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ORIGINAL RESEARCH ARTICLE

Historical occurrences of marine microalgal blooms in Indian peninsula: Probable causes and implications

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Abstract The Indian marine environment supports employment for over 200 million people, including revenue of nearly $7 billion per annum. However, ecological goods and services of the shallow coast and the marine environment of the Indian peninsula are being affected by recurrent blooms of microalgae. One hundred and six published literature, starting from the first report in 1908 to 2017, were reviewed to investigate the historical occurrences of marine microalgal blooms (MMBs) around the Indian peninsula. 154 MMBs comprising 24 genera and 7 classes were reported during the study period. *Noctiluca* (dinophyceae) and *Trichodesmium* (cyanophyceae) bloom contributed 34.4% and 31.8% of total blooms. PCA revealed that high sea surface temperature (SST) and salinity were significant driving forces for *Trichodesmium* blooms formation, while high nutrients (NO_3-N, PO_4-P, and SiO_4-Si) and low salinity triggered prymnesiophyceae, raphidophyceae, bacillariophyceae and most of the dinophyceae blooms. *Noctiluca* blooms were linked with both eutrophication and the abundance of prey organisms. HABs were generally dinophyceae dominated and were associated with mass mortality of aquatic fauna, human intoxication, paralytic, and ciguatera shellfish poisoning and even death. Increasing SST and anthropogenic influences around the Indian peninsula could increase the occurrences of MMBs (including HABs) and the number of causative taxa. Proper safety measures such as rou-

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tine monitoring of phycotoxin levels in the environment and local seafood are required to be put in place in other to protect the health of the public.

1. Introduction

Marine ecosystems are the major backbone of life on earth and constitute the largest source of habitat and biodiversity (Anderson et al., 2012). They are primarily supported by the microalgae, which provide the basic food in the food web/chain and play an important role in nutrient recycling and gaseous exchange (Chassot et al., 2010; Passow and Carlson, 2012). Microalgae are unicellular microscopic photosynthetic creatures which exist in different forms (single, filamentous or colonial), shapes (ovoid, cylindrical, spherical) and size (nano: 2—20 μm, micro: 2—200 μm, macro: $>$ 200 μm). They may be free-floating or moving in the water column (i.e., pelagic microalgae), settled on the sediment (benthic microalgae), macrophytes, or other substrates (epiphytic microalgae). They contain pigments for harvesting light/solar radiation and utilize sunlight, nutrients, and carbon dioxide for productivity, growth, and reproduction (Gireesh et al., 2015; Ignatiades, 2016). Marine microalgae are taxonomically diverse and comprise various groups, including diatoms, coccolithophores, chlorophytes, flagellate protists (dinoflagellates, raphidophytes) and cyanobacteria (Brierley, 2017). In total, it consists of about 5000 extant species as a whole.

Generally, microalgae respond rapidly to variations in environmental conditions. Such response includes a change in growth that differs among different taxa or groups (Sharma et al., 2012). Hence, certain changes in physicochemical conditions, e.g., temperature, salinity, nutrients, etc. can stimulate the proliferation of opportunistic micro-algae into large biomass or otherwise cell numbers capable of causing harm, a phenomenon referred to as "bloom" (Anderson et al., 2012). Typically, the cell, biomass, or chlorophyll-*a* concentration, which defines a bloom has not been delineated in the global scientific community. Though a few authors have proposed cell densities (Kim et al., 1993) and chlorophyll-*a* concentration (Binding et al., 2018) defining a bloom, none is yet unanimously accepted. Smayda (1997), in his opinion, discussed that defining this benchmark will vary according to species nature (i.e., whether toxic or non-toxic) and size, location, or habitat type (i.e., whether oligotrophic, mesotrophic or eutrophic) and season. Hence, the term "bloom" has been conventionally used in literature to describe the rapid increase or growth of one or more species of microalgae resulting into visible water discoloration, e.g., red tide, foam production and harm to aquatic biota, ecosystem and human health (Aleynik et al., 2016; Smayda, 1997).

The dominance of either single or multiple species of marine microalgae is called marine microalgal bloom (MMB), and this forms part of the natural cycle of photosynthetic organisms in marine ecosystems, and play a key role in maintaining their community structure and dynamics as well as ensuring sustained services/benefits to humans (Berdalet et al., 2015). However, harmful algal blooms (HABs) may bring severe health and socio-economic consequences to humans, organisms, and the environment (Willis et al., 2018). Six human syndromes namely; paralytic shellfish poisoning (PSP), neurotoxic shellfish poisoning (NSP), amnesic shellfish poisoning (ASP), diarrheic shellfish poisoning (DSP), ciguatera fish poisoning (CFP) and azaspiracid shellfish poisoning (AZSP) have been identified in association with HABs (Ferrante et al., 2012). Also, injury and death of fish, shellfishes and other marine animals following excessive respiration and or decomposition, production of exudates, reactive oxygen species (ROS) or noxious toxins during HABs have been reported (Narayana et al., 2014; Svendsen et al., 2018; Twiner et al., 2012; Walker et al., 2018). Some economic consequences of HABs already described include reduced demand for affected products (Getchis and Shumway, 2017), closure of important shellfisheries (Jin et al., 2008) and desalinization plants (Richlen et al., 2010), and loss of revenue (Anderson et al., 2000; Getchis and Shumway, 2017; Hoagland et al., 2002).

Increasing occurrences and adverse effects of MMBs in marine ecosystems have continued to stir interest in the scientific community (Anantharaman et al., 2009). Coastal habitats are amongst the most affected due to their shallow nature and high susceptibility to changing environmental conditions (Anderson et al., 2012). Changes in the physicochemical (temperature, salinity, dissolved nutrients) conditions of the water are mostly brought about by varying micro-climatic conditions, which usually differ from one geographical location to another (Guinder and Molinero, 2013). Hence, studies geared towards an understanding of major environmental factor/s promoting MMBs (including HABs) are required at regional levels for better environmental health management.

The resources from India's marine environment provide a livelihood to more than 3.5 million people and an estimated income of worth $7 billion in a year through recreation, fishing and other economic activities (Nayak, 2017; Saxena, 2012; Singh, 2003). However, the recurrent blooms of microalgae (including HABs) pose a threat to these ecosystems, as well as the economic, social, and ecological services which they provide (D'Silva et al., 2012; Padakumar et al., 2012). The environmental factors triggering such occurrences are not adequately understood. No study has been conducted that describes the specific physicochemical parameters conditions that exclusively responsible for marine microalgal bloom (MMBs) formation in and around the Indian peninsula. In this study, MMBs around the Indian peninsula coast from the first report in 1908 to 2017 were reviewed, and the various incidents, causative organisms, and relating physicochemical conditions reported were compiled. The relationship between these physicochemical conditions and

