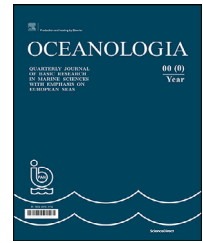




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SHORT COMMUNICATION

First report of *Protoperidinium steinii* (Dinophyceae) bloom from the coastal marine ecosystem – an observation from tropical Indian waters

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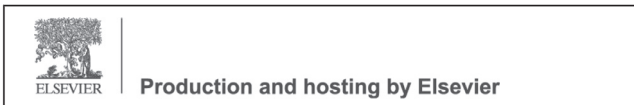
Protoperidinium steinii;
Red tide;
Non-toxic HAB;
Eutrophication;
Backwaters;
Bay of Bengal

Abstract A dense bloom of *Protoperidinium steinii* was observed in the backwaters adjoining the western Bay of Bengal, Kalpakkam coast, which might be the first report for the world oceans. The brownish-red bloom appeared on 2 October 2019, and it was monitored on alternate days up to 14 October. Surface water temperature was about 27.5°C and salinity was <17 PSU during the bloom. Dissolved inorganic nutrients like nitrate, ammonia, silicate, and phosphate were extremely high compared to that of the coastal waters. The chlorophyll-*a* maxima (20.95 mg m⁻³) coincided with the highest *Protoperidinium* density (113.9 × 10⁴ cells l⁻¹). The contribution of *P. steinii* ranged from 17–93% of the total phytoplankton population. Since *P. steinii* is a heterotroph and voracious grazer, low autotroph density was observed during the bloom. No mass mortality of fish or other organisms was observed, thereby indicating the non-toxic nature of the bloom.

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In recent years, an increase in the algal bloom events has been noticed in marine and estuarine waters, which poses a serious threat to environmental health (Glibert, 2017; Lassus et al., 2016; Sathishkumar et al., 2021). The root cause of algal bloom is attributed to the eutrophication of water bodies by natural and anthropogenic sources such as flooding, urbanization, desalination, and sewage (from industrial and domestic sources) disposal. Nutrient pollution/eutrophication in the marine environment (coastal and estuarine) is one of the largest concerns today, which is harmful to the water, soil, and biota (Boto, 1992; Ouyang and Guo, 2016). The bioavailability of nutrients, mainly phosphorus (P) and nitrogen (N) in excess concentrations, lead to unwanted algal blooms (Anderson et al., 2002; Carpenter, 2008; Diaz et al., 2017; Howarth and Marino, 2006) that creates many problems, including hypoxia (dead zones) thereby reducing fish and shellfish production (Wurtsbaugh et al., 2019). Algal blooms either by dinoflagellates, diatoms, or cyanobacteria have long been considered to be the major driver of biodiversity changes (Butchart et al., 2010; Davidson et al., 2012; Pysek and Richardson, 2010). Fishery production is considerably affected by the frequent bloom events by the dinoflagellates (Shaju et al., 2018). Moreover, harmful algal species can produce large amounts of toxins during their blooms, generally termed as harmful algal blooms (HAB), resulting in fish kills, human illness and other significant marine environmental changes (Lassus et al., 2016). Although severe poisoning of humans by fresh and brackish water cyanotoxins is rare, aquatic animals are frequently killed as they consume bloom impacted waters (Henriksen et al., 1997; Stewart et al., 2008). Despite this trouble, algal bloom events are also an important indicator of the hydrological health of the marine ecosystem and play a key responsibility in carbon cycling and aquatic dynamics. Thus, the monitoring of algal blooms is necessary to manage marine resources and the defense of general health (Gokul and Shanmugam, 2016).

This paper reports a dense bloom of the dinoflagellate *Protooperidinium steinii*, which is a heterotroph. Heterotrophic dinoflagellates (HTDs) have been recognized as omnipresent in the marine pelagic ecosystem (Sherr and Sherr, 2007). It is also found that about half of the dinoflagellate species in the marine ecosystem lack chloroplasts and consume other plankton cells as their staple food. Hence, often they are also considered microzooplankton-protists. The heterotrophic dinoflagellates potentially play an important role as herbivores. As herbivores, both thecate and athecate species of heterotrophic dinoflagellates consume diatoms, which has implications for biogeochemical cycles. Heterotrophic dinoflagellate grazing contributes to the recycling of silica, carbon, inorganic nitrogen, and phosphorus via excretion of dissolved and particulate matter (Caron et al., 1990; Kirchman, 2000; Sherr and Sherr, 2007). Apart from their role as herbivores, they (especially athecate heterotrophic dinoflagellates) serve as, both quantitatively and qualitatively, significant food reserves for the zooplankton community, i.e. mainly copepods and metazoans (Levinsen et al., 2000; Liu et al., 2005; Olsen et al., 2006; Suzuki et al., 1999; Vincent and Hartmann, 2001). Heterotrophic dinoflagellates also act as predators for bacteria, heterotrophic protists, some of the metazoans; eggs

and naupliar stages of some copepods, and other dinoflagellates (Jeong, 1999).

