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Bioluminescent bloom dynamics of *Gonyaulax spinifera* at Kumbalangi, Kochi, south-west coast of India

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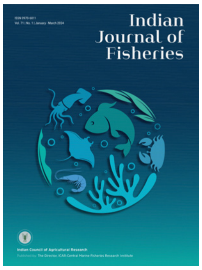

Abstract

Several bioluminescent bloom events have been reported in the coastal, oceanic, and island waters of India since 1890. In recent years, Kerala has experienced multiple episodes of bioluminescent blooms, with Kumbalangi, a well known bioluminescent bloom hotspot on the south-west coast of India, repeatedly witnessing such events for the past several years. To investigate the bloom dynamics and associated environmental drivers, the Kumbalangi bloom area was monitored regularly from May 2023 to September 2024. During this period, a total of 67 species of diatoms, 19 species of dinoflagellates, 10 species of Chlorophyceae, 11 species of Cyanophyceae, and a few representatives of Euglenophyceae and Amoebozoa, were identified, with diatoms constituting the dominant component of phytoplankton community. Bioluminescent blooms of the dinoflagellate *Gonyaulax spinifera* were observed during the pre-monsoon season. Principal component analysis (PCA) revealed that the aquatic environment was mainly influenced by salinity, dissolved inorganic nitrogen (DIN), and dissolved inorganic silicate (DISi). *G. spinifera* exhibited a strong positive correlation with salinity ($r=0.75$, $p<0.05$), suggesting that elevated salinity favoured its proliferation. The high Simpson dominance index, coupled with low Simpson diversity index, and Shannon–Wiener diversity index values, confirmed the occurrence of a monospecific bloom of *G. spinifera* during the bloom period. Presence of *G. spinifera* cysts were also recorded from the area, which indicates its potential for persistence and recurrence under favourable environmental conditions.

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Introduction

Bioluminescent algal blooms, commonly known as “sea sparkles”, and locally referred to as “kavaru”in malayalam, are natural phenomena observed in marine and coastal waters. The bioluminescence of these aquatic organisms is triggered by mechanical disturbances in the surrounding water, which cause physical deformation of the cell membrane (Maldonado and Latz, 2007), This generates an action potential across the vacuole membrane, leading to a decrease in pH within specialised luminogenic organelles known as scintillons (De Sa *et al*., 1963). The resulting acidic conditions activate the luciferase enzyme, which catalyses the oxidation of the light-emitting protein luciferin, resulting in the emission of intense flashes of blue-green light (Haddock *et al*., 2010).

According to the latest updates of AlgaeBase, 3912 species of dinoflagellates belonging to 711 genera have been documented (Guiry, 2024), of which 68 species are known to exhibit bioluminescence (Marcinko *et al*., 2013). Bioluminescent dinoflagellates include members of the genera *Noctiluca, Pyrocystis, Pyrodinium, Alexandrium, Gonyaulax,* and *Protoperidinium* (Baker *et al*., 2008). In photosynthetic bioluminescent dinoflagellates, light emission is regulated by an endogenous circadian clock, which modulates bioluminescence according to the time of the day. The oxidation of luciferin by luciferase, responsible for light production is most efficient under low light conditions/ darkness and at low oxygen tension (Soli, 1966). Therefore, bioluminescence is more pronounced during the night, even though low levels of light emission may also occur during daylight hours.

Bioluminescence serves several ecological functions, including reducing predation pressure by initiating a burglar-alarm mechanism, whereby light emission attracts secondary predators that may attack the initial predator (Burkenroad, 1943), Species-specific bioluminescence is believed to attract mates and as a camouflage tool (Widder, 2002). Despite their spectacular visual appeal, bioluminescent blooms can adversely affect the aquatic ecosystems and human health. Algal bloom formation can result in water discolouration, development of a slimy surface layer, and unpleasant orders, altering the water quality of the area. Certain bloom forming dinoflagellates produce potent toxins, such as saxitoxins (STXs) and yessotoxins (Cusick and Widder, 2020), which can cause fish kills, shellfish poisoning and other harmful ecological and public health impacts (Hallegraeff,1993).

