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Oceanography of Harmful Algal Blooms on the Ecuadorian Coast (1997–2017): Integrating Remote Sensing and Biological Data

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Ocean climate drivers and phytoplankton life strategies interact in a complex dynamic to produce harmful algal blooms (HABs). This study aims to integrate historical biological data collected during "red tide" events along the Ecuadorian coast between 1997 and 2017 in relation to five ocean variables derived from satellite remote sensing data to explain the seasonal drivers of coastal processes associated with HABs dynamics. Seasonality of the occurrence of HABs was assessed in relation to oceanographic variables by applying multiple correspondence analysis (MCA) to the Ecuadorian central coast (Zone 1) and at the outer and inner Gulf of Guayaquil (Zone 2). Sixty-seven HABs events were registered between 1997 and 2017. From a total of 40 species of phytoplankton identified, 28 were identified as non-toxic and the remaining 12 are well known to produce toxins. Dinoflagellates were the taxonomic group most highly associated with potential HABs events along the entire Ecuadorian coast. HABs appear to be constrained by the Humboldt coastal upwelling, high precipitation, and associated coastal runoff, with higher biomass abundance in the Gulf of Guayaquil than in the central coast. Results from the MCA reveal that in the central Ecuadorian coast (oligotrophic system), toxic HABs occurred with low abundance of dinoflagellates, while in the Gulf of Guayaquil (eutrophic system), toxic HABs corresponded to a high abundance of dinoflagellates. In both cases, high values were found for sea surface temperature, precipitation, and irradiance—characteristic of wet seasons or El Niño years. Non-toxic HABs occurred with a high abundance of dinoflagellates, ciliates, and centric diatoms, corresponding to colder waters and low levels of precipitation and irradiance. These findings confirm that dinoflagellates display several strategies that enhance their productive capacity when ocean conditions are warmer, allowing them to produce toxins at high or at low concentrations. Considering that the Gulf of Guayaquil is essential to tourism, the shrimp industry, fisheries, and international shipping, these findings strongly suggest the need to establish an ecosystem health research program to monitor HABs and the development of a preventive policy for tourism and public health in Ecuador.

Keywords: remote sensing, phytoplankton taxonomic groups (PTG), Gulf of Guayaquil, dinoflagellates, upwelling, Humboldt Current

INTRODUCTION

For decades, global coastal waters have experienced events known as "red tides" that are related to phytoplankton blooms, micro-algal blooms, and toxic algal or potentially harmful algal blooms (HABs) (Hallegraeff, 1993; Anderson, 2014; Anderson et al., 2017). Blooms are described as occurrences of a high biomass of plankton and benthic species, while HABs have been broadly classified as potent natural toxin producers created either by attaining high biomass levels or even through low numbers of toxic species. HABs may take place when a group of microalgae—photosynthetic cells found in the sea, brackish water, and freshwater—grow to very high numbers, producing toxic or harmful effects on shellfish, fish, marine mammals, birds, and humans (Hallegraeff, 1993; Zingone and Enevoldsen, 2002; Fleming et al., 2006; Jiménez and Gualancañay, 2006; Pitcher et al., 2017).

High-density algal blooms may cause anoxia to marine life, killing it and blocking sunlight on the surface of the water column. However, international research on HABs has recognized that some species have toxic effects even at low cells densities (Reguera et al., 2012; Anderson, 2014). The reasons why an algal bloom becomes toxigenic, either at high or low concentrations, is still not well understood. However, oceanographic and climatic conditions play an important role in HAB occurrence, which may be constrained by upwelling systems and stratification of the water column provoked by low wind stress and marine heat waves (Hallegraeff, 2010; Díaz et al., 2013; Pitcher et al., 2017). HABs may also be exacerbated by climatic variability, extreme events, like El Niño–Southern Oscillation (ENSO) (Sellner et al., 2003), and climate change due to a long-term increase in sea surface temperatures (Wells et al., 2015; Miller et al., 2006; Pitcher et al., 2017). In addition, anthropogenic nutrient loading from agricultural and urban watersheds, ballast water discharges from vessels, and nutrients released from mariculture activities, among others, are factors that drive HABs in coastal waters (Moore et al., 2008; Hallegraeff, 2010; Davidson et al., 2014; Berdalet et al., 2016).

Currently, the development of ocean remote sensing-derived data makes possible the exploration of the synoptic climatology of regions, biogeography of the primary productivity and HABs biomass, spring bloom growth, and even the identification of species at a good scale of resolution in space and time (McClain et al., 2004; Nair et al., 2008; Wei et al., 2008; McKibben et al., 2015). Thus, HAB dynamics can be explained by using *in situ* biological data and remote sensing observations of oceanographic variables (Moisan et al., 2011; Anderson, 2014; Blondeau-Patissier et al., 2014).

South America's Ecuadorian coast of the eastern tropical Pacific can be characterized by two biogeographical regions: the northern coast, influenced by the warm Panama Current, and the Gulf of Guayaquil, influenced by the Humboldt Current (Cucalon, 1989; Longhurst, 2006). Both regions are heavily affected by ENSO (Lee et al., 2014) and the eastern upwelling system, and these oceanographic structures can modify the ocean biogeochemistry periodically. All these oceanographic characteristics may trigger the occurrence of HABs along the Ecuadorian coast (Chavez et al., 2003; Pennington et al., 2006; Trainer et al., 2010). Following the global trend, the coast of Ecuador has experienced the occurrence of "red tides" for decades. Ecuadorian researchers have recorded approximately 132 events since 1968, resulting in reports of fish, juvenile shrimp, and shrimp larvae mortality (Torres, 2000, 2011, 2013, 2015, 2017; Torres and Tapia, 2002). Sixty-seven HABs events were registered between 1997 and 2017.

Despite their negative impacts on coastal activities, attempts to explain the oceanographic and climate drivers for the potential development of HABs are limited (Jiménez and Intriago, 2001; Jiménez and Gualancañay, 2006; Torres et al., 2017; Conde and Prado, 2018; Conde et al., 2018). Unfortunately, at this time there is no official HAB monitoring program for Ecuador that can analyze which toxins are generated by the phytoplankton species. Using a novel approach, this study intends to integrate ocean features, derived from synoptic remote sensing, and biological data, compiled from reports collected during "red tide" events, to identify which oceanographic conditions lead to the distribution and seasonal occurrence of HABs on the coast of Ecuador.

MATERIALS AND METHODS

Study Area

The study area is situated along the center and south of the Ecuadorian coast (South America) and was divided into two zones (**Figure 1**): Zone 1, corresponding to the area situated between the coastal localities of Manta (80.8°W, 0.8°S) and La Libertad (81°W, 2°S); and Zone 2, which includes the coastal area of the Gulf of Guayaquil (outer estuary) and the Guayas River estuary (inner estuary). The Guayas River estuary is connected to the El Morro and Jambelí channels and is comprised of two main bodies of water: Estero Salado and

