cryptogamie
Algologie
2020 • 41 • 7

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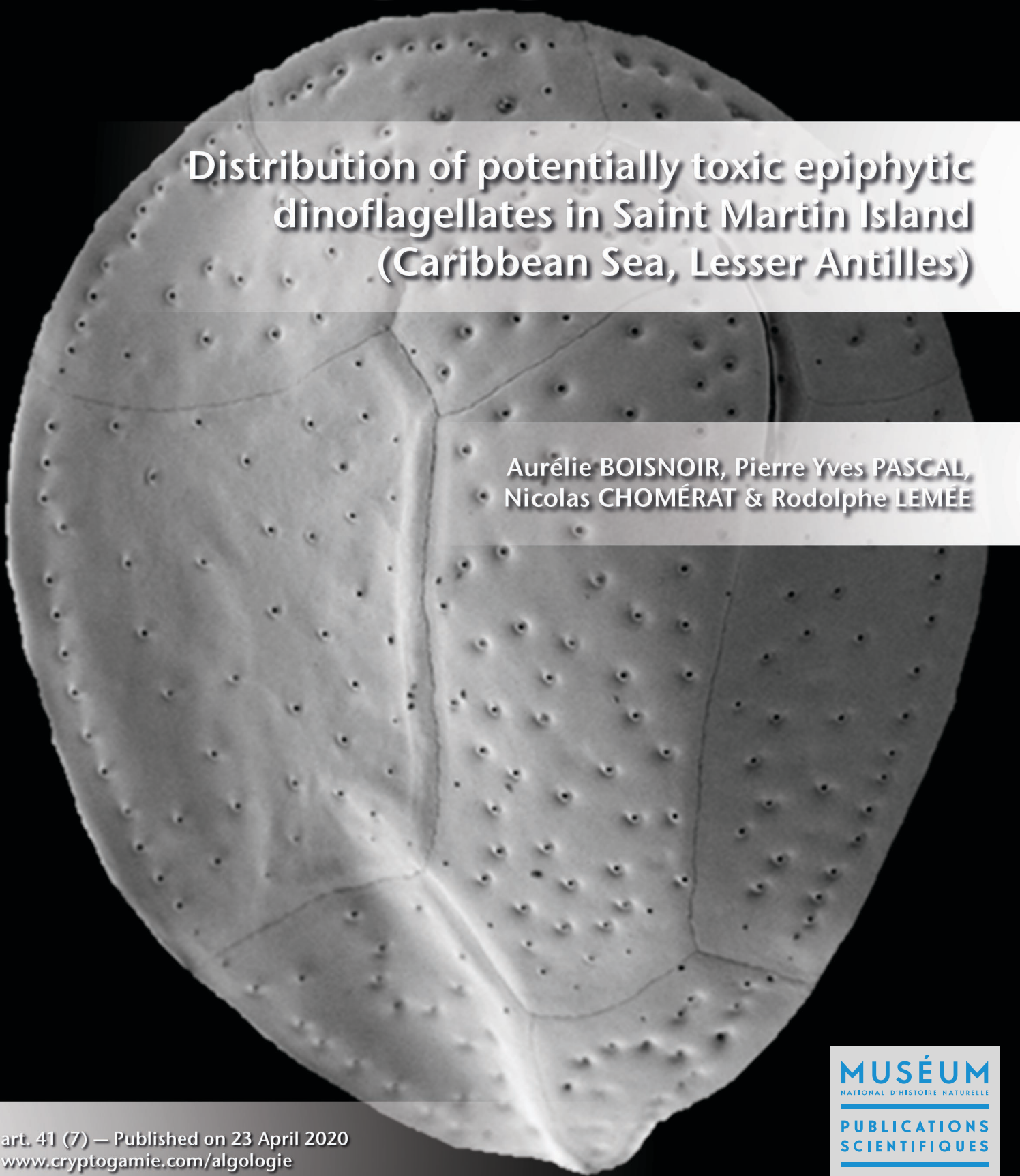

art. 41 (7) — Published on 23 April 2020
www.cryptogamie.com/algologie

MUSÉUM
NATIONAL D'HISTOIRE NATURELLE
PUBLICATIONS SCIENTIFIQUES

Couverture / *Cover* :
Ostreopsis sp. collected in the French West Indies (photo: Boisnoir & Chomérat).

Cryptogamie, Algologie est indexé dans / Cryptogamie, *Algologie is indexed in:*
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- Chemical Abstracts
- Current Contents
- Marine Science Contents Tables (FAO)
- Science Citation Index
- Publications bibliographiques du CNRS (Pascal).

