Coolia monotis* in the NW Mediterranean Sea. *CBM-Cah. Biol. Mar.* 53, 373–380.
- Cohu, S., Mangialajo, L., Thibaut, T., Blanfuné, A., Marro, S., Lemée, R., 2013. Proliferation of the toxic dinoflagellate *Ostreopsis* cf. *ovata* in relation to depth, biotic substrate and environmental factors in the North West Mediterranean Sea. *Harmful Algae* 24, 32–44.
- Delgado, G., Lechuga, C.H., Troccoli, L., Santos, K., 2006. Spatial-temporal variation of four species of toxic epiphytic dinoflagellates of *Prorocentrum* genus in NW of Cuba. *Rev. Cuba. Investig. Pesq.* 24, 5–9.
- Delgado, G., Lechuga-Devéze, C.H., Popowski, G., Troccoli, L., Salinas, C.A., 2005. Epiphytic dinoflagellates associated with ciguatera in the northwestern coast of Cuba. *Rev. Biol. Trop.* 54, 299–310.
- Delia, A.S., Caruso, G., Melcarne, L., Caruso, G., Parisi, S., Laganà, P., 2015. Biological toxins from marine and freshwater microalgae, in: *Microbial Toxins and Related*

- Contamination in the Food Industry, SpringerBriefs in Molecular Science. Springer International Publishing, pp. 13–55.
- den Hartog, C., 1970. The sea-grasses of the world. Amsterdam, London: North-Holland Publishing Company. Int. Rev. Gesamten Hydrobiol. Hydrogr. 56, 141–141.
- Dickey, R.W., Plakas, S.M., 2010. Ciguatera: a public health perspective. Toxicon 56, 123–136.
- Faust, M.A., 2009. Ciguatera-causing dinoflagellates in a coral-reef mangrove ecosystem, Belize. Atoll Res. Bull. 569, 1–30.
- Faust, M.A., 1997. Three new benthic species of *Prorocentrum* (Dinophyceae) from Belize: *P. norrisianum* sp. nov., *P. tropicalis* sp. nov., and *P. reticulaum* sp. nov. 1. J. Phycol. 33, 851–858.
- Faust, M.A., Gullledge, R.A., 2002. Identifying harmful marine dinoflagellates. Contrib. U. S. Natl. Herb. 42, 1–144.
- Fraga, S., Penna, A., Bianconi, I., Paz, B., Zapata, M., 2008. *Coolia canariensis* sp. nov. (Dinophyceae) a new nontoxic epiphytic benthic dinoflagellate from the Canary Islands. J. Phycol. 44, 1060–1070.
- Fraga, S., Rodríguez, F., 2014. Genus *Gambierdiscus* in the Canary Islands (NE Atlantic Ocean) with description of *Gambierdiscus silvae* sp. nov., a new potentially toxic epiphytic benthic dinoflagellate. Protist 165, 839–853.
- Friedman, M.A., Fleming, L.E., Fernandez, M., Bienfang, P., Schrank, K., Dickey, R., Bottein, M.-Y., Backer, L., Ayyar, R., Weisman, R., Watkins, S., Granade, R., Reich, A., 2008. Ciguatera Fish Poisoning: Treatment, Prevention and Management. Mar. Drugs 6, 456–479.
- García-Portela, M., Riobó, P., Franco, J.M., Bañuelos, R.M., Rodríguez, F., 2016. Genetic and toxinological characterization of North Atlantic strains of the dinoflagellate *Ostreopsis* and allelopathic interactions with toxic and non-toxic species from the genera *Prorocentrum*, *Coolia* and *Gambierdiscus*. Harmful Algae 60, 57–69.
- Gleibs, S., Mebs, D., 1999. Distribution and sequestration of palytoxin in coral reef animals. Toxicon 37, 1521–1527.
- Glibert, P., Anderson, D., Gentien, P., Granéli, E., Sellner, K., 2005. The global, complex phenomena of harmful algal blooms. Oceanography 18, 136–147.
- Graneli, E., Weberg, M., Salomon, P.S., 2008. Harmful algal blooms of allelopathic microalgal species: The role of eutrophication. Harmful Algae 8, 94–102.