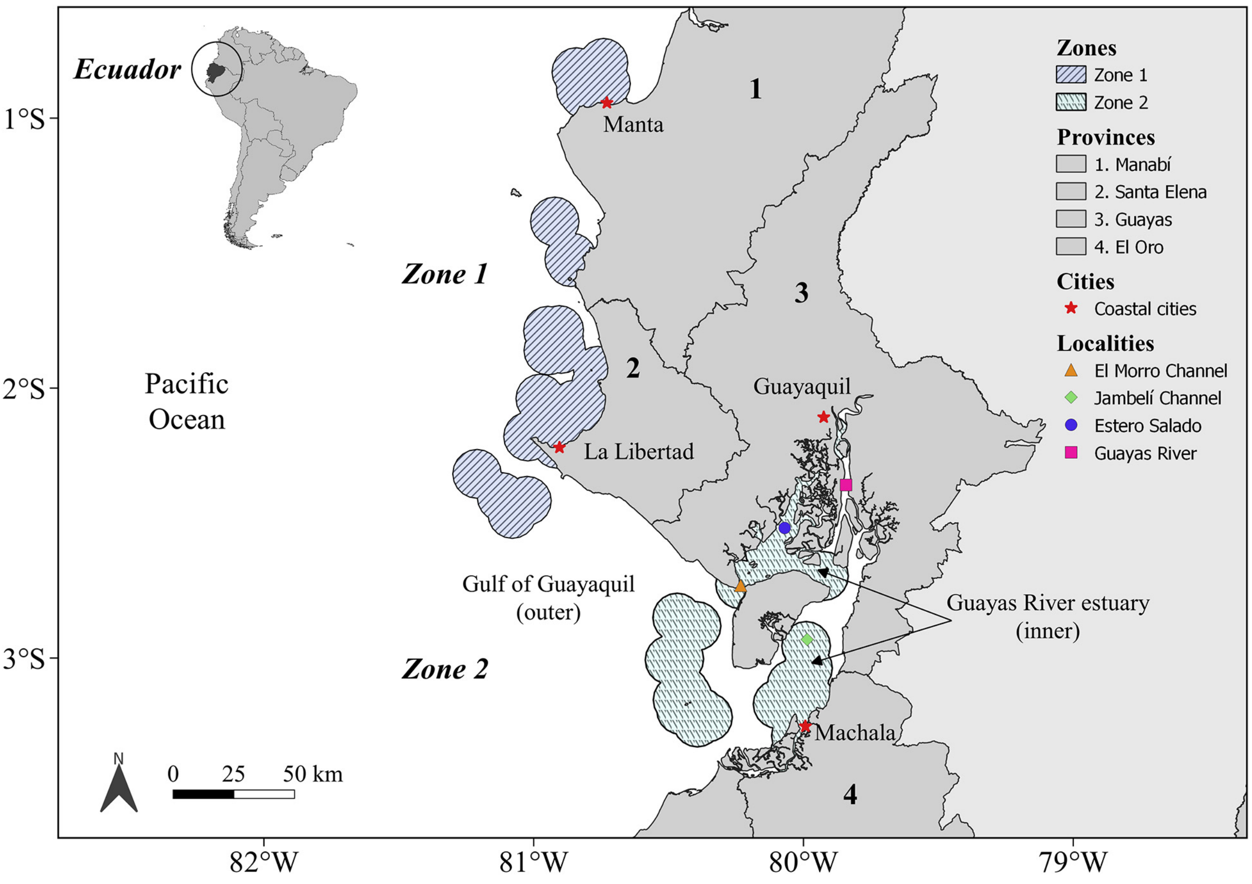

FIGURE 1 | Study area. Zone 1 is situated between the coastal cities of Manta and La Libertad; Zone 2 is located around the outer and inner (Estero Salado and Jambelí Channel) Gulf of Guayaquil estuary.

the Guayas River (**Figure 1**). Zone 1 is characterized mostly by sandy beaches used for tourism, and it is the location of important international cargo ports and fishery activities. Zone 2 includes the largest estuarine system on the South America coast adjacent to the Pacific Ocean and is where the cities of Guayaquil and Machala are located (**Figure 1**). The main economic activities carried out in Zone 2 are connected to shrimp farming, international cargo ports, and artisanal fisheries. Climate seasonality of the Ecuadorian coast is characterized by a wet season (December–May), with a unimodal peak of warm temperatures (March–April), and a dry season (June–November) characterized by the absence of rainfall and lower temperatures than those experienced during the wet season (Cucalon, 1989; Bendix et al., 2011).

Oceanographic and Atmospheric Data

Monthly averages of five variables recorded over the 1997–2017 period were derived from different satellite data compiled at ∼4 km of spatial resolution around Zones 1 and 2 on the Ecuadorian coast. Precipitation (PRE) was chosen as an atmospheric variable associated with climate seasonality (Nair et al., 2008; Shen et al., 2012) and therefore used as a proxy for seasonal atmospheric processes. In addition, seasonality of the region is strongly related to precipitation, which is also disturbed by the occurrence of El Niño and La Niña events in the equatorial eastern tropical Pacific (Pennington et al., 2006). The other four variables were oceanographic, representing select conditions of the ocean at specific times and places. Sea surface temperature (SST) is related to cold nutrient-rich currents and upwelling or with nutrient-poor warm currents (Pennington et al., 2006; Wei et al., 2008; Mélin and Hoepffner, 2011). Chlorophyll *a* (chl-a) was used as a proxy for phytoplankton abundance. Absorption due to phytoplankton at 443 nm (aph) represents the band of chlorophyll associated with the HABs peaks (Shen et al., 2012). Photosynthetically active radiation (PAR) was chosen as an indicator of the amount of light available for photosynthesis (Shi et al., 2014). Previously, SST and PRE have been related to the oceanographic and atmospheric processes of HABs, respectively (Wei et al., 2008). Satellite images were collected in NetCDF format and converted to GeoTiff files for the analyses using R software (version 3.5.0). Several satellites and sensors were used throughout the period of analysis (**Table 1**). Each variable was standardized with the respective global mean and standard deviation.

TABLE 1 | Description of oceanographic (SST, aph, chl-a, PAR) and atmospheric (PRE) variables from remote sensors.

Data (units)	Abbreviation	Satellite (sensor)	Temporal range	Source
Sea surface temperature (°C)	SST	Pathfinder	Monthly mean from September 1997 to December 2000	Casey et al., 2010
		GOES	Monthly mean from January 2001 to December 2016	NOAA NESDIS COASTWATCH and NOAA SWFSC ERD, 2018
Absorption due to phytoplankton at 443 nm (m^{-1})	aph	SeaWiFS	Monthly mean from September 1997 to January 2000	NASA Ocean Biology Processing Group, 2018c
		Terra MODIS	February 2000–December 2016	NASA Ocean Biology Processing Group, 2018a
Precipitation (mm)	PRE	Persiann	January 1997–August 2016	Sorooshian et al., 2014
Chlorophyll a (mg/m^3)	chl-a	Orbview-2 SeaWiFS	September 1997–December 2002	NASA Ocean Biology Processing Group, 2018d
		Aqua MODIS	January 2003–December 2016	NASA Ocean Biology Processing Group, 2017
Photosynthetically active radiation (Einstein/m^2/day)	PAR	SeaWiFS	September 1997–January 2000	NASA Ocean Biology Processing Group, 2018e
		Terra MODIS	February 2000–December 2016	NASA Ocean Biology Processing Group, 2018b

Phytoplankton Data

Phytoplankton data were compiled from 67 algal bloom events reported from 1997 to 2017 in the literature generated by the Ecuadorian Navy Army Oceanographic Institute (INOCAR), the National Institute of Fisheries, and reports from shrimp hatchery producers. Most of these data are included in the periodical research publications of INOCAR[1]. According to these reports, samples were collected from the sea surface. Data included taxa identification, abundance, location, and an observational description. This study also includes 8 unpublished reports from INOCAR and other researchers, increasing the original number of 59 registered events to 67 events in total. More detailed information on each event can be found in the publications and reports referenced in **Table 2**.

Some phytoplankton names have been updated according to the records in the World Register of Marine Species (WoRMS[2]). For the biological analysis performed in INOCAR, samples (a minimal volume of 250 mL of surface water) were collected from the "red tide" events and immediately transported to INOCAR's laboratories. All surface samples were fixed with Lugol solution until they changed to a light brown color (8–10 drops). The quantitative analysis was carried out using the Utermohl method described in Reguera et al. (2012) and adapted by Torres (2017). Samples were briefly homogenized and placed in a sedimentation chamber (25 mL) for 24 h.

Phytoplankton identification and abundance was assembled up to the genus or species level according to Jiménez (1983); Pesantes (1983), Balech (1988); Taylor et al. (1995), and Reguera et al. (2012) using a Leica (DMIL) inverted microscope. Cell abundance estimations were performed in horizontal transects of the chamber at 400× magnification, with a 15% error margin. Data were converted into cells L^{-1}. These data were further assembled in four phytoplankton taxonomic groups (PTG): dinoflagellates (DINO), centric diatoms (CDIAT), pennate diatoms (PDIAT), and ciliates (CILI), based on the GEOHAB criterion (WoRMS[3]; Pitcher et al., 2017). The species were categorized as toxic (TOX) or non-toxic (NOC) using the List of Harmful Microalgae (Moestrup et al., 2009).

Data Analysis

Each of four phytoplankton taxonomic groups, as well as the five remote sensing variables, were transformed into categorical variables (two categories: low and high) using the median as a cut-off. In addition, two categorical variables were also included: type of HAB event and season (identifying whether the event occurred during the wet or dry season) (Vila and Masó, 2005). All categorical variables were used for multi-correspondence analysis (MCA) for Zones 1 and 2. This analysis allowed for an investigation of the PTG patterns associated with the oceanographic and atmospheric variables in each zone.

RESULTS

Oceanographic Characteristics Associated With Potential HABs Using Remote Sensing Data

In Zone 1, chlorophyll *a* showed a unimodal peak at the end of the wet season, in April–May (∼1.5 mg m^{-3}), whereas a peak in April (∼5.0 mg m^{-3}) and a lower sustained value (3.0 mg m^{-3}) in September, during the dry season, were observed in Zone 2 (**Figures 2A,B**). The levels of chlorophyll *a* were higher in Zone 2 (2.5–5.0 mg m^{-3}) when compared to Zone 1 (0.5–1.5 mg m^{-3}).