In recent years, both the frequency and spatial extent of algal bloom events have increased. In India, blooms caused by a variety of phytoplankton species including *Cochlodinium polykrikoides*, *Karenia brevis*, *K. mikimotoi*, *Noctiluca scintillans*, *Trichodesmium erythraeum*, *T. thiebautii*, and *Chattonella marina*, have been reported from both the west and east coasts (Barathan and Sarangi, 2024). A total of 26 bioluminescent bloom events were reported from the coastal, oceanic, and island waters of India between 1890– and 2023 (Prasad *et al*., 2023). The apparent increase in bloom reports may partly reflect public awareness and rapid dissemination of information through social media and other digital platforms. Among the bloom forming phytoplankton, dinoflagellates are the predominant group reported from the different regions of the country. *Noctiluca scintillans* has been the most frequently reported bloom forming species, accounting for a large proportion of the reported bioluminescent events (Padmakumar *et al*., 2010, 2016; Vijayalakshmy *et al*., 2018; Parvathi *et al*., 2021; Samanta *et al*., 2023; Zedi *et al*., 2025).

Bioluminescent blooms in Kumbalangi have been reported regularly by major dailies since 2015. During a bloom event in 2020, *Gonyaulax spinifera* was identified as the causative species responsible for the occurrence of bioluminescence in Kumbalangi (Vishal *et al*., 2021). Similar bloom events have also reported at nearby locations, such as Kallanchery, Anjilithara, Attathadam, and Kulakaadavu, particularly during the month of March. The bioluminescent properties of *G. spinifera* were first confirmed by Kelly and Katona (1966) and several subsequent studies have investigated the mechanisms and ecological significance of bioluminescence in this species (Hanley and Widder, 2017; Vishal *et al*., 2021). Previous studies have also examined the water quality parameters such as dissolved oxygen, temperature, pH, salinity, and chlorophyll concentration, along with the nutrient contents (nitrite, nitrate, silicate, and phosphate) of the sites, which are known to influence bloom initiation and persistence (Venugopal *et al*.,1979; Padmakumar *et al*., 2010).

In this study, we attempted to quantitatively evaluate the differences in phytoplankton community composition between bloom and non-bloom periods and related these changes to the environmental and sediment characteristics of the Kumbalangi bloom area. Particular emphasis was placed on the occurrence of *G. spinifera* blooms and the associated shifts in the phytoplankton community structure of the water body.

Materials and methods

Study area and sampling site

The study area comprises confined waterbodies of Kumbalangi, a small coastal village in the Ernakulum District of Kerala State, along the west coast of India (Fig. 1). The area forms part of the Cochin Estuary, and it is connected to the main water body through sluice gates. The sampling locations were selected in light of recurrent bioluminescent blooms observed over the past several years. The study location is relatively sparsely populated, with minimal anthropogenic influences. Three sampling sites were chosen from the location: S1 (9.872892°N;76.287001°E); S2 (9.873552°N; 76.285636°E), and S3 (9.874155°N; 76.284858°E). The study area is characterised by shallow waters, with a depth ranging from around 2 m. Surface water and sediment samples were collected from the three sampling site at monthly intervals between May 2023 and September 2024, to facilitate regular monitoring of phytoplankton composition and physico-chemical characteristics, following standard procedures. During the bioluminescent bloom period (March-April 2024), sampling frequency was increased to weekly intervals (one sampling per week), to capture the rapid changes associated with the bloom development. A total of nine samples were collected during the bloom period, to enable a comprehensive assessment of bloom dynamics and associated environmental conditions.

Fig. 1. Location of the study area in Kumbalangi, Kerala

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Water sampling

The salinity, temperature, and pH of the water samples were recorded in the field. Temperature was measured using a mercury thermometer, salinity measured in a refractometer (ERMA, Japan 0–100%), and the pH using Eco Testr pH 2. Dissolved oxygen, carbon dioxide, biological oxygen demand (BOD), turbidity, and total suspended solids (TSS) were estimated standard methods (Gaarder and Gran, 1927); Strickland,1968; Subrahmanyan *et al*., 1979; Parsons *et al*., 1984; USEPA, 2001; APHA, 2017). The Chl-a, Chl-b, and Chl-c concentrations were estimated spectrophotometric method. Briefly, a known volume of water sample was filtered through a GF/F filter paper, then placed in 90% acetone solution and left in the dark for 24 h in a refrigerator. The extracted materials were separated by centrifugation and the absorbance of the extracted solution was measured at various wavelengths (750, 665, 645, and 630 nm) using a spectrophotometer (Vase *et al*., 2018). Nutrients such as ammonia (NH_4- N), nitrite (NO_2-N), nitrate (NO_3-N), silicate (SiO_3-Si), and phosphate (PO_4-P)) were determined using a segmented flow Auto Analyzer (SKALAR SAN ++) following established procedures (Grasshoff, 1983). A phytoplankton net made of bolting silk with a 20 µm mesh size was used for plankton collection. Ten liters of water was filtered and preserved in 5% formaldehyde solution (Rocky and Manual, 1991). Quantitative estimation of phytoplankton was performed using a Sedgwick-Rafter counting chamber. Identification was performed under an inverted microscope following standard keys (Gopinathan *et al*., 2007), and the results are expressed as cells l^{-1}**.**