- Grzebyk, D., Berland, B., Thomassin, B.A., Bosi, C., Arnoux, A., 1994. Ecology of ciguateric dinoflagellates in the coral reef complex of Mayotte Island (S.W. Indian Ocean). J. Exp. Mar. Biol. Ecol. 178, 51–66.
- Hallegraeff, G.M., 2010. Ocean climate change, phytoplankton community responses, and harmful algal blooms: a formidable predictive challenge 1. J. Phycol. 46, 220–235.
- Hallegraeff, G.M., 1993. A review of harmful algal blooms and their apparent global increase. Phycologia 32, 79–99.
- Heredia-Tapia, A., Arredondo-Vega, B.O., Nuñez-Vázquez, E.J., Yasumoto, T., Yasuda, M., Ochoa, J.L., 2002. Isolation of *Prorocentrum lima* (Syn. *Exuviaella lima*) and diarrhetic shellfish poisoning (DSP) risk assessment in the Gulf of California, Mexico. Toxicon 40, 1121–1127.
- Holmes, M.J., Lewis, R.J., Jones, A., Hoy, A.W.W., 1995. Cooliatoxin, the first toxin from *Coolia monotis* (dinophyceae). Nat. Toxins 3, 355–362.
- Holmes, M.J., Teo, S.L.M., 2002. Toxic marine dinoflagellates in Singapore waters that cause seafood poisonings. Clin. Exp. Pharmacol. Physiol. 29, 829–836.

- Jauzein, C., Couet, D., Blasco, T., Lemée, R., 2017. Uptake of dissolved inorganic and organic nitrogen by the benthic toxic dinoflagellate *Ostreopsis* cf. *ovata*. Harmful Algae 65, 9–18.
- Jauzein, C., Fricke, A., Mangialajo, L., Lemée, R., 2016. Sampling of *Ostreopsis* cf. *ovata* using artificial substrates: Optimization of methods for the monitoring of benthic harmful algal blooms. Mar. Pollut. Bull. 107, 300–304.
- Kumagai, M., Yanagi, T., Murata, M., Yasumoto, T., Kat, M., Lassus, P., Rodriguez-Vazquez, J.A., 1986. Okadaic acid as the causative toxin of diarrhetic shellfish poisoning in Europe. Agric. Biol. Chem. 50, 2853–2857.
- Landsberg, J.H., Van Dolah, F.M., Doucette, G.J., 2005. Marine and Estuarine Harmful Algal Blooms: Impacts on Human and Animal Health, in: Oceans and Health: Pathogens in the Marine Environment. Belkin and Colwell, pp. 165–215.
- Legrand, C., Rengefors, K., Fistarol, G.O., Granéli, E., 2003. Allelopathy in phytoplankton - biochemical, ecological and evolutionary aspects. Phycologia 42, 406–419.
- Lehane, L., Lewis, R.J., 2000. Ciguatera: recent advances but the risk remains. Int. J. Food Microbiol. 61, 91–125.
- Lenoir, S., Ten-Hage, L., Turquet, J., Quod, J.-P., Bernard, C., Hennion, M.-C., 2004. First evidence of palytoxin analogues from an *Ostreopsis mascarenensis* (Dinophyceae) benthic bloom in southwestern Indian Ocean. J. Phycol. 40, 1042–1051.
- Lewis, R.J., Holmes, M.J., 1993. Origin and transfer of toxins involved in ciguatera. Comp. Biochem. Physiol. C Pharmacol. Toxicol. Endocrinol. 106, 615–628.
- Loeffler, C., Richlen, M., Brandt, M., Smith, T., 2015. Effects of grazing, nutrients, and depth on the ciguatera-causing dinoflagellate *Gambierdiscus* in the US Virgin Islands. Mar. Ecol. Prog. Ser. 531, 91–104.
- Luo, Z., Zhang, H., Krock, B., Lu, S., Yang, W., Gu, H., 2017. Morphology, molecular phylogeny and okadaic acid production of epibenthic *Prorocentrum* (Dinophyceae) species from the northern South China Sea. Algal Res. 22, 14–30.