A review of available literature from all over the world indicated that the bloom of this particular species (*Protooperidinium steinii*) has never been reported from elsewhere (Encyclopedia of Life (EOL), 2012; D'Silva et al., 2012; Satpathy and Mohanty, 2008; Sahu et al., 2014). Thus, the present study is potentially the first report of *P. steinii* bloom observed in the backwaters of Sadras, Kalpakkam coast, Bay of Bengal (Figure 1a). Though sporadic appearances of *P. steinii* have been reported from estuarine, coastal, and offshore waters of India (Table 1S), it never formed a bloom. Moreover, there are only a few reports of bloom for this genus from Indian waters viz; *Protooperidinium divergens* (Raji and Padmavati, 2014), *Protooperidinium* sp. (Sanilkumar et al., 2009), *Protooperidinium pallidum* (Ramesh et al., 2019), *Protooperidinium quinquecorne* (Goswami et al., 2020). Here, we disseminate the results of ecological monitoring and exhaustive morphological observations of the heterotrophic dinoflagellate (HTD) bloom species. The bloom of *P. steinii* did not give the impression to cause any toxic incident (e.g., fish kills) during the present study. Although reports are available regarding the grazing behavior of *P. steinii* (Olseng et al., 2002), no reports were found on the toxic behavior of this species. Though the bloom was non-toxic, impacts of the bloom on water quality and phytoplankton community could be observed during the study. Thus, the present bloom can be categorized as non-toxic HAB as has been reported by various authors (Anderson, 2009; Fock and Greve, 2002; Montani et al., 1998; Smayda, 1997). The occurrence of non-toxic HABs is a common phenomenon throughout the world's oceans and more so in India, where species such as *Asterionellopsis glacialis*, *Trichodesmium erythraeum*, *Noctiluca* spp. etc have been reported to form non-toxic blooms frequently (Jyothibabu et al., 2017; Mishra et al., 2005; Mohanty et al., 2007; Mohanty et al., 2010; Padmakumar et al., 2012; Sahu et al., 2016).

An intense bloom of *Protooperidinium steinii* was observed on 2 October 2019 in the backwaters (12.510706°N, 80.160174°E) at Kalpakkam, southeast coast of India, during the early northeast monsoonal period. The water discoloration (brownish red tide) was observed in about 1.5 km length and 100 m width in the Sadras backwater region (Figure 1b). In general, this backwater is a biodiversity-rich area with oysters, bivalves, other edible fishes, and mangroves thriving in it. Also, the backwater is a visiting and breeding ground for many non-native birds (e.g., the rarely seen Siberian crane in the depths of winter). The backwater receives domestic and agricultural wastes directly from the catchment area and indirectly through the Buckingham Canal that runs parallel to the coast. A detailed description of the study area is available in previous literature (Mohanty et al., 2014). The backwater opens to sea for a brief period, 2–3 months, during the northeast monsoon (October–December) season and remains closed during the rest of the year. Generally, this backwater ecosystem is shallow, with the highest depth of ~2 meters. The bloom was monitored on alternate days from 2 to 14 October 2019 (The materials and methods of this manuscript are provided in the supplementary).

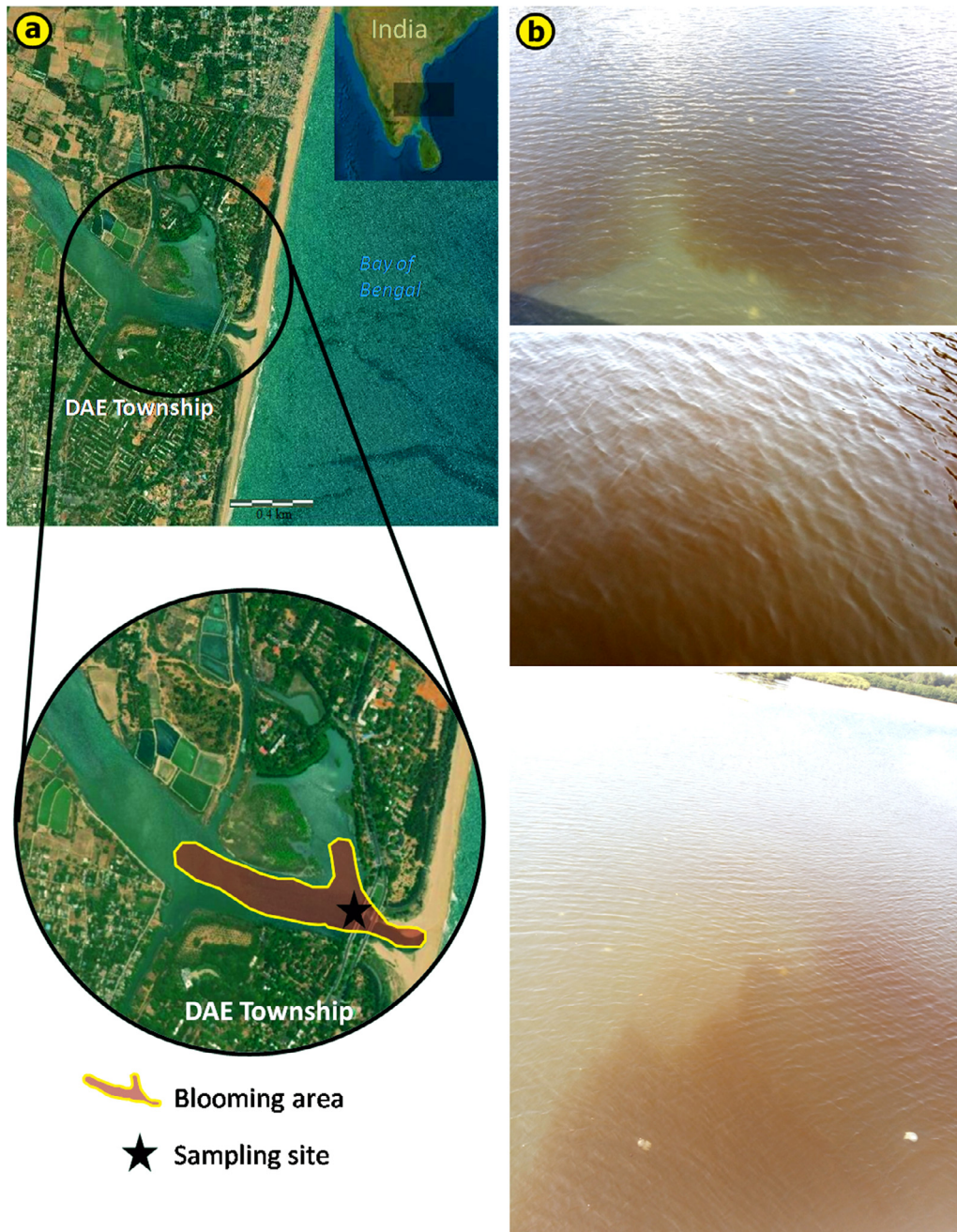


Figure 1 Map showing the bloom area (~) and sampling location (a); surface water discoloration of Sadras backwater, Southeast coast of India (b).