Sediment sampling

Sediment samples were collected from the top of the sediment layer using a Van Veen grab (0.05 m^2). Oxidation–reduction potential (ORP) readings of the sediment samples were recorded using an Oakton ORP 5 pocket tester, and the pH was measured using an Eco Testr pH 2 from the field. The sediment samples were dried and sieved using a 2 mm sieve for texture analysis according to the International Pipette Method, which is based on an improved dispersion procedure (Olmstead *et al*., 1930). Dried sediment samples sieved through a 0.5 mm mesh sieve were used for the estimation of total organic carbon (TOC) using Walkley and Black's titration method (Walkley and Black, 1934). The salinity of the soil was determined using Knudsen's argentometric titration (Mohr *et al*.,1856).

Diversity indices

The following diversity indices were calculated from the phytoplankton community dataset of the study area, using the PAST 4.03 software.

Shannon–Wiener diversity index (H')
The diversity index (H') was calculated by the formula (Shannon and Wiener, 1949):

$$H'=-\sum_{i=1}^{S} P_i \log2 P_i$$

which can be rewritten as

$$H'=\frac{3.3219(N \log N - \sum ni\text{-}\log ni)}{N}$$

where H'= Species diversity in bits of information per individual; n_i = Proportion of the samples belonging to the i^{th} species (no, of individuals of the i^{th} species); N = Total number of individuals in the collection

Margalef's richness index (d) (Margalef,1994).

$$d = \frac{(S-1)}{\log N}$$

S = No. of species
N = No. of individuals

Simpson's dominance index (D) (Simpson,1949)
$D = 1 - \lambda$

where $\lambda = \sum P_i^2$

$$P_i = \frac{n_i}{N}$$

n_i = No. of individuals of i, i^2,……………….
N = Total no, of individuals in the population.

Statistical analyses

A multivariate statistical analysis was performed to determine the correlation between the environmental variables and phytoplankton abundance during the bloom and non-bloom periods. Principal component analysis (PCA) was performed on the standardised environmental data. Canonical correspondence analysis (CCA) was used to assess species–environment relationships. Differences in the phytoplankton community composition between the bloom and non-bloom periods were evaluated using the Bray–Curtis dissimilarity matrix. A permutational multivariate analysis of variance (PERMANOVA) based on Bray–Curtis dissimilarity was performed to evaluate the significance of these differences. To verify that these differences were not due to the heterogeneity of multivariate dispersion, PERMDISP analysis was performed. PCA and CCA biplots were plotted using the R programming software (R Core Team, 2022). MS Excel was used for general plotting purposes. Maps were generated using QGIS 3.28.4 software.

Results and discussion

Physicochemical properties of the water and sediment

The abundance and distribution of *G. spinifera* are closely influenced by the aquatic environment. *Gonyaulax* blooms generally manifest as a pale yellowish-brown discolouration (Vishal *et al*., 2021) in water. The physicochemical properties of the water and sediment samples from the study area are presented in Table 1. Principal component analysis (PCA) revealed that the first eight principal components had eigenvalues greater than 1 and collectively explained 87.31% of the total variance in the dataset. PC1 accounted for 24.75% of the variance, followed by PC2 (17.01%) and PC3 (15.45%) (Table 2).PCA revealed that the aquatic environment of the Kumbalangi bloom area was influenced mostly by salinity, dissolved inorganic nitrogen (DIN), and dissolved inorganic silicate (DISi) (Fig. 2a). The highest concentration of inorganic nutrients were recorded during the monsoon season and the minimum during the pre-monsoon season. In a relatively homogeneous water column, elevated nutrient loads can reduce the number of limiting

Table 1. Physiochemical parameters of Kumbalangi bloom area during the sampling period

