Spatio-temporal dynamics and biotic substrate preferences of benthic dinoflagellates in the Lesser Antilles, Caribbean sea

Aurélie Boisnoir[a,b,*], Pierre-Yves Pascal[a], Sébastien Cordonnier[a], Rodolphe Lemée[b]

[a] Institut de Systématique, Évolution, Biodiversité, ISYEB, UMR 7205, Université des Antilles. Équipe Biologie de la mangrove. UFR SEN. 97100 Pointe-à-Pitre. France
[b] Sorbonne Université, CNRS, Laboratoire d'Océanographie de Villefranche, LOV, F-06230 Villefranche-sur-Mer, France

ABSTRACT

Epibenthic dinoflagellates were monitored monthly over an 18 month period in Guadeloupe and Martinique (Lesser Antilles, Caribbean Sea). These islands are located in the second most affected ciguatera fish poisoning (CFP) region of the world. Guadeloupe presented five times more total epibenthic dinoflagellates and two times less abundant *Gambierdiscus* spp. compared to Martinique, although the area of frequent CFP outbreaks covers Guadeloupe and not Martinique. Results did not show any clear seasonal variations of benthic dinoflagellates abundances. Temperature and salinity were not driving parameters in the evolution of total benthic dinoflagellate abundances. Preferential associations were found between macrophyte species and epibenthic dinoflagellates. The Phaeophyceae *Dictyota* spp. hosted the highest abundances of total epibenthic dinoflagellates, composed mainly of *Ostrepsis* and *Prorocentrum* genera. The seagrass *Halophila stipulacea* hosted the highest abundances of *Gambierdiscus* spp. and *Sinophysis* spp. whilst the highest abundance of *Coolia* was determined on *Galaxaura* spp. The pelagic *Sargassum* spp. hosted the lowest abundances of benthic dinoflagellates including the genus *Gambierdiscus*.

1. Introduction

Benthic dinoflagellates species are known to produce toxins involved in human poisonings that occur through the consumption of contaminated marine organisms (Bagnis et al., 1979; Friedman et al., 2017; Randall, 2005; Tripuraneni et al., 1997) or via the formation of toxic bio-aerosols (Ciminiello et al., 2014; Vila et al., 2016). These microalgae are also able to cause mass mortalities of marine organisms (Aguilar-Trujillo et al., 2017; Shears and Ross, 2009) by the direct toxic effect of its phycotoxins and/or indirectly due to the hypoxic conditions generated by bacterial activity in cases of massive blooms (Berdalet et al., 2015). Potentially toxic benthic dinoflagellates include *Ostreopsis*, *Prorocentrum, Gambierdiscus* (and associated *Fukuyoa*), *Coolia, Amphidinium,* and *Sinophysis*.

In tropical areas, some *Ostreopsis* species can synthesize putative palytoxin potentially involved in palytoxicosis and clupeotoxism poisonings after consuming contaminated crustaceans and fish (Alcala et al., 1988; Randall, 2005). In temperate areas, palytoxin and derivates involve skin and eye irritations (Tichadou et al., 2010). Poisonings can also occur in these temperate regions when inhaling toxic bio-aerosols (Durando et al., 2007; Gallitelli et al., 2005) but not through ingestion, even though *Ostreopsis* toxic compounds were found in edible marine

organisms (Aligizaki et al., 2008; Amzil et al., 2012, 2012; Biré et al., 2015, 2013; Taniyama et al., 2003).

The okadaic acid produced by some *Prorocentrum* species can accumulate in seafood and hence lead to diarrheic shellfish poisoning (DSP) (Lee et al., 2016; Tripuraneni et al., 1997). Species of this genus are also able to cause environmental and economic troubles due to massive mortalities of marine organisms (fish, octopus, crustaceans) particularly reported during bloom events (Aguilar-Trujillo et al., 2017; Shears and Ross, 2009).

Some *Gambierdiscus* species are the causal agent of ciguatera fish poisoning (CFP), the most widespread non-bacterial food poisoning in the world (Tester et al., 2009). The Caribbean area is the second most CFP affected region of the word, with incidence rates between 12 and 500 cases /100,000 hab. (Chinain et al., 2014). The CFP does not occur homogeneously in the Eastern Caribbean. There are three main Caribbean CFP outbreak zones which are the British Virgin Islands, Antigua, and Montserrat Islands (Olsen et al., 1983) with CFP incidence rates exceeding 10 / 10,000 hab. (Tester et al., 2010). The northern part of Martinique Island is on the border between the two identified regions in the West Indies, with high and low ciguatera prevalence (Olsen et al., 1983). Areas identified with a high CFP prevalence were regularly explored which lead to several monitoring and/or ecological studies of

benthic dinoflagellates in the Gulf of Mexico (Okolodkov et al., 2014, 2007), Florida Keys (Norris et al., 1985), Bahamas Archipelago (Bomber et al., 1988), Cuba (Delgado et al., 2005), Virgin Islands (Carlson and Tindall, 1985) and Puerto Rico (Ballantine et al., 1988, 1985). Areas identified with fewer CFP cases were less studied. Between 1996 and 2006, epidemiological studies showed that ciguatera occurred in Guadeloupe and Martinique Islands with similar incidence rates (Tester et al., 2010), although these islands are respectively inside and outside of the high CFP prevalence areas (Olsen et al., 1983). Moreover, between 17 and 20% of Collective Alimentary Toxi-Infections (CATI) cases declared in Guadeloupe and Martinique have an undetermined cause (Petit-Sinturel, 2015), which suggests that other toxic benthic dinoflagellates as *Ostreopsis* spp. and *Prorocentrum* spp. could potentially be involved in such health problem. To our knowledge, the effects of *Sinophysis* spp. on human health have not been documented. The other genera as *Coolia* spp. and *Amphidinium* spp. synthesize toxins, but human poisoning due to those species has never been demonstrated (Ben-Gharbia et al., 2016; Botana, 2014; Holmes et al., 1995).

Considering the potential impact of toxic benthic dinoflagellates on human health in the Caribbean Sea, ecological studies, including spatio-temporal distribution and substrate preferences, are needed in order to understand the dynamics of this community. In temperate areas, seasonal variations of benthic dinoflagellates were often observed and related to temperature fluctuations (Cohu et al., 2013; Mangialajo et al., 2011). Different periodicity patterns of benthic dinoflagellates abundances have also been reported in the Caribbean (Ballantine et al., 1985; Okolodkov et al., 2014), but without being able to clearly identify the environmental driving parameters (e.g. temperature, nutrient inputs, seasonal occurrence of main macrophytes).

In order to better manage the local risk of benthic dinoflagellate toxicity, several ecological studies only recently started considering both habitat heterogeneity and preferential associations between host macrophytes and benthic dinoflagellates. As mentioned by Yong et al., (2018), results on preferential associations between macrophytes and benthic dinoflagellates are often contradictory, even if habitat complexity seems to play an important role for several benthic dinoflagellate genera.

The genus *Ostreopsis* can be preferentially associated with hosts presenting an architecture with branched thalli (Totti et al., 2010; Vila et al., 2001a,b), macroblade shapes (Parsons and Preskitt, 2007) and with filamentous shapes (Yong et al., 2018). In temperate areas, macrophyte communities including *Jania rubens* and *Halopteris filicina* constitute favorable substrates for this association and such host preferences were also observed in tropical environments (Blanfuné et al., 2015) even though not systematically (Ballantine et al., 1985).

For the genus *Prorocentrum*, no preferential association was found in temperate areas (Foden et al., 2005) whereas, in tropical environments, this genus has been preferentially associated with filamentous turf (Parsons and Preskitt, 2007) and Phaeophyceae (Delgado et al., 2006).

In tropical areas, the genus *Gambierdiscus* can be preferentially associated with specific host species (Carlson et al., 1984; Saint Martin et al., 1988), with more broader host taxonomic groups such as Ulvophyceae (Bomber et al., 1989; Carlson et al., 1984), Florideophyceae (Yasumoto et al., 1980, 1979), or Phaeophyceae (Delgado et al., 2005; Lobel et al., 1988) as well as host morphology types such as microfilamentous algae (Parsons and Preskitt, 2007). These preferential associations are not systematically observed in tropical and temperate environments (Ishikawa and Kurashima, 2010; Litaker et al., 2010; Nishimura et al., 2018). Also, different preferential associations were found between host macroalgae and different *Gambierdiscus* species (Rains and Parsons, 2015).