A similar pattern was observed in the sea surface temperature (SST) monthly average in both zones, with a peak of 25–26°C in February, during the wet season, and lower values of 22.5–23°C in September (**Figures 2C,D**). Absorption due to phytoplankton at 443 nm (aph) showed a unimodal pattern, with high values in Zone 1 (peak in April; 0.05 m^{-1}) and the highest value in Zone 2 (April–May; 0.15 m^{-1}) (**Figures 2E,F**). Photosynthetically active radiation (PAR) presented a bimodal pattern in both zones. Zone 1 saw a maximum value in April (48 Einstein m^{-2} day^{-1}) and a lower peak in September (30 Einstein m^{-2} day^{-1}). In

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[1] http://www.inocar.mil.ec

[2] http://www.marinespecies.org/

[3] http://www.marinespecies.org/

TABLE 2 | List of potentially harmful algal blooms (HABs) recorded in events along the coast of Ecuador (1997–2017).

Species	PTG	Type	ZONE 1		ZONE 2				References for toxicity	References for HABs recurrences in Ecuador
			Wet season		Dry season		Wet season			
			N	Max log cells L^{-1}	*N*	Max log cells L^{-1}	*N*	Max log cells L^{-1}		
Diarrhetic Shellfish Poisoning (DSP)										
Dinophysis caudata (Saville-Kent, 1881)	DINO	TOX	1		1				Ignatiades and Gotsis-Skretas, 2010; Nagai et al., 2011; Anderson et al., 2017	Torres, 2000, 2006, 2011
Dinophysis spp. (Ehrenberg, 1839)	DINO	TOX	1						Yasumoto et al., 1985; Hallegraeff, 1993; Lloyd et al., 2013; Reguera et al., 2014	Torres, 2011
Gonyaulax spp. (Diesing, 1866)	DINO	TOX			1				Wang, 2008	Torres and Palacios, 2007a
Prorocentrum mexicanum (Osorio-Tafall, 1942)	DINO	TOX	1	3.37			1		Ignatiades and Gotsis-Skretas, 2010; Muciño-Márquez et al., 2015	Coello, 2010; Torres, unpublished data (u.d)
Prorocentrum micans (Ehrenberg, 1834)	DINO	TOX	1	3.37	2		1		Razali et al., 2015; Lee et al., 2016	Torres, 2000, u.d; Torres and Tapia, 2002; Torres and Palacios, 2007b
Diarrhetic Shellfish Poisoning (DSP) and Venerupin Shellfish Poisoning										
Prorocentrum cordatum (Ostenfeld) (Dodge, 1975)	DINO	TOX			1		3		Heil et al., 2005; Lundholm, 2011	Torres et al., 2004; Torres and Palacios, 2007b; Torres, 2011
Paralytic Shellfish Poisoning (PSP)										
Alexandrium spp. (Halim, 1960)	DINO	TOX			1				Wang, 2008; Anderson et al., 1990, 2017; Food and Agriculture Organization [FAO], 2004; Ignatiades and Gotsis-Skretas, 2010	Torres and Palacios, 2007a
Gymnodinium catenatum (Graham, 1943)	DINO	TOX	1		3	6.05	1		Ignatiades and Gotsis-Skretas, 2010	Jiménez and Intriago, 2001; Torres and Palacios, 2007a; Torres, u.d.
Gymnodinium spp. (Stein, 1878)	DINO	TOX	4	5.22	6	7.05	6	7.45	Wang, 2008	Torres, 2000, 2006, 2011, u.d.; Torres and Palacios, 2007a,b
Amnesic Shellfish Poisoning (ASP)										
Pseudo-nitzschia spp. (Peragallo and Peragallo, 1900)	DINO	TOX			1	6.68			Rhodes et al., 1998; Trainer et al., 2012; Anderson et al., 2017	Torres, 2006, 2011
Neurologic or Neurotoxic Shellfish Poisoning (NSP)										
Gonyaulax spinifera (Claparède and Lachmann) (Diesing, 1866)	DINO	TOX			1				Wang, 2008; Alexander et al., 2009; Anderson et al., 2017	Torres and Palacios, 2007a
Karenia brevis (C. C. Davis) (Daugbjerg et al., 2000)	DINO	TOX					4	7.72	Food and Agriculture Organization [FAO], 2004; Pierce and Henry, 2008; Corcoran et al., 2014	Torres et al., 2004

(Continued)

TABLE 2 | Continued

Species	PTG	Type	ZONE 1		ZONE 2				References for toxicity	References for HABs recurrences in Ecuador
			Wet season		Dry season		Wet season			
			N	Max log cells L^{-1}	*N*	Max log cells L^{-1}	*N*	Max log cells L^{-1}		
Potentially Ichthyotoxic Species										
Gyrodinium spp. (Kofoid and Swezy, 1921)	DINO	NOC	2	4.45	3		2	7.75	Alonso-Rodríguez and Páez-Osuna, 2003; Ignatiades and Gotsis-Skretas, 2010	Torres, 2000, 2011, u.d.; Torres et al., 2004; Torres and Palacios, 2007b
Margalefidinium catenatum (Okamura, 1916; Gómez et al., 2017)	DINO	NOC	2	6.94	1		1		Cortés et al., 2004; Matsuoka et al., 2008; Kudela and Gobler, 2012; Gómez et al., 2017	Torres et al., 2004; Torres, 2011, 2016, u.d.
Potentially Fish-killing and Bloom-forming Species										
Mesodinium rubrum (Lohmann, 1908)	CILI	NOC	9	6.69	4	7.06			Jiménez and Intriago, 2001; Cortés-Lara, 2002; Gárate-Lizárraga et al., 2002; Wang et al., 2008; Torres, 2011	Torres, 2000, 2006, 2011; Jiménez and Intriago, 2001; Coello, 2003; Jiménez and Gualancañay, 2006; Coello and Cajas, 2007
Coscinodiscus spp. (Ehrenberg, 1839)	CDIAT	NOC			1	5.20	1	4.30	Mathew et al., 1988; Torres, 2011	Torres and Palacios, 2007b; Coello et al., 2010
Skeletonema costatum (Greville) (Cleve, 1873)	CDIAT	NOC	1	6.10	1	5.88	4	6.14	Hallegraeff, 1993; Suaréz and Guzmán, 1994; Chen et al., 2007; Anderson et al., 2017	Torres et al., 2004; Torres and Palacios, 2007b; Coello et al., 2010; Torres, 2016
Akashiwo sanguinea (K. Hirasaka) (Daugbjerg et al., 2000)	DINO	NOC	1	7.15					Hallegraeff, 2004; White et al., 2014; Anderson et al., 2017	Coello, 2003; Torres et al., 2004; Torres, 2011
Ceratium tripos (O. F. Müller) (Nitzsch, 1817)	DINO	NOC	1						Suaréz and Guzmán, 1994; Hallegraeff, 2004; Torres et al., 2004; Torres, 2011	Torres, 2000
Cochlodinium spp. (Schütt, 1896)	DINO	NOC			2	6.72	1	6.64	Hallegraeff, 2004; Kudela and Gobler, 2012; Razali et al., 2015	Torres, 2000, 2011; Torres et al., 2004; Torres, 2011
Kryptoperidinium foliaceum (F. Stein) (Lindemann, 1924)	DINO	NOC					1	4.00	Kempton et al., 2002; Saburova et al., 2012; Merino-Virgilio et al., 2014	Jiménez and Gualancañay, 2006; Torres, 2011
Levanderina fissa (Levander) (Moestrup et al., 2014)	DINO	NOC	6	7.00					Alonso-Rodríguez and Páez-Osuna, 2003; Gárate-Lizárraga, 2014	Jiménez and Intriago, 2001; Jiménez and Gualancañay, 2006; Torres, 2011
Noctiluca scintillans (Macartney) (Kofoid and Swezy, 1921)	DINO	NOC	2	3.97	2	6.06	4	6.41	Thangaraja et al., 2007; Wang et al., 2008; Ibrahem and Al-Shawi, 2015; Razali et al., 2015	Torres, 2000, 2011, 2016, u.d.; Coello, 2003; Torres et al., 2004
Prorocentrum gracile (Schütt, 1895)	DINO	NOC	2						Gul and Saifullah, 2011; Muciño-Márquez et al., 2015; Anderson et al., 2017	Jiménez and Intriago, 2001; Torres et al., 2004
Tripos furca (Ehrenberg) (Gómez, 2013)	DINO	NOC	2		3				Edwards et al., 2006; Ibrahem and Al-Shawi, 2015; Razali et al., 2015; Yurimoto et al., 2015	Torres, 2000, 2006, 2011; Torres and Palacios, 2007a

(Continued)