Cryptogamie, Algologie est distribué en version électronique par / Cryptogamie, *Algologie is distributed electronically by:*
- BioOne® (http://www.bioone.org/loi/crya)

Cryptogamie, Algologie est une revue en flux continu publiée par les Publications scientifiques du Muséum, Paris
Cryptogamie, Algologie *is a fast track journal published by the Museum Science Press, Paris*

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Diffusion – Publications scientifiques Muséum national d'Histoire naturelle
CP 41 – 57 rue Cuvier F-75231 Paris cedex 05 (France)
Tél. : 33 (0)1 40 79 48 05 / Fax : 33 (0)1 40 79 38 40
diff.pub@mnhn.fr / http://sciencepress.mnhn.fr

ISSN (imprimé / *print*) : 0181-1568 / ISSN (électronique / *electronic*) : 1776-0984

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Aurélie BOISNOIR
Institut de Systématique, Évolution, Biodiversité, ISYEB, UMR 7205,
Équipe Biologie de la Mangrove, Université des Antilles,
BP 592, F-97159 Pointe-à-Pitre, Guadeloupe (France)
aurelie.boisnoir@gmail.com (corresponding author)

Pierre Yves PASCAL
Institut de Systématique, Évolution, Biodiversité, ISYEB, UMR 7205,
Équipe Biologie de la Mangrove, Université des Antilles,
BP 592, F-97159 Pointe-à-Pitre, Guadeloupe (France)

Nicolas CHOMÉRAT
Ifremer, Département Océanographie et Dynamique des Écosystèmes,
Unité Littoral, Laboratoire Environnement littoral et Ressources aquacoles
Bretagne-Occidentale, Station de Biologie Marine de Concarneau,
Place de la Croix, F-29900 Concarneau (France)

Rodolphe LEMÉE
Sorbonne Université, CNRS, Laboratoire d'Océanographie de Villefranche,
LOV, F-06230 Villefranche-sur-Mer (France)

Submitted on 7 January 2020 | Accepted on 18 February 2020 | Published on 23 April 2020

Boisnoir A., Pascal P. Y., Chomérat N. & Lemée R. 2020. — Distribution of potentially toxic epiphytic dinoflagellates in Saint Martin Island (Caribbean Sea, Lesser Antilles). *Cryptogamie, Algologie* 41 (7): 47-54. https://doi.org/10.5252/cryptogamie-algologie2020v41a7. http://cryptogamie.com/algologie/41/7

ABSTRACT
For the first time, distribution of epiphytic dinoflagellates was studied in Saint Martin Island (Lesser Antilles) during the cyclonic season (between September 1st and 3rd, 2015). The present study provides a semi-quantitative analysis because the fresh weight of each macrophyte was estimated around 10 g. The identified genera were: *Ostreopsis* J.Schmidt, *Prorocentrum* Ehrenberg, *Coolia* Meunier, *Amphidinium* Claperède & Lachmann, and *Gambierdiscus* Adachi & Fukuyo in order of decreasing abundance. Highest average abundance values of the genera *Ostreopsis* and *Amphidinium* were hosted by macrophytes of the Phaeophyceae class with *c.* 15 000 and 60 cells g^{-1} respectively. Epiphytic *Coolia* cells were mainly observed on seagrasses with the highest average abundance value of *c.* 1000 cells g^{-1} whereas the genera *Gambierdiscus* and *Prorocentrum* were most often associated with Florideophyceae with the highest average abundances of *c.* 70 and 1500 cells g^{-1} respectively. This preliminary study indicates the most relevant locations to survey the biodiversity of potentially toxic epiphytic dinoflagellates in Saint Martin Island.

KEY WORDS
Dinoflagellates,
Caribbean Sea,
Ostreopsis,
Gambierdiscus,
Prorocentrum,
ciguatera fish poisoning
(CFP).

RÉSUMÉ

Répartition des dinoflagellés épiphytes potentiellement toxiques dans l'île de Saint-Martin (mer des Caraïbes, petites Antilles).

Pendant la saison cyclonique (1-3 septembre 2015), la distribution des dinoflagellés épiphytes a été étudiée pour la première fois sur l'île de Saint-Martin (Petites Antilles). Cette étude présente une analyse semi-quantitative des abondances de dinoflagellés épiphytes, le poids frais de chaque macrophyte ayant été estimé à 10 g. Les genres identifiés par ordre d'abondance décroissante au cours de l'étude sont les suivants : *Ostreopsis* J.Schmidt, *Prorocentrum* Erhenberg, *Coolia* Meunier, *Amphidinium* Claperède & Lachman et *Gambierdiscus* Adachi & Fukuyo. Les abondances maximales pour les genres *Ostreopsis* et *Amphidinium* ont été trouvées sur les Phaeophyceae ; leurs abondances atteignaient respectivement 15 000 et 60 cellules g^{-1}. Les cellules appartenant au genre *Coolia* ont été observées principalement sur les phanérogames marines avec une abondance maximale d'environ 1000 cellules g^{-1}. Les cellules des genres *Gambierdiscus* et *Prorocentrum* ont surtout été observées sur les Florideophyceae avec des abondances maximales respectives de 70 et 1500 cellules g^{-1}. Cette étude préliminaire a mis en exergue des localisations intéressantes pour étudier la diversité des dinoflagellés épiphytes potentiellement toxiques présents sur le littoral de l'île de Saint-Martin.