The genus *Coolia* was hosted preferentially by seagrasses in the temperate area (Hachani et al., 2018) and by Florideophyceae in the tropical area (Parsons and Preskitt, 2007; Yong et al., 2018).

To our knowledge, preferential associations between macrophyte and *Amphidinium* and *Sinophysis* have never been observed.

Benthic dinoflagellate ecology, including seasonal variations and substrate preferences, has never been studied in Guadeloupe and Martinique (Lesser Antilles). These islands are respectively inside and outside of the currently identified prevalence CFP areas (Olsen et al., 1983). In the context of global change, this distribution can differ with an increase of *Gambierdiscus* spp. and associated CFP cases (Kibler et al., 2017, 2015). The main objectives of the present study are to follow spatio-temporal population dynamics of benthic dinoflagellates in Guadeloupe and Martinique islands, as well as to distinguish biotic substrate preferences and determine physico-chemical driving parameters.

2. Material and methods

A survey was carried out between February 2015 and August 2016 on the islands of Guadeloupe and Martinique, in order to evaluate, on a month basis, abundances of dinoflagellates on 3 different sampling sites and on each Island. In each sampling site, 2 or 3 local and perennial macrophytes exposing the highest spatial coverage were collected in triplicates. Pelagic *Sargassum* spp. were also sampled, as unusual and massive amounts of this Phaeophyceae are washed up on the coasts of the Caribbean area since 2011 (Maréchal et al., 2017) and can constitute a substratum for the development of benthic dinoflagellates. Sampling was carried out during both dry and cyclonic seasons in Guadeloupe and Martinique. The dry period lasted from January to May whereas the cyclonic period covered a period from June to

Table 1
Characteristics of samples sites sampled and identifications macrophyte.

Site	Island	Latitude	Longitude	Bottom	Depth (m)	Macrophyte
Chapelle	Guadeloupe	16°28'18.0"N	61°30'47.6"W	coral, sand	2	*Dictyota* spp. Lamouroux *Galaxuara* spp. Lamouroux *Penicillus* spp. Lamarck
Bois Jolan	Guadeloupe	16°14'08.2"N	61°20'59.8"W	coral, sand	0.5 - 1	*Penicillus* spp. Lamarck *Syringodium filiforme* Kützing *Sargassum* spp. Agardh *Thalassia testudinium* Koenig
Rivière Sens	Guadeloupe	15°58'49.2"N	61°42'54.3"W	sand	1.5 - 4	*Galaxaura* spp. Lamouroux *Halophila stipulacea* (Forsskål) Ascherson
Tartane	Martinique	14°45'30.8"N	60°55'16.6"W	sand	1.5	*Caulerpa* spp. Lamouroux *Thalassia testudinium* Koenig
Pointe Faula	Martinique	14°32'29.9"N	60°49'44.5"W	sand	0.5	*Halodule* spp. Endlicher *Syringodium filiforme* Kützing *Sargassum* spp. Agardh
Anse Tonnoir	Martinique	14°25'59.2"N	60°53'02.9"W	sand	2	*Halophila stipulacea* (Forsskål) Ascherson *Syringodium filiforme* Kützing *Thalassia testudinium* Koenig

December. Both periods are mainly marked by a difference in the rate of rainfalls. All samples were collected between 0.5 and 4 m depth (Table 1).

2.1. Abundance of benthic dinoflagellates

The macrophytes were carefully sampled with surrounding water in a 250 mL plastic flask avoiding the resuspension of microalgae growing on the macrophyte. Acidic Lugol at 1% (vol/vol) was added in all samples to fix the microalgae and 10 s agitation allowed benthic dinoflagellates to detach from the macrophyte. Samples were filtered through a 500 µm mesh to separate the macrophyte from the dinoflagellate suspension. In order to recover a maximum of dinoflagellates, the macrophyte was rinsed twice for 10 s with 100 mL of GF/F filtered seawater and then weighed. Total seawater volume was measured. Samples were stored at 4 °C in dark. A total of 923 samples of macrophytes were quantitatively analyzed within this study.

Benthic dinoflagellates were identified at a genus level in order to avoid misidentification based on morphological characters (Hoppenrath et al., 2013; Penna et al., 2005). Benthic dinoflagellates present in 1 mL were counted with a Sedgewick Rafter© counting cell using a standard light microscope (Leitz, Orthoplan) less than one week after the sampling. Abundance values and fresh weight of macrophyte allowed the calculation of the number of benthic toxic dinoflagellates per gram of fresh weight of macrophyte (cells g^{-1}).

2.2. Abundance of planktonic dinoflagellates

Triplicate of water samples were collected 20 cm above macrophyte in a 250 mL plastic flask. The water sampling was done carefully before the macrophyte sample without macrophyte disturbances to avoid the presence of artificially suspended benthic cells in the sample. Acidic Lugol at 1% (vol/vol) was added in all samples to fix the microalgae. Samples were homogenized during 10 s then placed in a 50 mL Uthermol's chamber (1958). Planktonic cells were counted after 24 h of sedimentation in the Uthermol's chamber using an inverted microscope (Optech inverted biological microscopes series IB). A total of 291 samples of seawater were quantitatively analyzed during this study.

2.3. Resuspension ratio

The planktonic: benthic abundance ratios (the number of dinoflagellates per liter divided by the number of dinoflagellates per gram of fresh weight of macrophyte) have been calculated for each genus in order to estimate the ability of benthic dinoflagellates to be suspended in the column water. Ratios below 0.5 indicate that benthic dinoflagellates stay strongly attached to their substratum, whereas a ratio higher than 0.5 suggests that benthic dinoflagellates can easily detach from their substratum and be suspended in the column water.

2.4. Temperature and salinity

Sea surface temperature and salinity were both measured from June 2015 to August 2016 in Guadeloupe and Martinique, in 250 mL seawater samples collected close to macrophytes (between 0.5 and 4 m depth). Temperature was measured immediately after the sampling with a Checktemps 4 by HANNA thermometer. The salinity was determined using a Master-S/MilliM ATAGO© manual refractometer. Average values of wind speed and direction were calculated 7 days before the sampling by using measurements from Météo France weather stations. These data were available for one station in Guadeloupe and for three stations in Martinique (Table 1). In Guadeloupe, data provided by Météo France weather station localized at Baillif (16°00′48″N, 61°44′30″W) were used for Rivière Sens because these two sites were close. In Martinique, data provided by Météo France weather station localized at Trinité (14°45′00″N, 60°55′24″W) were used for Tartane sampling site, data from the weather station localized at Vauclin (14°33′06″N, 60°50′12″W) were used for Pointe Faula and data from the weather station localized at Sainte Anne (14°26′12″N, 60°52′12″W) were used for Anse Tonnoir.

2.5. Data analysis

All descriptive analytical values are presented as mean ± standard error (SE). Non-parametric tests were used when Shapiro test did not reveal homogeneous variances of benthic dinoflagellates abundances. Kruskal-Wallis ANOVA was used to i) assess the distribution of benthic dinoflagellates between Guadeloupe and Martinique ii) recognize preferential associations between macrophytes and dinoflagellates and iii) determine if dinoflagellate abundances significantly varied over the time. Mann Whitney test was used to compare abundances of each genus between both islands. A principal component analysis was performed to describe the effect of ecological parameters on the growth of benthic dinoflagellates. Spearman correlation tests were applied to determine the relationship between dinoflagellates abundances and between benthic and planktonic cell abundances. Mann Whitney test was used to compared temperature and salinity in Guadeloupe and Martinique.