Taxon Description (morphology): (i) Cells sometimes medium or small-sized. (ii) The main cell body rounded (Figure 2). (iii) Epithea extending in a long apical horn and prominent three-winged antapical spines (Figure 3). (iv) Hypotheca hemispherical. (v) The left side of the sulcus is usually bordered by a pronounced list. Species heterotrophic and often pink or yellowish, feeding by means of a pallium. In live samples, “group attack” has been observed. One cell attaches to the prey, followed by several more individuals (Figure 2c). In culture, this species does not grow with immobile prey (Encyclopedia of Life (EOL), 2012).

The genera *Protoperidinium* is under the phylum of dinoflagellate and belongs to the order Peridiniales. Gómez (2005) described more than 260 species of *Protoperidinium*, which may be found worldwide. Its size may vary between 50 to 100 μm and the color of these organisms can be visible in red, brown or yellow, which mostly depends on their selection of food (Olenina et al., 2006). In our case, the average size of collected species ranged between 38–56 μm (Diameter) and 22–34 μm (Length) (Figures 2–3). In general, *Protoperidinium* is classified into two subgenera (*Protoperidinium* and *Archaeperidinium*) based on their numbers of thecal plates (2–6) (Gul and Nawaz, 2014). Commonly,

Table 1 Physicochemical variables at different day intervals during the bloom event (October 2019).

Parameters	Present study						Previous values 2016–17
	2-Oct	4-Oct	6-Oct	8-Oct	10-Oct	14-Oct	
Temperature (°C)	26.4	27.3	28.1	29.5	29.2	29.7	31.15 ± 0.8
pH	7.65	7.98	8.17	8.16	8.23	8.25	7.94 ± 0.3
Salinity (PSU)	16.8	16.82	17	17.13	17.23	17.29	21.27 ± 4.9
Turbidity (NTU)	15.9	5.1	5.3	3.6	3.1	3.2	NA
Dissolved Oxygen (mg l ⁻¹)	5.41	3.18	3.23	4.1	4.69	4.53	6.75 ± 1.4
Nitrate (μM l ⁻¹)	17.65	12.38	11.13	10.8	9.3	11.32	11.05 ± 7.6
Orthophosphate (μM l ⁻¹)	30.5	26.5	24.8	25.9	26.1	27.0	6.32 ± 2.1
Silicate (μM l ⁻¹)	239.2	248.4	230.3	211.2	197.8	223.0	102.72 ± 51.1
Ammonia (μM l ⁻¹)	21.15	27.96	19.15	40.2	30.76	31.1	6.55 ± 2.8
Total Nitrogen (μM l ⁻¹)	143.0	125.9	107.2	117.2	107.8	107.4	62.40 ± 8.4
Total Phosphate (μM l ⁻¹)	32.9	27.0	26.0	26.8	27.2	27.4	6.97 ± 1.8
Chlorophyll- <i>a</i> (mg m ⁻³)	20.95	5.33	2.21	0.28	0.32	0.33	5.80 ± 4.1