TABLE 2 | Continued

Species	PTG	Type	ZONE 1		ZONE 2				References for toxicity	References for HABs recurrences in Ecuador
			Wet season		Dry season		Wet season			
			N	Max log cells L^{-1}	*N*	Max log cells L^{-1}	*N*	Max log cells L^{-1}		
Potentially Bloom-forming Species										
Chaetoceros affinis (Lauder, 1864)	CDIAT	NOC	1		1		1		Vyas et al., 1986; Konno et al., 2010; Razali et al., 2015; Anderson et al., 2017	Torres, 2000; Torres et al., 2004
Chaetoceros curvisetus (Cleve, 1889)	CDIAT	NOC	1		1				Shen et al., 2012; Begum et al., 2015; Lo et al., 2016	Torres, 2000
Chaetoceros levis (Schütt, 1896)	CDIAT	NOC	1						Razali et al., 2015	Torres, 2000
Thalassiosira spp. (Cleve, 1873; Hasle, 1973)	CDIAT	NOC	1	4.37	2	6.70	1	5.48	Hallegraeff, 2004; Torres, 2011; Anderson et al., 2017	Torres and Palacios, 2007a; Coello et al., 2010; Torres, 2011, u.d.
Navicula spp. (Blainville, 1825)	PDIAT	NOC					1	4.48	Alonso-Rodríguez and Páez-Osuna, 2003; Razali et al., 2015	Coello et al., 2010
Asterionella frauenfeldii (Grunow, 1863)	PDIAT	NOC			1		1		Perumal et al., 1999; Jugnu and Kripa, 2008; Naha et al., 2014	Torres, 2000; Torres et al., 2004
Nitzschia longissima (Brébisson) (Pritchard, 1861)	PDIAT	NOC					1		Merino-Virgilio et al., 2014; Razali et al., 2015; Anderson et al., 2017	Torres et al., 2004
Thalassionema nitzschioides (Grunow) (Mereschkowsky, 1902)	PDIAT	NOC					2	4.78	Perumal et al., 1999; Merino-Virgilio et al., 2014; Begum et al., 2015; Padmakumar et al., 2018	Torres et al., 2004; Coello et al., 2010
Ceratium spp. (Schrank, 1793)	DINO	NOC	1						Thangaraja et al., 2007; Gómez et al., 2008; Padmakumar et al., 2018	Jiménez and Gualancañay, 2006; Torres, 2011
Ceratium trichoceros (Ehrenberg) (Saville-Kent, 1881; Kofoid and Swezy, 1921)	DINO	NOC	1				1		Jiménez and Intriago, 2001; Thangaraja et al., 2007; Torres, 2011; Ibrahem and Al-Shawi, 2015	Jiménez and Intriago, 2001
Protoperidinium quarnerense (B. Schröder) (Balech, 1974)	DINO	NOC			1				Torres et al., 2004; Gómez et al., 2008	Torres, 2000
Pyrophacus steinii	DINO	NOC	2		1				Razali et al., 2015; Wall and Cicily, 2015	Torres, 2000, 2011, u.d.
Triadinium polyedricum (Schiller) (Wall and Dale, 1971)	DINO	NOC			1				Shin et al., 2016	Torres and Palacios, 2007a
Tripos macroceros (Ehrenberg) (Gómez, 2013)	DINO	NOC	2				1		Thangaraja et al., 2007; Torres, 2011; Ibrahem and Al-Shawi, 2015	Torres, 2000
Tripos dens (Ostenfeld and Johannes Schmidt) (Gómez, 2013)	DINO	NOC	1		3	6.54	1		Horner et al., 1997; Pitcher and Calder, 2000; Alonso-Rodríguez and Páez-Osuna, 2003; Torres, 2011	Torres and Palacios, 2007a; Torres, 2011

The table includes potentially toxic (TOX) and non-toxic (NOC) species. The toxic species for humans are represented through syndromes. The non-toxic species are: (i) Potentially ichthyotoxic species—this group causes physical damage or irritation of the gills, are toxigenic, and cause hypoxia from oxygen depletion. It is also capable of causing the massive death of fish. The causal mechanisms are uncertain and the studies carried out are inconclusive (Andersen, 2012); (ii) Potentially fish-killing species—this group differs from the previous one because the death of the fish is caused by the decrease of oxygen as a consequence of the bloom's great biomass; (iii) Potentially bloom-forming species. The species are classified in four phytoplankton taxonomic groups (PTG): dinoflagellates (DINO), centric diatoms (CDIAT), pennate diatoms, and ciliates (CILI). N, number of occurrences. Log C, maximum abundances in log10 (cells/L). The occurrences and concentrations are shown by dry and wet seasonality in the study areas (Zone 1 and Zone 2).

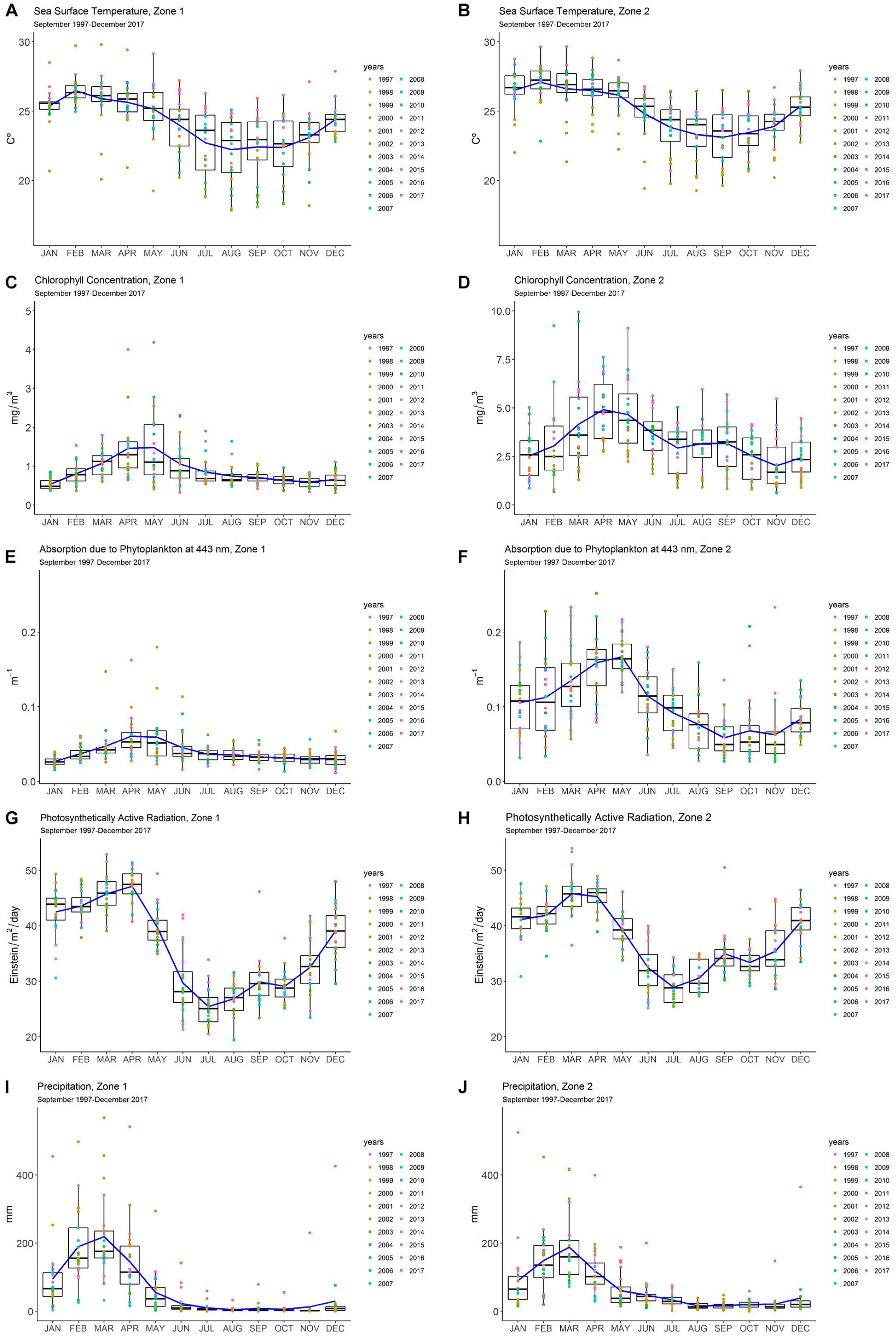

FIGURE 2 | Panel diagram of the monthly means of the remote sensing data of oceanographic variables: **(A,B)** sea surface temperature (SST); **(C,D)** chlorophyll *a* (chl-a); **(E,F)** absorption due to phytoplankton at 443 nm (aph); **(G,H)** photosynthetically active radiation (PAR) and atmospheric variable; **(I,J)** precipitation (PRE) for Zones 1 and 2 on the Ecuadorian coast (1997–2017). Seasonal pattern and inter-annual variability are shown with the blue line and the colored dots, respectively.