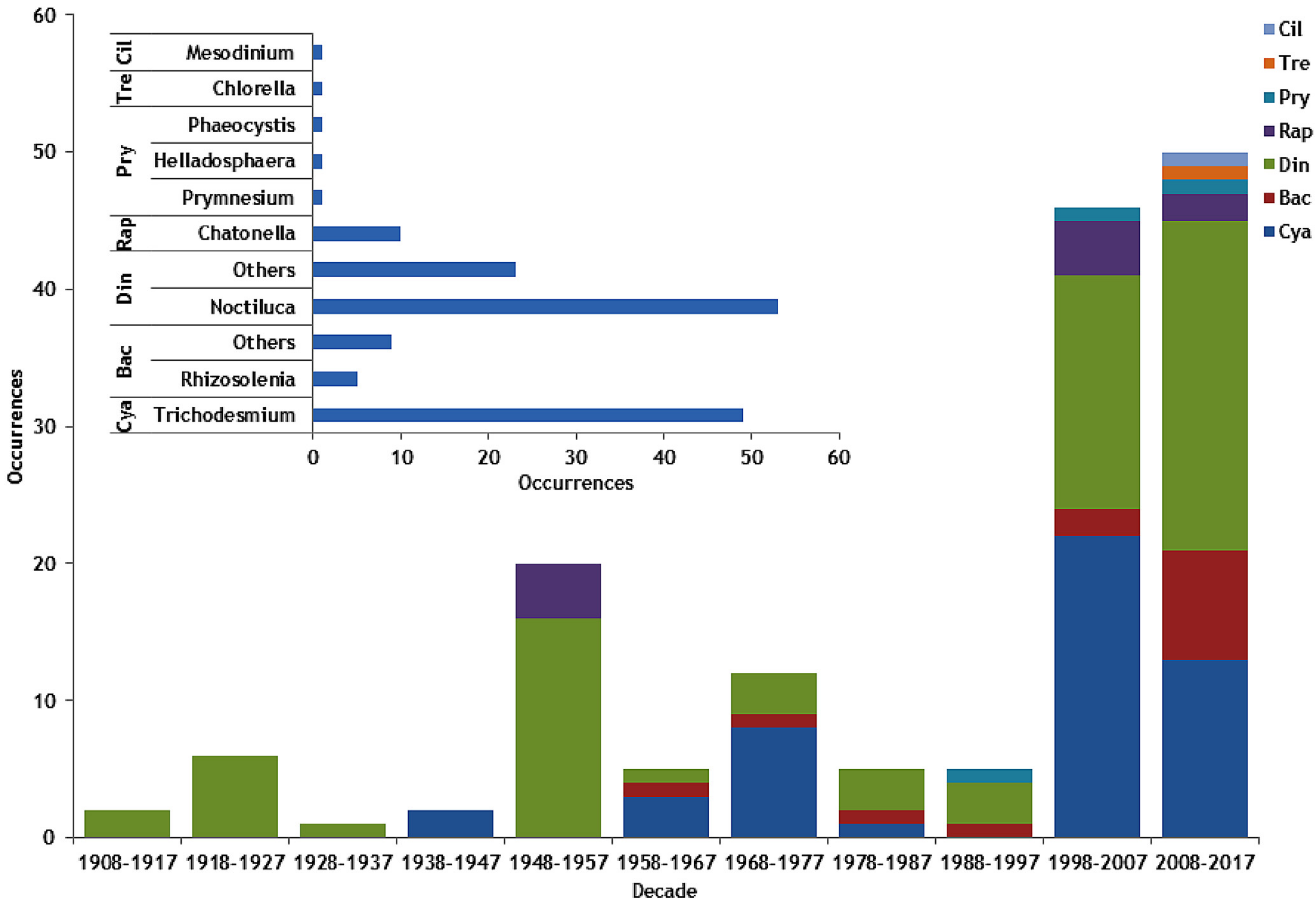

Figure 1 Incidences of marine microalgal blooms around the Indian peninsula from 1908 to 2017. Inset: Occurrences by different bloom-forming organisms. In general, and in the inserted figure, grouping was done by classes and genera, respectively. Cya — Cyanophyceae, Bac — Bacillariophyceae, Din — Dinophyceae, Rap — Raphidophyceae, Pry — Prymnesiophyceae, Tre — Trebouxiophyceae, Cil — Ciliatea.

blooms of the different taxa was also examined in other to determine the critical parameters influencing specific blooms along the coast of the Indian peninsula.

2. Data retrieval and analysis

A total of 106 articles published on occurrences of MMBs around the Indian peninsula coast from the first report in 1908 to 2017 (110 years) were accessed. Subsequently, information regarding period, location, causative organism, and taxonomy were retrieved (Supplementary Tables 1 and 2). Decadal and seasonal occurrences of such events were compiled concerning taxonomic class and dominant genera (Figures 1 and 2). In order to obtain the spatial distribution of blooms, latitude and longitude data obtained from the literature were inputted into Arc Map 10.5 software in decimal degrees (Figure 3). In instances where none was available in the source article, relevant values were obtained from https://google.com/maps.

Also, cell density and physicochemical conditions, e.g., sea surface temperature (SST), pH, salinity, dissolved oxygen (DO), NO_3-N, NO_2-N, NH_3-N, PO_4-P, and SiO_4-Si reported during each bloom event were obtained, and the average, standard deviation and range values for individual species and class were determined using Microsoft Excel 10 software (Table 1). Satellite datasets available for major parameters considered, i.e., SST, salinity, nitrate, phosphate, and silicate, including wind speed and mixed layer depth (MLD), were retrieved from relevant sources (Supplementary Table 3). The datasets acquired were limited to the area covered by bloom events reported in this study (Latitude 6.00° to 24.00°N and Longitude 64.00° to 93.08°E).

Indirect gradient analysis, like the Principal component analysis (PCA), was carried out in order to establish the correlation between blooms formed by different taxa and abi-

Table 1 Eigenvalues of the correlation matrix.

	Eigenvalue	Percentage of variance	Cumulative percentage of variance
1	2.08543	41.71	41.71
2	1.11257	22.25	63.96
3	0.98019	19.60	83.56
4	0.53595	10.72	94.28
5	0.28586	5.72	100.00

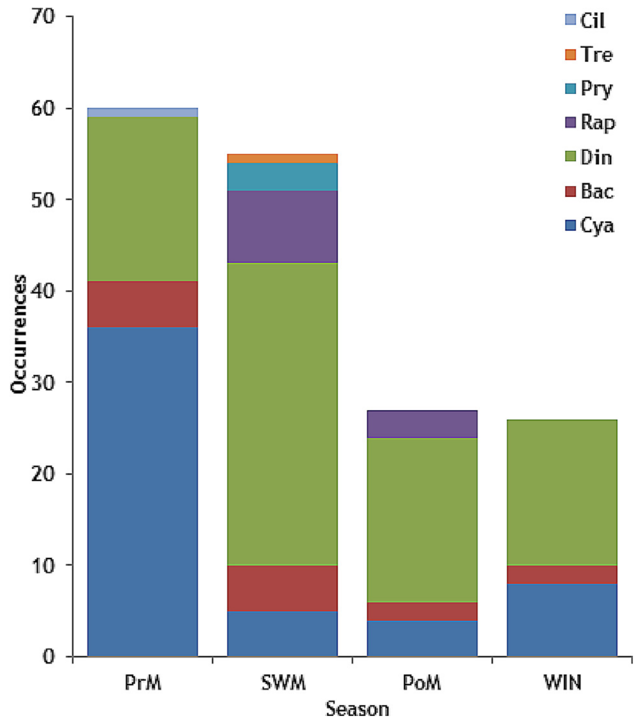

Figure 2 Seasonal occurrences of marine microalgal blooms around the Indian peninsula from 1908 to 2017. Cya — Cyanophyceae, Bac — Bacillariophyceae, Din — Dinophyceae, Rap — Raphidophyceae, Pry — Prymnesiophyceae, Tre — Trebouxiophyceae, Cil — Ciliatea, PrM — Pre-Monsoon, SWM — South-west monsoon, PoM — Post-monsoon, WIN — Winter.

otic factors by correlating the ordination scores (Figure 4). NO_2-N and NH_3-N values were not included in the PCA due to low/no availability of on the spot recorded data. In an instance where one or more physicochemical parameter(s) was not reported, the entire data for such an event was excluded from the PCA analysis. Log transformation, Log_{10} (X+1) was carried out before analyzing data using Origin software version 8.5.1. One way ANOVA was employed to evaluate the significant difference between decadal mean annual temperatures and salinities obtained from satellite database using SPSS 16.0 software (Supplementary Table 4).

Bloom events, as a result of the sudden proliferation of one or more species of microalgae, were included only in this study for doing cause and effect analysis based on the reported visible discoloration (red tide) or patches on water, injury or loss of aquatic life, and/or toxicity to humans (International Council for the Exploration of the Sea, 1984). The least cell concentrations attributed to the blooms of the various taxonomic classes in this study were 6.2×10^4 cells/L (Qasim, 1970) for cyanophyceae, 1.3×10^4 cells/L for bacillariophyceae (Sanilkumar et al., 2009a), 1.0×10^4 and 9.0×10^4 cells/L for *Noctiluca* (Padmakumar et al., 2016a) and other dinophyceae, respectively (Iyer et al., 2008), 24.0×10^4 cells/L for raphidophyceae (Jugnu, 2006), 186.0×10^4 cells/L for prymnesiophyceae (Ramaiah et al., 2005), 19.4×10^4 cells/L for trebuoxiophyceae (Asha et al., 2015) and 100.0×10^5 cells/L for ciliates (Sahu et al., 2016). A HAB event was identified as an incident associated with devastating impacts such as mortality of aquatic fauna (e.g., fish, and shellfish), human injury and death (e.g., respiratory difficulty, hospitalization, shellfish poisoning), and or economic hardship due to grounded or reduced fishing activity (Sanseverino et al., 2016).

3. Results and discussion

3.1. Biophysical and meteorological characteristics around the Indian peninsula coast

The Indian peninsula is bordered on the western side by the Arabian Sea (AS) and the eastern side by the Bay of Bengal (BOB). Both ecosystems form part of the North Indian Ocean and are influenced by intense, annually reversing monsoon winds and seasonally varying sea surface circulation (Chowdary et al., 2016). Strong southwesterly monsoon winds blowing from June to September induce the summer monsoon, also known as the south-west monsoon (SWM). This season is characterized by heavy precipitation, strong water mixing and upwelling of cold, saline, nutrient-rich, and oxygen-depleted waters from the subsurface to the surface along the coast. This effect is most pronounced along the south-west coast (Attri and Tyagi, 2010). Generally, low SST (27.7°C in AS and 28.5°C in BOB), high MLD (65 m in AS and 45 m in BOB), and nutrient concentration (NO_3-N of around 5 μM, PO_4-P up to 0.75 μM and SiO4-Si up to 20 μM) are recorded. Surface salinity is higher in the AS remains relatively high (~35.6 psu) during this period as compared to the BOB (~33.6 psu), owing to lower precipitation of around 130 cm/month in the AS than in the BOB (~350 cm/month). Surface salinity in the AS remains relatively high (~35.6 psu) during this period, while that in the BOB is low (~33.6 psu), due to higher precipitation (350 cm/month) in the BOB than in the AS (130 cm/month) (Supplementary Figures 3—7).

Another major cause of low salinity in the BOB is the large amount of run-off/freshwater which it receives from major rivers which are located along its northern part, e.g., River Brahmaputra and Ganges, Mahanadi, Godavari, Krishna, and Cauvery. The freshwater flux from these rivers reaches up to 14×10^4 m^3/s during SWM. About 60% of the entire freshwater received in the season (Chaitanya et al., 2014). The AS is fed by small rivers, e.g., Sabarmati, Mahi, Narmada, and Tapi. AS receives a comparatively lower input of freshwater as compared to BoB due to low precipitation. River run-off also contributes to the source of nutrient enrichment in both the AS and BOB during SWM. A southwesterly flow is known as the West Indian Coastal Current (WICC), which prevails during this season and carries colder and more saline water to the east coast (Panikkar and Jayaraman, 1966). Low saline water is observed along the west coast below 15°N due to the southward advection of low salinity surface water from the coastal margin up north by this current, as well as the input of run-off water from nearby areas (Behara et al., 2019).