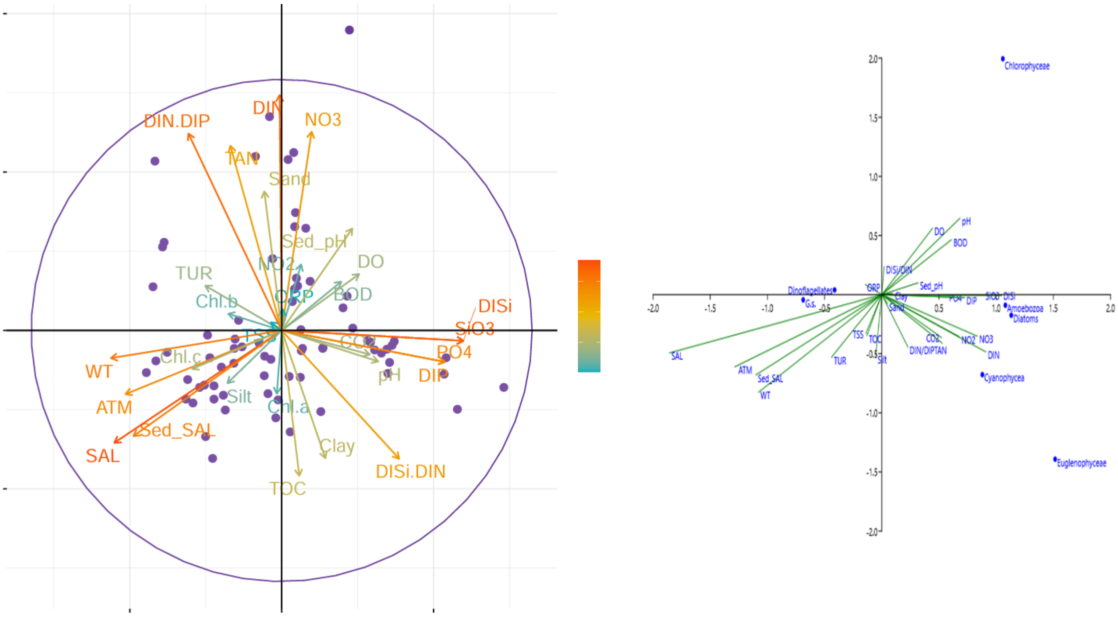
Parameter	Value (Mean±SD)
Atmosphere temperature	32±0.32°C
Water temperature	31±0.27°C
pH	7±0.04
Salinity	8±0.86 ppt
Turbidity	6±0.64 NTU
Dissolved oxygen	2±0.12 mg l^{-1}
BOD	1±0.10 mg l^{-1}
Chl a	16.36±1.54 mg m^{-3}
Chl b	3.52±0.53 mg m^{-3}
Chl c	15.17±2.29 mg m^{-3}
TSS	87.09±6.47 mg l^{-1}
CO_2	1± 0.08 mg l^{-1}
TAN	0.194±0.02 mg l^{-1}
Phosphate	0.285±0.02 mg l^{-1}
Silicate	1.886±0.16 mg l^{-1}
Nitrite	0.016±0.005 mg l^{-1}
Nitrate	0.115±0.03 mg l^{-1}
DISi	67±5.69 µM
DIN	23.2± µM
DIP	9.2±0.81 µM
Sediment salinity	3.3 ± 0.4 ppt
Sediment pH	7.2±0.1
Sediment ORP	-176±7.3 mV
Sediment TOC	0.87±0.1%
Sediment texture	Sand: 89±0.8%, Silt: 3±0.3%, Clay: 12±0.6%

nutrients, intensifying competitive pressure and leading to the dominance of certain phytoplankton species (Huisman *et al.*,1999). A similar pattern was observed in the present study in Kumbalangi, leading to the proliferation of *Gonyaulax spinifera* during the bloom period. The DIN values ranged from 4.8–85.2 µM. Significant monthly variations were observed in the in DIN (F= 4.67, p<0.05) and DIN:DIP ratio (F=33.70, p<0.05). Similar variations were found in the concentrations of dissolved inorganic silicate, DISi(F=33.48, p<0.05) and DISi:DIN ration (F=16.81, p<0.05). In contrast monthly variations recorded in the dissolved inorganic phosphorus (DIP) was minimal (F=3.56, p>0.05). Chlorophyll a was weakly positively correlated with DIN (r=0.099, p>0.05) and DIP (r=0.060, p>0.05), whereas it showed weak negative correlation (r=-0.123, p>0.05) with DISi. The significant temporal variation in the inorganic nitrogen and silicate levels suggests that these nutrients played an important role in driving seasonal shifts in the phytoplankton community, with dinoflagellates dominating during the pre-monsoon period and diatom becoming predominant during the monsoon season. Similar observations have been reported by Madhu *et al*. (2010), who demonstrated that nutrient availability is a key factor regulating the community composition of phytoplankton.