- Mangialajo, L., Bertolotto, R., Cattaneo-Vietti, R., Chiantore, M., Grillo, C., Lemee, R., Melchiorre, N., Moretto, P., Povero, P., Ruggieri, N., 2008. The toxic benthic dinoflagellate *Ostreopsis ovata*: Quantification of proliferation along the coastline of Genoa, Italy. Mar. Pollut. Bull. 56, 1209–1214.
- Mangialajo, L., Fricke, A., Perez-Gutierrez, G., Catania, D., Jauzein, C., Lemee, R., 2017. Benthic Dinoflagellate Integrator (BEDI): A new method for the quantification of benthic harmful algal blooms. Harmful Algae 64, 1–10.
- Mangialajo, L., Ganzin, N., Accoroni, S., Asnaghi, V., Blanfuné, A., Cabrini, M., Cattaneo-Vietti, R., Chavanon, F., Chiantore, M., Cohu, S., Costa, E., Fornasaro, D., Grossel, H., Marco-Miralles, F., Masó, M., Reñé, A., Rossi, A.M., Sala, M.M., Thibaut, T., Totti, C., Vila, M., Lemée, R., 2011. Trends in *Ostreopsis* proliferation along the Northern Mediterranean coasts. Toxicon, Palytoxin-group toxins 57, 408–420.
- Mariani, S., Alcoverro, T., 1999. A multiple-choice feeding-preference experiment utilising seagrasses with a natural population of herbivorous fishes. Mar. Ecol. Prog. Ser. 189, 295–299.
- Martinez-Cruz, Okolodkov, Y.B., aguilar-Trujillo, C., Herrera-silveira, J.A., 2015. Epiphytic dinoflagellates on the seagrass *Thalassia testudinum* at Dzilam, southeastern Gulf of Mexico. Cymbella 2–9.
- Monti, M., Minocci, M., Beran, A., Iveša, L., 2007. First record of *Ostreopsis* cf. *ovata* on macroalgae in the Northern Adriatic Sea. Mar. Pollut. Bull. 54, 598–601.
- Morton, S.L., Faust, M.A., 1997. Survey of toxic epiphytic dinoflagellates from the belizean barrier reef ecosystem. Bull. Mar. Sci. 61, 899–906.

- Morton, S.L., Norris, D.R., Bomber, J.W., 1992. Effect of temperature, salinity and light intensity on the growth and seasonality of toxic dinoflagellates associated with ciguatera. *J. Exp. Mar. Biol. Ecol.* 157, 79–90.
- Nascimento, S.M., Salgueiro, F., Menezes, M., Oliveira, F. de A., Magalhães, V.C.P., De Paula, J.C., Morris, S., 2016. *Prorocentrum lima* from the South Atlantic: Morphological, molecular and toxicological characterization. *Harmful Algae* 57, Part A, 39–48.
- Okolodkov, Y.B., Campos Bautista, G., Gárate-Lizárraga, I., González-González, J.A.G., Hoppenrath, M., Arenas, V., 2007. Seasonal changes of benthic and epiphytic dinoflagellates in the Veracruz reef zone, Gulf of Mexico. *Aquat. Microb. Ecol.* 47, 223–237.
- Okolodkov, Y.B., Del Carmen Merino-Virgilio, F., Aké-Castillo, J.A., Aguilar-Trujillo, A.C., Espinosa-Matías, S., Herrera-silveira, A., 2014. Seasonal changes in epiphytic dinoflagellate assemblages near the northern coast of the Yucatan Peninsula, Gulf of Mexico. *Acta Bot. Mex.* 107, 121–151.
- Onuma, Y., Satake, M., Ukena, T., Roux, J., Chanteau, S., Rasolofonirina, N., Ratsimaloto, M., Naoki, H., Yasumoto, T., 1999. Identification of putative palytoxin as the cause of clupeotoxicosis. *Toxicon* 37, 55–65.
- Parsons, M.L., Brandt, A.L., Ellsworth, A., Leynse, A.K., Rains, L.K., Anderson, D.M., 2017. Assessing the use of artificial substrates to monitor *Gambierdiscus* populations in the Florida Keys. *Harmful Algae* 68, 52–66. doi:10.1016/j.hal.2017.07.007
- Parsons, M.L., Preskitt, L.B., 2007. A survey of epiphytic dinoflagellates from the coastal waters of the island of Hawai'i. *Harmful Algae* 6, 658–669.