Cold, dry northeastern monsoon winds usher in the northeast monsoon or winter (WIN) season. The winds blow in the south-west direction and result in the vertical mixing of surface water with deeper nutrient-rich water due to heat loss resulting from cooling. The lowest average SST of 27.3°C and 27.9°C in the AS and BOB, respectively, is recorded during this period along with little rainfall (Attri and Tyagi, 2010). Mean salinity of around 32.3 psu is recorded in the

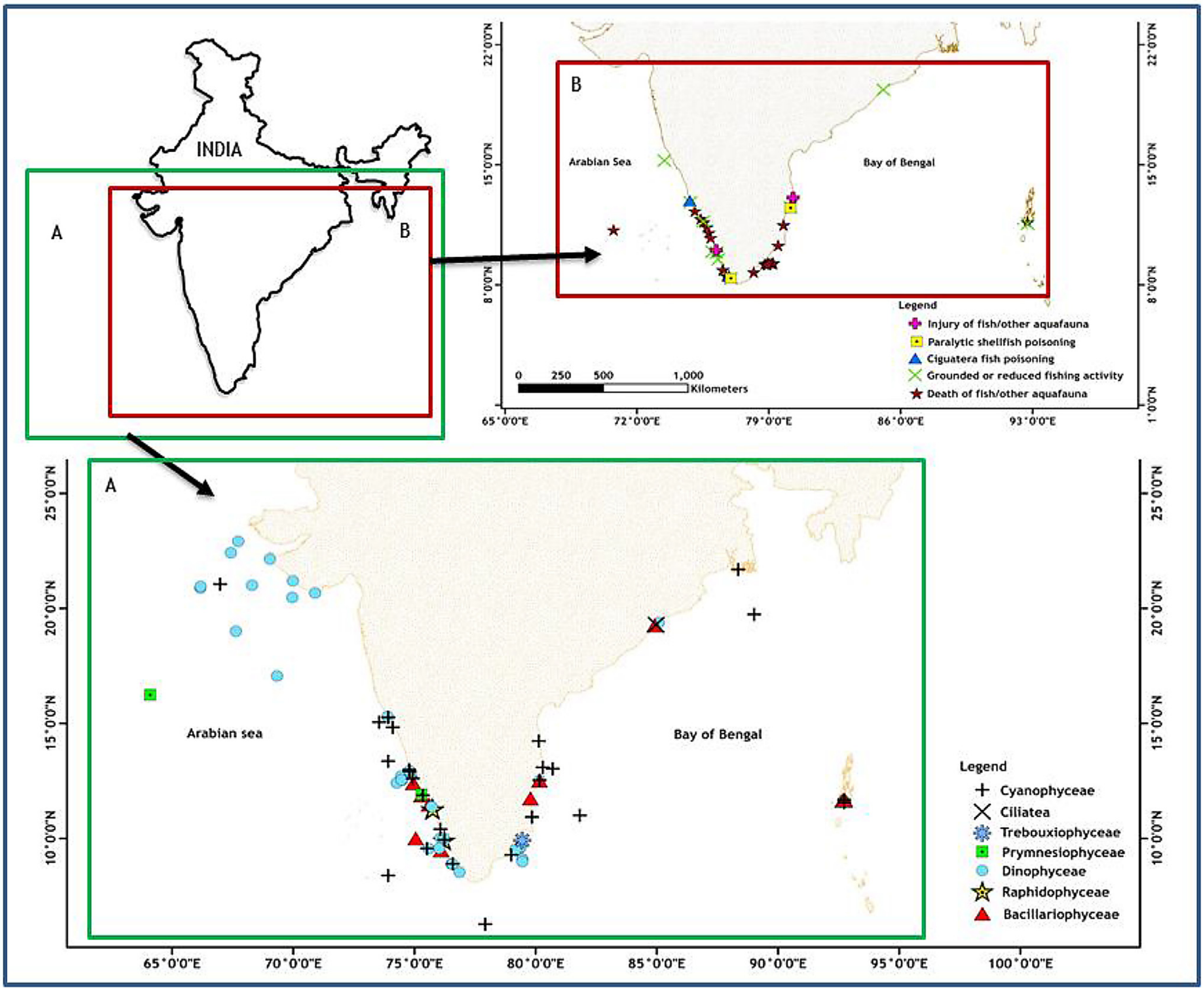

Figure 3 Distribution of marine microalgal blooms around the Indian peninsula from 1908 to 2017. A — Non-harmful occurrences. B — Harmful algal blooms.

BOB while that in the AS is around 35.4 psu. High nutrient levels, up to 8 μM of NO_3-N, 0.75 μM of PO_4-P, and 10 μM of SiO_4-Si are observed. Also, wind speed and mixed layer depth increase reaching a maximum of ~9 m/s and 75 m, respectively, around January. The utmost of these conditions generally occurs along the extreme north and south coasts of the peninsula (Supplementary Figs. 1—7). East Indian Coastal Current (EICC) flows along the eastern boundary towards the west direction and carries low salinity water from the BOB into the southern AS. The winter season runs from December to February (Akhil et al., 2014).

A period of transition known as the post-monsoon season (PoM) follows the SWM before the start of the NEM. It is generally characterized by the withdrawal of monsoon and high SST (28°C in AS and 28.5°C in BOB) along both coasts. Surface salinity is ~36 psu in the AS and ~33 psu in the BOB. Cyclonic depression and heavy, widespread rainfall occur along the eastern coast (Anoopa, 2017). Hot and dry winds characterize the pre-monsoon (PrM) season. A maximum average SST of above 29°C is recorded also recorded in both basins. Surface salinity is also high, around 35.5 psu in the AS and 33.5 psu in the BOB. The season is characterized by cyclonic storms which move in the north-western direction, and short durations of rainfall. Most of these occur in the Bay of Bengal (BOB) (Anoopa, 2017). According to the Asia-Pacific Data Research Centre (2018), the average salinity of the seawater increases from the northern part to the southern part in the BOB. The same increases from the southern part to the northern part in general in the AS. However, in the case of SST, both the BOB and AS exhibit a similar pattern of distribution, i.e., from north to the south gradient (Mohapatra et al., 2015).

3.2. Occurrences of MMBs around the Indian Peninsula

A total of 154 MMBs comprising 24 genera under the class: dinophyceae (9 genera), bacillariophyceae (8 genera), prymnesiophyceae (3 genera), cyanophyceae, raphidophyceae, trebouxiophyceae, and ciliateae (1 genus each) were reported around the Indian peninsula from 1908 to 2017 (Figure 1; Supplementary Tables 1 and 2). Among