MOTS CLÉS
Dinoflagellés, mer des Caraïbes, *Ostreopsis*, *Gambierdiscus*, *Prorocentrum*, ciguatera.

INTRODUCTION

Some benthic dinoflagellates are a major concern for public health due to their toxins production. However, few studies have focused on the taxonomy of benthic dinoflagellates (Momigliano *et al.* 2013) and the diversity of the microbenthic communities remains largely unexplored especially in the Caribbean Sea (Chomérat *et al.* 2018).

In the Caribbean Sea, *Gambierdiscus* Adachi & Fukuyo species are the causal agent of a worry health issue, the ciguatera fish poisoning (CFP) (Bagnis *et al.* 1980; Litaker *et al.* 2017; Díaz-Asencio *et al.* 2019). The Caribbean Sea presents a CFP incidence rate fluctuating between 12 and 500 cases/100 000 inhabitants and is consequently the second region of the world most affected by CFP after the Pacific Ocean (Chinain *et al.* 2010). Within the Caribbean Sea, Saint Martin is the most affected island with an estimated CFP incidence rate of 100 cases/10 000 habitants in 1981 (Tester *et al.* 2010). However, only a single survey focused on the abundances of the genus *Gambierdiscus* on corals in this area (Bourdeau & Bagnis 1989). In another study dealing with the distribution of *Gambierdiscus* in the Gulf of Mexico and the Caribbean Sea, three species have been found in Saint Martin without indications about the colonized substrate (Litaker *et al.* 2017). In both studies, the presence of *Gambierdiscus* on macrophytes was overlooked despite their potential contribution on fluxes of toxin in the food web. Herbivorous organisms can be contaminated through selective ingestion of the surficial biofilm containing the toxic epiphytes (Darius *et al.* 2018; Boisnoir *et al.* 2020) or through ingestion of the whole macrophyte covered with toxic epiphyte dinoflagellates (Yasumoto *et al.* 1976; Bourdeau & Bagnis 1989; Díaz-Asencio *et al.* 2019).

The genera *Ostreopsis* J.Schmidt and *Prorocentrum* Ehrenberg are commonly found associated with *Gambierdiscus* in tropical areas (Ballantine *et al.* 1988; Besada *et al.* 1982; Faust 2009), they are responsible for specific poisonings. In tropical environments, the toxins synthesized by the genus *Ostreopsis* are the causal agent of the palytoxicosis (Alcala *et al.* 1988) and clupeotoxism (Onuma *et al.* 1999; Randall 2005) that occur respectively after the consumption of crustaceans and fish bioaccumulating toxins produced by this genus. The genus *Prorocentrum*, and specifically the species *Prorocentrum lima* (Erhenberg) F.Stein is responsible for diarrhetic shellfish poisoning (DSP) not limited to tropical areas (Tripuraneni *et al.* 1997). Among the *Ostreopsis* species morphologically described in the Caribbean Sea (Faust & Morton 1995; Faust 1999) several are known to be toxic (Ukena *et al.* 2001; Scalco *et al.* 2012; Accoroni *et al.* 2017) but the presence of *Ostreopsis* species in this area has not been confirmed by molecular studies (Penna *et al.* 2010). Concerning the genus *Prorocentrum*, 15 species sampled in the Western part of the Caribbean Sea have been described morphologically in the 1990's by M. A. Faust (Faust 1990a, b, 1991, 1993a, c, 1994; Faust *et al.* 2008) but it is only recently that a taxonomic study conducted in the Eastern Caribbean area have confirmed the presence of species known to be toxic (Chomérat *et al.* 2018).

