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Epibenthic Dinoflagellates in the Southern Gulf of California: Species Composition and Abundance

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Abstract

Bahía de La Paz is the largest bay in the southern Gulf of California. This bay is an important area with a variety of commercial fish species and other natural resources and recreational activities. Epibenthic dinoflagellates are common inhabitants of harbors, inlets and semi-enclosed coastal lagoons; they produce potent toxins that may negatively affect human health and marine biota. The purpose of the present study was to identify potentially harmful epibenthic dinoflagellates growing on macroalgae from different coastal sites of the bay to determine their species composition, abundances, seasonal distributions, interannual and spatial variations. A total of 153 quantitative samples were collected in 2015–2019 (at 10 sites during four samplings in May, June and December) mainly from macroalgae. About 23 dinoflagellate species from the genera *Prorocentrum*, *Ostreopsis*, *Sinophysis*, *Gambierdiscus*, *Fukuyoa*, *Amphidinium*, *Blixaea*, *Bysmatrum*, *Cabra*, *Coolia*, *Durinskia* and *Plagiodinium* were found as epiphytes on at least 58 macroalgal species of 42 genera. Toxigenic genera, such as *Gambierdiscus*, *Ostreopsis*, *Coolia* and *Prorocentrum*, were widespread throughout the study area. Playa El Tecolote and Playa Costa Baja were the best habitats for dinoflagellates; therefore, the two locations can be considered the beaches with the greatest risk to human health.

Keywords: Dinoflagellata; epibenthos; epiphytic dinoflagellates; epiphytes; Gulf of California; interannual variation; Mexican Pacific; microalgae; microphytobenthos; species composition

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1. Introduction

Harmful algal blooms (HABs) have been increasing globally in extension, species diversity and economic impact [1–5], although it was recently shown that the perceived global trends are poorly evidenced and that they should be considered regional [6]. Epibenthic dinoflagellates (mostly sand-dwelling, but also epiphytic and epizoic) [7] are found globally and include many toxigenic species (including the causative agents of ciguatera fish poisoning—CFP) that negatively impact human health and marine animals. In addition to the impact caused by epiphytic dinoflagellates blooms, macroalgal blooms can also have

deleterious effects. These can produce a large amount of biomass that can be stranded on beaches along the coastline where it decomposes, triggering severe ecological impacts. Joniver et al. (2021) [8] pointed out that macroalgal blooms had a clear negative effect on aquatic plants (including seagrasses), fish and benthic invertebrates. Similarly, the decomposition of micro- and macroalgae blooms on various beaches in Bahía de La Paz may cause unpleasant smells impacting public access to the beaches, as well as ecological, economic, and human-health issues.

Marine benthic dinoflagellates have been much less studied than marine planktonic ones, and their role in marine food webs is still poorly understood. Over the past two decades, many benthic dinoflagellate species have attracted increasing attention as the causative agents of benthic harmful algal blooms (BHABs) and related syndromes, such as CFP and diarrhetic shellfish poisoning (DSP) in humans through consumption of seafood. Less than 10% of the total number of the known dinoflagellates appear to be benthic [9,10]. In general, 244 dinoflagellate species from 63 genera had been described by 2023 [7]. To our knowledge, marine dinoflagellates species have been found in all the oceans of the planet except the Antarctic Ocean in a range of habitats such as sand-dwelling, epiphytic on macroalgae, seagrasses and mangrove roots and floating detritus, in tide pools and subtidal areas, as epizoic beings attached to corals and other invertebrates, and also epilithic.

Epibenthic dinoflagellates are common inhabitants of harbors, inlets and semi-enclosed coastal lagoons. The known toxic benthic dinoflagellates reported for Latin America are within the genera *Gambierdiscus* R. Adachi et Y. Fukuyo, *Fukuyoa* F. Gómez, D.X. Qiu, R.M. Lopes et Senjie Lin, *Ostreopsis* Johs. Schmidt, *Prorocentrum* Ehrenberg, *Coolia* Meunier and *Amphidinium* Hulburt [11,12]; also see references in them. Such benthic harmful algal blooms (BHABs) have been described from tropical and subtropical coastal environments [13]. Few studies have been conducted on the BHABs along the Baja California Peninsula. Macroalgal assemblages in Bahía de La Paz usually comprise the phyla Rhodophyta, Ochrophyta (class Phaeophyceae) and Chlorophyta, with the families Rhodomelaceae and Ceramiaceae being the most abundant [14].

There are a few investigations regarding epibenthic dinoflagellates in the study area [15–19]. About 50% of them are master's theses dealing with the species composition, toxins, allelopathy, morphological and molecular characteristics of individual species, with an emphasis on *Coolia*, *Gambierdiscus*, *Ostreopsis* and *Prorocentrum* spp. All 240 ciguatera cases (including 200 in the La Paz area) reported from 1984 to 2013 in the Mexican Pacific have been documented in the state of Baja California Sur; the toxicity was assessed by mouse bioassay, as well as by immunoassay and HPLC [20].

Some benthic dinoflagellates have been reported in this bay because of the resuspension processes [21–23]. This process has favored the proliferation (blooms) of few benthic dinoflagellate species, such as *Prorocentrum rhathymum*, *P. lima, Blixaea quinquecornis* and *Amphidinium* cf. *carterae*, without consequences for the marine biota. Nevertheless, some of these blooms have contributed substantially to the phytoplankton biomass (13.20 to 17.75 mg/m chlorophyll-*a*) [22].

The goal of the present study was to identify potentially harmful benthic dinoflagellates growing on macroalgae from different coastal sites in the southern Gulf of California to carry out an assessment of their specific composition, cell abundances, seasonal distribution and their relationship with the macroalgal substrate, thus evaluating the risk of CFP in the study area.

2. Materials and Methods

2.1. Study Area

Bahía de La Paz is located on the Gulf of California western coast (24°28′27″ N, 110°33′2″ W), delimited by Isla San José to the north (24°58′23″ N, 110°36′52″ W), the Baja California Peninsula to the west and south, and Isla Espiritu Santo and Isla La Partida to the east (Figure 1). Bahía de La Paz is the largest bay on the Baja California Peninsular side of the Gulf of California. The bay constantly exchanges water with the latter via a northern and a southern opening [24]. Bahía de La Paz is subject to two main wind patterns. Southerly and southeasterly winds, locally called Coromuel, prevail from late spring to early autumn, with magnitudes of 4 m/s combined with frequent calm periods. Strong and persistent northerly and northwesterly winds prevail in late autumn and winter, reaching velocities of 12 m/s. Based on the temperature in the 0–25 m surface layer, two seasons are distinguished: the cold season (December to May, 22.5 ± 4.4 °C) and the warm season (July to November, 28.4 ± 1.9 °C) [25]. Similarly, in another study of the surface water, the temperate season (April to June, 23.55 ± 1.35 °C) and the warm season (July to September, 30.25 ± 0.95 °C) are distinguished [26].

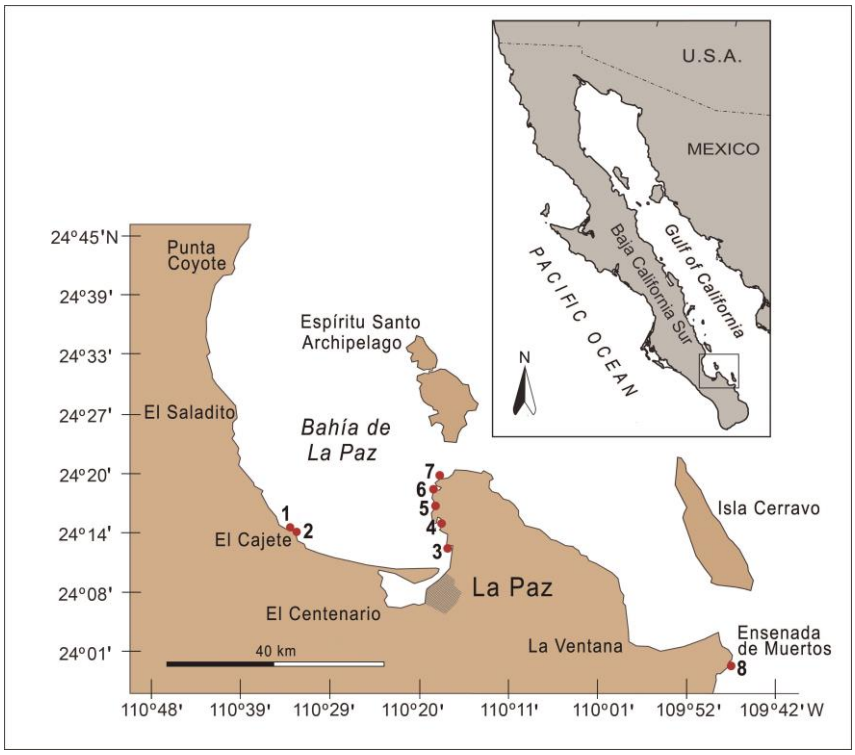


Figure 1. Sampling sites in Bahía de La Paz and adjacent waters in 2015–2019: 1—Agua de Yepiz, 2—Playa El Califin, 3—Costa Baja, 4—Playa El Tesoro (El Tesoro I and El Tesoro II), 5—Playa Las Brujas, 6—Balandra (Balandra-1 and Balandra-2), 7—Playa El Tecolote, 8—Playa Ensenada de Muertos (Bahía de los Sueños).