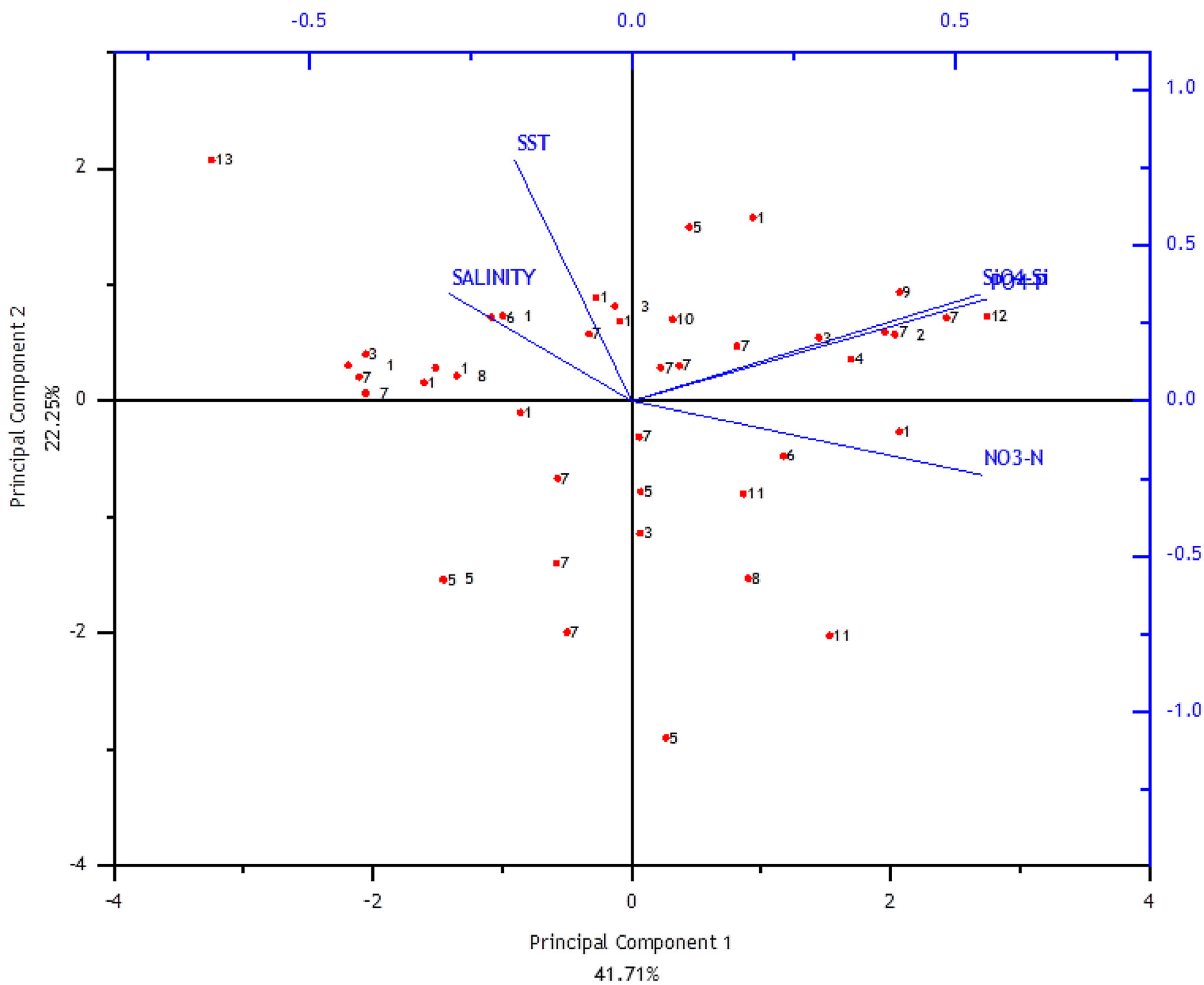

Figure 4 PCA biplot showing the relationship between the blooms of various phytoplankton with environmental variables. 1. Cyanophyceae (1. *Trichodesmium*), 2—6 Bacillariophyceae (2. *Coscinodiscus*, 3. *Rhizosolenia*, 4. *Leptocylindrus*, 5. *Asterionella*, 6. *Chaetoceros*), 7—10. Dinophyceae (7. *Noctiluca*, 8. *Protoperidinium*, 9. *Karenia*, 10. *Gonyaulax*), 11. Raphidophyceae (11. *Chatonella*), 12. Prymnesiophyceae (12. *Prymnesium*), 13. Trebouxiophyceae (13. *Chlorella*).

all the MMBs recorded from this region, *Noctiluca* (dinophyceae) and *Trichodesmium* (cyanophyceae) were the dominant bloom-forming genera and accounted for 34.4% and 31.8% respectively (Figure 1).

3.2.1. Temporal occurrences

In the first three decades (1908 to 1937), occurrences of MMBs recorded were limited to those of the dinophyceae. However, over time, blooms of additional taxa emerged. During the last decade alone (2008—2017), blooms of two new taxa, such as the trebouxiophyceae and ciliates were recorded. A remarkable increase in the incidence of MMBs along the Indian peninsula has been recorded from 1948 to 2017. The occurrences of MMBs were increased from 1948 to 2017. Twenty incidents were recorded from 1948 to 1957, 46 incidents occurred from 1998 to 2007, and 50 incidents were also recorded from 2008 to 2017. All through 1948 to 1957, only the dinophyceae remained dominant (80%), while in the second to the last decade, cyanophyceae was dominant (47.8%) followed by dinophyceae (37.0%). In the last decade, dinophyceae (48.0%) again replaced cyanophyceae (26.0%) and remained dominant. Appearances of dinoflagellate blooms were consistently recorded every decade except between 1938 to 1947 and 1988 to 1997. Also, those of bacillariophyceae appeared regularly from 1958 to 2017 (Figure 1).

MMBs were most pronounced during the PrM season, followed by the SWM season. Blooms of cyanophyceae dominated during the PrM season, while those of dinophyceae dominated during the SWM season. Events attributed to the raphidophyceae and prymnesiophyceae were most pronounced during the SWM season, while those associated with the bacillariophyceae were remarked during PrM and SWM. Blooms of ciliatea were featured only in the PrM season, whereas those of trebouxiophyceae were recorded only in the SWM season (Figure 2).

Table 2 Factor loading matrix of total variance explained by each vector of the principal component analysis.

	Coefficients of PC1	Coefficients of PC2
SST	−0.18153	**0.77412**
Salinity	−0.28219	**0.34455**
NO_3-N	**0.54157**	−0.23703
PO_4-P	**0.54986**	0.32851
SiO_4	**0.54016**	0.34339

Note: factors/parameters with significant weight are in bold.

3.2.2. Spatial occurrences

From the 154 MMBs reported, 103 were recorded along the western coast. Also, on both the east and west coast, higher incidences were observed along with the southern parts than the northern parts. For instance, 36 out of the 38 events of HABs recorded along the Indian peninsula coast occurred in the southern part. Blooms of the raphidophyceae and prymnesiophyceae were mainly recorded along the southwestern coast. Those of ciliatea and trebouxiophyceae occurred along the south-eastern coast alone, whereas, MMBs, those were dominated by the cyanophyceae and dinophyceae were featured both the west and east coast (Figure 3a).

3.3. Physiochemical conditions during occurrences of MMBs

3.3.1. Principal component analysis

PCA identified two principal components (PC1 and PC2) with eigenvalues greater than 1. Both components cumulatively explained 63.96% of the total variance in the conditions of the various blooms recorded. Principal component 1 (PC1) accounted for 41.71% (Eigenvalue = 2.08543) of the total variance recorded and had high positive loadings of NO_3-N (0.54), PO_4-P (0.55), SiO_4-Si (0.54). SST and salinity weight recorded were low (−0.18 and −0.28 respectively), implying that water eutrophication was the significant condition explained by this component. However, principal component 2 (PC2) represented 22.25% (Eigenvalue = 1.11257) of the total variance and had higher loading of SST (0.77) and salinity (0.35), indicating that both factors were mainly responsible for the blooms explained by it (Tables 1 and 2). As presented on the biplot, nutrients (NO_3-N, PO_4-P, and SiO_4-Si) had higher weight than SST and salinity, revealing that on the overall, they had more influence on the occurrences of blooms (Figure 4).

3.3.2. Cyanophyceae (*Trichodesmium*), Trebouxiophyceae and Ciliatea blooms

Blooms of cyanophyceae (*Trichodesmium*) and trebouxiophyceae (*Chlorella marina*) were recorded under the higher condition of SST (30.26±1.38°C and 31.42±0.00°C respectively) and salinity (34.29±1.16 and 51.75±0.00 psu respectively), as well as the low condition of NO_3-N (1.50±3.02 μM and 0.01±0.00 μM respectively), NO_2-N (0.16±0.12 μM and 0.04±0.00 μM respectively), PO_4-P (0.53±0.82 μM and 0.04±0.00 μM respectively) and SiO_4-Si (4.10±4.45 μM and 0.23±0.00 μM respectively) (Table 3). The PCA biplot further validated this, as appearances of both taxa were mainly positively correlated with SST and salinity, and negatively with the nutrients. However, some blooms of the cyanophyceae were positively correlated with PO_4-P and SiO_4-Si. The bloom of trebouxiophyceae was more closely associated with water salinity than SST due to the remarked salinity condition in which it was recorded (Figure 4). Hence, high water salinity was a significant driver in the occurrence of its bloom. *Chlorella* strains have been reported to be capable of active growth under high conditions of temperature and salinity up to 42.5°C (Ouyang et al., 2010) and 60 psu (Kakarla et al., 2018) respectively, as well as minimal nutrient conditions (Mata et al., 2010; Nigam and Singh, 2011).

Most of the MMBs dominated by cyanophyceae occurred during high SST and salinity, along with high PO_4-P and SiO_4-Si (Figure 4), which tallied with the PC2 in which SST, salinity, PO_4-P, and SiO_4-Si had positive loading (Table 2). Thus, the component mainly explained the principal factor responsible for the occurrence of blooms of this taxon — high SST and salinity. The dominance of cyanophyceae, during PrM when SST and salinity conditions were high (≥29°C and 33—35 psu respectively) furthered established the role of these parameters in driving its blooms (Supplementary Figure 1 and 2). Coincidentally, a significant increase in SST condition (at $p<0.01$) along the coast of India between 1938 and 1947 matched with the first record of blooms of cyanophyceae (Supplementary Table 4). Similar to this study, SST and salinity have been reported as significant parameters influencing the abundance and distribution of cyanophyceae (*Trichodesmium*) in different oceans (Agarwin et al., 2013; Jiang et al., 2017; Liu and Tang, 2012; Rodier and Borgone, 2008; Rouco et al., 2014, 2016; Walworth et al., 2015). Breitbarth et al. (2007) discussed that *Trichodesmium* (cyanophyceae) was capable of growing at a wide temperature range of 20 to 34°C, while Full and Bell (2003) prescribed that a salinity range of 22—43 psu as favorable for growth. The specific range of SST (27.50—33.50°C) and salinity (32.14—35.86 psu), also support the similar observation recorded around the Indian peninsula.

The low NO_3-N condition under which most blooms of the cyanophyceae (*Trichodesmium*) were recorded in this study (Figure 4) is associated with the diazotrophic nature of the organism and in agreement with available reports (Holl and Montoya, 2005; Mulholland and Capone, 1999). NO_3^-N deficient condition promotes diazotrophy — the fixation of atmospheric nitrogen into usable forms for growth in *Trichodesmium*, thus enabling it to outgrow other organisms (D'Silva et al., 2012). High SiO_4-Si level associated with some bloom of the cyanophyceae (*Trichodesmium*) could have resulted from its non-uptake. High PO_4-P levels recorded during certain events might be connected with its requirement for growth and metabolism (Qu et al., 2019). Also, low wind speed (~5 m/s), water mixing and high stratification prevalent during the PrM season (Supplementary Figures 3 and 4) could have also promoted the buoyancy of the organism, and its ability to form extensive blooms (Capone et al., 1997).