Table 2. Eigenvalues and the percentage variance explained by the principal components

Principal component	Eigenvalue	Variance (%)	Cumulative variance (%)
PC1	7.18	24.75	24.75
PC2	4.93	17.01	41.77
PC3	4.48	15.45	57.22
PC4	2.63	9.06	66.28
PC5	2.05	7.08	73.36
PC6	1.59	5.49	78.85
PC7	1.43	4.93	83.79
PC8	1.02	3.53	87.31

CCA demonstrated that the distribution of phytoplankton groups was strongly influenced by the prevailing environmental conditions (Fig. 2b). *G. spinifera* showed a close association with higher salinity, whereas Chlorophyceae was associated with higher DO, pH and BOD. Cyanophyceae was observed to be controlled by DIN, NO_2 and NO_3. Diatoms and Amoebozoa were positively associated with



(a) (b)

Fig. 2. (a) PCA and (b) CCA biplots showing the relationships between *G. spinifera* abundance and environmental variables in the Kumbalangi bloom area

DIP, DISi, SiO_3, and PO_4, indicating distinct ecological preferences among the major phytoplankton groups.

G. spinifera was identified as the causative species responsible for the bioluminescent blooms in the Kumbalangi bloom area. Previous studies from Cochin Estuary have shown that the abundance of dinoflagellates correlated well with environmental variables such as surface water temperature ($r=0.89$, $p<0.01$) and salinity ($r=0.64$, $p<0.05$) (Sathish *et al*., 2022). *G. spinifera* is a eurythermal and euryhaline species (Hand *et al*., 1965), and in the present study, its abundance showed significant positive correlation with salinity ($r=0.75$, $p<0.05$) (Fig. 3) and water temperature ($r=0.63$, $p<0.05$). Kim *et al*. (2024) reported a positive correlation between *G. spinifera* and water temperature followed by pH. The average pH of the Cochin Estuary was slightly alkaline (7.37±0.24) Dibu *et al*., 2025. In the present study, pH showed little temporal variation in the Kumabalangi bloom area (7±0.04), which is comparable to values reported for the Cochin estuary. In contrast, *G. spinifera* abundance was negatively correlated with silicate ($r=-0.59$, $p=>0.05$), phosphate ($r=-0.45$, $p>0.05$), and nitrate ($r=-0.50$, $p>0.05$). The reduced nutrient concentrations observed during the bloom period (March–April 2024) are likely attributable to to rapid nutrient uptake by the abundant phytoplankton population. The highest silicate (SiO_3-Si) concentration (2.695 mg l^{-1}) was observed at the time of peak diatom abundance during the monsoon season and decreased to 1.031 mg l^{-1} during the subsequent pre-monsoon season, which coincided with the *G. spinifera* bloom. Elevated silicate concentrations during monsoon can be attributed to increased freshwater runoff and terrestrial inputs resulting from intense rainfall (Thasneem *et al*., 2018, Dibu *et al*., 2025). The subsequent depletion of silicate during the pre-monsoon may reflect its utilisation by the dominant diatoms before the proliferation of *G. spinifera* (Mishra *et al*., 1993; Shruthi and Rajashekhar, 2014). The concentrations of other nutrients such as phosphate (PO_4-P) and nitrate (NO_3-N)), declined from 0.377 to 0.215 mg l^{-1} and from 0.037 to 0.018 mg l^{-1}, respectively. The nutrient concentrations measured during the bloom likely represent the residual unassimilated fraction remaining after rapid uptake by the phytoplankton population (Sommer, 1999).