Recently, the surface sediments of the eastern coast of Bahía de La Paz were studied, and the seafloor-unit-classification proposal was made [27]. This region corresponds to sites 3 to 7 in our study area. The surface sediments at our sampling sites were coarse (0.5–1 mm) and very coarse (1–2 mm) sands. Sites 3 to 6 (Figure 1) are within the Punta Coyote zone, while site 7 (Playa El Tecolote) belongs to Canal de San Lorenzo; the latter is characterized by coarse to very coarse sands with more than 90% $CaCO_3$ and the presence of bioclasts formed by mollusk, coral, rhodolith and foraminifera fragments. At sites 7 and 2 (Playa El Califin), rocky substrate was common. The southern area of the bay, called

Laguna de La Paz, separated from the rest of the bay by El Mogote sand barrier, which contains a wide range of sediments from coarse sands to fine limes of fluvial and eolic origin, was not sampled in this study.

2.2. Sampling

Before sampling, a visual survey of the area was conducted. With the aim of studying the epibenthic dinoflagellate taxocoenosis, 153 quantitative samples were collected from different substrates (mainly green, brown and red macroalgae attached to the sea bottom, as well as sediments, mangrove roots and floating macroalgae) at 10 sites (corresponding to 8 sites on the map below) along the western coast of the southern Gulf of California (9 sites in Bahía de La Paz from Playa El Califin to Playa El Tecolote and a site beyond the bay) between 09:15 and 13:30 on 22 May 2015; 15, 21 and 22 June 2016; 16, 23 and 30 June 2018; and 7 December 2019. Macroalgae were collected manually at nine selected sites in Bahía de La Paz and a site in Ensenada de Muertos by snorkeling (Figure 1). Recurrent sampling in different years was performed only at Playa El Tecolote. At Balandra, samples were taken at two separate sites. Additionally, three mangrove root samples were collected at Playa El Tesoro I and II, the two inlets surrounded by mangroves.

The samples were taken in shallow water (down to 1.5 m depth) with a temperature of 21.5–25.0 °C and salinity of 35–36. Additionally, the data of the sea surface temperature were obtained from online resources using the Ocean Virtual Laboratory [28] (Figure 2). Level 4 interpolated temperature products are from ODYSSEA/Ifremer. Macroalgae were detached gently from the sea bottom, manually or using a knife, and fixed with formalin (stock solution of 37%) to a final concentration of 4%.

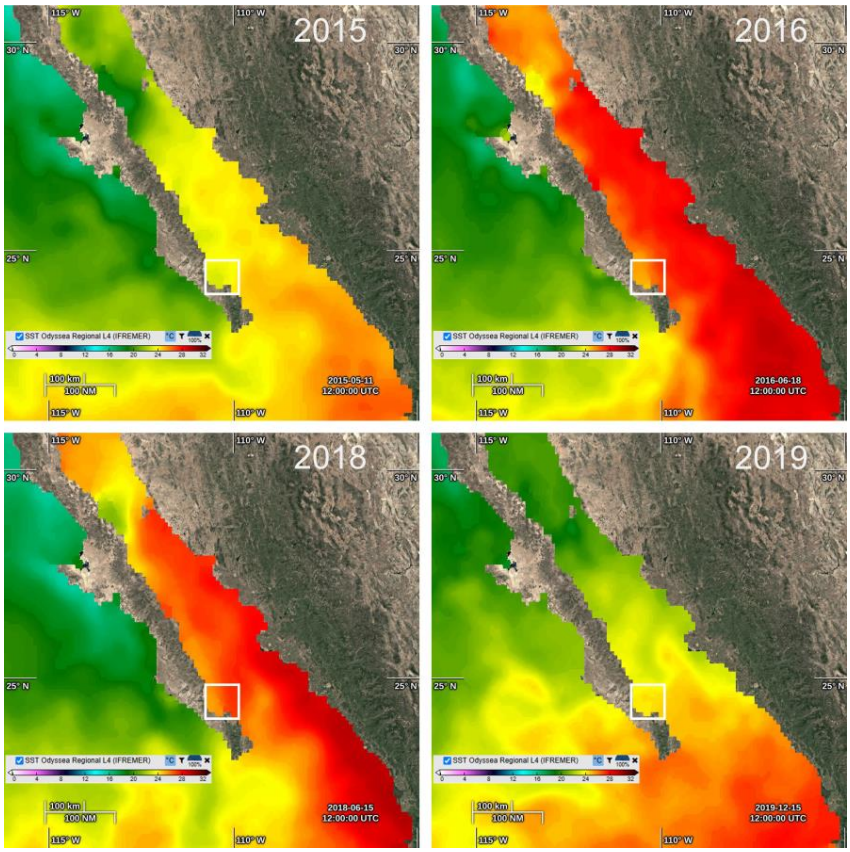


Figure 2. Sea surface temperature (SST) on 11 May 2015, 18 June 2016, 15 June 2018 and 15 December 2019 at 12:00. Temperature data were extrapolated regionally to an L4 level. The red box within the maps indicates the sampling area for this study.

2.3. Laboratory Analyses

Before cell counting in a 1 mL Sedgwick–Rafter chamber, a sample was vigorously shaken for one minute. Cells were counted using an Olympus CKX41 (Olympus Optical Co., Ltd., Tokyo, Japan) inverted microscope equipped with the phase-contrast objectives; the whole chamber or a part of it was scanned, depending on the total dinoflagellate cell abundance. Smaller cells of the genera *Amphidinium*, *Cabra* Sh. Murrat et D.J. Patterson emend. Chomérat, Couté et Nézan and *Plagiodinium* M.A. Faust et Balech were counted using the 40× objective, while larger cells of other genera were counted using the 10× objective. The results were expressed as the number of cells per gram (cells/g) of wet weight substrate (WWS). For taxonomic identification of dinoflagellates, both light and scanning electron microscopy were used together with the specialized literature [7,29–31]. The nomenclature of the algal taxa was updated following [7,32].

An epifluorescence compound microscope Axio Scope.A.1 (Carl Zeiss, Oberkochen, Germany) equipped with an Axiocam 506 color six-megapixel digital camera was used to observe the cell shape and size, as well as the thecal plate arrangement. Staining was performed with Calcofluor White M2R 0.2% [33] in epifluorescence, and Trypan Blue 0.2% [34,35] in bright field.

A JEOL JSM-7600F field emission scanning electron microscope (FESEM; JEOL, Ltd., Tokyo, Japan) was used at 5 kV at a working distance of 17.2–20.6 mm in the LEI regime to study the thecal morphology of dinoflagellate species in some samples. The samples were preliminarily washed in distilled water, followed by dehydration in a series of ethanol solutions of increasing concentration (30, 50, 70, 90 and 100%—twice in the latter). Subsequently, cells were air dried on 0.5″ aluminum mounts and sputter-coated with gold–palladium using a Polaron SC7640 high-resolution sputter coater (Quorum Technologists, Newhaven, SXE, UK).

Morphological features of the entire macroalgal thalli were observed using a stereomicroscope of low magnification Motic SMZ-168 (Kowloon, Hong Kong, China). When necessary, cross-sections of algal thalli were made and observed using a compound Motic B3 microscope (Kowloon, Hong Kong, China). Specimens were identified using the specialized literature [36–39]. The status of the current names for each species, as well as the synonyms, were checked using AlgaeBase [32] and a checklist of macroalgae [40].

2.4. Data Analysis

All analyses were performed in an open-source environment in R (version 4.2.2) and RStudio (1.6.4) [41]. Statistical differences between different cell abundances of epiphytic dinoflagellates, different sampling sites and years of study were analyzed using a two-level permutational multivariate test (PERMANOVA) [42]. Alpha diversity was estimated using the ecological descriptors: Shannon diversity, Pielou evenness, Simpson dominance and richness and evaluated with two-way PERMANOVA. Differences in the species assemblage composition between sites and years (beta diversity) were analyzed using Bray–Curtis dissimilarity on log-transformed abundance data. Structural patterns in taxonomic composition were investigated by performing a non-metric multidimensional scaling (NMDS) analysis on the beta diversity dissimilarity matrix [43].

A one-way analysis of similarities (ANOSIM) test was performed to determine whether the species composition of epiphytic dinoflagellates assemblages differed significantly between study years. Similarity percentage analysis (SIMPER) was then used to determine dinoflagellate taxa that accounted for the largest observed differences between NMDS assemblage patterns. Species contributing > 2% of the average dissimilarity within a single assemblage pattern by the mean of each pairwise comparison between years were considered potential “indicator” taxa that are more representative.

An interaction analysis based on UpSetR visualization matrices was used to assess and identify the years that shared or showed exclusivity of cell abundances and the different genera of epiphytic dinoflagellates across the years. The effect of different sampling sites was analyzed using a two-way cluster analysis and visualized in a full-linkage heatmap for each sampling site and years with spatial variation. The abundances of different species were first log-transformed (log + 1). Different clusters were selected with more than 30% similarity. Analysis and visualization were performed using the heatmap function of the '*stats*' (version 4.6.0) package.

Dinoflagellate–macroalgae association was evaluated using a differential ternary composition graph showing the distribution of dinoflagellates among the three major taxa of macroalgae: Chlorophyta, Rhodophyta and Ochrophyta (Phaeophyceae). The graph was constructed using the *ggtern* function and package with confidence intervals of 95%.

3. Results

3.1. Species Composition of Macroalgae

In the sampling sites during the period of 2015–2019, no seagrasses were found, so samples of the epiphytic dinoflagellates were taken only from macroalgae. Species composition of macroalgae differed between years and sites (Table 1). The number of species of Rhodophyta was more than twice of that of Phaeophyceae and Chlorophyta combined. Many taxa were identified only to the generic level and some to the family level. In the genera *Laurencia* J.V. Lamouroux, *Dictyota* J.V. Lamouroux and *Padina* Adanson, two or three morphologically different species were identified in each of them. In total, at least 58 macroalgal species of 42 genera and 26 families were distinguished: 33 Rhodophyta species of 26 genera, 13 Phaeophyceae species of 10 genera, and 12 Chlorophyta of 6 genera. The thalli of all the examined species served as a habitat for epiphytic dinoflagellates.