3. Results

3.1. Temperature and salinity

Temperature fluctuated between 26.2 °C and 31.7 °C during the survey. Monthly average temperature was 27.9 ± 0.3 °C at Chapelle, 28.1 ± 0.3 °C at Bois Jolan and 28.1 ± 0.3 °C at Rivière Sens (Guadeloupe, Fig. 1) and 27.8 ± 0.3 °C at Tartane, 29.2 ± 0.4 °C at Pointe Faula and 29.1 ± 0.3 °C at Anse Tonnoir (Martinique, Fig. 2). Salinity varied between 31 and 38 during the survey. Salinity presented an average value of 35 ± 1 in each site. The temperature and salinity values were not significantly different between Guadeloupe and
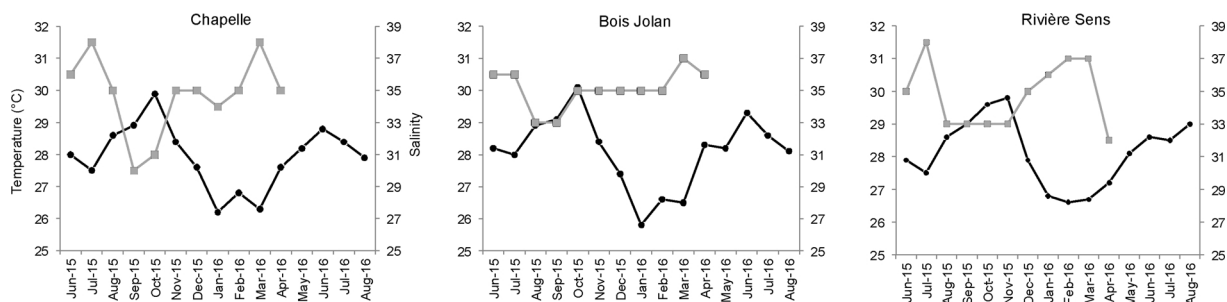

Fig. 1. Variation of temperature (black), salinity (grey) in Guadeloupe. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).
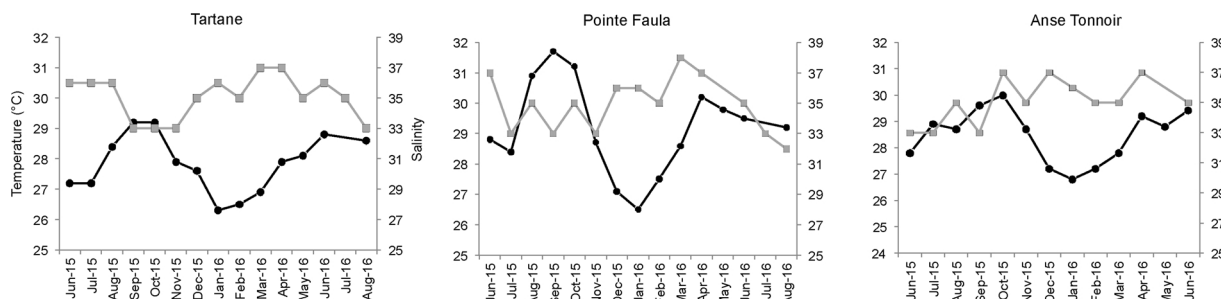
Fig. 2. Variation of temperature (black), salinity (grey) in Martinique. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

Martinique during the survey (p < 0.118) but the temperature of seawater (Kruskal Wallis, p < 0.021) and salinity (Kruskal Wallis, p < 0.034) fluctuated between the seasons on both islands. Temperature of seawater was the highest during the wet season with an average of $29 \pm 1\,°C$ in Guadeloupe and $28 \pm 1\,°C$ in Martinique, whereas during the dry season the average temperature of seawater was $27 \pm 1\,°C$ in Guadeloupe and $28 \pm 1\,°C$ in Martinique. Conversely, the highest salinity was found during the dry season in both islands. Indeed, average salinity was 36 ± 2 in Guadeloupe and 36 ± 1 in Martinique during the dry season while 34 ± 2 were found in both islands during the wet season.

3.2. Spatial distribution

The genera as *Ostreopsis, Prorocentrum, Gambierdiscus, Amphidinium, Sinophysis*, and *Coolia* were identified in Guadeloupe and in Martinique during the survey. Mean abundances of genera estimated over the 18-month period were statistically different between both islands (Kruskal Wallis, p < 0.0001), with 5 times more benthic dinoflagellates in Guadeloupe than in Martinique. The distribution of dinoflagellate genera differed between islands. Around 61 times more *Ostreopsis* spp., and 2.5 times more *Coolia* spp. were found in Guadeloupe compared to Martinique (Fig. 3). On the other hand, 3.5 times more *Sinophysis* spp., 2 times more *Gambierdiscus* spp. and 0.9 times more *Prorocentrum* spp. were found in Martinique compared to Guadeloupe (Mann Whitney, p < 0.021). The distribution of *Amphidinium* spp. was statistically the same on both islands (Mann Whitney, p = 0.981). Differences in abundances were found between sites (Kruskal Wallis, p < 0.0001). In Guadeloupe, statistically more benthic dinoflagellates were found at Chapelle than at Bois Jolan and Rivière Sens (Kruskal Wallis, p < 0.002), while in Martinique, more benthic dinoflagellates were found at Anse Tonnoir than Tartane and Pointe Faula (Kruskal Wallis, p < 0.0004, Fig. 4). In Guadeloupe, *Ostreopsis* spp. dominated all sampling sites and represented between 55% and 87% of the community. Proportion of this genus decreased from North to South in opposition to *Prorocentrum* spp. (Fig. 4). Similar trends were observed with proportions of *Gambierdiscus* spp., *Coolia* spp., *Amphidinium* spp., and *Sinophysis* spp., who increased from North to South but never exceeding
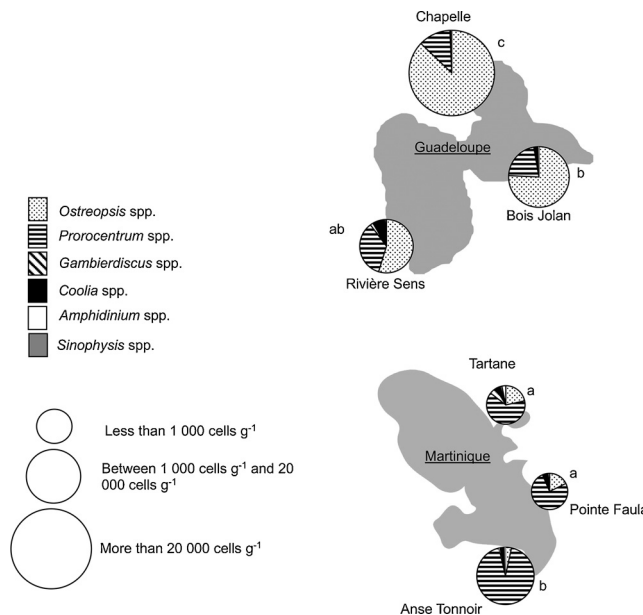

Fig. 4. Total mean abundance of benthic dinoflagellates present in Guadeloupe and in Martinique from March 2015 to August 2016. Letters (a, b, c) indicate significant differences of average abundances between sites (Kruskal Wallis p < 0.0001, alpha = 0.05).