NA: not available

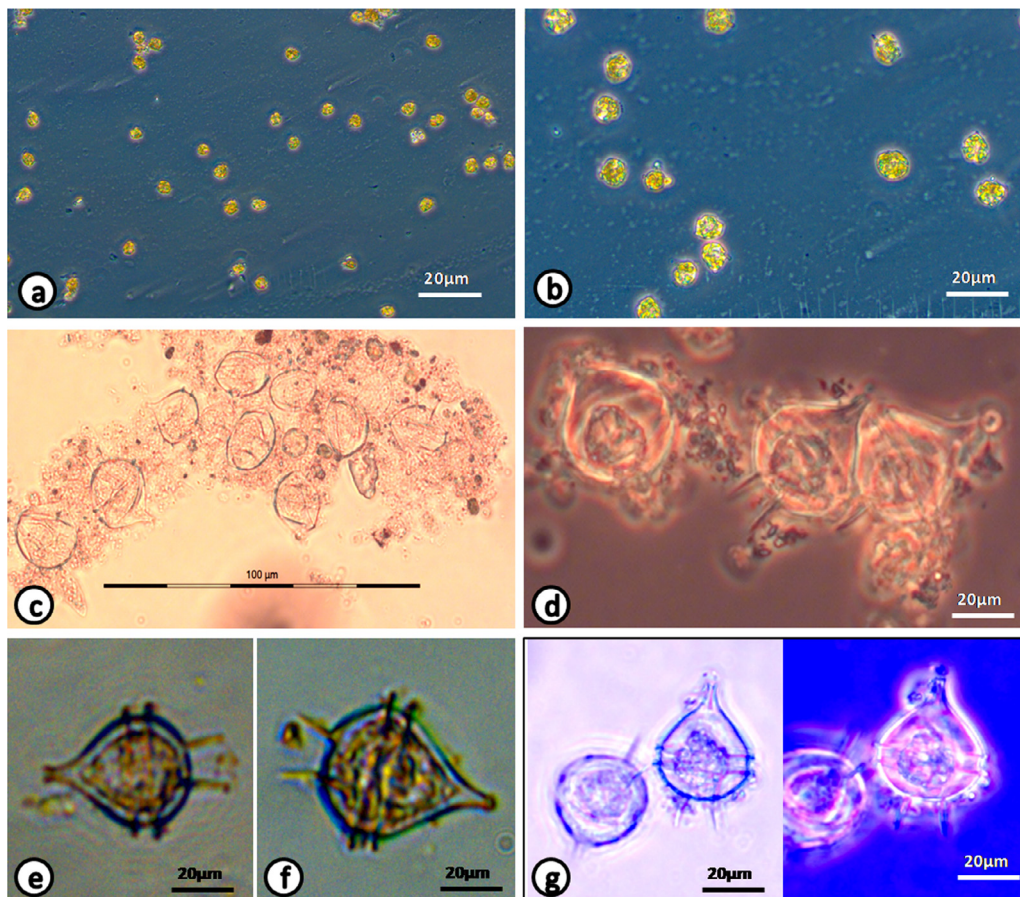


Figure 2 Microscopic view of the blooming dinoflagellate *Protoperidinium steinii*; Figure shows the cyst of *P. steinii* at 200 × and 400 × magnifications (panels a, b); different magnifying views of *P. steinii* (c, d); developmental stages of the *P. steinii* (e, f); Fluorescence image of adult species (g).

these organisms are found in both coastal and oceanic waters, rarely occur in estuarine and brackish waters, preferring warmer to tropical climates (Gribble et al., 2007). The heterotrophic dinoflagellates (HTDs) do not filter small particles from the water as some ciliates do (Jacobson and Anderson, 1986); instead, they capture individual phytoplank-

ton cells, which can be approximately as large as them or larger, and either engulf the entire cell or move the captured cell's body fluids into themselves through a pallium or peduncle (Jacobson and Anderson, 1986). In *Protoperidinium*, the pallium is made from the cytoplasm. Its prey foremost of diatoms (e.g., *Ditylum brightwellii*

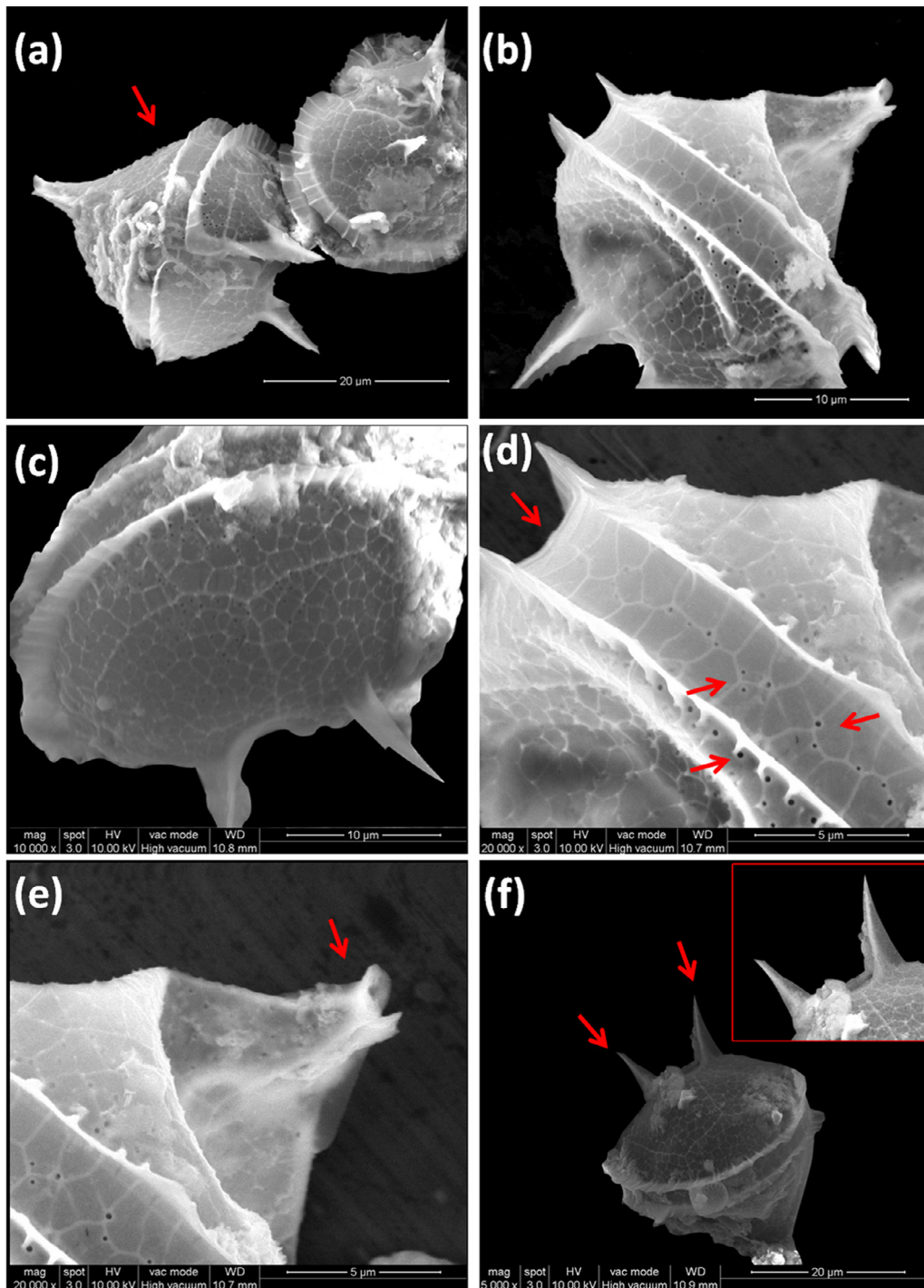


Figure 3 Morphological characteristics of bloom forming dinoflagellate *Protoperidinium steinii* under FE-SEM at different scaling views: (a) ventral view; (b) dorsal view; (c) antapical view; (d) cingulum with pores; (e) apical horn; (f) antapical horns.

and *Thalassiosira* sp.) and dinoflagellate (*Gonyaulax polyedra*) (Buskey, 1997). *Protoperidinium* is known to be “picky eaters”. Some species of this particular taxa can survive very longer periods; for example, *Protoperidinium depressum* can survive up to 71 days in conditions of starvation or lower food availability (Gribble et al., 2007). Smaller to larger sizes of diatoms and dinoflagellates are the prime food source for *Protoperidinium*, and their proliferation may stimulate to cause a red tide of *Protoperidinium*.