Table 1. Macroalgal taxa found in Bahía de La Paz and adjacent waters in the southern Gulf of California in 2015–2019 at ten sampling sites. Sampling sites: 1—Agua de Yepiz, 2—Playa El Califin, 3—Costa Baja, 4a—Playa El Tesoro I, 4b—Playa El Tesoro II, 5—Playa Las Brujas, 6a—Balandra-1, 6b—Balandra-2, 7—Playa El Tecolote, 8—Playa Ensenada de Muertos (Bahía de los Sueños); also see Figure 1. Identification was performed based on the entire individuals or thallus fragments.

Taxa	May 2015	June 2016	June 2018	December 2019
Rhodophyta				
Acanthophora spicifera (Vahl) Børgesen	3, 4b	1, 2, 6a,b, 7	7	
Amphiroa cf. *vanbosseae* Me. Limoine		7		
Amphiroa sp.		7	8	7
Asparagopsis sp.			8	
Bostrychia radicans (Montagne) Montagne	4a *			
Callithamnion sp.				7
Centroceras sp.	4a			
Ceramium sp.		2, 7	7	7
Champia sp.				7
Corallinaceae gen. sp.	4b, 7			
Crouania sp.				7
Digenea simplex (Wulfen) C. Agardh		5, 8	8	
Ganonema cf. *farinosum* (J.V. Lamouroux)				
K.-C. Fan et Y.-C. Wang		7		

Table 1. *Cont.*

Taxa	May 2015	June 2016	June 2018	December 2019
Gayliella sp.		2		
Gelidiella sp.			8	
Gelidium sp.		6a		
Gigartinaceae gen. sp.		8		
Gracilaria sp.	2	8		
(?)*Gracilariopsis* sp.				7
Herposiphonia cf. *littoralis* Hollenberg				7
Herposiphonia sp.				7
Hypnea valentiae (Turner) Montagne		1, 2, 6b, 7		
Hypnea sp.	3	5, 8	8	7
Laurencia cf. *masonii* Setchell et N.L. Gardner		2		
Laurencia spp.	3, 7	1, 2, 5, 6a,b, 7, 8	7	7
Lithophyllum sp.		7		
Lomentaria sp.	4b			
Neosiphonia sp.	3	1	7, 8	7
(?)*Pterocladia* sp.				7
Spyridia filamentosa (Wulfen) Harvey	3, 7	2, 6b, 7		
Spyridia sp.	4a,b, 7	2, 5, 6a, 8	7	7
Wrangelia sp.				7
Yuzurua sp.	6a			
Phaeophyceae				
Chnoospora sp.			8	
Colpomenia sp.			7	
Dictyopteris sp.				7
Dictyota spp.	7	1, 2, 7	8	7
Hydroclathrus clathratus (C. Agardh) M. Howe		1, 2, 6b		
Hydroclathrus sp.			7	
Myrionema sp.		1, 2 **		
Padina mexicana E.Y. Dawson var. *erecta*				
Avila-Ortíz	1	5		
Padina spp.	3, 7	2, 8	7, 8	
Sargassum agardhianum Farlow		1, 2, 7		
Sargassum sp.	3, 7	1, 5, 8	7, 8	7
Sphacelaria furcigera Kützing		1, 2 ***		
(?)*Taonia* sp.		1		
Chlorophyta				
Caulerpa racemosa (Forsskål) J. Agardh		5, 8	8	
Caulerpa sertularioides (S.G. Gmelin) R. Howe		2	8	
Chaetomorpha cf. *californica* Collins				7
Cladophora cf. *stimpsonii* Harvey				7
Cladophora sp.			8	7

Table 1. *Cont.*

Taxa	May 2015	June 2016	June 2018	December 2019
Codium cuneatum (Setchell) N.L. Gardner		1, 2, 6b		
Codium sp.	3, 4b, 7	6a,b, 7	7, 8	
Halimeda sp.	3, 7	6a, 7	7	7
Ulva clathrata (Roth) C. Agardh		6b		
Ulva intestinalis Linnaeus				7
Ulva sp.1 (laminar)		5, 6b, 7, 8	7, 8	7
Ulva sp.2 (tubular)	4b	6b		7

Note: * as epiphyte on mangrove roots; ** as epiphyte on *Sargassum agardhianum*; *** as epiphyte on *S. agardhianum, Padina* sp. and *Hypnea valentiae*.

3.2. Species Composition of Dinoflagellates

In total, about 23 dinoflagellate species from the genera *Prorocentrum* (8), *Ostreopsis* (3), *Sinophysis* Nie et Wang (3), *Gambierdiscus* (2), *Fukuyoa*, *Amphidinium*, *Blixaea* Gottschling, *Bysmatrum*, *Cabra*, *Coolia* Meunier, *Durinskia* S. Carty et E.R. Cox and *Plagiodinium* (one species each) were found (Figures 3–6). Microscopic observations did not allow us to identify some taxa to species level.

3.3. Abundance of Dinoflagellates

The maximum cell abundance was observed at Playa El Califin in June 2016: 14,441 cells/g of macroalgal wet weight (WWS: wet weight substrate; *Padina* sp. with attached cyanobacterial clumps). Usually, *Prorocentrum lima*, *P. rhathymum* and *P. sculptile* were dominant (up to 76%). *Gambierdiscus* was dominant only once (64%; Playa El Tecolote, December 2019). Occasionally, *Ostreopsis* dominated (up to 94%; Playa El Tecolote, December 2019). In all 13 macroalgal samples taken at Playa El Tecolote in 2019, *Gambierdiscus* and *Ostreopsis* occurred; their abundance reached 5697 cells/g MWW; *Ostreopsis* contributed up to 5195 cells/g. *Coolia* reached rather high abundances on both sides of Bahía de La Paz (1979 cells/g at Playa El Califin on the west coast of the bay and 1433 cells/g at Playa El Tecolote on the east coast, with up to 42% of the dominance in May–June).

3.4. Interannual and Spatial Changes in Cell Abundance of Dinoflagellates

The results of the PERMANOVA analysis indicated that interannual (r^2 = 0.02, p = 0.001) and spatial variation (r^2 = 0.12, p = 0.001) induced changes in the abundance and structure of epiphytic dinoflagellates. In May 2015, the cell abundance was represented mainly by *Coolia* cf. *malayensis*, with 13,828 cells/g WWS (~3 orders of magnitude) (Figure 7), followed by *Ostreopsis* cf. *lenticularis* and *Prorocentrum sculptile* with 3669 cells/g and 2872 cells/g WWS, respectively. The lowest cell abundance was observed for *Prorocentrum* sp. and *P. hoffmannianum* with 7 to 8 cells/g WWS. Sites 7 and 3 showed the highest abundances, whereas site 4 showed the lowest cell abundance. *Prorocentrum lima* and *P. rhathymum* showed the highest abundances with 48,327 and 20,133 cells/g WWS in June 2016, in addition to 7438 cells/g and 7486 cells/g WWS in June 2018, followed by *Coolia* sp. with 14,064 cells/g WWS and *Bysmatrum gregarium* with 12,537 cells/g WWS in June 2016. Similarly, in 2016, sites 1 and 7 hosted the highest abundances. In June 2018, site 8 showed the highest abundance of epiphytic dinoflagellates. *Ostreopsis* and *Gambierdiscus* were the dominant genera in December 2019, with 10,172 cells/g and 1699 cells/g WWS, respectively. The least represented were *Sinophysis stenosoma* and *Prorocentrum* cf. *cassubicum*, with 1.9 cells/g and 3.8 cells/g WWS.