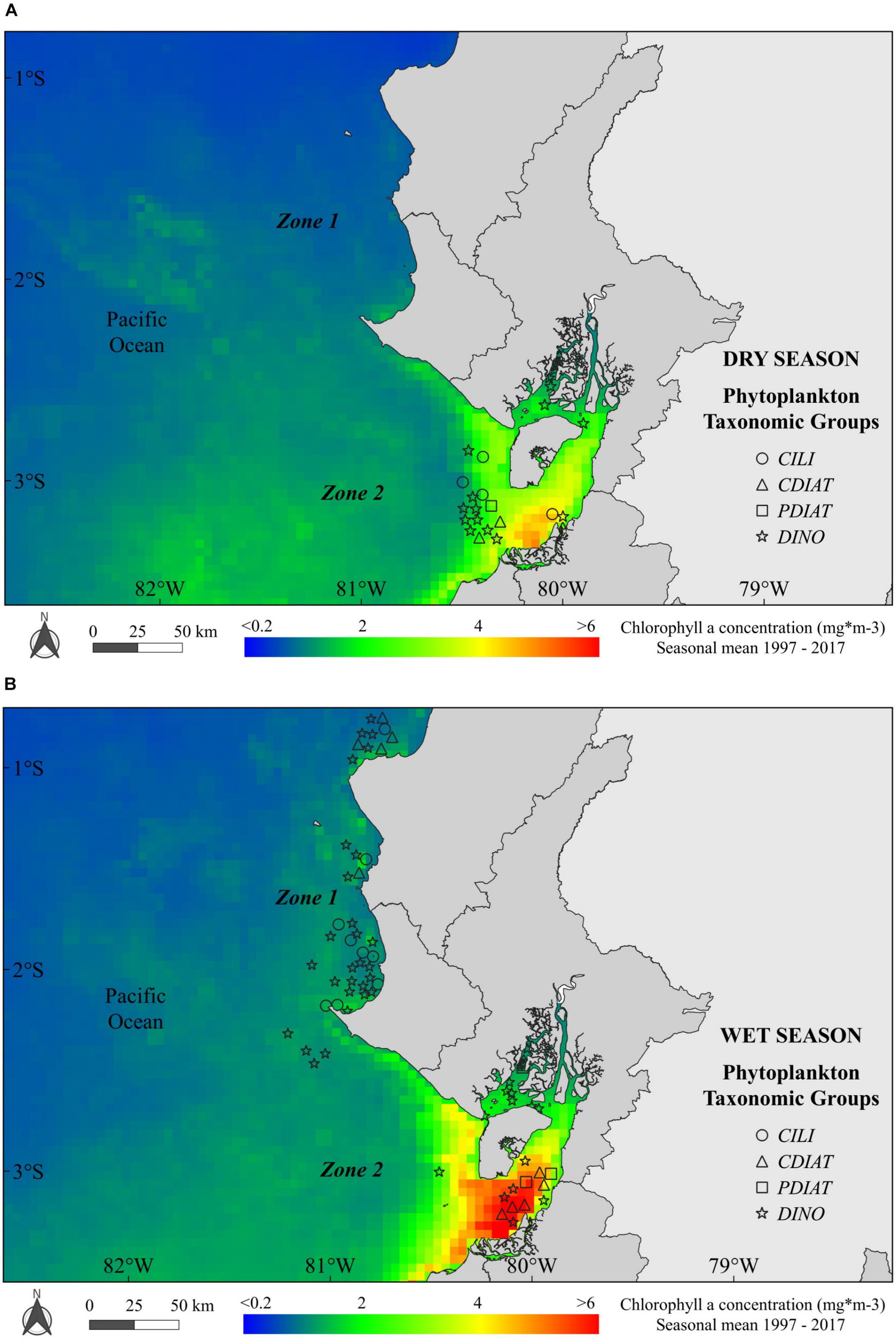

FIGURE 3 | Spatial distribution of occurrences of phytoplankton taxonomic groups (PTGs: ciliates, centric diatoms, pennate diatoms and dinoflagellates) along the Ecuadorian coast during **(A)** the dry season—occurrences of PTGs and **(B)** the wet season—occurrences of PTGs in Zones 1 and 2 of the study area. Background colors show the seasonal mean of chlorophyll *a* for the dry and wet seasons.

Zone 2, the maximum average value was registered in March (48 Einstein m^{-2} day^{-1}) and a second peak in September (32 Einstein m^{-2} day^{-1}) (**Figures 2G,H**). Precipitation showed a similar pattern for both zones, with an average peak in the wet season (March) both for Zone 1 (~200 mm) and Zone 2 (180 mm) (**Figures 2I,J**).

Distribution and Seasonality of HAB and Phytoplankton Taxonomic Groups

A detailed checklist of the four PTGs is presented in **Table 2** and includes 40 species, 67 HAB occurrences, maximum abundance levels according to category in log (log base 10) of cells L^{-1}, HAB category (NOC or TOX), season (dry and wet), and the respective toxicity and reporting references (See **Suplementary Tables S1, S2**).

Harmful algal blooms showed strong seasonal characteristics: (a) there were 46 registered occurrences of PTG in Zone 2 during the dry season (**Figure 3A**; there were no data for Zone 1; see section "Materials and Methods"); and b) 48 (Zone 1) and 40 (Zone 2) PTG occurrences during the wet season (**Figure 3B**). Regarding the spatial distribution during the dry season, the chl-a ranged from ~1–1.5 mg m^{-3} in Zone 1 (from Manta to La Libertad) to ~2–3 mg m^{-3} in Zone 2 at the Gulf of Guayaquil, and it varied along with the clusters of PTG (**Figure 3A**). On the other hand, during the wet season, most of the PTG were DINO, both in Zones 1 and 2. In particular, PTGs coincided with higher chl-a (3–5 mg m^{-3}) in Zone 2 at the Jambelí Channel (**Figure 3B**).

During the dry season, in Zone 2, DINO were the most common PTG (72% of occurrences), followed by CDIAT (13%), PDIAT (4%), and CILI (11%) (**Figure 4**). On the other hand, during the wet season, in both zones DINO reached ~70%, while CDIAT comprised only 10% in Zone 1 and 18% in Zone 2. PDIAT amounted to 13% in Zone 2 and 19% was CILI, but only in Zone 1 (**Figure 4**).

Regarding the abundance of PTG, dinoflagellates presented great variability in their abundance, ranging from 3.4 to 7.8 log of cells L^{-1} during both the dry and wet seasons, reaching a maximum in Zone 2 of the Gulf of Guayaquil. Centric diatoms were higher during the dry season (5.2–6.7 log of cells L^{-1}) than in the wet season (4.3–6 log of cells L^{-1}), reaching a maximum in Zone 2. Pennate diatoms were reported only 4 times in 20 years of data, with a maximum concentration of 6.7 log of cells L^{-1} (**Figure 5**).

Harmful Algal Bloom Species Assembled Along the Ecuadorian Coast

Harmful algal blooms reports from 1997 to 2017 determined a total of 40 species of phytoplankton: 28 were identified as non-toxic, whereas the other 12 are well known to produce toxins (**Table 2**). The most recurrent genera were *Gymnodinium* (21 occurrences) and *Prorocentrum* (10). Other observed genera

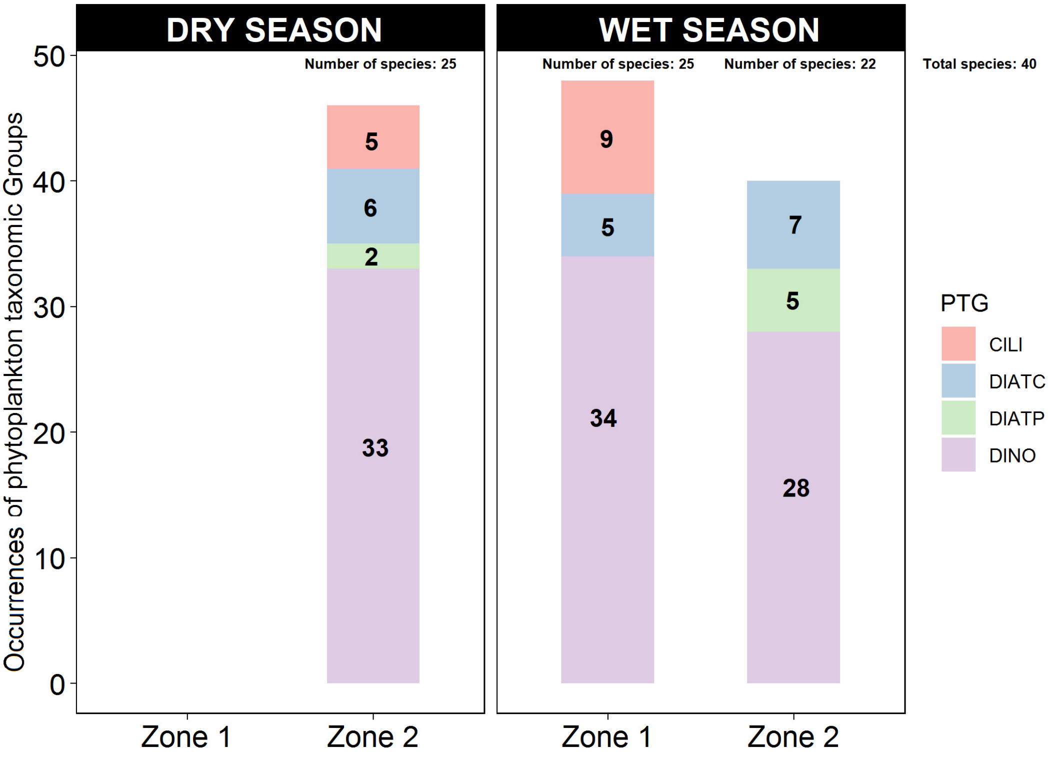

FIGURE 4 | Occurrences of phytoplankton taxonomic groups (PTGs) in Zones 1 and 2 of the study area during the dry and wet seasons. For the period 1997–2017, a total of 46 PTG occurrences with 25 species were reported in the dry season in Zone 2, 48 PTG occurrences with 25 species were reported in Zone 1, and 40 PTG occurrences and 22 species were reported in Zone 2 in the wet season.