The variations in physicochemical parameters during the bloom event (2–14 Oct 2019) are given in Table 1. Surface water temperature during this period ranged from 26.4°C to 29.7°C. The observed temperature seems to be conducive for the bloom of this genus, as has been reported by Raji and Padmavati (2014) during the *Protoperidinium divergens* bloom in the Andaman Bay region. The correlation results showed a negative relation between dinoflagellates and temperature (Table 2) which could be attributed

Table 2 Correlation matrix (Pearson (n)) of environmental variables and biological parameters measures during *Protoperidinium steinii* bloom.

Variables	Temp	pH	Salinity	Turbidity	DO	Nitrate	Phosphate	Silicate	Ammonia	TN	TP	Chl-a	Dino	Diatoms	Cyano	<i>P. steinii</i>	
Temp	1																
pH	0.904	1															
Salinity	0.953	0.847	1														
Turbidity	-0.831	-0.948	-0.710	1													
DO	-0.051	-0.386	0.155	0.534	1												
Nitrate	-0.821	-0.955	-0.733	0.964	0.465	1											
Phosphate	-0.597	-0.844	-0.448	0.871	0.766	0.896	1										
Silicate	-0.775	-0.639	-0.819	0.512	-0.303	0.656	0.365	1									
Ammonia	0.713	0.470	0.557	-0.573	0.046	-0.502	-0.267	-0.560	1								
TN	-0.824	-0.975	-0.809	0.878	0.389	0.915	0.841	0.599	-0.270	1							
TP	-0.653	-0.878	-0.495	0.936	0.770	0.913	0.978	0.324	-0.359	0.848	1						
Chl-a	-0.863	-0.975	-0.748	0.990	0.518	0.973	0.897	0.562	-0.548	0.920	0.942	1					
Dino	-0.970	-0.948	-0.941	0.840	0.127	0.879	0.703	0.810	-0.565	0.913	0.717	0.891	1				
Diatoms	-0.788	-0.941	-0.647	0.986	0.622	0.968	0.939	0.488	-0.512	0.886	0.976	0.990	0.826	1			
Cyano	-0.409	-0.711	-0.233	0.813	0.920	0.764	0.932	0.040	-0.162	0.702	0.954	0.804	0.483	0.871	1		
<i>P. steinii</i>	-0.830	-0.649	-0.906	0.434	-0.373	0.523	0.273	0.878	-0.453	0.640	0.251	0.515	0.848	0.405	-0.033	1	
<i>P. steinii</i> C	-0.759	-0.931	-0.621	0.987	0.654	0.952	0.929	0.421	-0.477	0.878	0.979	0.982	0.792	0.995	0.893	0.349	1

Values in bold are significantly different from 0 with a significance level $\alpha=0.05$ (Dino – total dinoflagellates; Cyano – cyanobacteria; *P. steinii* C – Cysts)

to the fact that the abundance of dinoflagellates including *P. steinii* gradually decreased with an increase in temperature. The pH values (7.65–8.25) showed a gradual increase from the 2nd to 14th October. A change in pH is mostly fluctuated by environmental influence and carbon (CO₂) removal through the autotrophic process by phytoplankters as well as freshwater influx and decomposition of organic matter (Rajasegar et al., 2002). In the present study, the increase in pH during the post-bloom period could be attributed to the rate of photosynthesis. As *Protoperidinium steinii* is a heterotroph and voracious grazer (Archer et al., 1996; Hansen 1991; Lessard 1991), the low autotroph density, mainly diatoms, and cyanobacteria, during the bloom could have resulted in a reduced primary production rate, thereby decreasing the water pH. On the other hand, when the dinoflagellate density gradually decreased from bloom to post-bloom period, the diatom and cyanobacteria density gradually increased (Figure 4). This could have caused an increase in photosynthesis rate which further led to the increase in water pH. The above hypothesis is supported by the fact that, when florae eradicate carbon dioxide (CO₂) by photosynthesis process, carbonate gather and after that undergoes hydrolysis to supply the OH⁻. The higher concentration of OH⁻ increases pH (Boyd and Pillai, 1985). A similar increase in water pH due to enhanced photosynthesis rate has been reported in confined water bodies (Satpathy, 1996; Mohanty et al., 2017). In the present study, pH developed a negative correlation with phytoplankton density. This could be due to the fact that pH values were low during the initial phases of bloom when the autotroph density was high. Though during the post-bloom periods, the autotroph densities gradually increased, the overall correlation between them was negative due to large differences in autotroph abundance from bloom to post-bloom period. Salinity (16.80–17.29 PSU) was relatively low during the bloom and post-bloom period. Though the salinity variations were not high enough, a gradual increase in salinity was noticed during the study. Similar to that of temperature and pH, salinity also developed a negative correlation with dinoflagellate cell density. Low salinity of the water has been reported to favor the dinoflagellate proliferation especially the benthic species (Accoroni and Totti, 2016). Considerably high turbidity was (15.90 NTU) observed during the bloom which coincided with the high cell density (*Protoperidinium* cyst) and the water turbidity gradually decreased during the post-bloom period. The above observation was supported by the positive correlation of turbidity with all the biological components of the study. Various authors also have reported a similar increase in water turbidity due to high phytoplankton densities (Kalimurthy, 1973; Satpathy et al., 2010). The dissolved oxygen (DO) contents varied between 3.18–5.41 mg L⁻¹. The highest concentration was observed on the day of bloom whereas the lowest concentration was recorded on the 3rd day of bloom. This abrupt decrease in DO might be due to the rapid consumption of oxygen by *Protoperidinium*, which is a heterotroph. Besides, as described earlier, the low autotroph density during that period could also have caused a low photosynthetic DO production. Similarly, the gradual increase in DO content during the post-bloom period could be attributed to the increased photosynthetic activity of the autotrophs. The positive correlation of DO with cyanobacteria that dominated the autotroph popula-