The bloom of ciliatea (*Mesodinium rubrum*) was rare, and no information about physicochemical conditions was recorded. However, studies published have identified high

Table 3 Parameters recorded in association with blooming phytoplankton along the coasts of India (APDRC, 2019, Lotliker et al., 2018, Madhav and Kondalarao, 2004, Madhu et al., 2011a, Madhu et al., 2011, Madhupratap et al., 2000, Martins et al., 2010, Mathew et al., 1988, Annamalai et al., 2016, Matondkar et al., 2004, Matondkar et al., 2006, Minu et al., 2015, Mishra et al., 2005, Mohanty et al., 2007, Nagabhushanam, 1967, Nashad et al., 2017, Nayak et al., 2000, Nayar and Prabhu, 2001, Nunez et al., 2011, Padmakumar et al., 2008, Padmakumar et al., 2010a, Padmakumar et al., 2011, Padmakumar et al., 2016b, Arun et al., 2012, Peter et al., 2016, Prabhu et al., 1965, Prasad, 1958, Raghavan et al., 2010, Raji and Padmavati, 2014, Ramamurthy, 1973, Rao, 1969, Rekha et al., 2012, Sachithanandam et al., 2013, Sahu et al., 2018, Sanilkumar et al., 2009b, Baliarsingh et al., 2016, Sanilkumar et al., 2012, Sargunam et al., 1989, Sasamal et al., 2005, Satpathy et al., 2007, Shaju et al., 2018, Shetye et al., 2013, Shunmugam et al., 2017, Subrahmanyan, 1954, Sulochanan et al., 2014, Tada et al., 2016, Thomas, 2014, Thomas et al., 2014b, Berdalet et al., 2019, Turner et al., 2017, Venugopal et al., 1979, Vijayalakshmy et al., 2018, Xu et al., 2019, Brand and Compton, 2007, Capone et al., 2005, Chandrasekhararao et al., 2018, Chellam and Alagarswami, 1978, Choudhury and Panigrahy, 1989, Cicily et al., 2013, Daniel et al., 1979, Desa et al., 2005, Devassy, 1974, Devassy et al., 1978, Dharani et al., 2004, Dwivedi et al., 2015, Dwivedi et al., 2012, Dwivedi et al., 2006, Eashwar et al., 2001, Edwards et al., 2006, Ferrante et al., 2012, Figler et al., 2019, Garcia et al., 2019a, Garcia et al., 2019b, Gobler et al., 2017, Gomes et al., 2014, Gopakumar et al., 2009, Al-azri et al., 2007, Harrison et al., 2011, Heil et al., 2014, Hemalatha et al., 2016, Hiremath and Mathad, 2010, Hornell, 1908, Hornell, 1917, Hornell and Nayudu, 1923, Indian Space Research Organization, ISRO 1999, Jabir et al., 2013, Jasmine et al., 2005, Jones et al., 2017, Joseph et al., 2008, Jyothibabu et al., 2017, Jyothibabu et al., 2003, Karthik and Padmavati, 2018, Katti et al., 1988, KNMI Climate Explorer website 2018, KNMI Climate Explorer website 2018, Kumar et al., 2015, Kumar et al., 2009).

Class	Cell density ($\times 10^5$ cells L^{-1})	SST (°C)	pH	Salinity	DO (mg L^{-1})	NO_3-N (µM)	NO_2-N (µM)	NH_3-N (µM)	PO_4-P (µM)	SiO_4 (µM)	Chlorophyll *a* (µg L^{-1})	Reference(s)
1. Bacillariophyceae												
Asterionella japonica (n=6)	61013.07±181495.78 (0.84-545000.00)	26.86±2.83 (24.00-31.58)	7.82±0.00 (7.82-7.82)	32.29±2.45 (28.66-34.83)	5.85±1.78 (3.08-7.46)	1.62±2.06 (0.02-5.05)	0.03±0.04 (0.00-0.09)	-	0.27±0.53 (0.00-1.43)	1.47±2.19 (0.03-5.10)	53.39±51.01 (5.63-132.17)	7; 26; 59; 68; 69
Chaetoceros spp. (n=1)	4.90±0.00	-	-	-	-	-	-	-	-	-	7.50±0.00 (7.50-7.50)	38
C. curvisetus (n=1)	2.75±0.00 (2.75-2.75)	31.30±0.00 (31.30-31.30)	8.05±0.00 (8.05-8.05)	31.96±0.00 (31.96-31.96)	7.03±0.00 (7.03-7.03)	0.29±0.00 (0.29-0.29)	0.01±0.00 (0.01-0.01)	0.74±0.00 (0.74-0.74)	0.02±0.00 (0.02-0.02)	4.22±0.00 (4.22-4.22)	5.80±0.00 (5.80-5.80)	Begum et al. 2015
C. tortissimum (n=1)	617.86±0.00 (617.86-617.86)	29.14±0.00 (29.14-29.14)	7.93±0.00 (7.93-7.93)	28.43±0.00 (28.43-28.43)	3.40±0.00 (3.40-3.40)	4.27±0.00 (4.27-4.27)	0.33±0.00 (0.33-0.33)	-	0.28±0.00 (0.28-0.28)	10.90±0.00 (10.90-10.90)	0.19±0.00 (0.19-0.19)	Karthik and Padmavati (2014)
Coscinodiscus asteromphalus var. *centralis* (n=1)	35.07±0.00 (35.07-35.07)	27.50±0.00 (27.50-27.50)	8.00±0.00 (8.00-8.00)	34.33±0.00 (34.33-34.33)	7.12±0.00 (7.12-7.12)	2.70±0.00 (2.70-2.70)	0.00±0.00 (0.00-0.00)	-	1.75±0.00 (1.75-1.75)	37.90±0.00 (37.90-37.90)	104.90±0.00 (104.90-104.90)	26; 63
Fragilaria oceanica (n=1)	368.00±0.00 (368.00-368.00)	-	-	32.36±0.00 (32.36-32.36)	-	0.03±0.00 (0.03-0.03)	-	-	0.03±0.00 (0.03-0.03)	-	123.48±00.00 (123.48-123.48)	11
Hemidiscus hardmannianus (n=1)	0.32±0.00 (0.32-0.32)	-	-	-	-	-	-	-	-	-	-	71
Leptocylindrus sp. (n=1)	14.79 ± 0.00 (14.79-14.79)	29.30±0.00 (29.30-29.30)	-	29.30±0.00 (29.30-29.30)	8.16±0.00 (8.16-8.16)	2.62±0.00 (2.62-2.62)	-	-	1.77±0.00 (1.77-1.77)	9.83±0.00 (9.83-9.83)	-	43
Pleurosigma sp. (n=1)	20.00±0.00 (20.00-20.00)	-	-	-	-	-	-	-	-	-	-	11
Rhizosolenia sp. (n=1)	10.00±0.00 (10.00-10.00)	-	-	-	-	-	-	-	-	-	-	11
R. alata (n=3)	1.02±0.53 (0.41-1.36)	27.00±2.29 (24.50-29.00)	8.30±0.14 (8.20-8.40)	34.67±0.58 (34.00-35.00)	4.25±0.69 (3.46-4.76)	0.72±0.90 (0.10-1.76)	0.11±0.04 (0.08-0.14)	-	0.82±0.56 (0.40-1.45)	16.38±8.55 (11.40-26.26)	12.31±3.19 (8.64-14.30)	8; 21

(*continued on next page*)

Table 3 (*continued*)