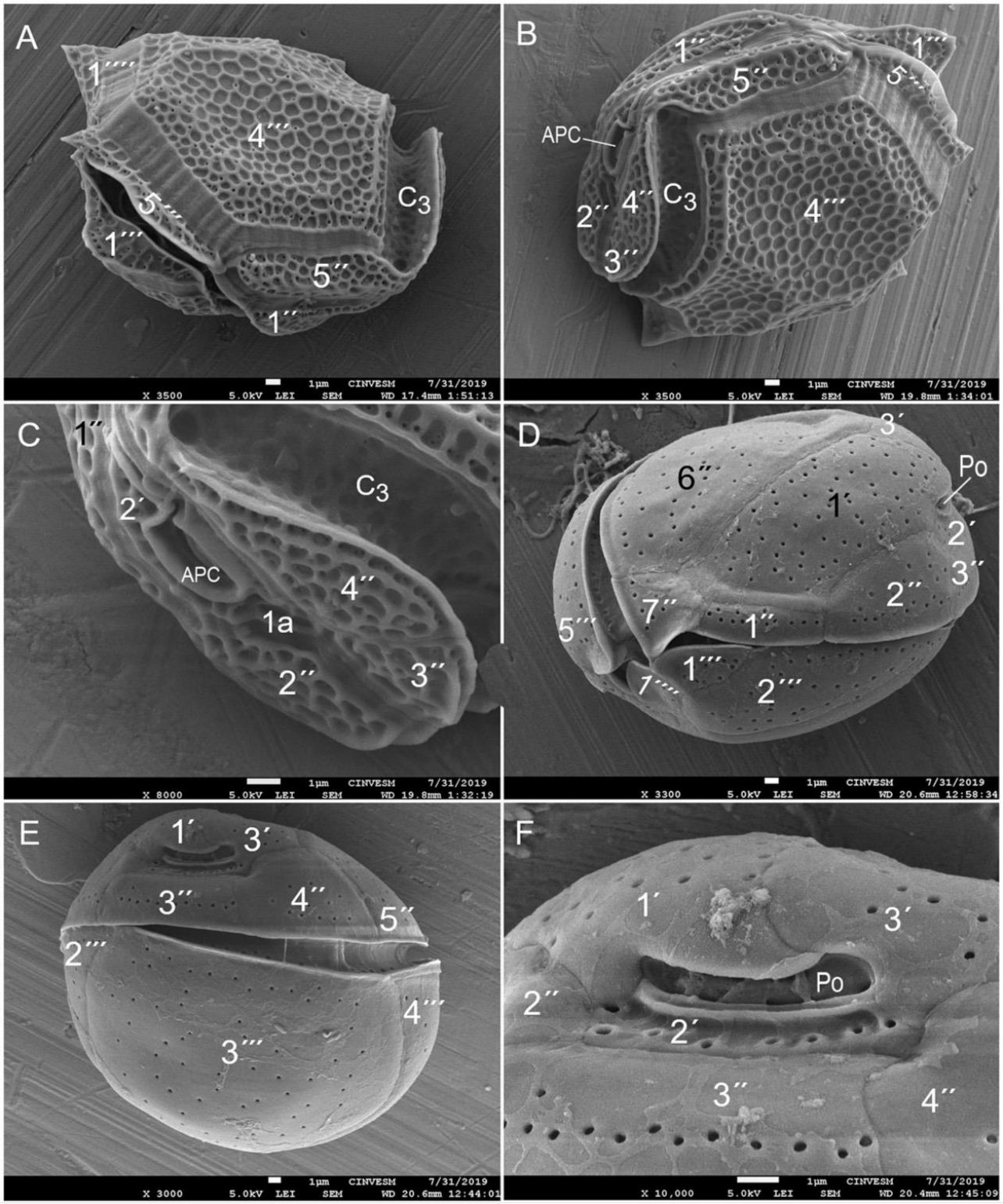


Figure 3. *Cabra* cf. *aremonica* (**A**–**C**) and *Coolia* cf. *malayensis* (**D**–**F**): (**A**) cell in right-side-ventral view; (**B**) cell in apical-right-side-ventral view; (**C**) epitheca and cingulum; (**D**) cell in apical-ventral view; (**E**) left-side-dorsal view; (**F**) fragment of the epitheca showing the Po and adjacent plates. Symbols for thecal plates: 1′–3′—the apical plates; 1″–7″—the precingular plates; 1a—the anterior intercalary plate; 1‴–5‴—the postcingular plates; 1⁗—the first posterior plate; APC—the apical pore complex; c_3—the third cingular plate; Po—the pore plate. Scale bars: 1 µm.

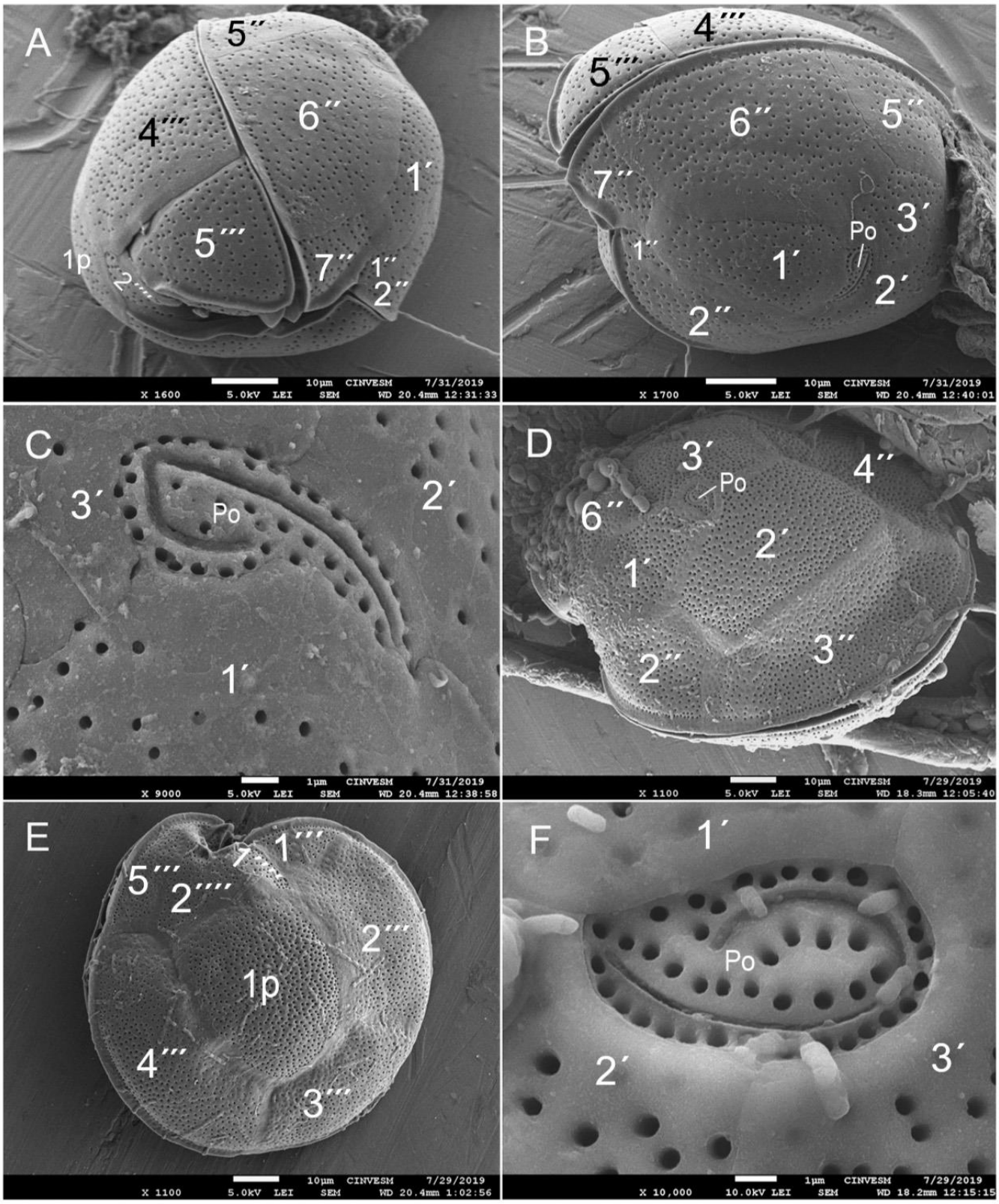


Figure 4. *Fukuyoa paulensis* (**A**–**C**) and *Gambierdiscus toxicus* (**D**–**F**): (**A**) cell in right-side view; (**B**) cell in apical-right-side view; (**C**) the Po and adjacent plates; (**D**) cell in apical view; (**E**) cell in antapical view; (**F**) the Po and adjacent plates. Symbols for thecal plates: 1′–3′—apical plates; 1″–7″—precingular plates; 1‴–5‴—postcingular plates; 1⁗, 2⁗ and 1p—antapical plates; Po—the pore plate. Scale bars: 10 μm in (**A**,**B**,**D**,**E**); 1 μm in (**C**,**F**).