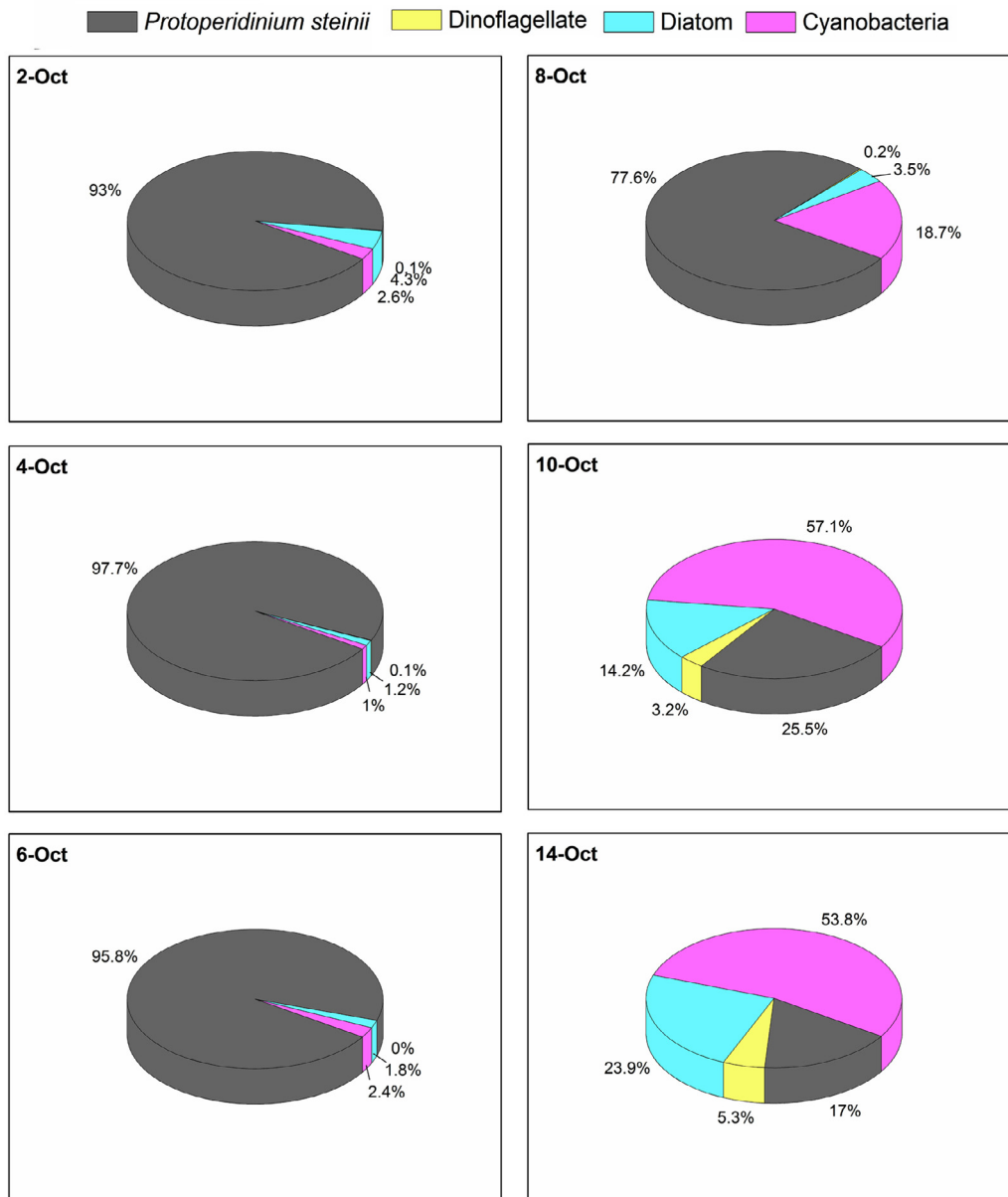


Figure 4 Pie chart shows the percentage contribution of *Protoperdinium steinii* along with other phytoplankton groups during the bloom event (2–14 October 2019).

tion during the post-bloom period supported the above observations (Table 2).