- Penna, A., Vila, M., Fraga, S., Giacobbe, M.G., Andreoni, F., Riobó, P., Vernesi, C., 2005. Characterization of *Ostreopsis* and *Coolia* (Dinophyceae) isolates in the western Mediterranean Sea based on morphology, toxicity and internal transcribed spacer 5.8s rDNA sequence. *J. Phycol.* 41, 212–225.
- Pezzolesi, L., Guerrini, F., Ciminiello, P., Dell'Aversano, C., Dello Iacovo, E., Fattorusso, E., Forino, M., Tartaglione, L., Pistocchi, R., 2012. Influence of temperature and salinity on *Ostreopsis cf. ovata* growth and evaluation of toxin content through HR LC-MS and biological assays. *Water Res.* 46, 82–92.
- Pezzolesi, L., Pistocchi, R., Fratangeli, F., Dell'Aversano, C., Dello Iacovo, E., Tartaglione, L., 2014. Growth dynamics in relation to the production of the main cellular components in the toxic dinoflagellate *Ostreopsis cf. ovata*. *Harmful Algae* 36, 1–10.
- Pistocchi, R., Pezzolesi, L., Guerrini, F., Vanucci, S., Dell'Aversano, C., Fattorusso, E., 2011. A review on the effects of environmental conditions on growth and toxin production of *Ostreopsis ovata*. *Toxicon* 57, 421–428.
- Procaccini, G., Acunto, S., Famà, P., Maltagliati, F., 1999. Structural, morphological and genetic variability in *Halophila stipulacea* (Hydrocharitaceae) populations in the western Mediterranean. *Mar. Biol.* 135, 181–189.
- Rahman Sha, M.M., An, S.-J., Lee, J.-B., 2014. Occurrence of sand-dwelling and epiphytic dinoflagellates including potentially toxic species along the coast of Jeju Island, Korea. *J. Fish. Aquat. Sci.* 9, 141–156.
- Randall, J.E., 2005. Review of clupeotoxicosis, an often fatal illness from the consumption of clupeoid fishes. *Pac. Sci.* 59, 73–77.
- Rhodes, L., Adamson, J., Suzuki, T., Briggs, L., Garthwaite, I., 2000. Toxic marine epiphytic dinoflagellates, *Ostreopsis siamensis* and *Coolia monotis* (Dinophyceae), in New Zealand. *N. Z. J. Mar. Freshw. Res.* 34, 371–383.

- Richlen, M.L., Lobel, P.S., 2011. Effects of depth, habitat, and water motion on the abundance and distribution of ciguatera dinoflagellates at Johnston Atoll, Pacific Ocean. *Mar. Ecol. Prog. Ser.* 421, 51–66.
- Ruiz, H., Ballantine, D.L., 2004. Occurrence of the seagrass *Halophila stipulacea* in the tropical West Atlantic. *Bull. Mar. Sci.* 75, 131–135.
- Sghaier, Y.R., Zakhama-Sraieb, R., Benamer, I., Charfi-Cheikhrouha, F., 2011. Occurrence of the seagrass *Halophila stipulacea* (Hydrocharitaceae) in the southern Mediterranean Sea. *Bot. Mar.* 54, 575–582.
- Shears, N.T., Ross, P.M., 2009. Blooms of benthic dinoflagellates of the genus *Ostreopsis*; an increasing and ecologically important phenomenon on temperate reefs in New Zealand and worldwide. *Harmful Algae* 8, 916–925.
- Shumway, S.E., 1990. A review of the effects of algal blooms on shellfish and aquaculture. *J. World Aquac. Soc.* 21, 65–104.
- Sugg, L.M., VanDolah, F.M., 1999. No evidence for an allelopathic role of okadaic acid among ciguatera-associated dinoflagellates. *J. Phycol.* 35, 93–103.