Distribution of potentially toxic benthic dinoflagellates in the Caribbean justifies special attention to Saint Martin Island. Although CFP incidence rate has not been recently updated for this Island, CFP is still occurring (Boucaud-Maitre *et al.* 2018) despite the regulation of fish consumption by a decree (decree no. 2002-1249, https://bit.ly/2OfU8Ut). This decree includes three different prohibitions that concern fifteen species. Some species (*Carangoides bartholomaei* (Cuvier), *Sphyraena barracuda* (Edwards), *Seriola dumerili* (Risso), *Seriola rivoliana* Valenciennes) are constantly prohibited from fishing and sale in Saint Martin, Saint Barthelemy and Guadeloupe islands. Other species (*Caranx latus* Agassiz, *Caranx lugubris* Poey, *Caranx ruber* (Bloch), *Mycteroperca venenosa* (Linnaeus), *Mycteroperca tigris* (Valenciennes), *Alphestes afer* (Bloch), *Epinephelus morio* (Valenciennes), *Gymnothorax funebris* Ranzani) are prohibited from fishing and sale beyond the parallel 16°5N. The species *Lutjanus buccanella* (Cuvier) cannot be sold if its weight exceeds 1 kg whatever the fishing place. The species *Lutjanus jocu* (Bloch & Schneider) adds up the two last prohibitions.

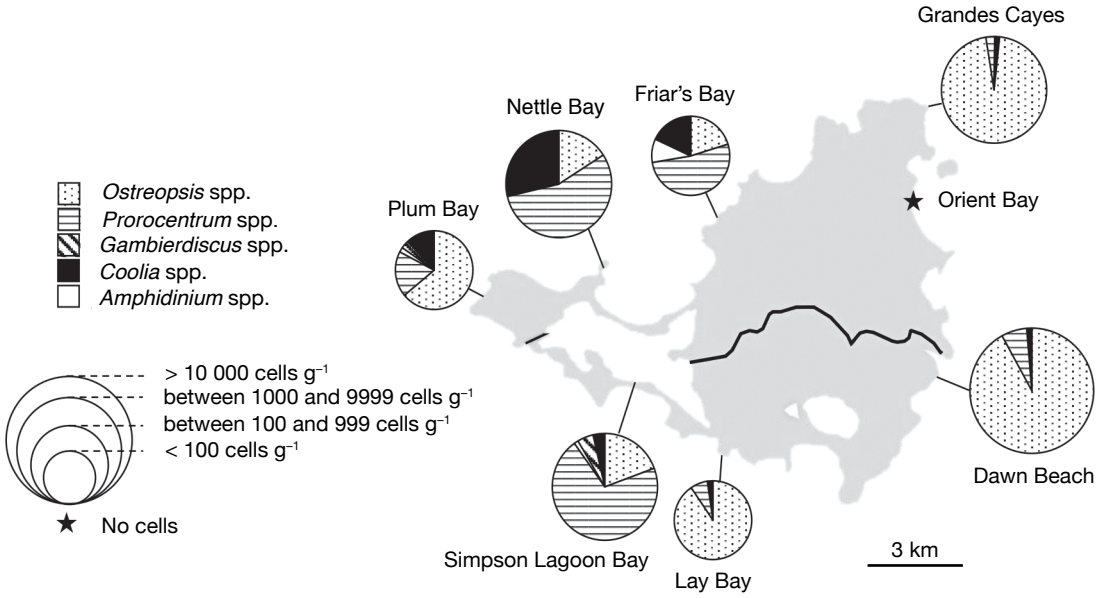

Fig. 1. — Distribution of potentially toxic benthic dinoflagellates abundances (cells g^{-1}) in Saint Martin Island.

Genera like *Coolia* Meunier, *Amphidinium* Claperède & Lachmann and *Sinophysis* Nie & C.Wang need to be considered even if their toxicity to human health is unknown (Botana 2014; Holmes *et al.* 1995). In the framework of a program studying the diversity of benthic dinoflagellates present in the Lesser Antilles, the aim of the present study is to describe the distribution of the benthic dinoflagellates community hosted by macrophytes in Saint Martin Island during the cyclonic period, which extends from June to December in the Caribbean area.

MATERIAL AND METHODS

Abundance of benthic dinoflagellates

Samples were collected between September 1st and 3rd, 2015 at eight sites along the Atlantic and Caribbean coast of Saint Martin Island (Fig. 1). All samples were collected between 0.5 and 2 m depth in shore waters.

The most abundant benthic macrophytes, which were locally present all year round, as well as the floating *Sargassum* spp., were sampled on each site. Approximately 10 g of macrophyte were carefully sampled with surrounding water in a 250 mL plastic flask avoiding the release of microalgae attached to 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 sieve (Retsch©, Ø 100 mm) to separate the macrophyte from the release dinoflagellates. Total seawater volume was measured. Microalgae samples were stored in the dark at 4°C. In total, 42 samples of macrophytes were semi-quantitatively analyzed because the fresh weight of the macrophyte was estimated (10 g).

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 were counted with a 1 mL Sedgewick Rafter© counting cell using a standard light microscope (Leitz, Orthoplan) within one week after sampling. Abundance values and the approximate fresh weight of macrophyte (10 g) allowed the calculation of the number of benthic toxic dinoflagellates per gram of fresh weight of macrophyte (cells g^{-1}).