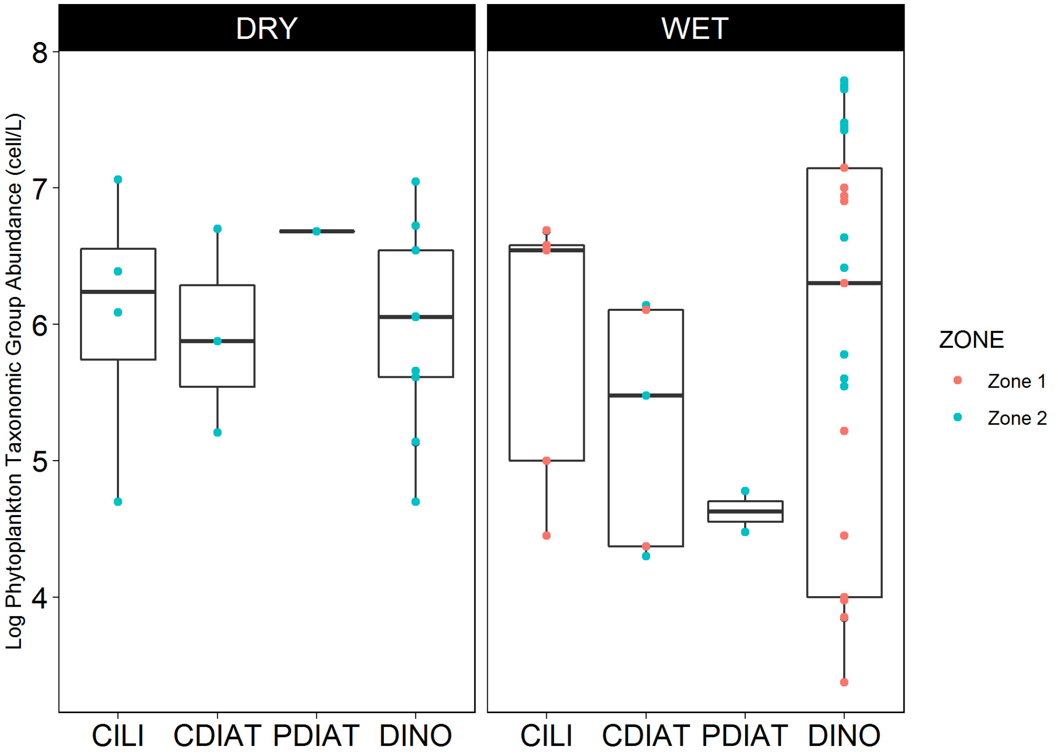

FIGURE 5 | Seasonal abundance of phytoplankton taxonomic groups during HABs events in Zones 1 and 2 of the study area.

were *Karenia* (4), *Dinophysis* (3), and *Pseudo-nitzschia* (1). *Gymnodinium catenatum* (5 occurrences) was observed in the years 2000, 2004, 2008, and 2014 in several locations in Zone 1 and in the Jambeli Channel in Zone 2, with a maximum abundance of 6.05 log of cells L^{-1}. *Prorocentrum cordatum* (4 occurrences) was observed in 2003 and 2004 in the Jambelí Channel and Estero Salado in Zone 2, but unfortunately without abundantly available data. *Prorocentrum mexicanum* (2 occurrences) with a maximum abundance of 3.4 log of cells L^{-1} in 2009 and 2016 was reported in Manta in Zone 1 and in Puerto Bolivar and the Jambelí Channel in Zone 2. *Prorocentrum micans* (4 occurrences), with a maximum abundance of 3.4 log of cells L^{-1}, was reported in Manta in Zone 1 and in Isla Santa Clara, Puerto Bolivar, in Zone 2. Microphotographs of Lugol-preserved colonies of *Gymnodinium catenatum* are shown in **Figures 6A,B**. This sample was found in San Pedro (Zone 1) in March 2018. A potentially harmful, non-toxic *Cochlodinium catenatum*, a synonym of *Margalefidinium catenatum*, is shown in **Figure 6C**. This sample was found in La Libertad in March 2018. However, the HAB-forming dinoflagellate *Cochlodinium catenatum* needs further samplings/taxonomic studies to ensure a precise identification.

Other groups of 28 species were categorized as non-toxic algal blooms in order of occurrence: 16 taxa of dinoflagellates, including *Noctiluca scintillans*, *Gyrodinium* spp., *Levanderina fissa*, *Tripos dens*, and *Tripos furca*, six centric diatoms, including *Skeletonema costatum*, *Thalassiosira* spp., and *Chaetoceros affinis*, four pennate diatoms, including *Asterionella frauenfeldii*, *Thalassionema nitzschioides*, *Nitzschia longissima*, and *Navicula* spp., and just one ciliate—*Mesodinium rubrum* (**Table 2**). The highest NOC species abundance was represented by *Gyrodinium* spp., attaining 7.75 log of cells L^{-1}, found in Estero Salado (Zone 2) during 1999's wet season. The highest abundance of *Mesodinium rubrum* was 7.06 log of cells L^{-1}, found in Jambeli Channel (Zone 2) during the 2007 dry season. A greater variability in abundance was observed during the wet season for most of the PTG.

Multi-Correspondence Analysis of PTG and Remote Sensing Data

In Zone 1 (**Figure 7**), the occurrence of toxic HABs corresponded to low abundances of DINO and CDIAT. These biological features seem to be associated with high values of SST, PRE, and PAR and to low chl-a and aph values (443 nm). All these environmental features characterized the wet season (**Figure 7**). Conversely, non-toxic HABs corresponded to a high abundance of DINO and CILI and to low SST and PRE, but with high aph (**Figure 7**).

During the wet season in Zone 2 (**Figure 8**), TOX events corresponded to high biomass levels of DINO, coupled with high SST, PAR, and PRE. However, during the dry season, low PRE and PAR and colder waters were linked to a high abundance of CDIAT. These features are simultaneously related to NOC species.

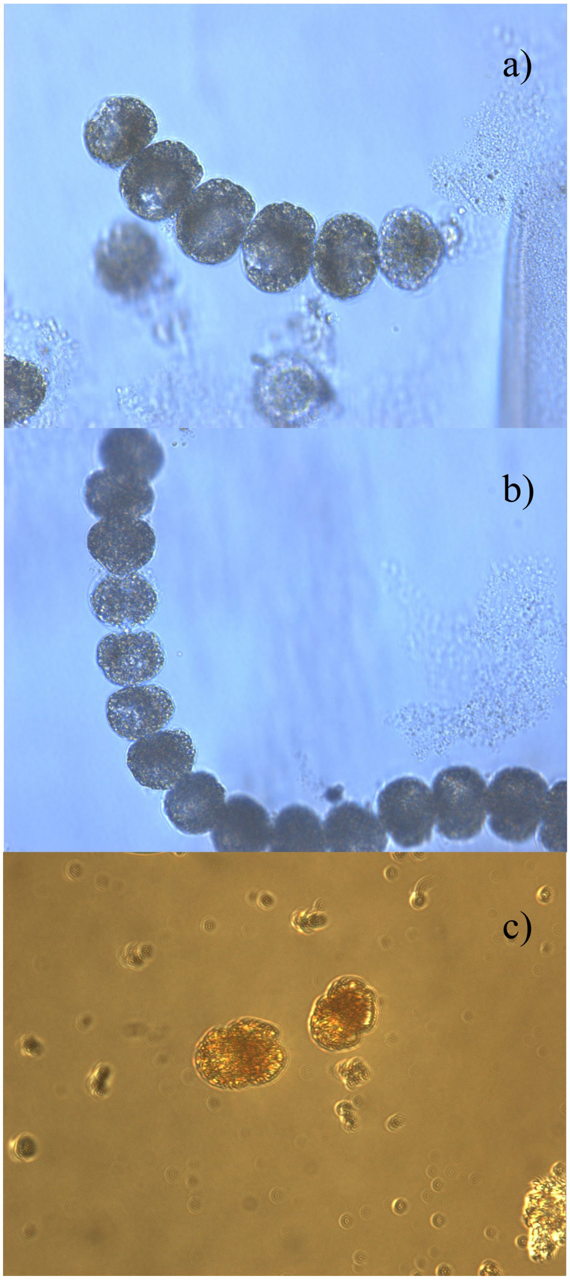

FIGURE 6 | Microphotographs of Lugol-preserved colonies associated with toxic or non-toxic species collected on the Ecuadorian coast: **(A,B)** *Gymnodinium catenatum* (Graham, 1943) found in San Pedro (Zone 1) in 2018. This taxon is associated with a paralytic toxin; **(C)** *Cochlodinium catenatum* (Schütt, 1896), found in La Libertad in Zone 1 in March 2018.