- Taylor, F.J.R., 1985. The distribution of the dinoflagellates *G. toxicus* in the Eastern Caribbean, in: Proceedings Of The Fifth International Coral Reef Congress. Tahiti, pp. 423–428.
- Ten-Hage, L., Turquet, J., Quod, J.-P., Puiseux-Dao, S., Coute, A., 2000. *Prorocentrum borbonicum* sp. nov. (Dinophyceae), a new toxic benthic dinoflagellate from the southwestern Indian Ocean. *Phycologia* 39, 296–301.
- Tester, P.A., 1994. Harmful marine phytoplankton and shellfish toxicity potential consequences of climate change. *Ann. N. Y. Acad. Sci.* 740, 69–76.
- Tester, P.A., Feldman, R.L., Nau, A.W., Faust, M.A., Litaker, R.W., 2009. Ciguatera fish poisoning in the Caribbean. *Smithson. Contrib. Mar. Sci.* 0, 301–311.
- Tester, P.A., Kibler, S.R., Holland, W.C., Usup, G., Vandersea, M.W., Leaw, C.P., Teen, L.P., Larsen, J., Mohammad-Noor, N., Faust, M.A., Litaker, R.W., 2014. Sampling harmful benthic dinoflagellates: Comparison of artificial and natural substrate methods. *Harmful Algae* 39, 8–25.
- Totti, C., Accoroni, S., Cerino, F., Cucchiari, E., Romagnoli, T., 2010. *Ostreopsis ovata* bloom along the Conero Riviera (northern Adriatic Sea): Relationships with environmental conditions and substrata. *Harmful Algae* 9, 233–239.
- Valdiglesias, V., Prego-Faraldo, M.V., Pásaro, E., Méndez, J., Laffon, B., 2013. Okadaic acid: More than a diarrheic doxin. *Mar. Drugs* 11, 4328–4349.
- Vanucci, S., Guerrini, F., Milandri, A., Pistocchi, R., 2010. Effects of different levels of N- and P-deficiency on cell yield, okadaic acid, DTX-1, protein and carbohydrate dynamics in the benthic dinoflagellate *Prorocentrum lima*. *Harmful Algae* 9, 590–599.
- Vila, M., Garcés, E., Masó, M., 2001. Potentially toxic epiphytic dinoflagellate assemblages on macroalgae in the NW Mediterranean. *Aquat. Microb. Ecol.* 26, 51–60.
- Willette, D.A., Ambrose, R.F., 2012. Effects of the invasive seagrass *Halophila stipulacea* on the native seagrass, *Syringodium filiforme*, and associated fish and epibiont communities in the Eastern Caribbean. *Aquat. Bot.* 103, 74–82.
- Willette, D.A., Chalifour, J., Debrot, A.O.D., Engel, M.S., Miller, J., Oxenford, H.A., Short, F.T., Steiner, S.C.C., Védie, F., 2014. Continued expansion of the trans-Atlantic invasive marine angiosperm *Halophila stipulacea* in the Eastern Caribbean. *Aquat. Bot.* 112, 98–102.
- Williams, S.L., 2007. Introduced species in seagrass ecosystems: Status and concerns. *J. Exp. Mar. Biol. Ecol., The Biology and Ecology of Seagrasses* 350, 89–110.

- Xu, Y., Richlen, M.L., Morton, S.L., Mak, Y.L., Chan, L.L., Tekiau, A., Anderson, D.M., 2014. Distribution, abundance and diversity of *Gambierdiscus* spp. from a ciguatera-endemic area in Marakei, Republic of Kiribati. Harmful Algae 34, 56–68.
- Yasumoto, T., Nakajima, I., Bagnis, R., Adachi, R., 1977. Finding of a dinoflagellate as a likely culprit of ciguatera. Nippon Suisan Gakkaishi 43, 1021–1026.
- Yasumoto, T., Seino, N., Murakami, Y., Murata, M., 1987. Toxins produced by benthic dinoflagellates. Biol. Bull. 172, 128–131.
- Zingone, A., Siano, R., D'Alelio, D., Sarno, D., 2006. Potentially toxic and harmful microalgae from coastal waters of the Campania region (Tyrrhenian Sea, Mediterranean Sea). Harmful Algae 5, 321–337.