Phytoplankton diversity

High diversity and abundance of phytoplankton were observed in the bloom area, during the study period, comprising 67 species of diatoms, 19 species of dinoflagellates, 10 species of Chlorophyceae, and 11 species of Cyanophyceae and a few representatives of Euglinophyceae, and Amoebozoa (Table 2). Diatoms formed the dominant phytoplankton group accounting for 78.9% of the total species diversity. Similar phytoplankton assemblages dominated by diatoms have been reported from Cochin estuarine waters (Nandan *et al*., 2018, Soumya *et al*., 2019, Sathish *et al*., 2022). Among the diatoms, *Pleurosigma* species particularly *Pleurosigma normanii* and *Pleurosigma elongatum* were the most abundant, followed by *Navicula distans*, *Diadesmis nitzschioides*, *Surirella* spp., *Pseudonitzschia* spp., *Gyrosigma* spp., *Gyrosigma balticum*, *Bacillaria paxillifera* and *Amphora* spp., etc. The dinoflagellate assemblage was dominated by *Gonyaulax spinifera*, along with other species, such *as Protoperidinium pellucidum, Protoperidinium leonis,* and *Ceratium furca.*

G. spinifera accounted for 80% of the total dinoflagellate diversity in the study area, followed by *P. pellucidum* (10%), *P. leonis* (1%), and *C. furca* (1%). Diatoms were most abundant during the monsoon season, specifically in August, reaching a maximum density of 37633 cells l^{-1}, which could be attributed to elevated silicate concentrations associated with monsoon runoff. The abundance of diatoms may, in turn, have supported higher populations of

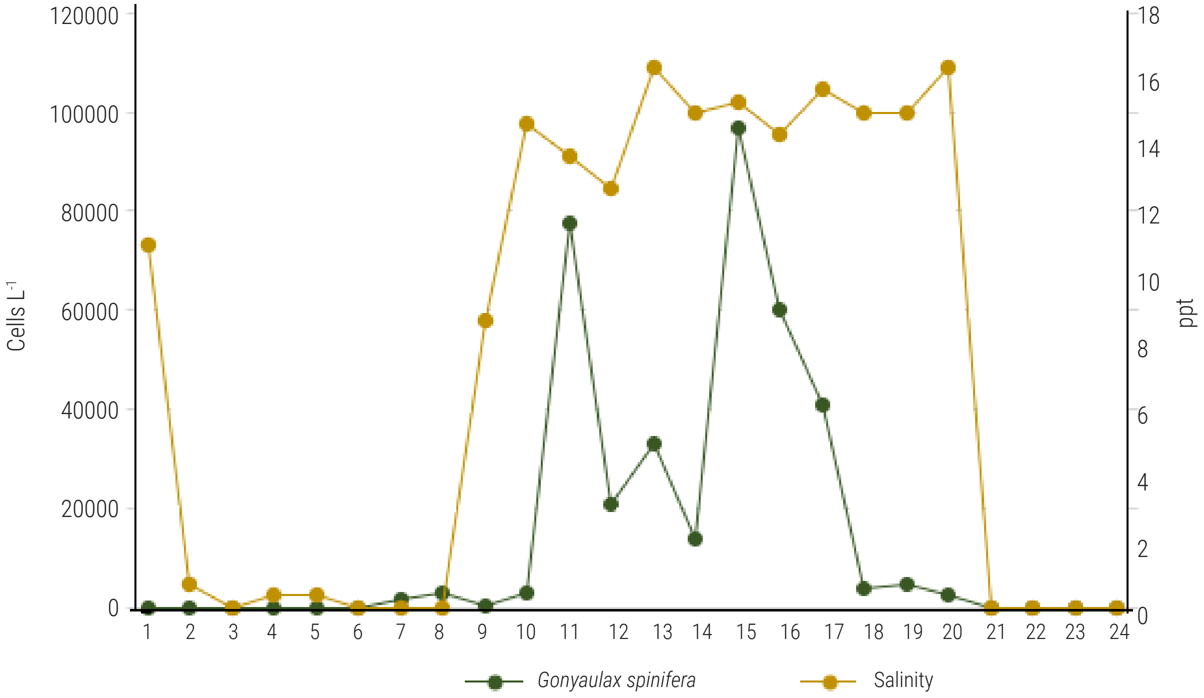


Fig. 3. Relationship between salinity and abundance of *G. spinifera*

Table 2. Phytoplankton diversity recorded in the Kumbalangi bloom area during the study period