Nitrogen and phosphorus are the two essential nutrients that cause eutrophication leading to luxuriant algal growth when their concentrations exceed certain limits (Vollenweider et al., 1998; Nasrollahzadeh et al., 2008). In the present study, nitrate concentration was very high ($17.65 \mu\text{M l}^{-1}$) on the 1st day of bloom, and relatively low values were observed during the 3rd and 5th day (Table 1). The concentration of nitrate was significantly low during the post-bloom period, about 6–7 times that of during the bloom. It indicated that nitrate was consumed by the diatom and cyanobacteria species which were present in good numbers during the early stages of bloom. However, the subsequent increase in the adult population of *P. steinii*, which

resulted in a decrease in other phytoplankton densities, could be the reason for the almost similar nitrate concentrations observed during the post-bloom periods. The above observation was supported by the positive correlation of nitrate with diatoms and *P. steinii* cysts. Interestingly, adult *P. steinii* did not show any significant correlation with nitrate, downplaying its role in the HTD proliferation. Though nitrate is thermodynamically the most stable form of combined inorganic nitrogen, the fluctuation in nitrate and its reduction mainly depends on biological activities such as quick utilization by phytoplankton and nitrogen fixers (De Souza, 1983; Moran and Zepp, 1997; Qasim, 1977). The ranges of other nitrogenous nutrients like ammonia (61.15 to $19.15 \mu\text{M l}^{-1}$), total nitrogen (143 – $107.20 \mu\text{M l}^{-1}$) also indicated that the backwater is severely affected by eu-

trophication. Relatively low ammonia concentrations were observed during the bloom as compared to the post-bloom period. Ammonia is an important nutrient, sometimes which is preferred more than nitrate by the phytoplankton species in particular environmental conditions (Gilbert et al., 1982; Olson, 1980). Besides, the excretory release of ammonia by invertebrates also significantly impacts its dynamics in the aquatic environment. The present observation of relatively low ammonia concentration during early bloom could be attributed to its utilization by autotrophs. Phosphate and total phosphorus concentrations ranged from 24.80–30.50 $\mu\text{M l}^{-1}$ and 26–32.90 $\mu\text{M l}^{-1}$ respectively. The values did not show any particular trend except the relatively high concentration recorded on the 1st day of bloom. Phosphate showed a positive correlation with diatoms, cyanobacteria and *P. steinii* cysts. Similar to that of nitrate, adult *P. steinii* did not show any significant correlation with phosphate as well. Silicate concentrations ranged from 197.8–248.4 $\mu\text{M l}^{-1}$. The highest silicate content coincided with the peak density of adult *P. steinii* and its concentration decreased subsequently during the post-bloom period. Silicate showed a positive correlation with adult *P. steinii* density. It indicated the release of silicate due to grazing on diatoms and utilization of silicate by autotrophs during low heterotroph (*P. steinii*) densities (Caron et al., 1990; Kirchman, 2000; Sherr and Sherr, 2007). The phosphate was four times higher and the silicate was two times higher as the previous values in the same saltwater region, respectively. The higher concentration of phosphate and silicate was mostly loaded by the terrestrial runoff that contains more quantities of wastes from agriculture, aquaculture, and domestic sewage etc.

A comparison of present nutrient concentration with previous data (2016–2017) from the same location (Table 1) indicated a considerable increase in phosphate, silicate, ammonia, TN, and TP concentrations during this particular period. Since *P. steinii* is a heterotroph, nutrients may not directly affect the trigger mechanism of its bloom. However, as reported by others, the present *P. steinii* bloom could be a successor of a diatom or dinoflagellate bloom (Nakamura et al., 1995, 1995a; Tiselius and Kuylenstierna, 1996) that might have occurred in the recent past. The present observation of the heterotrophic bloom could be categorized into the GM1 (Generation mechanism 1) out of the four GMs theorized by Jeong et al. (2015). In GM1, the growth of red tide forming organisms takes place in the presence of nutrients and light, which ultimately end by increased heterotrophic population as they graze upon the autotrophs. The present instance falls in GM1, as the vertical migration, which is an essential component of GM2–GM4, will be negligible in the present study due to low water depth (2 m). It has been proved that heterotrophic dinoflagellates, which are opportunistic, grow well after autotrophic blooms, especially diatom blooms (Olseng et al., 2002). While the majority of *Protoberidinium* species appear to be diatom grazers, some can utilize, and may even require, dinoflagellate prey for their proliferation (Buskey, 1997; Buskey et al., 1994; Hansen, 1991; Jacobson and Anderson, 1986; Jeong and Latz, 1994; Jeong, 1999). While *Protoberidinium* spp. can feed on prey larger than themselves (Jacobson and Anderson, 1986), they occasionally have difficulty feeding on small organisms. For example, *P. pellucidum* and *P. huberi* generally consume dinoflagellates

and diatoms but do not prefer to feed on small flagellates belonging to the class prymnesiophyceae, cryptophyceae, and chlorophyceae (Jeong, 1999). Chl-*a* concentration was relatively high in the brownish water with a maximum of 20.95 mg m^{-3} during the bloom period (2 October). Various reports have also found a similar higher concentration of chl-*a* during the bloom of dinoflagellate around the Indian coasts (Baliarsingh et al., 2016; Baliarsingh et al., 2017; Padmakumar et al., 2018; Vijayalakshmy et al., 2018). Very low chl-*a* concentration during post-bloom periods could be attributed to the low autotrophic biomass during that period.

Phytoplankton community structure showed a remarkable variation from bloom to post-bloom period. During the study, 33 species of phytoplankton were recorded, which comprised of 11 dinoflagellates, 21 diatoms, and 1 cyanobacterium species (Table 2S). The total phytoplankton density varied from 2.8×10^4 – 122.5×10^4 cells l^{-1} . The highest density was recorded on the day of bloom (2 October) in which the contribution of *P. steinii* cysts was about 1.5 times higher than the adults (Figure 5). However, on the 3rd day of bloom (4 October), the adult density exceeded the cyst density by 20 times. This indicated the rapid growth of the cysts to adults in two days. The contribution of *Protoberidinium steinii* during the study ranged from 17–93% of the total phytoplankton population (Figure 4). The diatom densities showed a gradual decrease from the day of the bloom up to the 6th day (from 5.27×10^4 to 0.54×10^4 cells l^{-1}) and after that, a steady increase in density was observed (Figure 5). Among the diatoms, the abundance of *Nitzschia sigma* showed drastic changes during the bloom. The population density of *Oscillatoria* sp. (cyanobacterium) also showed a similar trend as that of diatoms. The above observations indicated a significant impact of the early phase of bloom on other phytoplankton groups, during which *P. steinii* cysts grew into adults rapidly. Similar observations of low diatom density during dinoflagellate blooms have been reported earlier (Alkawri et al., 2016; Baliarsingh et al., 2016, 2017; Mohanty et al., 2007).