10% of total benthic dinoflagellates at the 3 sites. In Martinique, *Prorocentrum* spp. abundances increased from North to South and dominated the dinoflagellate population with between 64% and 93% depending on the site. Abundances of *Ostreopsis* spp. represented between 3% and 22% of dinoflagellates and were negatively correlated with abundances of *Prorocentrum* spp. The proportions of *Gambierdiscus* spp., *Amphidinium* spp., *Sinophysis* spp., and *Coolia* spp. never exceeded 10% of total benthic dinoflagellates and decreased with a North to South gradient as described for *Prorocentrum* spp.
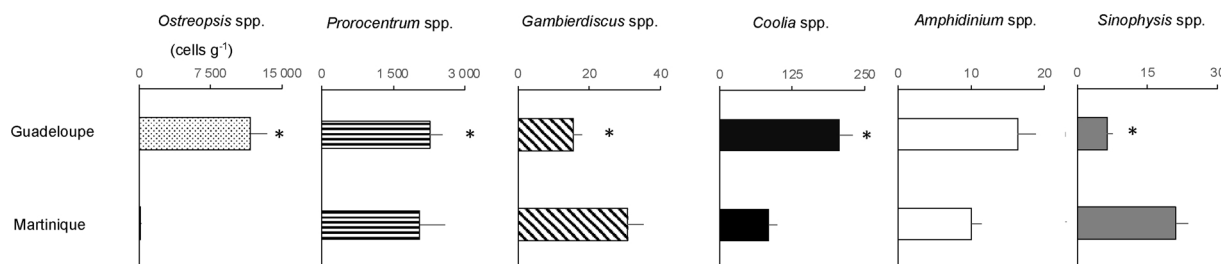

Fig. 3. Average abundance of different benthic dinoflagellates genera during 18 months (March 2015 – August 2016) in Guadeloupe and Martinique Islands. Mann Whitney, p < 0.01, alpha = 0.05. The symbol * indicates significant p-values (p < 0.05).
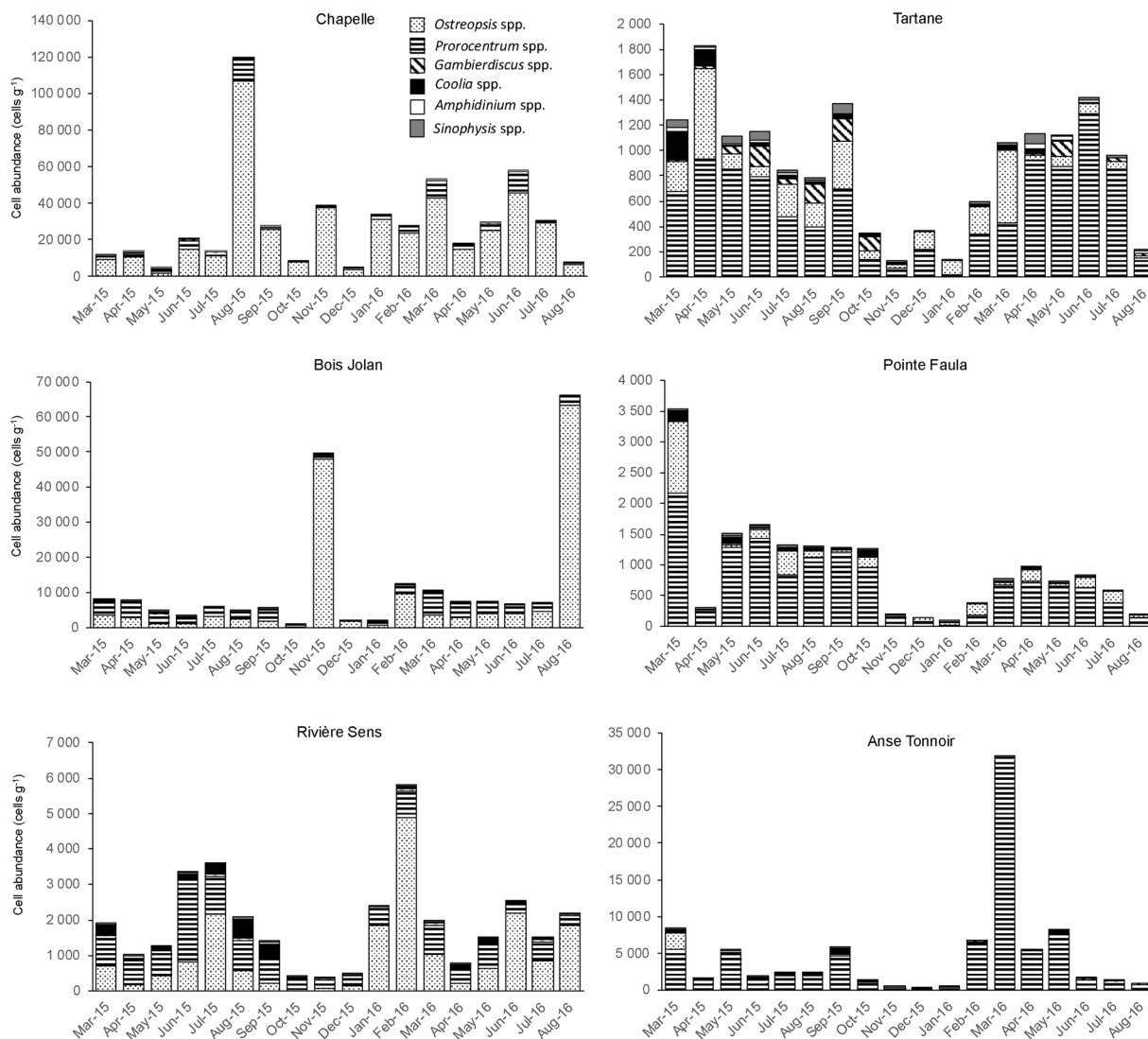
Fig. 5. Fluctuation of benthic dinoflagellates abundances (cells g^{-1}) from March 2015 to August 2016 in Guadeloupe (left) and Martinique (right).

3.3. Temporal variations

Total abundance of epiphytic dinoflagellates did not show marked seasonal variations in Guadeloupe and Martinique (Fig. 5, Kruskal Wallis, p > 0.05) but the lowest total abundances of benthic dinoflagellates occurred between October and January when seawater temperatures were lower, except at Chapelle and Bois Jolan.

The genus *Ostreopsis* spp. was found with abundances varying between 0 and 106,675 cells g^{-1}. In Guadeloupe, *Ostreopsis* spp. presented the highest abundance peaks, being 2–20 times more abundant than other species. This dinoflagellate occurred at Chapelle and Bois Jolan during the wet season while highest abundance values were reached during the dry season at Rivière Sens. *Ostreopsis* spp. were found with a monthly average abundance of 24,939 ± 5 757 cells g^{-1} at Chapelle, 8786 ± 4092 cells g^{-1} at Bois Jolan and 1049 ± 283 cells g^{-1} at Rivière Sens. In Martinique, at Anse Tonnoir, there were 6 times more *Ostreopsis* spp. during the dry season (374 ± 267 cells g^{-1}) compared to the wet season (60 ± 18 cells g^{-1}, Kruskal Wallis, p = 0.026). In the two other sampling sites of Martinique, the highest abundances of *Ostreopsis* spp. were also recorded during the dry season. *Ostreopsis* spp. were present with a monthly average abundance of 190 ± 45 cells g^{-1} at Tartane, 168 ± 63 cells g^{-1} at Pointe Faula and 199 ± 121 cells g^{-1} at Anse Tonnoir.

The genus *Prorocentrum* was found with abundance values varying between 0 and 66,761 cells g^{-1}. In Guadeloupe, they were 2 times more *Prorocentrum* spp. during the dry season (3486 ± 512 cells g^{-1}) than in the wet season (1715 ± 930 cells g^{-1}) at Bois Jolan (Kruskal Wallis, p = 0.013) whereas no difference was found between seasons at Chapelle and Rivière Sens (Kruskal Wallis, p > 0.183). This genus was present with a monthly average abundance of 3471 ± 896 cells g^{-1} at Chapelle, 2502 ± 345 cells g^{-1} at Bois Jolan and 671 ± 111 cells g^{-1} at Rivière Sens. In Martinique, peaks of total abundances were represented by high abundances of *Prorocentrum* spp. Temporal distribution profiles were different in Martinique. The genus *Prorocentrum* was found with the highest abundances during the dry and the wet season at Tartane and Pointe Faula whereas a single abundance peak of was found at Anse Tonnoir. Eight times more *Prorocentrum* spp. were found during the dry season (7942 ± 3481 cells g^{-1}) than the wet season (1483 ± 401 cells g^{-1}) at Anse Tonnoir (Kruskal Wallis, p = 0.010). This seasonal difference of abundances was not found at Tartane and Pointe Faula (Kruskal Wallis, p > 0.374). Species of *Prorocentrum* presents a monthly average abundance of 562 ± 86 cells g^{-1} at Tartane, 718 ± 135 cells g^{-1} at Pointe Faula and 4353 ± 1694 cells g^{-1} in Martinique.