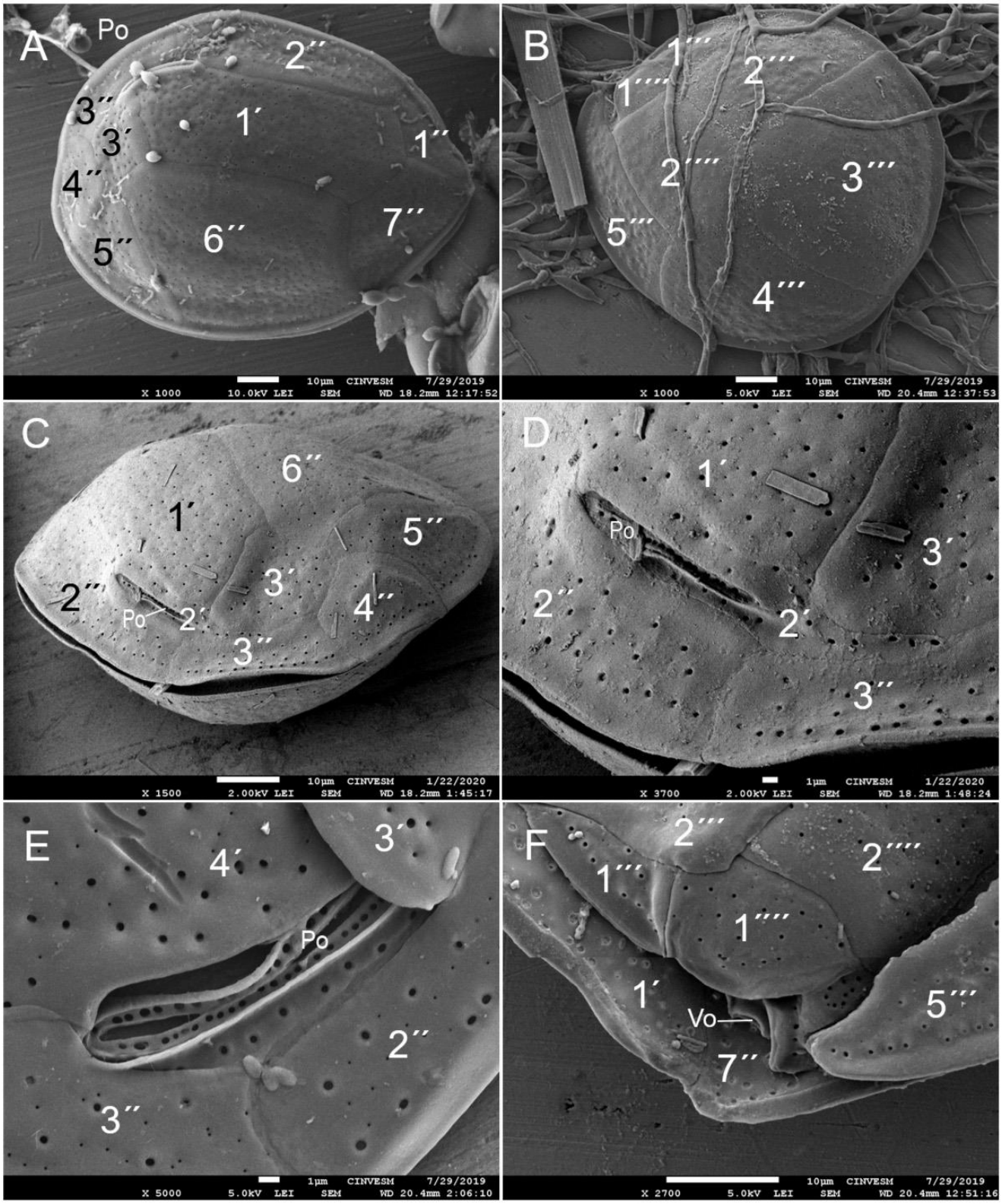


Figure 5. *Ostreopsis* cf. *lenticularis*: (**A**) cell in apical view; (**B**) cell in antapical view; (**C**) cell in apical-dorsal view; (**D**,**E**) the Po and adjacent plates; (**F**) fragment of the theca showing plates adjacent to the sulcal area in antapical-ventral view. Symbols for thecal plates: 1′–4′—apical plates; 1″–7″—precingular plates; 1‴–5‴—postcingular plates; 1⁗ and 2⁗—posterior plates; Po—the pore plate; Vo—ventral opening. Scale bars: 10 µm in (**A**–**C**,**F**); 1 µm in (**D**,**E**).

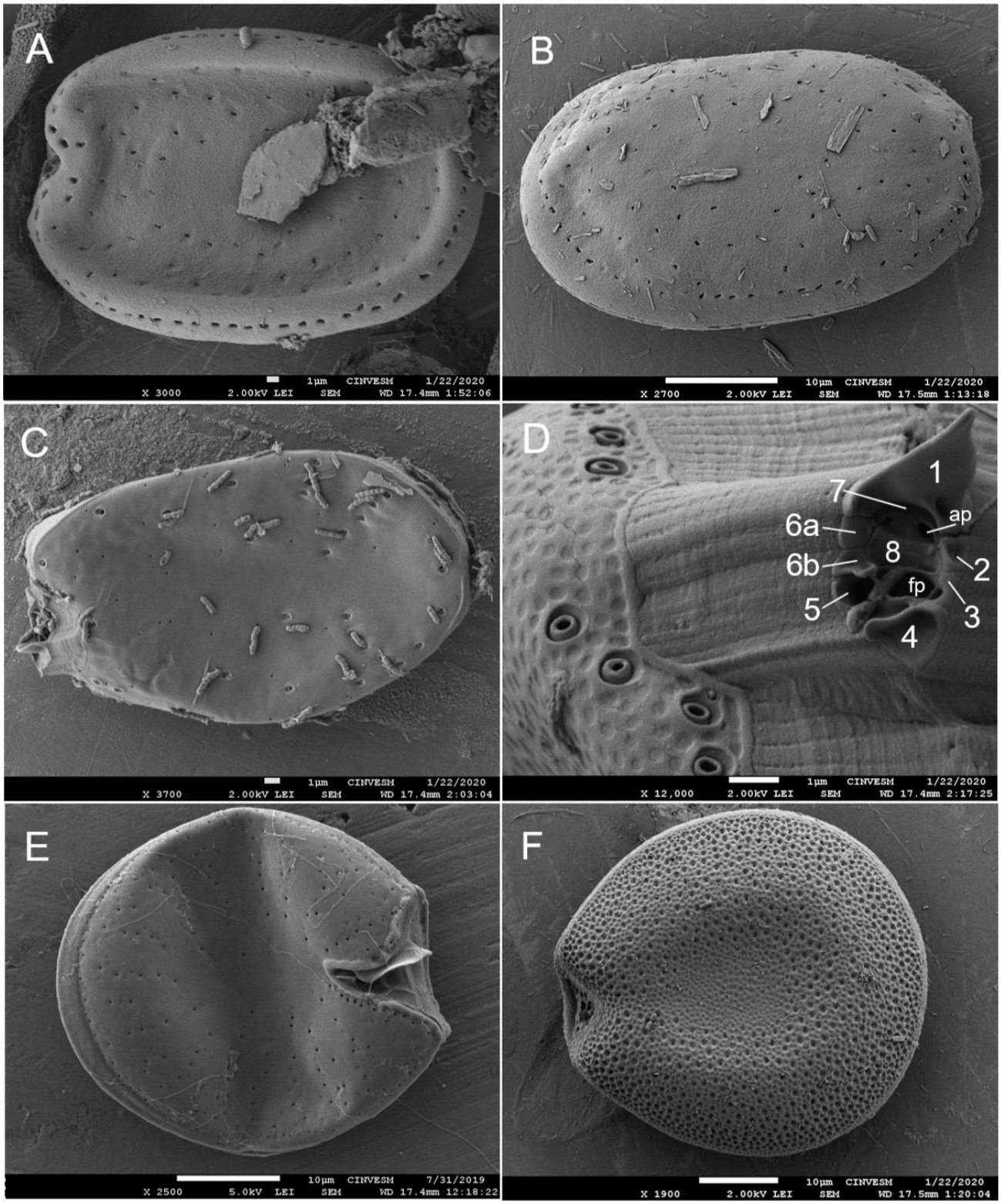


Figure 6. *Prorocentrum* species: (**A**) the *Prorocentrum lima* complex sp. 1 (cell in right-side view); (**B**) the *Prorocentrum lima* complex sp. 2 (cell in left-side view); (**C**) *P. rhathymum* (cell in left-side view); (**D**) *P. rhathymum* (the apical zone showing the trichocyst pores and the sagittal suture on the left plate, and the periflagellar area on the right plate); (**E**) *P. sculptile* (cell in right-side view); (**F**) *P. hoffmannianum* (cell in left-side view). Symbols for thecal plates: 1–8—platelets of the periflagellar area; ap—the accessory pore, fp—the flagellar pore. Scale bars: 10 µm in (**A**,**B**,**E**); 1 µm in (**C**,**D**,**F**).

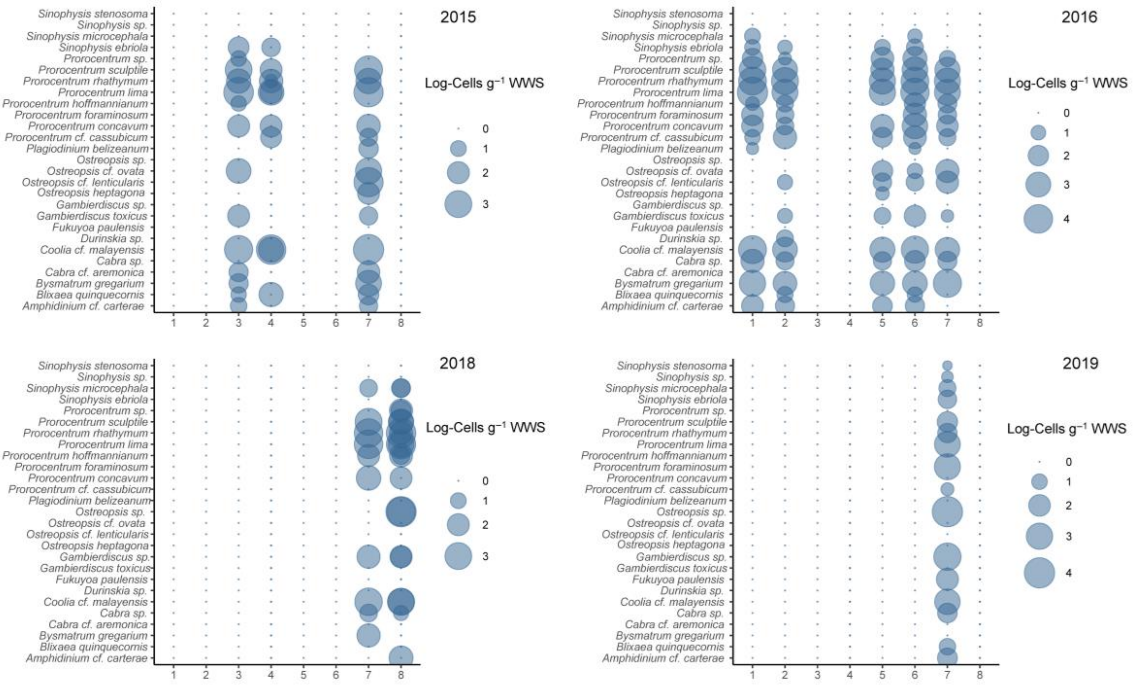


Figure 7. Interannual and spatial variation in the abundance of epiphytic dinoflagellates in Bahía de La Paz and adjacent waters in 2015–2019, showing the highest abundances in 2016 and 2019.

3.5. Seasonal Variation in Epibenthic Dinoflagellates

The genera *Blixaea*, *Bysmatrum*, *Coolia*, *Fukuyoa*, *Plagiodinium* and *Sinophysis* showed seasonal variation at the Tecolote site (H = 10.46, p = 0.01), respectively. However, no preference was observed for any season (month) in terms of increasing or decreasing abundance, so their behavior is differential throughout the months of study. The maximum variability was detected for the genera *Prorocentrum*, although it is associated with the richness within this genus. *Bysmatrum* showed a maximum abundance of four orders of magnitude in June 2016, followed by *Coolia* in May 2015 (Figure 8).