Group	Species identified
Diatom	*Actinoptychus undulatus, Achnanthes* sp., *Amphora lineolata, Amphora lineolata, Amphora spectabilis, Amphiprora gigantea, Bacillaria paxillifera, Bacteriastrum* sp., *Bacteriastrum delicatulum, Biddulphia aurita, Biddulphia mobiliensis, Biddulphia sinensis, Campylodiscus* sp., *Campylodiscus noricus, Coscinosira polychorda, Cocconeis littoralis, Coscinodiscus oculus-iridis, Coscinodiscus concinnus, Coscinodiscus centralis, Coscinodiscus granii, Coscinodiscus lineatus, Coscinodiscus rothii, Cyclotella striata, Cymbella* sp., *Cylindrotheca closterium, Diploneis* sp., *Entomoneis* sp., *Fragilaria oceanica, Fragilariopsis* sp., *Gyrosigma* sp., *Gyrosigma balticum, Mastogloia exilis, Mastogloia minuta, Melosira distans, Navicula* sp., *Navicula clavata, Navicula cuspidata, Navicula distans, Diadesmis nitzschioides, Navicula spectabilis, Nitzschia closterium, Nitzschia longissima, Nitzschia sigma, Nitzschia spathulata, Nitzschia sigmoidea, Pseudonitzschia* sp., *Odontella mobilensis, Paralia sulcata, Planktoniella sol, Pleurosigma angulatum, Pleurosigma carinatum, Pleurosigma elongatum, Pleurosigma normanii, Pleurosigma strigosum, Rhaphoneis amphiceros, Rhaphoneis surirella, Rhaphoneis discoides, Streptotheca indica, Surirella ovalis, Surirella fluminensis, Surirella fastuosa, Surirella spiralis, Thalassiosira subtilis, Thalassiothrix longissima, Triceratium reticulatum*
Dinoflagellates	*Ceratium furca, Ceratium extensum, Dinophysis caudata, Gonyaulax spinifera, Noctiluca scinillans, Peridinium conicum, Protoperidinium leonis, Protoperidinium minutum, Protoperidinium depressum, Protoperidinium pellucidum, Peridinium subpyriforme, Protoperidinium steinii, Protoperidinium tuba, Protoperidinium balticum, Protoperidinium claudicans, Prorocentrum gracile, Prorocentrum micans, Pyrophacus* sp., *Pyrophacus fusa*
Cyanophyceae	*Coelosphaerium* sp., *Gomphosphaeria* sp., *Lyngbya* sp., *Merismopedia* sp., *Microcystis* sp., *Synechococcus, Spirulina* sp., *Phormidium* sp., *Trichodesmium erythraeum, Trichodesmium thiebautii, Oscillatoria* sp.
Chlorophyceae	*Ankistrodesmus falcatus, Cosmarium* sp., *Microspora* sp., *Pediastrum simplex, Pediastrum duplex, Scenedesmus acuminatus, Scenedesmus quadricauda, Closterium navicula, Closterium setaceum, Spirogyra* sp.
Euglenophyceae	*Euglena viridis*
Amoebozoa	*Arcella* sp.

the heterotrophic protoperidiniaceandinoflagellate *P. pellucidum*. Protoperidiniacean dinoflagellatesare known to feed on diatoms (Jacobson and Anderson, 1986). *P. pellucidum*, which is reported to exhibit bioluminescence (Baker *et al.*,2008), dominated (39667 cells l^{-1}) during the pre-bloom period (June 2023), however no visible bioluminescence was observed during this period. The abundance of *G. spinifera* drastically increased in March 2024 reaching a peak density of 97000 cells l^{-1} and remained the dominant phytoplankton taxon throughout the bloom period (Fig. 4). This marked increase resulted in a monospecific bloom, with a subsequent decline in the abundance of other dinoflagellates and diatoms Such bloom formation is consistent with the habitat specialisation and