Class	Cell density ($\times 10^5$ cells L^{-1})	SST (°C)	pH	Salinity	DO (mg L^{-1})	NO_3-N (μM)	NO_2-N (μM)	NH_3-N (μM)	PO_4-P (μM)	SiO_4 (μM)	Chlorophyll *a* (μg L^{-1})	Reference(s)
R. imbricata (n=1)	240.00±0.00 (240.00-240.00)	31.14±0.00 (31.14-31.14)	8.23±0.00 (8.23-8.23)	34.21±0.00 (34.21-34.21)	6.50±0.00 (6.50-6.50)	0.27±0.00 (0.27-0.27)	0.00±0.00 (0.0-0.00)	-	0.00±0.00 (0.0-0.00)	0.00±0.00 (0.0-0.00)	-	Saravanae et al., 2016
Mean ± SD (Range) n = 17	**25019.74±116139.89 (0.32-545000.00)**	**27.71±2.65 (24.00-31.58)**	**8.09±0.20 (7.82-8.40)**	**32.52±2.38 (28.43-35.00)**	**5.73±1.74 (3.08-8.16)**	**1.46±1.67 (0.18-5.05)**	**0.08±0.11 (0.00-0.33)**	**0.37±0.52 (0.00-0.74)**	**0.51±0.68 (0.00-1.77)**	**8.15±10.92 (0.00-37.90)**	**44.12±49.46 (0.19-132.17)**	
2. Ciliatea												
Mesodinium rubrum (n=1)	100.00±0.00 (100.00-100.00)	-	-	-	-	-	-	-	-	-	-	61
3. Cyanophyceae												
Trichodesmium erythraeum (n=21)	13064.38±38283.15 (0.62-115142.40)	30.23±1.53 (27.50-33.50)	8.13±0.18 (7.90-8.40)	33.99±1.10 (32.14-35.47)	6.03±2.00 (2.66-9.11)	1.61 ± 3.25 (0.00-10.00)	0.19 ± 0.11 (0.03-0.29)	31.04±49.06 (0.10-125.00)	0.58±0.87 (0.00-2.80)	4.28±4.64 (0.00-14.00)	19.71 ± 38.98 (0.08-127.00)	4; 10; 13; 23; 27; 28; 29; 31; 37; 41; 42; 48; 52; 57; 69; 70
T. thiebautii (n=2)		29.07±0.00 (29.07-29.07)	-	35.26±0.00 (35.26-35.26)	9.11±0.00 (9.11-9.11)	0.03 ± 0.00 (0.03-0.03)	-	0.84 ± 0.00 (0.84-0.84)	0.11 ± 0.00 (0.11-0.11)	1.29 ± 0.00(1.29-1.29)	-	48; 57
T. hildebrantii (n=1)	3.00±0.00 (3.00-3.00)	-	-	-	-	-	-	-	-	-	-	51
Trichodesmium sp. (n=4)	0.04±0.00 (0.04-0.04)*	30.38±0.28 (30.00-30.61)	-	35.40±0.52 (34.67-35.86)	5.84±0.06 (5.80-5.89)	0.79±0.31 (0.58-1.01)	0.03±0.00 (0.03-0.03)	14.25±18.60 (1.10-27.40)	0.22±0.13 (0.13-0.31)	2.27±0.00 (2.27-2.27)	14.82±18.02 (2.50-35.50)	13; 23; 54
Mean ± SD (Range) n = 49	**11758.24±36329.26 (0.73-115140.00)**	**30.26±1.38 (27.50-33.50)**	**8.13±0.18 (7.90-8.40)**	**34.29±1.16 (32.14-35.86)**	**6.00±1.83 (2.66-9.11)**	**1.50±3.02 (0.00-10.00)**	**0.16±0.12 (0.03-0.29)**	**26.85±42.77 (0.10-125.0)**	**0.53±0.82 (0.00-2.80)**	**4.10±4.45 (0.00-14.00)**	**18.58±34.62 (0.08-127.00)**	
4. Dinophyceae												
Noctiluca miliaris (n= 38)	511.14± 1695.85 (0.01-8100.00)	28.14±1.90 (25.02-32.13)	8.05±0.24 (7.54-8.40)	34.12±2.75 (25.00-40.00)	5.42±1.51 (2.20-9.16)	2.13±2.75 (0.00-11.06)	0.51±0.86 (0.00-3.28)	5.18±6.05 (1.21-14.90)	0.91±1.28 (0.00-4.56)	6.38±9.49 (0.11-32.61)	9.01±8.08 (0.34-26.50)	2; 3; 6; 11; 12; 14; 15; 16; 17; 18; 19; 20; 24; 25; 30; 32; 35; 36; 37; 39; 40; 41; 44; 45; 46; 47; 48; 49; 53; 62; 65; 66; 69; 72; 75; 76

(*continued on next page*)

Table 3 *(continued)*

Class	Cell density (× 10^5 cells L^{-1})	SST (°C)	pH	Salinity	DO (mg L^{-1})	NO_3-N (μM)	NO_2-N (μM)	NH_3-N (μM)	PO_4-P (μM)	SiO_4 (μM)	Chlorophyll *a* (μg L^{-1})	Reference(s)
Karenia mikimotoi (n=3)	38.46±64.18 (0.90-112.57)	29.25±1.52 (28.37-31.00)	7.56±0.39 (7.25-8.00)	32.04±4.78 (26.52-34.80)	2.40±0.71 (1.90-2.90)	2.26±1.62 (0.80-4.00)	0.14±0.16 (0.02-0.25)	4.85±0.00 (4.85-4.85)	5.74±3.71 (1.46-8.00)	32.30±0.00 (32.30-32.30)	56.80±0.00 (56.80-56.80)	22; 33; 59
Cochlodinium sp. (n=1)	1.40±0.00 (1.40-1.40)	27.0 0±0.00 (27.00-27.00)	7.40±0.00 (7.40-7.40)	33.00±0.00 (33.00-33.00)	-	2.40±0.00 (2.40-2.40)	24.52±0.00 (24.52-24.52)	14.72±0.00 (14.72-14.72)	15.95±0.00 (15.95-15.95)	-	1.20±0.00 (1.20-1.2)	40
Gonyaulax polygramma (n=2)	2555.00±3457.75 (110.00-5000.00)	29.55±0.00 (29.55-29.55)	-	34.10±0.00 (34.10-34.10)	6.38±0.00 (6.38-6.38)	1.65±0.00 (1.65-1.65)	-	-	0.60±0.00 (0.60-0.60)	10.00±0.00 (10.00-10.00)	13.15±0.00 (13.15-13.15)	52; Padmakumar et al. 2018
Dinophysis sp. (n=1)	3.10±0.00 (3.10-3.10)	-	-	-	-	-	-	-	-	-	-	38
Prorocentrum sp. (n=1)	1.50±0.00 (1.50-1.50)	-	-	-	-	-	-	-	-	-	-	38
Protoperidinium sp. (n=1)	5000.0±0.0 (5000.0-5000.0)	29.00±0.00 (29.00-29.00)	8.34±0.00 (8.34-8.34)	34.64±0.00 (34.64-34.64)	8.65±0.00 (8.65-8.65)	0.00±0.00 (0.00-0.00)	-	-	0.25±0.00 (0.25-0.25)	1.68±0.00 (1.68-1.68)	0.90±0.00 (0.90-0.90)	63
Protoperidinium divergens (n=1)	350.00±0.00 (350.00-350.00)	26.00±0.00 (26.00-26.00)	7.70±0.00 (7.70-7.70)	31.00±0.00 (31.00-31.00)	2.23±0.00 (2.23-2.23)	1.12±0.00 (1.12-1.12)	1.12±0.00 (1.12-1.12)	-	0.29±0.00 (0.29-0.29)	9.33±0.00 (9.33-9.33)	10.96±0.00 (0.13-0.13)	55
Mean±SD (Range)	**644.19±1785.35 (0.01-8100.00)**	**28.22±1.83 (25.02-32.13)**	**7.94±0.33 (7.25-8.40)**	**33.80±2.84 (25.00-40.00)**	**5.03±1.72 (1.90-9.16)**	**2.12±2.47 (0.00-11.06)**	**1.61±5.31 (0.00-24.52)**	**5.99±5.83 (1.21-14.90)**	**1.87±3.45 (0.00-15.95)**	**7.93±10.41 (0.11-32.61)**	**10.36±12.27 (0.13-56.80)**	
5. Prymnesiophyceae												
Prymnesium parvum (n=1)	800.00±00.00 (800.00-800.00)	28.00±0.00 (28.00-28.00)	8.00±0.00 (8.00-8.00)	34.00±0.00 (34.00-34.00)	1.50±0.00 (1.50-1.50)	5.60±0.00 (5.60-5.60)	-	-	1.90±0.00 (1.90-1.90)	62.00±0.00 (62.00-62.00)	13.54±0.00 (13.54-13.54)	73
Helladosphaera spp. (n=1)	135.23±0.00 (135.23-135.23)	-	7.72±0.00 (7.72-7.72)	36.36±0.00 (36.36-36.36)	6.51±0.00 (6.51-6.51)	6.84±0.00 (6.84-6.84)	0.97±0.00 (0.97-0.97)	9.10±0.00 (9.10-9.10)	1.22±0.00 (1.22-1.22)	8.27±0.00 (8.27-8.27)	-	56
P. globose (n=1)	25800.00±0.00 (25800.00-25800.00)	-	-	-	-	0.00±0.00 (0.00-0.00)	-	-	0.30±0.00 (0.30-0.30)	-	5.06±0.00 (5.06-5.06)	33
Mean ± SD (Range)	**8911.74±14629.44 (135.23-25800.00)**	**28.00±1.00 (26.00-28.00)**	**7.86±0.20 (7.72-8.00)**	**32.09±3.78 (28.00-36.36)**	**6.03±3.96 (1.41-11.00)**	**5.45±3.14 (0.00-7.80)**	**0.32±0.56 (0.00-0.97)**	**9.10±0.00 (9.10-9.10)**	**1.78±1.91 (0.30-5.00)**	**19.18±28.64 (3.00-62.00)**	**8.82±3.76 (5.06-13.54)**	
6. Raphidophyceae												
Chatonella marina (n=4)	768.18±1355.44 (45.00-2800.00)	27.08±2.12 (25.56-30.20)	7.55±0.43 (7.06-7.86)	32.30±2.79 (29.33-34.87)	2.99±2.57 (0.22-6.42)	3.34±3.90 (0.14-9.02)	0.06±0.05 (0.02-0.12)	0.51±0.01 (0.50-0.51)	1.23±1.23 (0.27-2.99)	4.26±2.04 (2.81-5.70)	16.96±14.12 (8.30-37.97)	26; 39; 50; 64; 65; 70; 74
7. Trebouxiophyceae												
Chlorella marina (n=1)	2.12±0.00 (2.12-2.12)	31.42±0.00 (31.42-31.42)	7.62±0.00 (7.62-7.62)	51.75±0.00 (51.75-51.75)	5.40±0.00 (5.40-5.40)	0.01±0.00 (0.01-0.01)	0.04±0.00 (0.04-0.04)	6.75±0.00 (6.75-6.75)	0.04±0.00 (0.04-0.04)	0.23 ±0.00 (0.23-0.23)	18.41±0. 00 (18.41-18.41)	5

Note: Reference number is mentioned in the reference section in []

* implies value presented in filament/L, n = number of events

water temperature, salinity, irradiance, column stratification stability, and low nutrient conditions as factors favoring its bloom (Liu et al., 2012; van Beusekom et al., 2009). The PrM season in which its bloom occurred was characterized by similar conditions along the coast of India (Supplementary Figures 1—7). Considering the ability of the cyanophyceae (*Trichodesmium*), trebouxiophyceae (*Chlorella marina*) and ciliatea (*Mesodinium rubrum*) to grow favorably under high water temperature and salinity, the incidence of their blooms could increase along the Indian peninsula coast in the near future, as the SST and salinity conditions increase rapidly (Supplementary Figure 3).