3.6. Alpha and Beta Diversity of Epiphytic Dinoflagellates

Shannon diversity (r^2 = 0.11, p = 0.001), richness (r^2 = 0.10, p = 0.001) and Simpson dominance (r^2 = 0.08, p = 0.002) were influenced by interannual changes at all sampling sites (Table 2). During the four years of study, a total of 27 epiphytic dinoflagellate species from 12 genera of epiphytic dinoflagellates were observed. Six genera (*Amphidinium*, *Prorocentrum*, *Coolia*, *Ostreopsis*, *Gambierdiscus* and *Fukuyoa*) include potentially toxigenic species. *Prorocentrum* was the most represented genus (eight species), followed by *Ostreopsis* and *Sinophysis* genera with three species each. In June 2016, the highest richness (20 species) was observed (sites 6 and 7), while in June 2018 only 13 species were found (site 8). In May 2015 and December 2019, 16 and 17 species of epiphytic dinoflagellates, respectively, were observed (at site 7 in particular) (Figure 9).

The highest species diversity was observed in 2016, particularly at site 7, with values of 2.1 (maximal) and 1.7 (minimal), while the lowest diversity related to an increase in observed dominance occurred in 2015 at site 4 with diversity values of 0.3 and 0.4 and dominance of 0.82 and 0.88. In 2018 and 2019, the values of diversity and dominance were 0.2 and 0.8, respectively (Figure 9).

The ANOSIM analysis associated with the NMDS (Figure 10A) indicated that the epiphytic dinoflagellate taxocoenosis differed in the study years (dissimilarity > 0.65, *Stres* = 0.18, R = 0.57, p = 0.001), translating into the different patterns observed (p = < 0.001, Table 3).

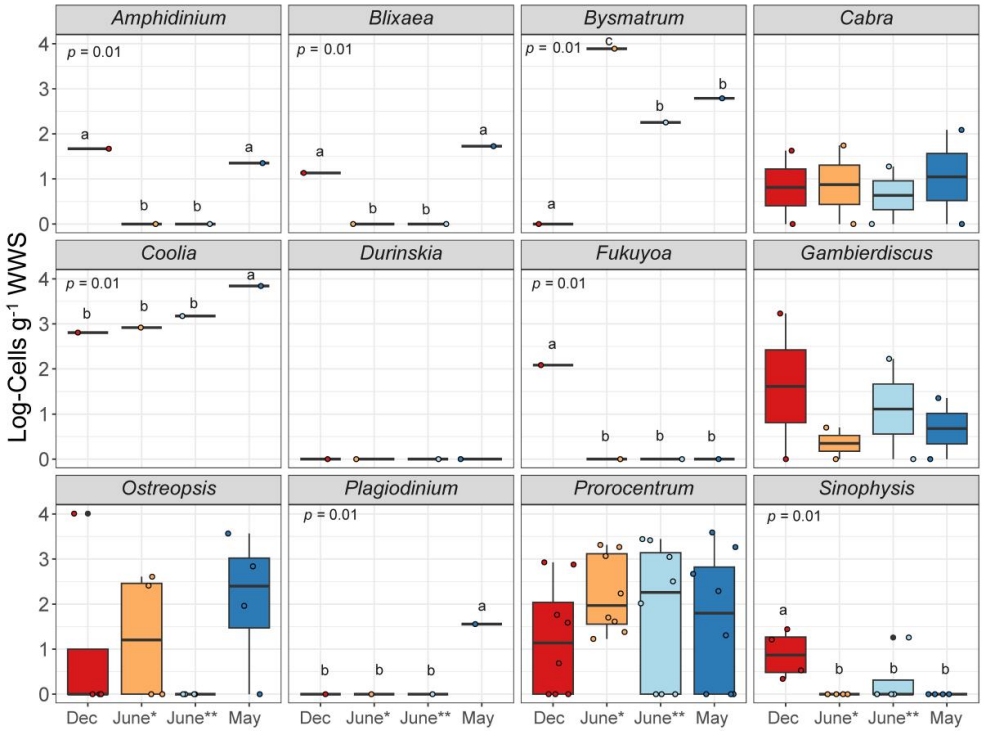


Figure 8. Seasonal variation in the main genera of epibenthic dinoflagellates. The total abundance of dinoflagellates was represented at the Tecolote site in Bahía de La Paz, Mexico. On the *X*-axis, May–May (2015), Jun *–June (2016), Jun **–June (2018), Dec–December (2019). Kruskal–Wallis analysis was performed to explore statistically significant differences. The letters above the boxplots indicate significant differences at the 95% level, based on Wilcox multiple comparisons.

Table 2. Summary of the permutational multivariate analysis of variance (PERMANOVA) based on Bray–Curtis dissimilarities and applied to the taxocoenosis structure of epiphytic dinoflagellates observed at 10 sampling sites for four years. Bold numbers indicate a significant effect in the models. Asterisks indicate the interaction between the models.

Factor	Pseudo-*F*	*p* (Perm)	R^2
Density			
Years	1.36	**0.001**	0.02
Sites	3.23	**0.001**	0.12
Years * Sites	3.62	0.912	0.01
Shannon diversity			
Years	0.45	0.508	0.003
Sites	7.60	**0.007**	0.05
Years * Sites	15.78	**0.001**	0.11
Richness			
Years	8.09	**0.001**	0.15
Sites	4.47	**0.032**	0.03
Years * Sites	15.28	**0.001**	0.10
Equitability index			
Years	14.09	**0.001**	0.10
Sites	4.26	**0.010**	0.03
Years * Sites	2.76	0.106	0.01
Simpson index (λ)			
Years	4.29	**0.048**	0.03
Sites	6.35	**0.016**	0.04
Years * Sites	11.28	**0.002**	0.08

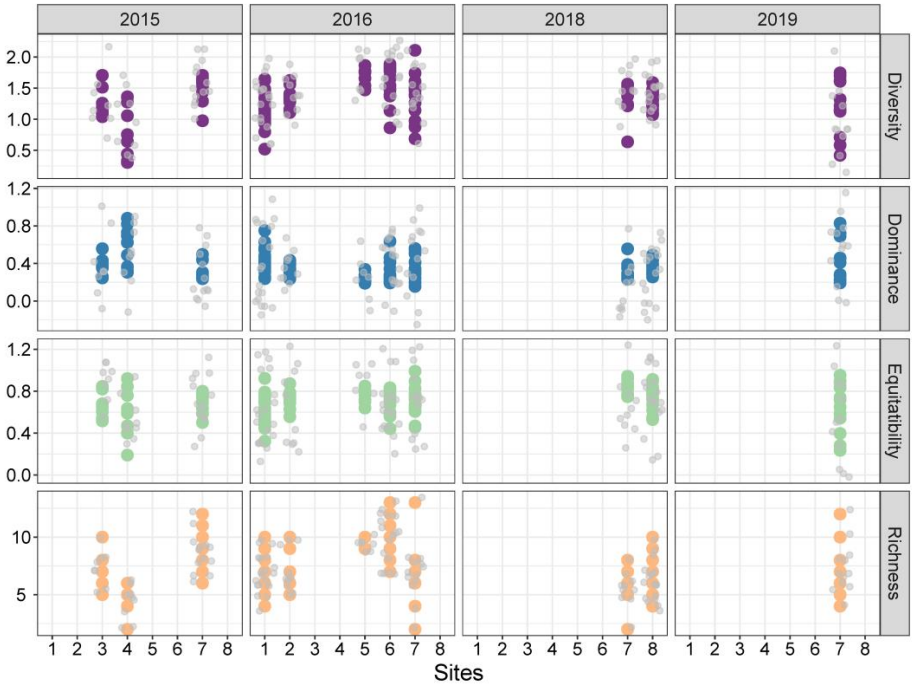


Figure 9. Interannual and spatial variation in the associated ecological descriptors in the coastal waters of Bahía de La Paz and adjacent waters in 2015–2019. The colored points show the dispersion of the data and the gray points indicate the modeled distribution. The highest species richness and diversity were observed in 2016 and 2019.