The genus *Coolia* was the third most abundant and was present in both islands with abundances varying between 0 and 1464 cells g^{-1}. This genus was 2 times more abundant during the dry season (236 ± 44 cells g^{-1}) than in the wet season (118 ± 47 cells g^{-1}) at Chapelle

(Kruskal Wallis, p = 0.041) whereas none seasonal fluctuations were found at Bois Jolan and Rivière Sens (Kruskal Wallis, p > 0.328). In Guadeloupe, this genus was found with a monthly average abundance of 170 ± 35 cells g^{-1} at Chapelle, 290 ± 48 cells g^{-1} at Bois Jolan and 131 ± 34 cells g^{-1} at Rivière Sens. In Martinique, *Coolia* spp. were found with similar monthly average abundance levels at Tartane (33 ± 13 cells g^{-1}) and Pointe Faula (38 ± 12 cells g^{-1}) whereas the abundance was 5 times more at Sainte Anne, reaching 159 ± 46 cells g^{-1}. No seasonal variation of *Coolia* spp. abundances was found in Martinique (Kruskal Wallis, p > 0.304).

The abundances of *Gambierdiscus* spp. varied between 0 and 301 cells g^{-1} and none *Gambierdiscus* cell was found in 74% of the samples. This genus was frequently observed at Rivière Sens, Tartane and Anse Tonnoir, but was absent in certain periods in other sites: Rivière Sens (April 2015), Tartane (November-December) and Anse Tonnoir (December). The absence of *Gambierdiscus* spp. was observed during the fall of seawater temperature at Tartane and Anse Tonnoir. This genus was found with the highest monthly average abundances at Rivière Sens (34 ± 5 cells g^{-1}), Tartane (52 ± 15 cells g^{-1}) and Anse Tonnoir (28 ± 6 cells g^{-1}), when the temperature was increasing or was highest. Despite rising temperature, no seasonality was highlighted between the wet and the dry season for this genus.

Abundances of *Amphidinium* spp. fluctuated between 0 and 163 cells g^{-1}. This genus was found in Guadeloupe with a monthly average abundance of 19 ± 10 cells g^{-1} at Chapelle, 21 ± 8 cells g^{-1} at Bois Jolan and 16 ± 4 cells g^{-1} at Rivière Sens whereas it occurred in Martinique with 13 ± 3 cells g^{-1} at Tartane, 6 ± 1 cells g^{-1} at Pointe Faula and 10 ± 3 cells g^{-1} at Anse Tonnoir.

The abundances of *Sinophysis* spp. were the fewest and this genus was the less frequent dinoflagellate in the area. *Sinophysis* spp. were present in this study with abundances varying between 0 and 133 cells g^{-1}. In Guadeloupe, this genus was found with a monthly average abundance of 3 ± 1 cells g^{-1} at Chapelle and Bois Jolan and 16 ± 4 cells g^{-1} at Rivière Sens. In Martinique, a monthly abundance average reached 29 ± 7 cells g^{-1} at Tartane, 13 ± 3 cells g^{-1} at Pointe Faula, and 19 ± 5 cells g^{-1} at Anse Tonnoir. About 4 times more *Sinophysis* spp. were found during the wet season (27 ± 7 cells g^{-1}) than in the dry season (8 ± 5 cells g^{-1}) (p = 0.031).

3.4. Benthic versus planktonic cells

No significant relation was found between benthic and planktonic abundances (Table 2). *Ostreopsis* spp. and *Coolia* spp. had a higher resuspension ratio than *Prorocentrum* spp., *Amphidinium* spp. and *Sinophysis* spp. suggesting *Ostreopsis* spp. and *Coolia* spp. can be more detached from their host than *Amphidinium* spp. and *Sinophysis* spp. An intermediate resuspension ratio for *Gambierdiscus* spp. was found (Fig. 6).

3.5. Interactions between genera

Total abundances of benthic dinoflagellates were strongly correlated with abundances of *Ostreopsis*, *Prorocentrum* and *Coolia* genera

Table 2
Coefficient of determination of linear regression between planktonic and benthic abundances of different genera of dinoflagellates.

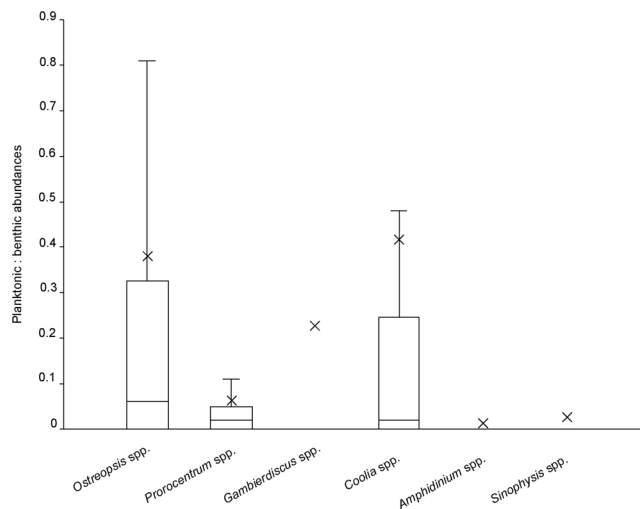|	R^2
Ostreopsis spp.	0.057
Prorocentrum spp.	0.079
Gambierdiscus spp.	0.007
Coolia spp.	0.004
Amphidinium spp.	0.001
Sinophysis spp.	0.07

Fig. 6. Resuspension ratio for different benthic dinoflagellates genera present in Guadeloupe and Martinique. Box plots indicate first quartile, median and third quartile. The mean is indicated by a cross.

(r_s > 0.601, p < 0.0001). A weak negative correlation was found between the abundance of *Ostreopsis* spp. and *Gambierdiscus* spp. (r_s = - 0.158, p = 0.025). The same trend was found between *Ostreopsis* spp. and *Sinophysis* spp. (r_s = - 0.238, p = 0.001). The abundance of *Amphidinium* spp. was weakly correlated with *Prorocentrum* spp., *Gambierdiscus* spp. and *Coolia* spp (r_s = 0.324, p < 0.001). A weak positive correlation existed between abundances of *Sinophysis* spp., *Gambierdiscus* spp., and *Coolia* spp. (r_s < 0.039, p < 0.0001, Table 3).

3.6. Host effect

Dinoflagellate species present preferential associations with macrophyte hosts (Fig. 7). All genera of benthic dinoflagellates were present in lowest abundance on *Sargassum* spp. Another Phaeophyceae, *Dictyota* spp., supported the highest abundance of benthic dinoflagellates, particularly with *Ostreopsis* spp. and *Prorocentrum* spp. Highest abundances of *Gambierdiscus* spp. and *Coolia* spp. were respectively found on *Halophila stipulacea* and *Galaxaura* spp.

3.7. Multivariate analysis

A principal component analysis based on physico-chemical characteristics and abundances of benthic dinoflagellates (total variability = axis1 + axis2 = 53.13%) indicated that all environmental factors were poorly represented (Fig. 8). The abundances of *Prorocentrum* spp. and *Ostreopsis* spp. were inversely proportional and independent with abundances of *Gambierdiscus* spp., *Coolia* spp., *Amphidinium* spp. and *Sinophysis* spp. These four last genera co-occurred in dinoflagellate populations. High abundance of *Prorocentrum* spp. was rather driven by temperature and low salinity whereas *Ostreopsis* spp. was promoted by low temperature and high salinity. *Gambierdiscus* spp., *Coolia* spp., *Amphidinium* spp. and *Sinophysis* spp. were rather found under light wind conditions. The same analysis at Pointe Faula showed a more homogeneous abundance of benthic dinoflagellates despite seasons but the principal component analysis did not highlight changes of dinoflagellate abundances according to seasons.