DISCUSSION

Oceanography of HABs and Remote Sensing Data

This study confirms that HAB dynamics in the Ecuadorian coastal zone seem to be constrained by the Humboldt upwelling system, high precipitation, and terrestrial nutrients from the Guayas Basin, aligning with other HAB studies in coastal ecosystems and upwelling zones (Kudela et al., 2005; Vila and Masó, 2005; Borbor-Cordova et al., 2006; Anderson et al., 2017; Conde et al., 2018; Oyarzún and Brierley, 2018). In addition, high sea surface temperature during ENSO and ocean heat waves seem to affect all the aforementioned drivers, along with the adaptive strategies of the phytoplankton species and their community assemblage (Masó and Garcés, 2006; Anderson, 2014; Anderson et al., 2017).

The findings of this study reveal that a higher biomass of HABs was found in Zone 2 than in Zone 1 when considering eutrophic and oligotrophic systems, respectively, based on chl-a concentration. Dinoflagellates were the taxonomic group most highly associated with HABs all along the Ecuadorian coast. An interesting finding is that toxic species of DINO appeared either at low or high levels of abundance in Zone 1 or Zone 2, respectively, mostly during the wet season.

These results agree with the findings presented in previous research, demonstrating that dinoflagellate species that form blooms utilize diverse ecological strategies as colonists and r-strategists in nutrient-rich, disturbed environments, or are nutrient stress tolerant in oligotrophic systems (Smayda and Reynolds, 2003; Smayda and Trainer, 2010). Dinoflagellates use a C-strategy (as colonists) to adapt, reaching high levels of biomass and becoming potentially toxic species in nutrient-enriched, high irradiance, estuarine habitats, such as that found in Zone 2. Whereas in the oligotrophic Zone 1, with its highly stratified and high irradiance conditions, a nutrient stress-tolerant ensemble of dinoflagellate species occurred at very low biomass levels (Smayda and Reynolds, 2003; Suparna, 2005; Smayda and Trainer, 2010; Corcoran et al., 2014). For instance, *Gymnodinium catenatum* and *Karenia brevis*, considered toxic species, were found at high levels of abundance in Zone 2, mostly in the wet season, while *Prorocentrum micans* and *Prorocentrum mexicanum* were reported at low concentrations in the oligotrophic Zone 1, but also in Zone 2, in the wet season.

Considering the bloom behavior of diatoms, previous research found that they occur in coastal and upwelling zones and are annually recurrent and prolonged in duration, with high species diversity (Smayda and Reynolds, 2003). In our work, annual periodicity and high diversity were not evident, with only 7–5 occurrences of CDIAT (6 species) and PDIAT (5 species), respectively, mostly in the Jambeli Channel in Zone 2. Non-toxic HABs occurred with high abundance values of DINO, CILI, and CDIAT and were mostly associated with the cold water from the upwelling system, low precipitation, and irradiance, both in Zones 1 and 2 in environmental conditions more related to the dry season. This work suggests that there is a higher risk of HABs in the Gulf of Guayaquil, at the entrance of the Guayas Estuary (dry season), in the Jambeli Channel and Estero Salado (wet season), and in La Libertad and Manta in the dry season (**Figures 2A,B**).

However, the question remains as to the biological drivers of the presence of potentially toxic or non-toxic HABs on the Ecuadorian coast (in the eastern Pacific Ocean). It is known that species-specific adaptive strategies within the phytoplankton

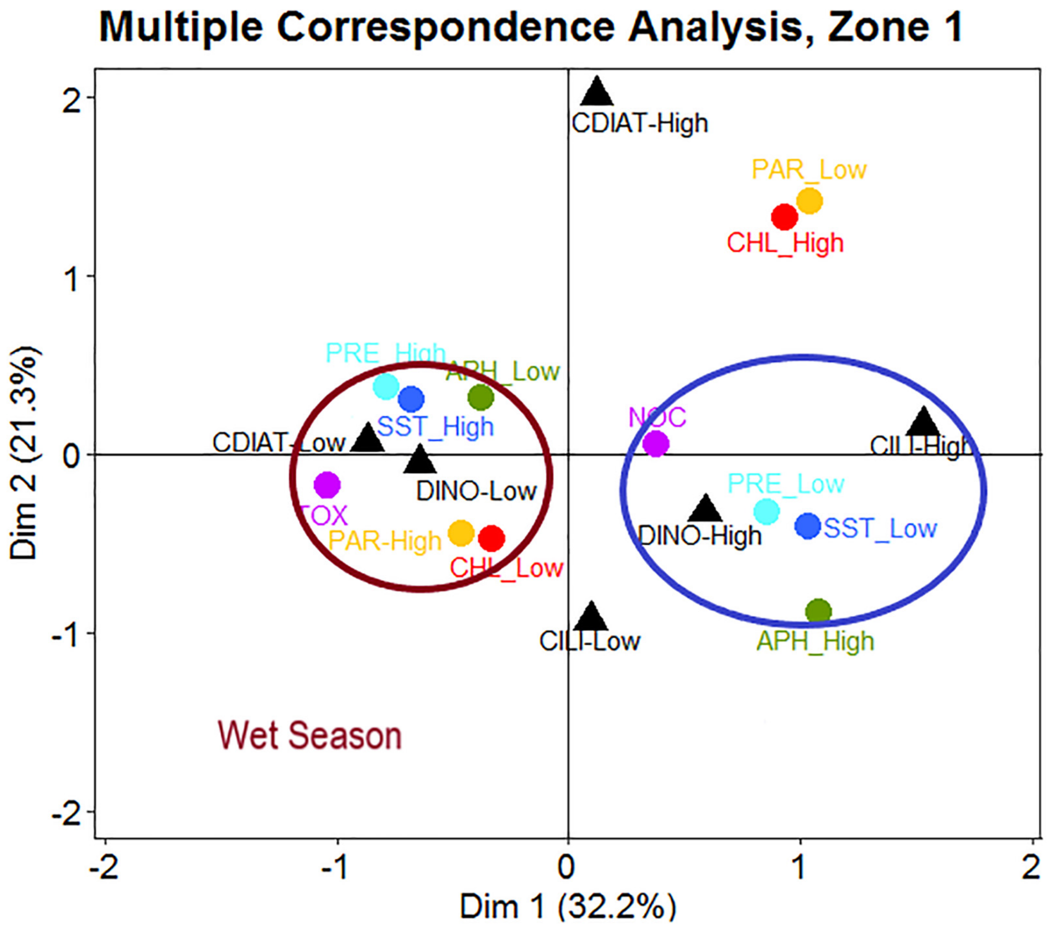

FIGURE 7 | In Zone 1, occurrences of toxic HABs (TOX) linked to low concentrations of dinoflagellates (DINO) and centric diatoms (CDIAT) are associated with high levels of sea surface temperature (SST), precipitation (PRE), and photosynthetic active radiation (PAR) as well as low levels of absorption coefficient of phytoplankton at 443 nm (aph) and chlorophyll *a* (chl-a) appearing during the wet season. Events of non-toxic HABs (NOC) appearing with high concentrations of DINO and ciliates (CILI) are associated with low levels of SST and PRE, accompanied by high values of aph.

community enable adaption to specific habitats and climate conditions (e.g., ENSO) (Prado et al., 2015). Adaptive and behavioral adaptation strategies of HABs may include mobility behavior, such as vertical migration, swimming patterns, phototaxis, and life cycle strategies as resting cysts, and phytoplankton development phases (Masó and Garcés, 2006; Anderson, 2014; Anderson et al., 2017). Future research on these aspects of the adaptive strategies of HABs are necessary for the region.

On the other hand, this study suggests that upwelling systems are related to HABs in the Gulf of Guayaquil. The Humboldt upwelling system is considered to be one of the most productive systems globally (Daneri et al., 2000; Taylor, 2008; Oyarzún and Brierley, 2018). Research groups, such as GEOHAB (Hallegraeff, 2004), have highlighted the potential impacts of HABs on upwelling systems in the context of climate change (Kudela et al., 2005; Edwards et al., 2006; Wei et al., 2008; Trainer et al., 2010; Díaz et al., 2016; Pitcher et al., 2017). In the case of Ecuador and Peru, the Humboldt upwelling system is the foundation of both countries' fishery productivity and the economic benefits of the fishery industry, which can be impacted by emergent HABs (Pennington et al., 2006; Trainer et al., 2010). Considering that there are limited studies on the upwelling systems in the Gulf of Guayaquil region (Oyarzún and Brierley, 2018), understanding these dynamics is critical to assess the future impacts of a changing climate in this very productive ecosystem.