Temperature and salinity

Temperature and salinity were measured in triplicates at each site in 250 mL seawater samples collected close to macrophytes (between 0.5 and 2 m depth).

Temperature was measured using a Hanna© thermometer and salinity by a Master-S/MilliM ATAGO© manual refractometer.

Data analysis

The descriptive analytical values of temperature and salinity are presented as mean ± standard error (SE). Due to a semi-quantitative approach, only the mean is presented for the abundance values of benthic dinoflagellates.

RESULTS

Temperature and salinity

The temperature of the seawater fluctuated between 29.7 ± 0.1°C and 30.8 ± 0.1°C (n = 3) and the salinity varied between 35 ± 1 and 40 ± 1 during the sampling at the different sites at Saint Martin Island. Generally, the average temperature

TABLE 1. — Temperature (°C), salinity and macrophytes collected in Saint Martin Island. Temperature and salinity were recorded in triplicates and macrophytes were sampled three times at each site.

Date	Station	Macrophyte	Temperature (°C)	Salinity
01.IX.2015	Grandes Cayes	*Thalassia testudinium* Koenig Benthic *Sargassum* spp.	30.2 ± 0.1	35 ± 0.1
01.IX.2015	Friar's Bay	*Padina* spp. *Laurencia* complex	30.0 ± 0.1	35 ± 0.1
01.IX.2015	Nettle Bay	*Thalassia testudinium* Koenig	30.5 ± 0.1	35 ± 0.1
02.IX.2015	Plum Bay	*Gracilaria* spp. *Halimeda* spp.	30.8 ± 0.1	35 ± 0.1
02.IX.2015	Simpson Lagoon Bay	*Halophila stipulaceae* Forsskål (Ascherson) *Gracilaria* spp.	30.3 ± 0.1	36 ± 0.1
02.IX.2015	Lay Bay	*Dasycladus* spp. *Gracilaria* spp.	30.5 ± 0.1	35 ± 0.1
03.IX.2015	Orient Bay	Pelagic *Sargassum* spp.	29.7 ± 0.1	40 ± 0.1
03.IX.2015	Dawn Beach	Benthic *Sargassum* spp. *Udotea* spp.	30.4 ± 0.1	37 ± 0.1

of the seawater was 30.3 ± 0.3°C and the average salinity was 36.0 ± 1 (n = 8) during the period study (Table 1).

DISTRIBUTION OF BENTHIC DINOFLAGELLATES. — The genera *Ostreopsis*, *Prorocentrum* and *Coolia* were absent at Orient Bay. The genus *Amphidinium* was absent at Lay Bay, Dawn Beach and Orient Bay. The genus *Gambierdiscus* was present only at Plum Bay and Simpson Lagoon Bay.

The genus *Ostreopsis* was observed mostly on Phaeophyceae and with decreasing abundances on Ulvophyceae, seagrasses, and Florideophyceae. The highest average abundance was found on benthic *Sargassum* spp. at Dawn Beach. Indeed, this macrophyte hosted on average 15 000 cells g^{-1} (Fig. 2).

Observed *Prorocentrum* were mostly on Florideophyceae with an average abundance of 1500 cells g^{-1} at Simpson Lagoon Bay. This genus was found to a lesser extent on Phaeophyceae, seagrasses, and Ulvophyceae.

The genus *Coolia* was found preferentially on seagrasses than on Phaeophyceae and Ulvophyceae and Florideophyceae. This genus was hosted with the highest abundance of *c.* 1000 cells g^{-1} on the seagrass *Thalassia testudinium* Koenig collected at Nettle Bay.

The genus *Amphidinium* was found with the highest average abundance on Phaeophyceae, seagrasses, Florideophyceae and Ulvophyceae. The highest average abundance of *Amphidinium* cells has been observed at Friar's Bay on the Phaeophyceae, *Padina* spp., with *c.* 60 cells g^{-1}.

The genus *Gambierdiscus* was found only at Simpson Lagoon Bay (on average *c.* 60 cells g^{-1}) and Plum Bay (on average *c.* 20 cells g^{-1}). This genus was mainly associated with *Florideophyceae* and to a lower extent to seagrasses. The highest average abundance of this genus was found on the Florideophyceae, *Gracilaria* spp. collected at Simpson Lagoon Bay (on average *c.* 70 cells g^{-1}). At Simpson Lagoon Bay up to 125 cells g^{-1} were found in a sample. None *Gambierdiscus* cell was observed on Phaeophyceae and Ulvophyceae.