4. Discussion

4.1. Abundance of benthic dinoflagellates in the Caribbean

Several benthic toxic dinoflagellates such as *Ostreopsis*, *Prorocentrum*, *Gambierdiscus*, *Coolia*, and *Amphidinium* genera were

Table 3

Correlation between abundance of benthic dinoflagellates (cells g-1 FW, temperature (°C) and salinity. Correlation r_s of Spearman with $p < 0.05$ (*), $p < 0.001$ (**) and $p < 0.0001$ (***).

|	*Ostreopsis* spp.	*Prorocentrum* spp.	*Gambierdiscus* spp.	*Coolia* spp.	*Amphidinium* spp.	*Sinophysis* spp.	Temperature	Salinity
Total	**0.789*****	**0.831*****	-0.042	**0.601*****	0.107	−0.112	-0.057	0.021
Ostreopsis spp.		**0.464*****	**-0.158***	**0.438*****	0.020	**-0.238****	**−0.23****	0.016
Prorocentrum spp.			0.029	**0.573*****	**0.223****	0.056	0.029	0.089
Gambierdiscus spp.				0.035	**0.224****	**0.397*****	0.084	−0.038
Coolia spp.					**0.279*****	0.090	0.081	−0.061
Amphidinium spp.						**0.324*****	-0.003	0.073
Sinophysis spp.							**0.174***	0.093
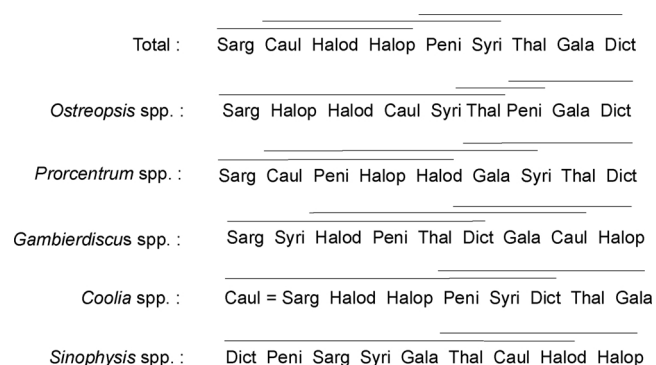
Fig. 7. Preferential associations between benthic dinoflagellates and several macrophytes species. Sarg: floating *Sargassum* spp., Caul: *Caulerpa* spp., Halod: *Halodule*, Halop: *Halophila*, Peni: *Penicillus* spp., Syri: *Syringodium* spp., Thal: *Thalassia testutinium*, Gala: *Galaxaura* spp., Dict: *Dictyota* spp. In the pairwise tests conclusions, significantly similar factors ($p < 0.05$) are joined by crossed-bar.

found in all the sites studied in Guadeloupe and Martinique islands. These genera have already been reported in other studies carried out in Florida (Norris et al., 1985), Bahamas Archipelago (Bomber et al., 1988), Belize (Faust, 2000, 1993), Gulf of Mexico (Tester et al., 2013), Cuba (Delgado et al., 2005), Porto Rico (Ballantine et al., 1988), and Virgin Islands (Carlson and Tindall, 1985). The genus *Sinophysis* was never found before the present study in Guadeloupe although this genus has already been identified in the Mexican Caribbean, Belize and Martinique islands (Almazán-Becerril et al., 2015; Chomérat, 2016;

Chomérat et al., 2018; Faust, 1993). Despite some variations, total abundances of benthic dinoflagellates in Guadeloupe and in Martinique were comparable with other Caribbean islands (Ballantine et al., 1988, 1985; Bomber et al., 1989; Delgado et al., 2005; Martinez-Cruz et al., 2015; Okolodkov et al., 2014, 2007).

The genus *Ostreopsis* was dominant in the present study in Guadeloupe as described in Puerto-Rico with similar monthly average abundances (Ballantine et al., 1985) but the dominance of this genus is unusual in the Caribbean area (Boisnoir et al., 2018). The maximum abundance levels of *Ostreopsis* spp. reached in this present study (106,875 cells g^{-1}) were the highest abundance for this genus ever reported in the Caribbean basin. Indeed, *Ostreopsis* reaches 1202 cells g^{-1} in the Gulf of Mexico (Okolodkov et al., 2007), less than 1000 cells g^{-1} in the Florida Keys and Cuba (Bomber et al., 1988; Delgado et al., 2005) and 43,000 cells g^{-1} in Puerto-Rico (Ballantine et al., 1985). In the Lesser Antilles, the abundance levels of *Ostreopsis* never exceeded 2000 cells g^{-1} in Guadeloupe (Boisnoir et al., 2018) and a similar trend was observed in Belize (Faust, 2009). Prevalence of *Ostreopsis* spp. is common in temperate environments and can be found with higher densities (Cohu et al., 2013; Mangialajo et al., 2017) reaching abundances of 10^5 cells g^{-1} (Vila et al., 2001a,b). In temperate areas, high abundances of *Ostreopsis* genus would be maintained under low nitrate and nitrite concentrations in the seawater (Carnicer et al., 2015; Cohu et al., 2013, 2011). Other environmental factors such as low hydro-dynamics induced by currents, waves or wind could also offer favorable conditions for the development of *Ostreopsis* spp. (Carlson, 1985; GEOHAB, 2012; Richlen and Lobel, 2011; M. Vila et al., 2001a,b). According to other studies, the effect of rainfall on *Ostreopsis* spp. abundance was not clear (Ballantine et al., 1988; Cohu et al., 2011;
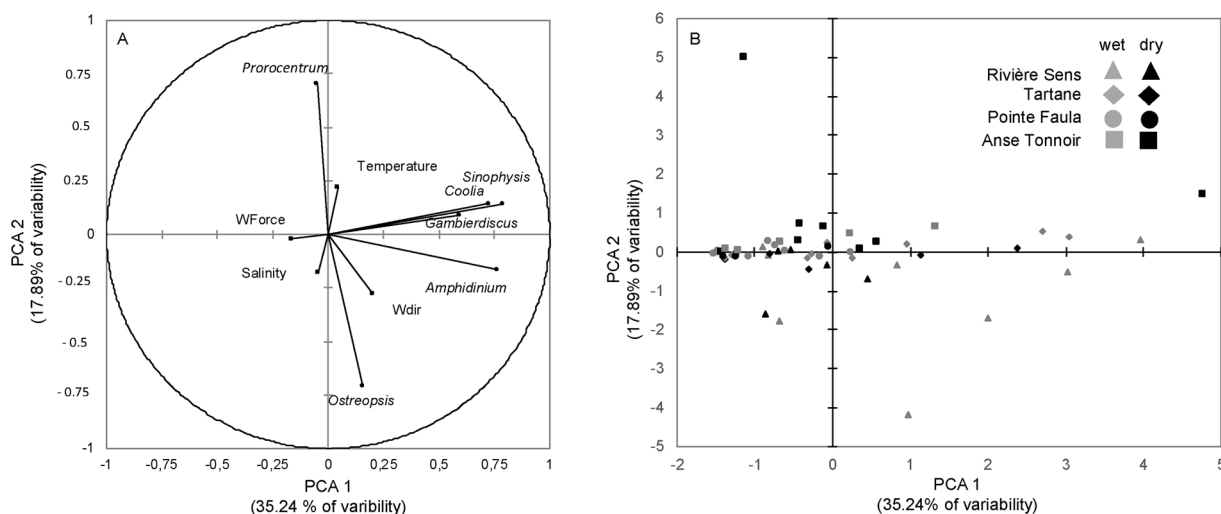

Fig. 8. Principal Component Analysis based on a) relation between abundances of epibenthic dinoflagellates (active variables in italic) and ecological factors (additional variables). b) Structuration of benthic dinoflagellates community according to site (shape) or season (color). The wet season is indicates in grey and the dry weason in black. Data of wind force (WForce) and wind direction (WDir) were available for only one station in Guadeloupe and for all three stations in Martinique (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article).

GEOHAB, 2012; Morton et al., 1992), whereas Parsons and Preskitt, (2007) showed that rainfall was negatively correlated to the abundance of *Ostreopsis* spp.

The genus *Prorocentrum* spp. was dominant in Martinique, as reported in Cuba (Delgado et al., 2005) and in the Gulf of Mexico (Martinez-Cruz et al., 2015; Okolodkov et al., 2014, 2007). The dominance of *Prorocentrum* spp. is typical in dinoflagellate communities reported in the Caribbean area (Bomber et al., 1988; Okolodkov et al., 2014) and on the Great Barrier Reef, off the coast of Australia (Skinner et al., 2013).