Harmful Algal Blooms and Human Health

Emergent issues concerning upwelling systems and HABs relate to the occurrence of phytoplankton species able to produce phycotoxins and jeopardize human health through paralytic shellfish poisoning, diarrhetic shellfish poisoning, and amnesic shellfish poisoning, as well as other harmful non-toxic blooms resulting in hypoxic and anoxic environments with potentially high negative impacts on fishery resources (Trainer et al., 2010; Pitcher et al., 2017). Phycotoxins can be transferred to human beings through the ingestion of contaminated seafood, thereby posing a potential risk to human health (Fleming et al., 2001; Alonso-Rodríguez and Páez-Osuna, 2003; Backer et al., 2003; Berdalet et al., 2016). Since the Gulf of Guayaquil and Zone 1 are very important for tourism activities, and are particularly known

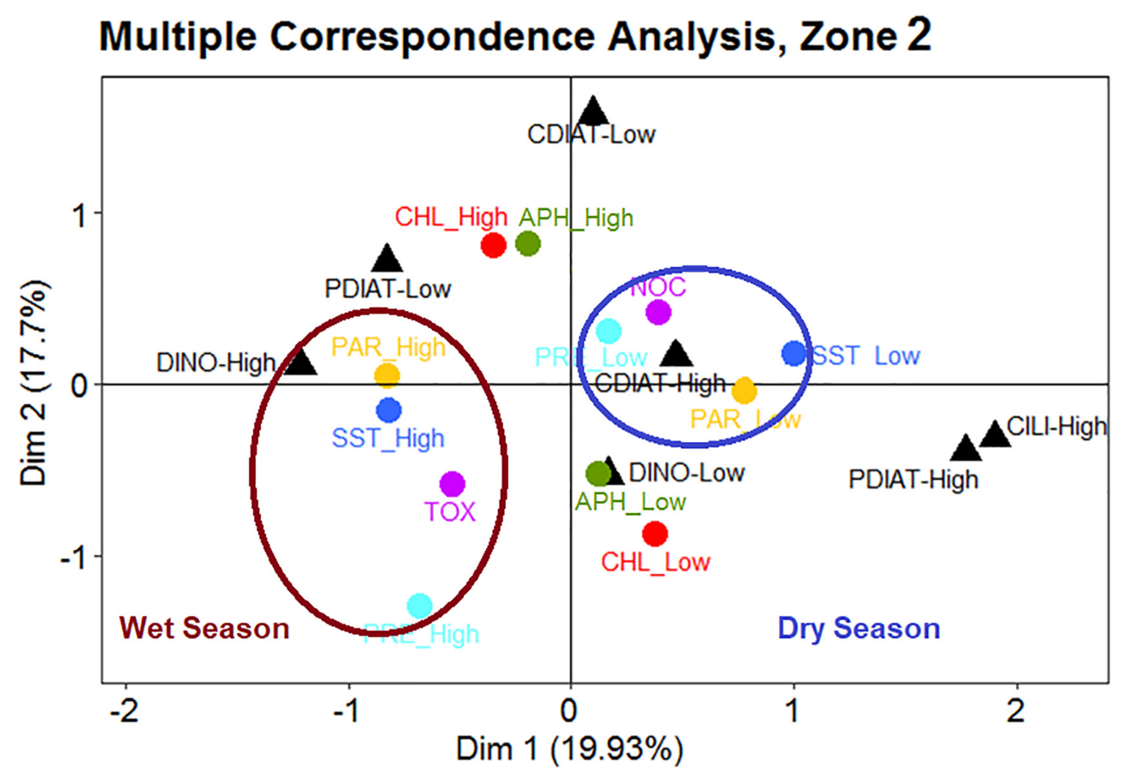

FIGURE 8 | In Zone 2, occurrences of toxic HABs (TOX) are associated with high levels of sea surface temperature (SST), photosynthetic active radiation (PAR), and precipitation (PRE), accompanied by high concentrations of dinoflagellates during the wet season. Events of non-toxic HABs (NOC) seem to be associated with low levels of SST, PRE and PAR and high levels of centric diatoms during the dry season.

for their seafood, a HABs monitoring program, by research and academic institutions, and a preventive policy to protect tourism and public health should be developed as a priority.

A recent study on the risk perceptions of coastal managers, public health officers, and coastal communities in Ecuador revealed that there is limited knowledge of the health impacts of "red tides" and HABs (Borbor-Cordova et al., 2018). While there have not been any reports of human beings affected by HAB toxins in Ecuador to date, this may be explained by the lack of awareness of the syndromes they cause (Borbor-Cordova et al., 2018). *Gymnodinium catenatum*, *Prorocentrum cordatum*, *Prorocentrum mexicanum*, *Prorocentrum micans*, *Karenia brevis*, *Alexandrium* spp., *Dinophysis caudata*, and *Pseudo-nitzschia* spp. are species found along the Ecuadorian coast that are associated with syndromes related to seafood toxicity. The toxins associated with algal blooms and affected seafood for the aforementioned species are described in **Supplementary Table S3**. The main vectors of algal toxins to humans are filter-feeding bivalve mollusks and finfish that ingest toxic algae. The main shellfish toxic syndromes include: paralytic shellfish poisoning, associated with *Gymnodinium catenatum*, diarrhetic shellfish poisoning, associated with *Dinophysis* spp. and *Prorocentrum* spp., neurotoxic shellfish poisoning, associated with *Karenia brevis*, and amnesic shellfish poisoning, linked to *Pseudo-nitzschia* (**Supplementary Table S3**). Symptoms depend upon the toxin and can be temporary, chronic, or even lethal (Backer et al., 2003, 2005). A main limitation of this study is that no analysis of toxins was done during the HABs events, thus an important further step would be to implement a toxins analysis in Ecuador.

Finally, HAB research has shown that exotic species of dinoflagellates can be introduced into the environment through ballast water from shipping (Barry et al., 2008). The intense harbor activities carried out within the Gulf of Guayaquil, with its high volume of international traffic, makes it a site of great risk for the introduction of exotic harmful microalgae, which is therefore another important reason to develop a HABs monitoring program in Ecuador.

Management Implications for Monitoring Ecosystem Health on the Ecuadorian Coast

The findings of this study raise many questions about high levels of productivity and HABs, upwelling conditions and their interaction with extreme events, such as El Niño or La Niña, and the associated impact on human health on the Ecuadorian coast. There are many knowledge gaps in terms of how climate ocean drivers, vertical patterns of mixing and stratification, and upwelling nutrients trigger high levels of productivity, as well as HABs. Thus, this study recommends the design of an integrated ecosystem health research program for the Gulf of Guayaquil and the central Ecuadorian coast. This program would attempt to increase knowledge of the drivers of algal growth, analyze the effects of extreme climatic events and upwelling systems on phytoplankton communities, monitor eutrophication indicators, and identify toxins (Hallegraeff, 2010; Anderson et al., 2017). The program would also develop an early warning system for potentially toxic algal blooms and introduced HAB species. Such an ecosystem health research program would be based on a collaborative framework of stakeholders from the scientific community, public health institutions, and marine resources management organizations, such as scientific institutions, health promoters, residents, and the tourism industry—whoever is interested in participating in citizen science (Fleming et al., 2006; Anderson, 2014). Finally, considering the intrinsic relationship between ocean and human health in relation to HABs, it is important to develop policies related to seafood safety, sanitary controls of shellfish, and deploy a fully equipped monitoring system for a biotoxin analysis program in Ecuador.

FINAL CONSIDERATIONS

Using remote sensing information combined with *in situ* historical data might help increase understanding of the drivers of high biomass phytoplankton within Ecuadorian coastal sites and indicate when those high biomass events might become toxic, harmful algal blooms. *In situ* sampling is critical to determine the composition and distribution of phytoplankton taxonomic groups and biotoxins, thus an integrated ecosystem health research program to monitor HABs in the Gulf of Guayaquil needs be developed and implemented in the near future. Upwelling studies linked to the ecology of the HABs in the Gulf of Guayaquil and the Humboldt Current are critical to maintaining the productivity of the coastal zone and managing its estuarine resources.

AUTHOR CONTRIBUTIONS

MB-C was responsible for the study design, developing an integrated framework, analyzing the data, and drafting the manuscript. GM-S and AC-T pre-processed and analyzed the data. GT collected and analyzed phytoplankton samples and analyzed the data. WR collected samples and reviewed all sections. Together, MB-C, BB, RB, and AC-T drafted the article. All authors discussed the results and reviewed and approved the final manuscript for submission.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2019.00013/full#supplementary-material

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