This could be mainly attributed to the heterotrophic nature of *P. steinii* that creates a tremendous grazing pressure on other phytoplankton (Archer et al., 1996; Hansen, 1991; Kjæret et al., 2000; Lessard, 1991). With the decline of the bloom biomass, the population density of other phytoplankters gradually increased due to the reduction of grazing. Grazing by HTDs in natural populations and laboratory studies has been well documented (Jeong, 1999; Jeong et al., 2015; Olseng et al., 2002). Though the rate of grazing in the case of HTDs is low as compared to ciliates, the presence of the HTDs in high numbers results in the removal of prey by them in larger quantities as compared to other heterotrophs (Jeong, 1999). Due to this process, HTD grazing is also thought to contribute to the decline of autotroph bloom in some coastal waters (Eppley and Harrison, 1975; Jeong et al., 2015; Nakamura et al., 1992; Williams and Eppley, 1967).

Protoberidinium spp. Have been observed to graze upon diatoms and dinoflagellates such as *Leptocylindrus danicus*, *Ditylum brightwellii*, *Thalassiosira* sp., *Skeletonema costatum*, *Gonyaulax polyedra*, *Gymnodinium sanguineum*, *Prorocentrum micans*, *Ceratium furca* etc. (Jeong, 1999; Olseng et al., 2002). During the present study, many of

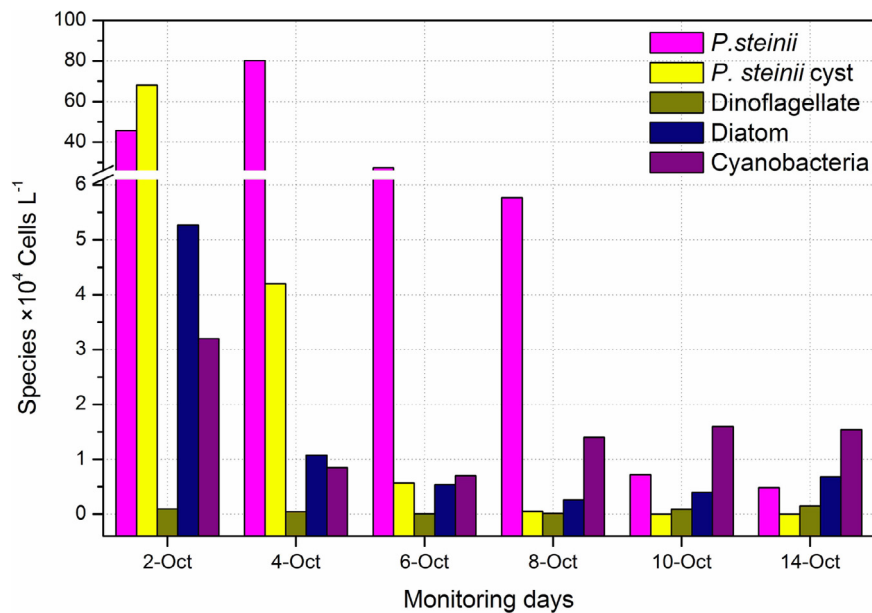


Figure 5 Abundance of *Protoperidinium steinii*, *P. steinii* cysts and other co-occurring phytoplankters during the bloom period in Sadras backwaters.

these species were not available in the autotrophic biomass. However, the significantly declined abundance of *Nitzschia sigma* and *Oscillatoria* sp. indicated that *Protoperidinium steinii* perhaps preyed upon these autotrophs, which has never been reported earlier. Maximum ingestion and clearance rates of HTDs on phytoplankton generally range from 0.01–1 ng C per grazer per h and 0.01–3 μ l per grazer per h, respectively (Jeong, 1999). For *Protoperidinium* spp., the ingestion rate varies from 0.06–0.74 ng C per grazer per h and the clearance rate is 0.05–28.3 μ l per grazer per h. The growth rate of *Protoperidinium* spp. has been reported in the range of 0.005–0.05 per h. Considering the highest growth rate, the doubling time of the *P. steinii* would be about 48 h. Thus, the abundance of adult *P. steinii*, which was almost double on the 3rd day as compared to the 1st day, could be attributed to their rapid growth rate. However, the total dinoflagellate population density including *P. steinii* cysts showed some reduction on the 3rd day, which could be attributed to the decline in prey biomass as well as cannibalistic effects in absence of suitable prey. It has been reported that *Protoperidinium divergens* uses cannibalism, in the absence of unfavorable prey, for prolonged survival and to maintain similar bioluminescence levels as observed under favorable prey conditions (Latz and Jeong, 1996).

The *P. steinii* bloom persisted for a brief period in the backwaters. Though we have been monitoring these water bodies for more than a decade, such a phenomenon has never been encountered. The bloom had a significant impact on the phytoplankton community and other physicochemical properties of the water body. Being a heterotrophic dinoflagellate, *P. steinii* bloom is mainly dependent on food availability rather than water quality. Continuous monitoring and in-depth analysis of the environmental conditions are required to ascertain the triggering mechanisms for such an event.

Declaration of Competing Interest

The authors declare that there is no conflict of interest in this manuscript.

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.oceano.2021.04.003>.

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