In this present study, *Gambierdiscus* genus was found with lowest maximal abundances compared to other studies carried out in the Gulf of Mexico and in the Caribbean Sea (Ballantine et al., 1988, 1985; Bomber et al., 1989; Delgado et al., 2005; Okolodkov et al., 2014). All these studies reported maximum abundances of *Gambierdiscus* spp. ranging from 2×10^3 to less than 10^5 cells g^{-1} while only a maximum of 301 cells g^{-1} was recorded in this present study. Besides these maximum values, abundance peaks of *Gambierdiscus* spp. generally remained below 400 cells g^{-1} in the Gulf of Mexico (Okolodkov et al., 2014), Florida (Bomber et al., 1989), Cuba (Delgado et al., 2005), and Puerto Rico (Ballantine et al., 1988, 1985). In a previous Guadeloupean study, the maximum abundance of *Gambierdiscus* was less than 150 cells g^{-1}, thereby confirming the low abundance of *Gambierdiscus* in the French West Indies (Boisnoir et al., 2018). According to these results, it appears that bloom threshold needs to be established regionally in the Caribbean area. Usually, for the genus *Gambierdiscus*, the bloom formation threshold is 1000 cells g^{-1}, for at such cell densities the amount of toxins begins to substantially accumulate in the food web (Litaker et al., 2010). This threshold would be suitable and could be applied for islands such as the Florida Keys, Cuba and Puerto Rico where the abundance of *Gambierdiscus* spp. can exceed 1000 cells g^{-1}. On the other hand, in other islands like Guadeloupe and Martinique where abundance values of this genus have never been found to exceed 400 cells g^{-1}, the bloom formation threshold should be lower. By referring to the method developed by Litaker et al. (2010), which determines the bloom threshold of 1000 cells g^{-1}, our present study showed that 85% of the samples had less than 50 cells g^{-1}, hence revealing a much lower bloom threshold. This cell density seems adequate to determine the bloom formation of *Gambierdiscus* in areas where the abundance of this genus never exceed 1000 cells g^{-1} and where CFP cases occur (Boucaud-Maitre et al., 2018; Tester et al., 2010).

Observed abundances of *Coolia* spp. were similar to abundances observed in the Gulf of Mexico (Martinez-Cruz et al., 2015) but a previous study also carried out in the Gulf of Mexico, showed that *Coolia* spp. exposed higher average abundances (Okolodkov et al., 2007).

Abundances of *Amphidinium* spp. have been reported with higher values in the Gulf of Mexico compared to Guadeloupe and Martinique (Okolodkov et al., 2014, 2007). A maximum of 3.69×10^3 cells g^{-1} were found in the Gulf of Mexico (Okolodkov et al., 2014) whereas, in the present study, the highest abundance only reached 163 cells g^{-1}.

In the Gulf of Mexico, *Sinophyis* spp. were present in most of the samples, and with very low abundance values (Okolodkov et al., 2014). Other surveys carried out in the Gulf of Mexico identified several *Sinophysis* species but cell counts were not undertaken (Martinez-Cruz et al., 2015; Okolodkov et al., 2007).

Results showed that certain benthic dinoflagellate genera were able to detach more easily than others from a colonized substrate and hence occupy the planktonic zone. Indeed, by studying the relationship between benthic and planktonic cells, *Ostreopsis* spp. and *Coolia* spp. were resuspended in the water column more easily than other genera. On the other hand, the benthic: planktonic ratios of *Amphidinium* spp. and *Sinophysis* spp. were very low, suggesting that these genera are strongly attached to the substratum. The intermediate benthic: planktonic ratios of *Gambierdiscus* spp. suggest that this genus can be present with comparable abundances in the water column and attached on the macrophyte.

4.2. Temporal distribution

Temporal variations of dinoflagellate abundances in the present study were not related to temperature nor to salinity variations even though variations were found between the wet and dry seasons. In the Gulf of Mexico, fluctuation of benthic dinoflagellate abundances might be linked to the seasonal occurrence of predominant macrophyte species (Okolodkov et al., 2014), whereas discontinuous benthic dinoflagellate abundances were shown to sustain under high nutrient runoff inputs and elevated temperatures (Ballantine et al., 1985). Other studies carried out in the Gulf of Mexico and in the Caribbean showed that benthic dinoflagellate abundances followed different periodicity patterns (Ballantine et al., 1988; Carlson, 1985; Carlson and Tindall, 1985; Delgado et al., 2005; Okolodkov et al., 2014, 2007; Taylor, 1985). These conclusions have to be regarded with caution considering that different methods were used for analyzing the data (Ballantine et al., 1988). For instance, maximum monthly abundances or variation of total bio-volume calculated over the whole dinoflagellate population made interpretation difficult in terms of periodicity of benthic dinoflagellate abundances (Carlson and Tindall, 1985; Taylor, 1985).

In the Gulf of Mexico, several abundance peaks of benthic dinoflagellates were found over the monitoring period, from May to December, although sampling sites were geographically close and environmental conditions, like precipitations, temperature, wind speed, and direction were similar (Okolodkov et al., 2007). Authors hence suggested that the occurrence of abundance peak events might rather be related to local inputs, such as nutrients or sediment load.

In the Caribbean Sea, one single abundance peak was reported in Cuba, from March to July, and seemed related to physico-chemical conditions, associating high water temperatures and nutrient concentrations, with low turbidity (Delgado et al., 2005). Two abundance peak events were reported in Puerto Rico, in July then between September and October (Ballantine et al., 1988) as well as in Florida, in April and in November (Bomber et al., 1989). In Puerto Rico, a weak positive correlation was found between the abundance of *Gambierdiscus* and seawater temperature suggesting that temperature was partly responsible for this variability in the data (Ballantine et al., 1988).

In French Polynesia, seasonal fluctuations of *Gambierdiscus* were found during a three-year survey starting in 1993, with higher abundances during the hot season (Chinain et al., 1999). Conversely, in the same area, another survey starting at the same period but, lasting 8 years, did not reveal any significant seasonal fluctuations in mean dinoflagellates cell densities (Chateau-Degat et al., 2005). The different results obtained in both studies could be due to different temperature ranges, mainly lower in Chateau-Degat et al., (2005) than Chinain et al., (1999). Notably, temperature ranges recorded in Chateau-Degat et al., (2005) were similar to those observed in this present study. A six-year study deployed in Japanese coastal areas revealed higher *Gambierdiscus* abundances in summer and autumn. Nevertheless, this study was set up in a temperate area where higher temperature fluctuations would lead to a higher variation of dinoflagellate abundance.

In order to obtain more accurate data to identify fluctuations periods of benthic dinoflagellates in the Caribbean Sea, further monitoring will have to be set up with more frequent and longer sampling periods.

4.3. Biotic substrate preferences

In the present study, only biotic substrates were considered because they are more abundant than artificial habitats in the marine environment. Results showed that most dinoflagellates were found colonizing *Dictyota* spp. and *Padina* spp. as reported in previous studies undertaken in Puerto Rico (Ballantine et al., 1988, 1985) and in Cuba (Ballantine et al., 1985; Delgado et al., 2005). In this present study, host preference was observed with *Ostreopsis* spp. which preferentially colonized *Dictyota* spp. (Phaeophyceae) while in Puerto Rico, this genus was rather found with higher abundances on seagrass (Ballantine et al., 1985).

Several studies reported higher abundances of *Prorocentrum* on Phaeophyceae in Cuba, (Delgado et al., 2005) and on Ulvophyceae or Phaeophyceae in Florida, (Bomber et al., 1989). Aligizaki and Nikolaidis (2006) reported the highest abundances of *Coolia* spp. on Florideophycea in the North Aegean Sea. In this present study, the highest abundances of *Gambierdiscus* genus were found on the macrophyte *Halophila stipulacea*, thereby suggesting a preferential association. This macrophyte is initially native to the Red Sea and Indian Ocean (Gessner, 1970), but was identified for in the Caribbean Sea in 2002, on the Island of Grenada (Ruiz and Ballantine, 2004), and progressively expanded to another dozen islands of the Lesser Antilles (Willette et al., 2014). This invasive angiosperm established in the Caribbean Sea by taking over the indigenous seagrass species, such as *Syringodium filiforme* (Willette and Ambrose, 2012). *H. stipulacea* develops rapidly into large mono-specific meadows (Willette and Ambrose, 2009) and its invasive potential is driven by high nutrient concentrations (van Tussenbroek et al., 2016). Today, *H. stipulacea* covers hundreds of hectares in the Caribbean Sea (Willette et al., 2014).