3.3.3. Blooms of Bacillariophyceae, Prymnesiophyceae, and Rapdidophyceae

Blooms attributed to the bacillariophyceae, prymnesiophyceae, and raphidophyceae were mainly recorded under a lower water temperature condition of 27.71±2.65°C, 28.00±1.00°C, and 27.08±2.12°C respectively, and lower salinity of 32.52±2.38, 32.09±3.78 and 33.30±2.79 psu respectively as compared to those of the cyanophyceae, trebouxiophyceae, and dinophyceae. Nutrient levels in water during the incidents of prymnesiophyceae and raphidophyceae were much higher (5.45±3.14 and 3.34±3.90 μM for NO_3-N, 1.78±1.91 and 1.23±1.23 μM for PO_4-P, 19.18±28.6 and 4.26±2.04 μM for SiO_4-Si respectively). SiO_4-Si concentration was also high (8.15±10.9 μM), while NO_3-N, NO_2-N, NH_3-N and PO_4-P (1.46±1.67 μM, 0.08±0.11 μM, 0.37±0.52 μM, and 0.51±2.04 μM respectively) were low (Table 3; Figure 4). PC1 indicates that the high and positive weightage of nutrients, i.e., NO_3-N (0.54), PO_4-P (0.55), and SiO_4-Si (0.54), might have been played a crucial role in developing the prymnesiophyceae and raphidophyceae dominated blooms around the Indian peninsula. Hence, PC1 primarily described the key physicochemical factors, i.e., nutrients, which were responsible for the blooms of both taxa. The lower factor weight recorded for SST and salinity revealed that they had minimal influence on the occurrence of their blooms (Table 2).

During the SWM season when blooms of the raphidophyceae and prymnesiophyceae were mostly recorded, eutrophication was apparent along the coast of India (Figure 2; Supplementary Figures 5—7). This high nutrient condition occurred as a result of the upwelling of nutrient-rich deep water and the input of run-offs. Blooms of bacillariophyceae may be primarily triggered by the bioavailability of high nutrients concentration (eutrophication), including silicates, and secondarily influenced by rainfall and river runoff. Therefore, bacillariophyceae blooms were reported in both the PrM and SWM period. Blooms of raphidophyceae and prymnesiophyceae appeared mainly along the southern coast (mainly the south-west), where these conditions were most prevalent (Supplementary Figures 3—7; Figure 4). The low surface salinity associated with their occurrences might be due to the input of freshwater from local rainfall and run-off, as well as the southward advection of low saline waters from the northwest coast by the West Indian coast current, WICC (Behara et al., 2019; Kumar and Mathew, 1997; Subrahmanyam et al., 2011).

Low nutrient conditions observed during the blooms of the bacillariophyceae could be as a result of the fast consumption of nutrients during bloom. Previous studies carried out in the field as well as in the laboratory revealed that the concentration of macronutrients, e.g., NO_3-N, PO_4-P and SiO_4-Si (in the case of diatoms) mostly limited the growth and biomass development of the bacillariophyceae, rapdidophyceae and prymnesiophyceae, wherein faster growth and higher cell density was reached under nutrient replete conditions (Gypens et al., 2007; Schoemann et al., 2005; Wang et al., 2011). The persistent appearance of their blooms in recent decades could be an indication of increasing eutrophication along the coast of India. Madeswaram et al. (2018) assessed the water quality along the coast of India from 1990 to 2015 and revealed that the annual average of NO_3-N increased from < 5 μM to 6 μM, NH_3-N from < 0.5 to 1 μM, PO_4-P from < 1 to 1.7 μM, and SiO_4-Si from < 2 to 10 μM at Kerala coast, Southwest India where most bloom incidents have been reported. This observation might be attributed to increasing sewage discharge, industrial wastes, and agricultural run-off as a result of an increase in population and urbanization (Prema et al., 2017).

3.3.4. Dinophyceae bloom

In general, blooms of the dinophyceae were recorded under wide-ranging SST (25.02—32.13°C), pH (7.25—8.40), salinity (25.00—40.00 psu), NO_3-N (0.00—11.60 μM), NO_2-N (0.00—24.52 μM), NH_3-N (1.21—14.90 μM), PO_4-P (0.00—15.95 μM) and SiO_4-Si (0.11—32.61 μM) conditions (Table 3; Figure 4). This observation corroborates the apparent appearance of blooms of this taxon every season along the coast of India. However, the dominance of its blooms during SWM and along the west coast (particularly south-west coast) suggested that water eutrophication had a major influence. Blooms of *Karenia* and *Cochlodinium* mostly occurred under high NO_3-N (2.26±1.62 and 2.40±0.00 μM respectively) and PO_4-P (5.74±3.71, 15.95±0.00 μM respectively), while those of *Noctiluca, Gonyaulax*, and *Protoperidinium* were recorded under low conditions (2.13±2.75, 1.65±0.00 and 1.12±0.00 μM respectively for NO_3-N, and 0.91±1.28, 0.60±0.00 and 0.27±0.03 μM respectively for PO_4-P). SiO_4-Si concentration was high during the bloom of most of the genera in this taxon (Table 3).

The low nutrient condition recorded during the bloom of *Noctiluca, Gonyaulax*, and *Protoperidinium* could be as a result of high nutrient uptake by bloom biomass, and or their ability to exhibit mixotrophy by simultaneously taking up nutrients in the water and also feeding on other smaller (5 to 60 μm) phytoplankton which is increasing in abundance in response to nutrient input (Jeong et al., 2005; Zhang et al., 2016). Both laboratory and field studies have revealed that diatoms, prymnesiophytes, cryptophytes and other small-sized phytoplankton of 5 to 60 μm constitute important food source for these dinoflagellates (Gomes et al., 2014; Gribble, 2007; Jeong et al., 2005; Kopuz et al., 2014; Stoecker et al. 2017; Turkoglu, 2013; Zhang et al., 2016). These taxa have been reported to be dominant along the southwestern part of the Indian peninsula coast and increase in biomass during the SWM season, which is characterized by nutrient upwelling (Ahmed et al., 2016; Rai and Rajashekhar, 2014; Thomas et al., 2013). The highest incidence of blooms of *Noctiluca,* mainly red *Noctiluca* was recorded in the same location and season (Supplementary Table 1; Figures 2 and 3).

It was observed that green *Noctiluca* predominantly formed bloom in the northwest coast of India, where lower water mixing and higher water column stability and stratification are recorded. The supply of SiO_4-Si in the upper mixed layer of the area is limited as compared to NO_3-N and PO_4-P due to mixing, which does not reach the silicline (Sarma et al., 2019). This condition is likely to have conferred a better condition for the photosynthetic green *Noctiluca* than the heterotrophic red one. It was observed that the range of SST and salinity conditions (25.02—32.13°C and 25.00—40.00 psu respectively) under which blooms of *Noctiluca* were recorded in this study exceeded the optimum of 10—30°C and 28—36 psu respectively specified in the literature (Harrison et al. 2011; Huang and Qi, 1997; Miyaguchi et al., 2006; Tada et al., 2004). This phenomenon implies that the strains which form bloom along the coast of India are adapted to high temperature and salinity. Hence the rising SST and salinity conditions along the Indian peninsula might not pose a hindrance to growth and the formation of their blooms under favorable environmental conditions of high nutrients and prey abundance. Increasing eutrophication, SST, and surface salinity (Supplementary Table 4) could be promoting blooms of the dinophyceae along the coast of India.

3.4. Consequences of MMBs around the Indian peninsula

3.4.1. Impact on human health

Harmful blooms of marine microalgae around the Indian peninsula coast were associated with an adverse impact on human health on different occasions during the study period. Two paralytic shellfish poisoning (PSP) outbreaks were recorded. The first, which occurred in 1981 at Valayar village, Tamil Nadu, southeast coast of India, resulted in the death of 3 individuals while 85 others were hospitalized. The incident happened following the consumption of contaminated *Meretrix casta* by the affected persons (Silas et al., 1982). During the second occasion, which was recorded in September 1997 along Vizhinjam, Kerala, southwest coast of India, *Perna indica* was the vector involved, and 7 deaths, including over 500 hospitalizations were documented (Karunasagar et al., 1998). In general, the victims displayed symptoms typical of PSP, including vomiting, numbness of limbs, and tingling sensation in the facial area. The causative taxa could not be identified in both instances. Similar outbreaks in neighboring waters of Malaysia and the Philippines were recently attributed to the toxic blooms of *Alexandrium tamivayanchi* (Mohammad-Noor et al., 2018) and *Pyrodinium bahamense* (Ching et al., 2015; Suleiman et al., 2017).