DISCUSSION

TEMPERATURE AND SALINITY

The present study was set up during the cyclonic period in the Caribbean Sea. This period is characterized by a high seawater temperature (above 28°C) and a low salinity (below 35) due to heavy rainfall (Ballantine *et al.* 1988; Delgado *et al.* 2006; Boisnoir *et al.* 2018; Boisnoir *et al.* 2019a; Arbeláez M. *et al.* 2020). Temperature and salinity measured in Saint Martin Island were above means recorded during ecological studies conducted on benthic dinoflagellates in the Caribbean area (Ballantine *et al.* 1988; Delgado *et al.* 2006; Boisnoir *et al.* 2018; Boisnoir *et al.* 2019a; Arbeláez M. *et al.* 2020). These results suggest low rainfall and high light irradiance before and during the period sampling. In the Caribbean area, the wet season is watched because this period is supposed to promote the occurrence of high abundance values of benthic dinoflagellates (Ballantine *et al.* 1988) and to be related with high CFP cases (Tosteson 2004) due to long period with high seawater temperature (Tester *et al.* 2010; Tosteson 2004). However, these trends were not always found (de Fouw *et al.* 2001; Carlson & Tindall 1985). Furthermore, the relation between abundance values of *Gambierdiscus* cells and environmental conditions are complex and must consider parameters such as the salinity (Ballantine *et al.* 1988), light irradiance (Morton *et al.* 1992), substrate preferences (Lobel *et al.* 1988; Boisnoir *et al.* 2019a), and nutrients (Morton & Faust 1997; Delgado *et al.* 2006; Irola-Sansores *et al.* 2018).

BENTHIC DINOFLAGELLATES COMMUNITY

The species found in Saint Martin Island confirm that the benthic dinoflagellates community composition is in agreement with other studies performed in the Caribbean Sea (Morton & Faust 1997; Delgado *et al.* 2006; Irola-Sansores *et al.* 2018; Boisnoir *et al.* 2019a). In the present study, the abundance values of benthic dinoflagellates have to be considered with caution as samples were semi-quantitatively analyzed (the fresh weight of macrophyte was estimated around 10 g). The present study provides order of magnitude and not usual quantitative parameters such as the mean and the associated standard error to appreciate the global distribution of benthic dinoflagellates in Saint Martin Island during the cyclonic season.

Potentially toxic epiphytic *Ostreopsis*, *Prorocentrum* and *Gambierdiscus* genera accompanied by the genera *Coolia* and *Amphidinium* were found in Saint Martin Island for the first time in the present study. The genus *Sinophysis* was not found in Saint Martin although this genus was previously observed in the benthic dinoflagellate community of other areas of the Caribbean Sea (Faust 1993b; Chomérat 2016; Boisnoir *et al.* 2019a).