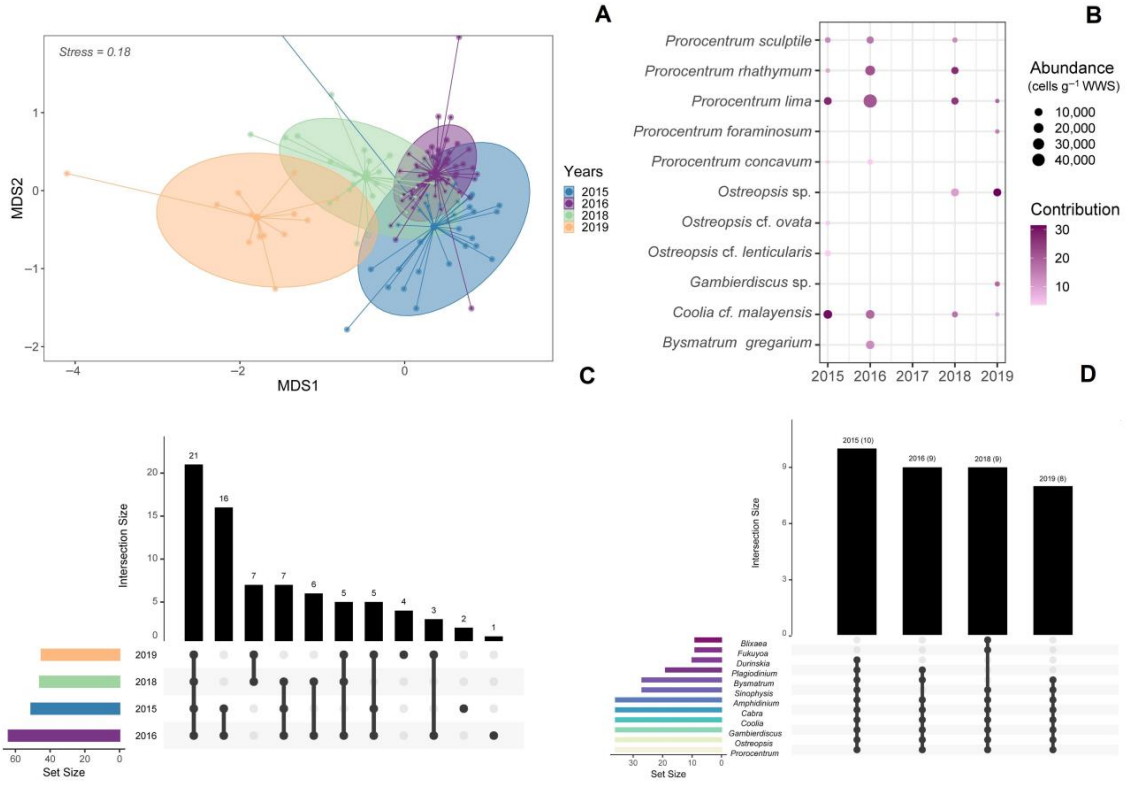


Figure 10. Analysis of beta diversity of epiphytic dinoflagellates from Bahía de La Paz and adjacent waters in 2015–2019. (**A**) Non-metric multidimensional scaling (NMDS) plot for epiphytic dinoflagellate taxocoenoses over four years of study. (**B**) Contribution of species during the different years of study. (**C**) UpSetR annual intersection map of cell density. Black bars indicate the number of interactions based on total dinoflagellate cell abundance. (**D**) Shared genera of epiphytic dinoflagellates and shared species richness.

Table 3. ANOSIM tests and interannual pairwise comparison of epiphytic dinoflagellate taxocoenoses in the study area.

Groups	Global R	Significance Level (%)
All years	0.570	0.0001
Year 2015 vs. 2016	0.463	0.0006
Year 2015 vs. 2018	0.386	0.0006
Year 2015 vs. 2019	0.795	0.0006
Year 2016 vs. 2018	0.485	0.0012
Year 2016 vs. 2019	0.96	0.0006
Year 2018 vs. 2019	0.638	0.0006

SIMPER analysis indicated a total of 11 epiphytic dinoflagellate species that had contributed significantly to the composition of the different patterns observed. In 2015, *Coolia* cf. *malayensis*, *Prorocentrum lima* and *P. sculptile* contributed up to 70% of the taxocoenosis, while in 2016 and 2018, *P. rhathymum*, *P. lima* and *Coolia* cf. *malayensis* contributed up to 60.5% and 69%, respectively. In 2019, taxocoenosis was represented mainly by *Ostreopsis* sp., *P. lima* and *Gambierdiscus* sp. (68.2%; Figure 10B). Interaction analysis based on UpSetR visualization matrices (Figure 10C,D) indicated that *Amphidinium* cf. *carterae*, *Coolia* cf. *malayensis*, *P. lima*, *P. rhathymum* and *P. sculptile* were the only species with maximum abundances (together contributing up to 66,079 cells/g WWS) shared during the entire study period. In 2016, the highest number of shared abundances with seven interactions was observed, while in 2015, only four similar abundances were shared. The UpSetR indicated 10 of the 12 reported genera in 2015, 9 in 2018, and 8 genera in 2016 and 2019.

The Clustering-Heatmap applied to the years with the greatest spatial variability (2015 and 2016) indicated that in May 2015 sites 3 and 4 showed similar cell abundances. Similarly, in June 2016, sites 1, 2 and 7 formed the first similar group, and the second cluster was formed by sites 5 and 6. *Prorocentrum lima*, *P. rhathymum*, *P. sculptile*, *P. concavum* and *Coolia* cf. *malayensis* were the key species in the clusters in both years (Figure 11).

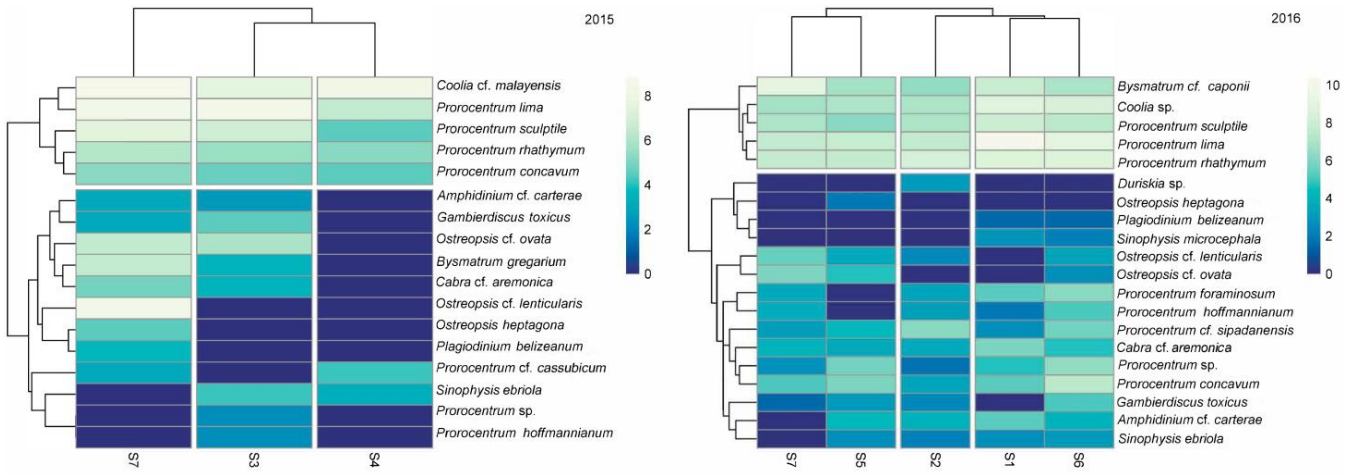


Figure 11. The Clustering-Heatmap of the similarity-based relationship between epiphytic dinoflagellates (*Y*-axis) and the different sampling sites in this study (*X*-axis).

3.7. Dinoflagellate-Macroalgae Associations

A total of 43 genera of macroalgae were identified; however, only the dominant genera (27) in the samples were plotted in Figure 12A. Of these, 17 belong to Rhodophyta, 5 to Phaeophyceae and 5 to Chlorophyta. *Dictyota*, *Laurencia*, *Spyridia* and *Ulva* showed the most extended distributions during the study period. The ternary graph revealed that 95%

of the epiphytic dinoflagellate taxocenosis showed preferences for Rhodophyta (*Spyridia filamentosa*, *Hypnea valentiae* and *Laurencia* cf. *masonii*), mainly in 2016 and 2019 (Figure 12B).

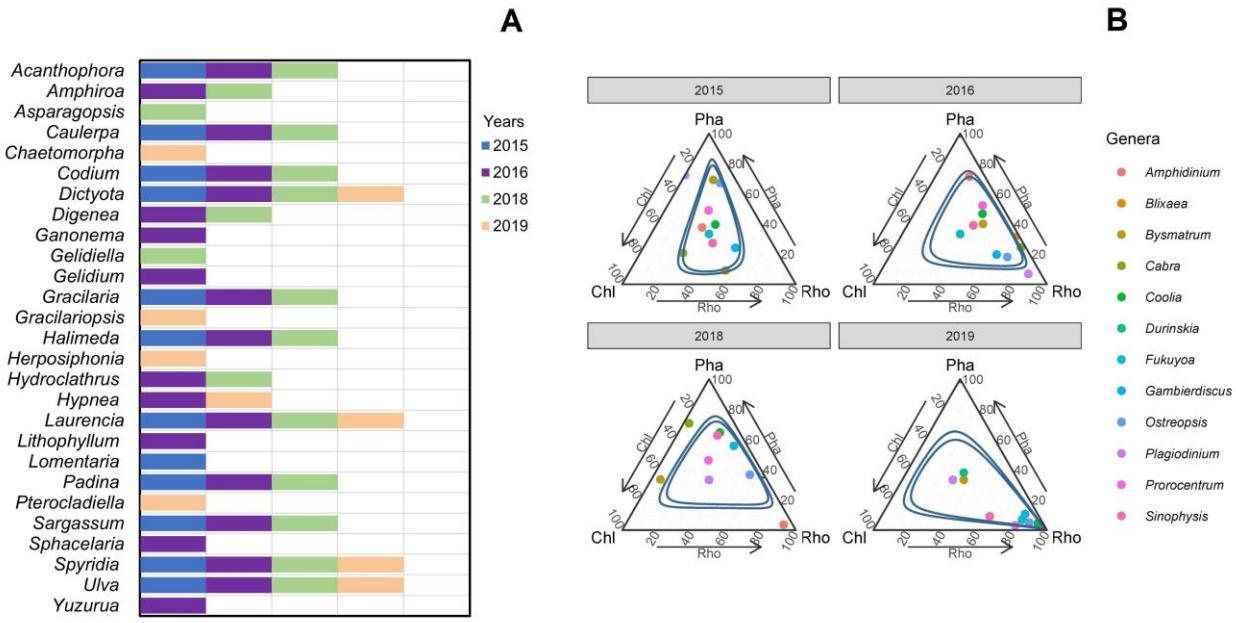


Figure 12. Interannual relationship between epiphytic dinoflagellate species and macroalgae. (**A**) Composition of the macroalgae identified in this study. (**B**) Ternary composition graph between dinoflagellates and macroalgae. The *X*-axis indicates the year when the different macroalgae were present. The genera *Dictyota*, *Laurencia*, *Spyridia* and *Ulva* were reported for all the study years. Red algae showed greater association with dinoflagellates compared to green and brown algae. Abbreviations: Chl—Chlorophyta, Ph—Phaeophyceae, Rh—Rhodophyta.