Two human intoxication events linked to ciguatera fish poisoning (CFP) were also recently reported. Both events resulted from the consumption of red snapper (*Lutjanus bohar*) contaminated with ciguatoxin (CTX) from an unknown toxic dinoflagellate suspected to be *Gambierdiscus* (dinophyceae). The initial episode, which was recorded in June 2015 along with Mangalore, Karnataka, involved two individuals (Rajeish et al., 2016), while the second one recorded in January 2016 along Trivandrum, Kerala, involved 6 individuals (Rajisha et al., 2017). No human death was recorded during both events. However, the victims presented symptoms including abdominal pain, vomiting, diarrhea, chest burning, paresthesia of the upper and lower limbs, the reversal of hold and old sensations, and tingling sensation in the throat and tip of the tongue within 4—6 hours of consuming the contaminated fish. Mice injected with extract prepared from the tissue of the fish sample displayed signs typical of ciguatera poisoning, including reduced movement activity, diarrhea, paralysis of hind limbs, gasping for air, difficulty in breathing, and finally death. Ciguatoxin-1 (CTX-1) was detected at 17 ng and 16.25 ng per 100 g of flesh during the respective events. The authors emphasized the need for the country to institute a surveillance system that will be geared towards screening seafood landed across the coast of the country as well as consumer's awareness for their safety.

On particular occasions, the strong stench emanating from the massive bloom of *Helladosphaera* sp. (prymnesiophyceae) and *Karenia brevis* (dinophyceae) along Malabar shore, southwestern coast of India was associated with respiratory difficulty in children living in nearby areas (Ramaiah et al., 2005; Robin et al., 2013). The particular event related to *Helladosphaera* sp. resulted in the hospitalization of over 200 children who developed symptoms like chest pain, nausea, and short periods of breathlessness (Ramaiah et al., 2005). In other to confirm whether the toxicity observed during *K. brevis* bloom was due to the production of the neurotoxin, Robin and colleagues subjected extract of mussel (*P. indica*) sampled from the site of bloom to mouse bioassay and observed that the symptoms recorded were not due to such (Robin et al., 2013). Generally, HAB forming species produce toxins under physiological stress conditions. The observation of Robin et al. (2013) might have occurred due to very little or no accumulation of brevetoxins within a primary consumer-like *P. indica*, as *P. indica* can sustain a long time without opening its valves, and avoiding siphoning in adverse hydrological conditions.

3.4.2. Impact of HABs on the ecosystem and associated biota

Three events of harmful *Trichodesmium erythraeum* (cyanophyceae) blooms were associated with the mortality of aquatic animals (Chacko, 1942; Chidambaram and Unny, 1944; Ramamurty, 1970). In a severe case reported by Chacko (1942) at Krusaddai Island, 756 holothurians, 250 fishes belonging to 16 genera and other bottom fauna like crabs, sea urchins, and mollusks were killed along a shoreline of about 2.4 km in one day. Death of the affected animals was mainly attributed to asphyxiation, due to hypoxic conditions in water that resulted from excessive respiration and decay of bloom. Water discoloration, the emanation of noxious smell, and low fish catch were also reported during other blooms of *T. erythraeum* (Karthik and Padmavati, 2017; Krishnan et al., 2007; Mohanty et al., 2010; Verlancar, 1978).

Six incidents of *Noctiluca scintillans* (dinophyceae) bloom were associated with the death of aquatic fauna (Aiyar, 1936; Anantharaman et al., 2010; Bimachar and George, 1950; Mohammed, 2003; Mohammed et al., 2007; Shayak et al., 2005). Marked reduction in fish catch was also documented on five occasions (Bimachar and George, 1950; Devassy and Nair, 1987; Jugnu, 2006; Padmakumar et al., 2010b, 2016a) while in another event fishes caught by fishermen were more or less in exhausted condition (Aiyar, 1936). The death of aquatic biota recorded during blooms of this organism was mainly linked to the release of mucoid substances, which altered the viscosity of water and caused mechanical obstruction, low oxygen condition, and asphyxiation. On another occasion, Naqvi et al. (1998) reported that the mucoid substance released during a bloom of the same organism made smaller fishes bioluminescent at night and therefore exposed them to the predatory ones.

On two occasions, the harmful bloom of *Karenia mikimotoi* (dinophyceae) produced hypoxic conditions in water and also obstructed the gill lamellae of fish, causing asphyxiation and death (Iyer et al., 2008; Robin et al., 2013). Many economic fish species, e.g., *Sardinella longiceps, Arius arius, Seganus javus, Psettodes erumei, Monacanthus hispidus, Diodon hystrix, Anguilla* sp. and *Rastrelliger kanagurta* were killed and the livelihood of local fishermen was also adversely impacted. Iyer et al. (2008) reported that the concentration of H_2S in water reached 1.6 mg L^{-1} following the decomposition of biomass at the end of the bloom. Detrimental *Gonyaulax* (dinophyceae) blooms have also impacted marine waters around the Indian peninsula in a similar manner to those of *K. mikimotoi* (Modayil, 2004; Prakash and Sarma, 1964).

Chatonella marina (raphidophyceae) blooms were implicated in the mass mortality of bivalves, e.g., *Mactra violacea*, demersal fishes, e.g., Eel, sciaenids, croakers, green mussels, and mole crab, and shrimp fishes, e.g., *Chanos chanos, Mugucephalus* sp., *Penaeus monodon, Penaeus indicus, Melapenaeus dobsoni,* and *M. affinis,* etc. (Jugnu, 2006; Sarangi and Mohammed, 2011). In a particular event, an unusually high catch of catfish in disoriented condition was reported (Jugnu, 2006). The toxicity was proposed to be due to the production of haemolytic compounds and hypoxia. A bloom of *Hemidiscus hardmannianus* (bacillariophyceae) was also associated with massive mortality of *Sardinella longiceps, Muraenesox cinerus, Arius maculatus, Lutjanus malabaricus, M. dobsoni,* etc., (Subramanian and Purushothaman, 1985), while that of *Asterionella glacialis* (bacillariophyceae) was linked with a decline in the fish catch (Satpathy and Nair, 1996).

3.4.3. Impact of MMBs on socio-economic status

Harmful events of MMBs around the Indian peninsula pose adverse socio-economic implications. Such effects could be linked with the cost of cleaning affected areas, purifying water for various use, loss of income and revenue associated with a reduction in yield of fish resource and demand for seafood, loss of jobs and productivity, morbidity and treatment, investigation, as well as local aesthetics (Adams et al., 2018; Hoagland et al., 2002). According to Hoagland and Scatasta (2006), economic losses from HABs could be a difficult task, owing to indirect effects that might not be readily accounted for. Financial losses regarding HABs around the Indian peninsula have not been estimated and reported to date. However, it is worthy to note that the west coast of the Indian peninsula where HABs were most pronounced contributes the majority (69.8%) of marine fish landings in the country (Sathianandan, 2017). Substantial impacts could occur in the near future amidst increasing occurrences of blooms. A comprehensive evaluation of economic losses associated with the occurrences of MMBs around the Indian peninsula is highly required for the effective management of India's fisheries potential.

4. Conclusions

A total of 154 events of MMBs were recorded from 1908 to 2017 around the Indian peninsula. Bloom forming species of these MMBs were related to 24 genera belonging to seven taxonomic classes, including cyanophyceae, bacillariophyceae, dinophyceae, raphidophyceae, prymnesiophyceae, trebouxiophyceae, and ciliatea. In the initial years of the 20th century, only dinophyceae blooms were reported. Those of cyanophyceae were reported only after 1937. After that, the bacillariophyceae became reported as bloom-forming species after 1957. The trebouxiophyceae and ciliatea appeared as new bloom-forming taxa in the last decade (2008—2017). Blooms of *Noctiluca* (dinophyceae) and *Trichodesmium* (cyanophyceae) were most predominant around the Indian peninsula and accounted for 34.4% and 31.8% of all incidents, respectively. Occurrences related to the cyanophyceae (*Trichodesmium*) were mainly driven by high SST and salinity, while those of bacillariophyceae, dinophyceae, raphidophyceae and, prymnesiophyceae were promoted by eutrophication. In addition to high nutrient conditions, blooms of *Noctiluca* (dinophyceae) were related to the abundance of prey organisms. Mainly, the cyanophyceae, bacillariophyceae, dinophyceae, raphidophyceae, and prymnesiophyceae caused HABs around the Indian peninsula. The impacts these HABs included environmental perturbation, mass mortality of aquatic fauna, altered fishing activity, human intoxication, e.g., paralytic and ciguatera shellfish poisoning, and even death. The knowledge of the environmental conditions promoting blooms along the coast of India is useful for bloom management planning and decisions. Surveillance programs for phycotoxins levels in the environment and local seafood, as well as sustainable environmental practices, will help to curtail the occurrences and spread of MMBs as well as related HABs around the Indian peninsula.

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Supplementary materials

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The numbers in sqaure brackets refer to Table 3.

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