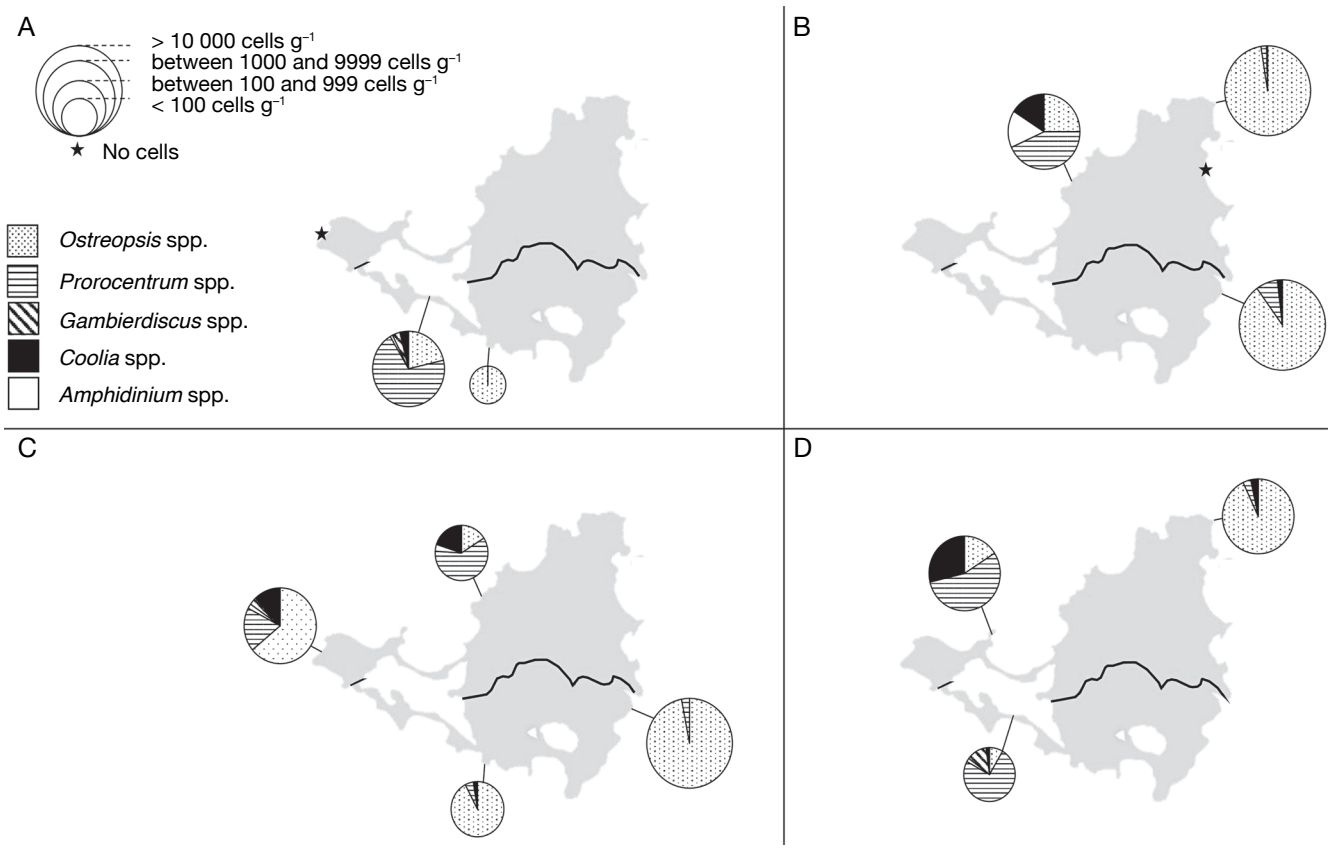

Fig. 2. — Distribution of potentially toxic benthic dinoflagellates abundances (cells g–1): **A**, Florideophyceae; **B**, Phaeophyceae; **C**, Ulvophyceae; **D**, seagrasses in Saint Martin Island.

The abundance densities of the genus *Ostreopsis* were lower in Cuba and Martinique islands than abundances values found in the present study. Indeed, during the cyclonic period less than 1500 cells g–1 were found in both islands (Delgado *et al.* 2006; Boisnoir *et al.* 2019a) while densities reached 15 000 cells g–1 in the present study. Similar abundances of *Ostreopsis* spp. were found in Puerto-Rico (Ballantine *et al.* 1988) and at Puerto Morelos along the Caribbean coast of Mexico (Irola-Sansores *et al.* 2018) where average cell densities reached respectively 16 000 cells g–1 and 13 000 cells g–1 during the wet season (Ballantine *et al.* 1988; Irola-Sansores *et al.* 2018). However, up to 100 000 cells g–1 were found at Bois Jolan in Guadeloupe during the wet season (Boisnoir et al. 2019). The dominance of the genus *Ostreopsis* was reported along the Caribbean coast of Mexico (Irola-Sansores et al. 2018), Puerto-Rico Island (Ballantine *et al.* 1988) and Guadeloupe (Boisnoir *et al.* 2019a). In the present study, this trend must be interpreted with caution. Indeed, the dominance of the genus *Ostreopsis* was recorded in Martinique Island between January and February 2014 (Boisnoir *et al.* 2019b) but it was not observed during a seasonal monitoring settled during 18 months (Boisnoir *et al.* 2019a) suggesting that the dominance of *Ostreopsis* can be occasional. In the present study, highest abundances of the genus *Ostreopsis* were found on benthic *Sargassum* spp. while none cells were found on pelagic *Sargassum* spp. In other studies carried out in the Gulf of Mexico and the Caribbean Sea, less than 200 cells g–1 were recorded on pelagic *Sargassum* spp. (Bomber *et al.* 1988; Boisnoir *et al.* 2019a). These results suggest that benthic *Sargassum* spp. should contribute to the potential toxic risk of benthic dinoflagellates contrarily to pelagic *Sargassum* spp. However, pelagic *Sargassum* spp. can be an important vector for exchanging microalgae populations (Kim *et al.* 2019). Arrival of toxic benthic dinoflagellates species has been observed in southeast of Australia after long distances on drifting macrophytes and plastic debris (Larsson *et al.* 2018). The dinoflagellate populations can be harbored by pelagic *Sargassum* and homogenized between the West Indies, Gulf of Mexico and the African coasts (Boisnoir *et al.* 2019a).