4. Discussion

Regarding the data on sea surface temperature in the months of sampling (Figure 2), the temperature conditions were similar in June 2016 and 2018 and also in May 2015 and December 2019.

4.1. Dinoflagellate-Macroalgae Associations

During the study period, species of red algae as substrates were more than twice those of brown and green algae (Table 1), unlike in the shallow coastal zone of the southern Gulf of Mexico, where green algae and seagrasses are the most common substrate for epiphytic dinoflagellates [44–47]. In general, for the macroalgal flora of Bahía de La Paz, a similar prevalence of the red algae over brown and green algae was found [14].

In 2016, *Blixaea*, *Cabra*, *Plagiodinium*, *Ostreopsis* and *Gambierdiscus* were the genera that showed specific associations in the mutualistic spectrum, while in 2019 they were *Duriskia*, *Fukuyoa*, *Gambierdiscus*, *Ostreopsis*, *Prorocentrum* and *Sinophysis*. In 2015, the brown algae *Sargassum* sp., *Padina* sp. and *Dictyota* sp. were the preferred hosts for species of *Plagiodinium*, *Ostreopsis* and *Bysmatrum*. In 2018, no significant associations in comparison to other years were revealed. Therefore, epiphytic dinoflagellates in Bahía de La Paz did not show preferences for any specific macroalgae, and at the 95% confidence level they demonstrated generalist behavior (Figure 12B).

The preference of epiphytic dinoflagellates (individual species or the entire dinoflagellate taxocoenoses) for macrophyte substrate has been previously discussed in the literature; however, more studies are necessary. Some publications are dedicated to only one or two seagrass host species [44,45]. Others investigated individual dinoflagellate species, with a special emphasis on the CFP-causative species of the genus *Gambierdiscus* [46–50].

Apart from *Gambierdiscus*, *Ostreopsis* and *Coolia* are another two genera that have served as subjects of numerous studies in tropical and subtropical waters [7,50]; also see references in these reviews. Among toxigenic genera, *Amphidinium* has remained the least studied, morphologically, taxonomically and ecologically.

Various authors investigated epiphytic dinoflagellates in a range of macrophytes, most of which were macroalgal assemblages/taxocoenoses [51–71]. Conclusions of the authors who worked in different geographical regions differ as the species composition of macrophytes does. In some publications, an emphasis is put on the preference of macroalgal substrate in terms of major taxonomic groups (red, brown or green algae) or the preference between macroalgae and seagrass. Other authors study only one or several host or epiphytic species and compare the dinoflagellate cell abundances in different parts of the leaves (seagrasses) or thalli (macroalgae). Some investigations compare cell abundance between different morpho-functional types of macroalgae, considering the weight to surface area ratio. Rare studies are focused on the allelopathic effect of macroalgal extracts on epiphytic dinoflagellates or, in general, on allelopathic interactions between a macrophyte and dinoflagellates. Finally, sampling procedures and protocols of cell counting also affect the reliability of the results obtained. Selection between a natural or an artificial substrate to study cell abundances and preferences for substrate has also been under discussion (for references, see [45,71]).

4.2. Potentially Toxic Dinoflagellates

Although in the present study a number of species were not identified to the species level and toxicological analyses were not performed, the following taxa can be listed as potentially toxic: *Gambierdiscus* cf. *toxicus*, *Gambierdiscus* sp., *Fukuyoa paulensis* (ciguatoxins and maitotoxins); the *Prorocentrum lima* complex spp., the *P. hoffmannianum* complex spp., *P. concavum* (okadaic acid, diarrhetic shellfish toxins–dinophysistoxins and their analogs and others); *Ostreopsis* cf. *ovata*, *O.* cf. *lenticularis*, *O.* cf. *heptagona* (palytoxin, palytoxin-like compounds and ovatoxins); *Coolia* cf. *malayensis* (cooliatoxin, gambierone and yessotoxin analogs) and *Amphidinium* cf. *carterae* (species of this genus produce different cytotoxic, antibacterial and antifungal compounds). The toxins produced by these genera pose a major threat to marine ecosystems and human health [72]. The most recent reviews of benthic dinoflagellate toxins, including numerous references, can be found in [7,72,73].

The differences in the species composition of benthic dinoflagellates between the sampling sites, as well as between years, did not show significant changes. This may be due to fact that the samples were not always taken in the same months. Similarly, the taxocoenosis that was observed in this study, not only at the generic level but also at the species level, is comparable to that in studies performed in other regions.

4.3. Areas with the Highest Potential Toxic Impact

Macroalgae are exposed to tidal action, wind and upwelling events. These conditions can cause the algae to break free from their substrate and be released to the water column. Similarly, epiphytic dinoflagellates can detach from macroalgae and cause blooms. Some of the dinoflagellate species reported in this study, such as *Amphidinium* cf. *carterae*, *Blixaea quinquecornis*, *Prorocentrum lima* and *P. rhathymum* [22,23], have caused blooms in coastal areas in Bahía de La Paz. The occurrence of blooms in the bay could represent a risk for aquaculture (shrimp farming and the fattening of tuna in captivity), touristic activities and human health.

In comparison to other studies, herein, benthic dinoflagellate abundances were expressed as cells per gram of the macroalgal wet weight. The abundance values of potentially toxic dinoflagellates found in our study are moderate (Figures 7 and 10B), and they do not

develop as a bloom according to the data reported from elsewhere, e.g., 1.7×10^6 cells/g of *Ostreopsis ovata* in the northern Adriatic Sea [74]. However, the possibility of the occurrence of a potential bloom of some of the aforementioned toxic species should not be excluded. Usually, benthic dinoflagellate blooms in the Bahía de La Paz have occurred during the upwelling season [22,23].

Although the abundances of toxic benthic dinoflagellates in Bahía de La Paz were not so high, the possibility exists of a feasible benthic bloom occurring. This fact could have a significant impact on marine fauna as well as on human health, as has happened in other parts of the bay. Among all sampling sites, Playa El Tecolote can be considered a locality of maximum risk for human health (Figure 1), probably due to the richest subaquatic vegetation (*Caulerpa* J.V. Lamour., *Codium* Stackhouse, *Halimeda* J.V. Lamour., *Dictyota* J.V. Lamour., *Padina* Adanson, *Sargassum* C. Agardh; *Acanthophora* J.V. Lamour., *Hypnea* J.V. Lamour., *Laurencia* J.V. Lamour., *Spyridia* Harvey, Corallinaceae gen. sp., etc.) inhabited by potentially toxigenic epiphytic dinoflagellates.

Playa Costa Baja, closest to the City of La Paz, a recreational zone with human activities and characterized by diverse macroalgae, had abundances of epiphytic dinoflagellates up to 1526 cells/g (*Padina*) and 2139 cells/g (*Codium*), with *Prorocentrum lima* as the dominant species (55.6–57.9%), followed by *Coolia* cf. *malayensis* (up to 25.7% of the dominance).

Both localities are popular sites for human recreational activities. Therefore, these are preferential zones for establishing a regular all-year round monitoring of the CFP-causative (*Gambierdiscus* and *Fukuyoa*) and other toxigenic species (*Amphidinium*, *Coolia*, *Ostreopsis* and *Prorocentrum*) that can impact human health or diverse invertebrate and vertebrate marine fauna. Other recreational beaches, such as Balandra, also have the potential for CFP, although low to moderate abundances of *Coolia*, *Ostreopsis* and *Gambierdiscus* species were detected there.

5. Conclusions

The same level of cell abundances in May–June and December can be explained by similar seasonal characteristics (warm and dry), particularly the moderate water temperature and low precipitation. Little variation in both water temperature and salinity during the studied period was possibly one of the reasons why a great similarity was observed between the benthic dinoflagellate taxocoenoses of the sampling sites. High dinoflagellate abundance in Playa El Tecolote in December 2019 was one of the most unexpected findings. Toxigenic genera, such as *Gambierdiscus*, *Ostreopsis*, *Coolia* and *Prorocentrum*, are widespread throughout the study area. Playa El Tecolote and Playa Costa Baja can be considered the localities of maximum risk for human health, probably due to the richest subaquatic vegetation as a habitat for epiphytic toxigenic dinoflagellates tending to prefer red and brown algae growing on a range of substrates (sand, rocks and dead corals).

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Conflicts of Interest: The authors declare no conflicts of interest.

Abbreviations

The following abbreviations are used in this manuscript:

HABs	harmful algal blooms
CFP	ciguatera fish poisoning
BHABs	benthic harmful algal blooms
DSP	diarrhetic shellfish poisoning
HPLC	high-performance liquid chromatography
Ifremer	Institut Français de Recherche pour l'Exploitation de la Mer
WWS	wet weight substrate
FESEM	field emission scanning electron microscope
PERMANOVA	permutational multivariate analysis of variance
NMDS	non-metric multidimensional scaling
ANOSIM	analysis of similarities
SIMPER	similarity percentage analysis
UpSetR	a package for visualization of set intersections
CINVESTAV-IPN	Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional
FOMIX	Fondos Mixtos
CONACyT	Consejo Nacional de Ciencia y Tecnología (Mexico)
COFAA	Comisión de Operación y Fomento de Actividades Académicas del IPN

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