Since 2011, large amounts of *Sargassum* spp. are regularly found washed up on coasts in the Gulf of Mexico, in Africa (from Sierra Leone to Ghana) and along the beaches of islands in the Lesser Antilles, including Guadeloupe and Martinique islands (Gower et al., 2013; Maréchal et al., 2017; Wang and Hu, 2016). This impressive phenomenon, called "Golden tides", involves two species of Phaeophyceae, *Sargassum natans,* and *Sargassum fluitans* which form the drifting algal communities found in the Sargasso Sea (de Szechy et al., 2012). Whilst drifting through the Caribbean Sea, *Sargassum* rafts progressively accumulate large communities of marine organisms including attached epibionts and mobile fauna, ranging from microbiota to fishes (Huffard et al., 2014). Such floating structures are suspected to also host high abundances of harmful dinoflagellates, as it is often reported for Phaeophyceae (Delgado et al., 2005) but results obtained in the present survey showed that among the studied macrophytes, *Sargassum* spp. hosted the lowest abundance of benthic dinoflagellates, such as *Ostreopsis* spp., *Prorocentrum* spp., and *Gambierdiscus* spp. Low abundances of benthic dinoflagellates hosted by the pelagic *Sargassum* spp. as described above, can be the result of allelopathic interactions which involve the production of specific molecules able to inhibit the growth of attached benthic dinoflagellates (Accoroni et al., 2015; Grzebyk et al., 1994; Morton and Faust, 1997). The toxic risk of benthic dinoflagellates colonizing *Sargassum* spp. would consequently be limited. On the other hand, *Sargassum* spp. drifting rafts can act as important vectors for exchanging different benthic dinoflagellate populations between the West Indies, Gulf of Mexico and African coasts.

4.4. Trophic transfer

The seagrass *Halophila stipulacea* could substantially contribute to the spreading of CFP cases in the West Indies. Indeed, grazers consuming *H. stipulacea* are liable to introduce ciguatoxins into the food chain.

Parrotfish species are the most represented coral fish in the Caribbean representing an important commercial interest value (Polunin and Roberts, 1993). Parrotfish found along the Kenyan coasts have been seen grazing *H. stipulacea* (Mariani and Alcoverro, 1999) but to our knowledge, this has never been observed in the Caribbean Sea. Only a little attention has been given to food web modifications occurring with the introduction of non-native species (Byrnes et al., 2007) and to whether long periods of time could be needed to establish new trophic links among species (Schlaepfer et al., 2011). Grazers evolving in the Caribbean area could start including *H. stipulacea* in their diet, and hence allow *Gambierdiscus* toxins to enter the marine food web thereby contaminating new marine species. In other Caribbean islands, *Gambierdiscus* spp. has been reported to colonize selectively Phaeophyceae and Florideophyceae (Bomber et al., 1989; Delgado et al., 2005). In addition, results have shown that *Sinophysis* spp. were also

found colonizing *H. stipulacea* with high abundance levels.

Other potential consumers of *H. stipulacea* is the marine turtle *Chelonia mydas* (Becking et al., 2014). Even if the consumption of marine turtles is illegal for a major part of the Caribbean (Humber et al., 2014). Illegal consumption exists, notably in developing tropical countries (Buitrago et al., 2008) and is still legal in a few countries, like in the Caribbean waters of Nicaragua (Barrios-Garrido et al., 2017). Deadly poisoning cases have never been reported after the consumption of marine turtles in the Caribbean Sea (Fussy et al., 2007), but have been observed in Micronesia (Pavlin et al., 2015).

4.5. The ciguatera in the Caribbean

The increase of sea surface temperature was suspected to be the major environmental factor driving ciguatera outbreaks in the Caribbean area (Tester et al., 2010) but Radke et al., (2013) showed that ciguatera occurred with a constant incidence rate in the US Virgin Islands, despite an increase of sea surface temperatures over the last 30 years. The fact that none of the ecological factors measured in the present study directly affected benthic dinoflagellate abundances, suggests the existence of complex interactions between environmental factors. For instance, the growth of *Gambierdiscus* spp. studied in Cuba, was associated with different environmental conditions such as light wind conditions, calm seas, increasing water transparency, and high water temperatures (Delgado et al., 2005). Also, this genus was found to occur at low depths in the Gulf of Mexico (Okolodkov et al., 2014) as well as in Guadeloupe (Boisnoir et al., 2018).

The Caribbean area is the second region of the world the most impacted by CFP cases (Chinain et al., 2014; Lewis, 1986; Pottier et al., 2001). The northern part of Martinique Island is on the border between high and low CFP prevalence areas identified in the West Indies (Olsen et al., 1983). In the high prevalence area, three main ciguatera outbreak centers are described with CFP incidence rates exceeding 10 / 10 000 hab. (Tester et al., 2010). The CFP incidence rates reported in Guadeloupe and Martinique islands were relatively similar between 1996 and 2006 with an incidence of 0.3 / 10 000 hab. in Guadeloupe and 0.2 / 10 000 hab. in Martinique (Tester et al., 2010). Between 2013 and 2016, the CFP incidence rate in Guadeloupe was 1.47 / 10 000 hab. i.e. 5 times higher than the previous study (Boucaud-Maitre et al., 2018). In Martinique, the CFP incidence rates have not been officially published these last years while, while 15 new CFP cases occurred in August 2018 on this same Island (unpublished data). The present study revealed higher abundances of *Gambierdiscus* spp. in Martinique compared to Guadeloupe. Depending on the toxicity of the species present in Martinique, the CFP incidence rate might have increased these last years as described in Guadeloupe. Moreover, Guadeloupe and Martinique are located respectively inside and outside the high prevalence CFP area, which suggests that both islands might have different population species of *Gambierdiscus*. Identification of benthic dinoflagellates by using molecular tools is recommended in CFP surveys in order to bring valuable information on the toxicity level of dinoflagellate species present in the Caribbean area, as for instance *G. excentricus* is the most toxic species in this genus found in the Caribbean (Litaker et al., 2017; Pisapia et al., 2017).

This study, carried out in Guadeloupe and Martinique, questions the local belief regarding the origin of ciguateric fish poisoning in those islands. A great majority of inhabitants from both French islands believe that poisoned fish came from fishing activities in Northern Caribbean islands, where incidence rates of CFP are much higher (Tester et al., 2010). The presence of *Gambierdiscus* spp. shown in this study on both islands can explain the occurrence of local cases of CFP in Guadeloupe and Martinique islands. Moreover, fish consumption is not regulated in Martinique, while in Guadeloupe a decree prohibits the consumption of several fish species. Toxin measurements must be done in sedentary marine organisms in order to determine if ciguatoxins are locally present in the marine food web especially in Martinique where

data are actually lacking. Furthermore, okadaic acid, potentially responsible for DSP (Lee et al., 2016; Tripuraneni et al., 1997), and palytoxin and derivates should also be looked for after seafood poisoning, for these toxins can be the cause of up to 17% of unexplained CATI (Petit-Sinturel, 2015).

5. Conclusion

In Guadeloupe and Martinique, total abundances of epibenthic dinoflagellates fluctuated through time but were not related to temperature nor to salinity variations. Important spatial disparities were found between both islands, with about 5 times more benthic dinoflagellates in Guadeloupe than in Martinique. *Halophila stipulacea*, a new invasive seagrass species in the Caribbean Sea, hosted high amounts of *Gambierdiscus* spp. in both islands and could be considered as a potential vector in spreading CFP cases within the Caribbean. Moreover, although outside the high prevalence CFP area, Martinique Island showed two times more *Gambierdiscus* spp. compared to Guadeloupe, suggesting that the ciguatera prevalence border might be shifting southwards in the Lesser Antilles. Morphogenetic analyses of benthic dinoflagellates of Martinique and Guadeloupe are under investigation in order to determine the occurring species for each Island.

Acknowledgments

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