The genus *Prorocentrum* is usually dominant in ecological studies settled in the Gulf of Mexico (Okolodkov *et al.* 2007; Martínez-Cruz *et al.* 2015), and in the Caribbean Sea (Delgado *et al.* 2006; Morton & Faust 1997; Arbeláez M. *et al.* 2020) but this dominance was not observed in Saint Martin Island. As in the present study, low abundance values of *Prorocentrum* were found in Cuba, Guadeloupe and Martinique where less than 2000 cells g–1 where found during the wet season (Delgado *et al.* 2006; Boisnoir *et al.* 2019a). However, abundance values reached more than 20 000 along the Caribbean coast of Colombia during the rainy season (Arbeláez M. *et al.* 2020). During the rainy season in the

Caribbean Sea, the dominance of *Prorocentrum* genus seems to occur with fewer cells than when the benthic dinoflagellates community is dominated by *Ostreopsis*.

The presence of the genus *Gambierdiscus* at only two sites in Saint Martin Island is surprising because this Island is located in the high CFP prevalence (Olsen *et al.* 1984). Furthermore, this genus was previously observed at eight sites (nine sites in total) on undamaged corals, *Acropora palmata* (Lamarck) (Bourdeau & Bagnis 1989). In this previous study, *Gambierdiscus* would be associated with maximal abundance values close to 20 cells g^{-1} of macrophyte fresh weight (Bourdeau & Bagnis 1989) lower than in the present study. The increase of abundance values of *Gambierdiscus* spp. can be explained with the probable increase of anthropic pressures near the coral reefs of Saint Martin Island (Chinain *et al.* 2010; Hoegh-Guldberg 1999) between the study of Bourdeau & Bagnis (1989) and the present study. Anthropic disturbances such as dredging and construction activities near coral reefs often involve a phase shift from coral reefs ecosystem to macrophytes (Hoegh-Guldberg 1999). Hence, this new ecosystem with abundant macrophytes provides additional and ideal substrate for the attachment of benthic dinoflagellates responsible for the CFP (Chinain *et al.* 2010; Rongo & Van Woesik 2011; Morrison *et al.* 2008).

Usually the bloom formation threshold for this genus is 1000 cells g^{-1} because at such cell densities the amount of toxins begins to substantially accumulate in the food web (Litaker *et al.* 2010). However, in some areas as Saint Barthelemy, Guadeloupe, Martinique, Caribbean cost of Colombia and Mexico, abundance values of *Gambierdiscus* have never been found to exceed 1000 cells g^{-1} (Boisnoir *et al.* 2019a; Boisnoir *et al.* 2018; Boisnoir *et al.* 2019b; Arbeláez M. *et al.* 2020; Irola-Sansores *et al.* 2018; Lobel *et al.* 1988) and CFP cases occurred (Boucaud-Maitre *et al.* 2018; Tester *et al.* 2010; Gaitán 2007; Núñez-Vázquez *et al.* 2019) suggesting that the amount of toxins begins to affect the food web at a lower cell density in some areas. It appears that the bloom threshold needs to be established regionally in the Caribbean Sea (Boisnoir *et al.* 2019b). Saint Martin could be a part of islands of the Lesser Antilles where abundance values of *Gambierdiscus* never exceed 1000 cells g^{-1} and where CFP still occur. The bloom formation threshold of 50 cells g^{-1} proposed by Boisnoir *et al.* (2019a) could be suitable for Saint Martin Island. A seasonal monitoring is necessary to know if abundance values of *Gambierdiscus* can exceed or not 1000 cells g^{-1} in order to determine if samples were collected during a bloom at Simpson Lagoon Bay.

The genera *Coolia* and *Amphidinium* are rarely mentioned in ecological studies carried out in the Caribbean basin. The low abundances found in this present study are similar to abundances observed in Guadeloupe and Martinique (Boisnoir *et al.* 2019a).

Spatial distribution

Due to the high dinoflagellate abundance, the sites of Dawn Beach, Nettle Bay, Friar's Bay, Simpson Lagoon Bay and Plum Bay are interesting to assess the diversity of benthic dinoflagellates in Saint Martin Island. Before the exclusion of Orient Bay, this site need to be explored again without pelagic *Sargassum* grounding.

CONCLUSION

Potentially toxic epiphytic dinoflagellates including the genus *Ostreopsis, Prorocentrum,* and *Gambierdiscus* were found for the first time in Saint Martin Island. These genera were accompanied by the non-toxic genera *Coolia* and *Amphidinium.* The species found in Saint Martin Island confirm that the benthic dinoflagellates community composition is in agreement with other studies performed in the Caribbean Sea. The present study revealed different distributions for each genus highlighting stations that will have to be explored to assess the diversity of benthic dinoflagellates species present in Saint Martin Island. In order to study the diversity of benthic dinoflagellate species present in the Caribbean area, it is now necessary to define morpho-genetically the species previously described according to morphological criteria.

Acknowledgements

This study was funded by the "Collectivité Territoriale de Martinique". We thank the reviewers for giving us the opportunity to improve our manuscript

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Submitted on 7 January 2020;
accepted on 18 February 2020;
published on 23 April 2020.