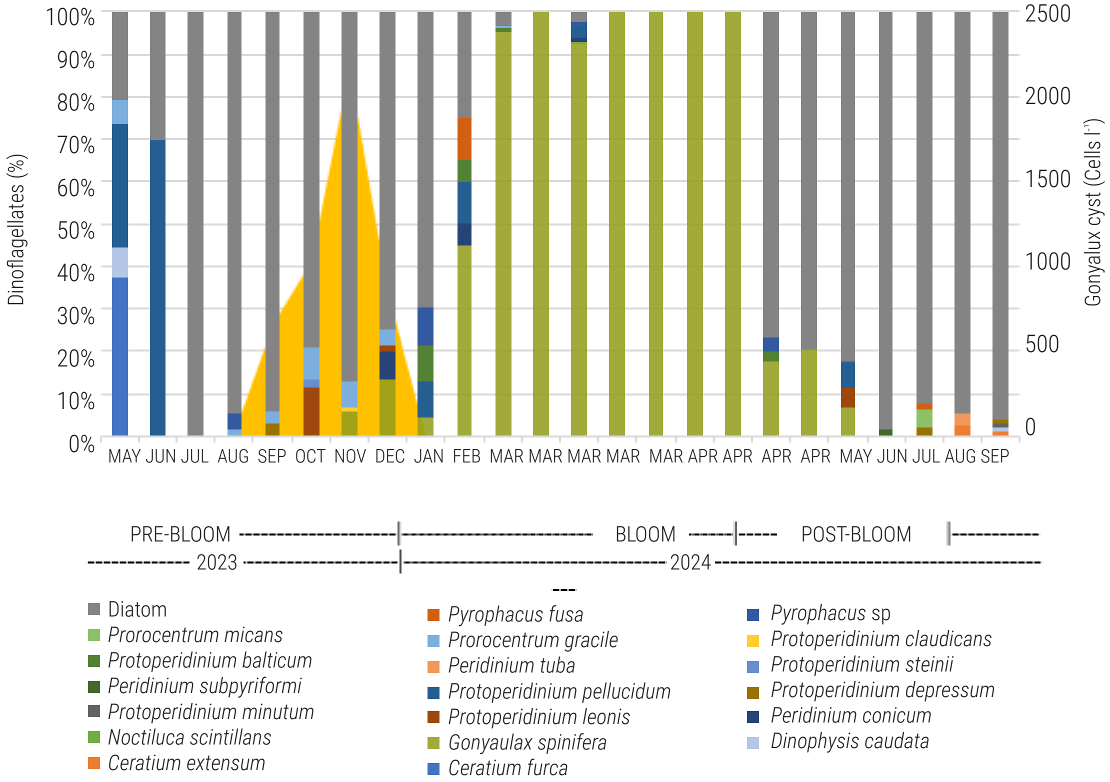


Fig. 4. Relative contribution of dinoflagellate species during different stages of the bioluminescent blooms in the Kumbalangi bloom area. The shaded area represents the period during which *G. spinifera* cysts were observed.

soloist behaviour exhibited by certain dinoflagellates under favourable environmental conditions (Smayda, 2002). *G. spinifera* (Fig. 5a) showed maximum abundance during the bloom episode, whereas densities of all other dinoflagellates and diatoms were relatively low. Emission of intense endogenous blue–green light under circadian regulation has been reported from *Gonyaulax* cells (Johnson *et al*., 1985). Similar episodes of bright blue–green bioluminescence was observed in the study area at night hours during the bloom period, with light emission being triggered by mechanical agitation of the water (Fig. 5 b).

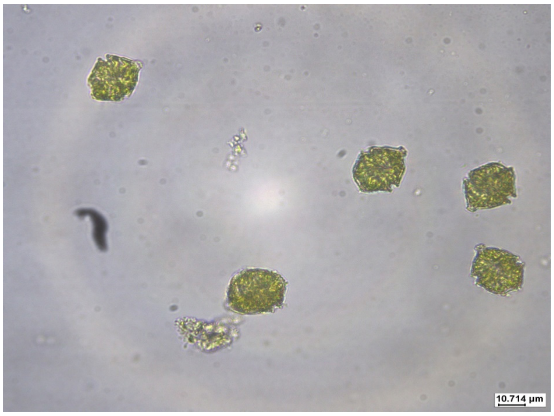


Fig. 5a. Photomicrograph of *G. spinifera* isolated from Kumbalangi bloom area

Fig. 5b. Bioluminescence caused by *G. spinifera* in the Kumbalangi bloom area captured at night in March 2024

Cluster analysis based on Bray–Curtis dissimilarity supported the patterns observed from the *in-situ* data. Samples collected during the bloom period (March and April 2024) clustered together exhibiting <0.4 dissimilarity, that is, >60% similarity in phytoplankton species composition and abundance, whereas samples collected during the non-bloom period formed distinct clusters. The high similarity among bloom samples, reflects dominance of a few bloom-forming species, while the non-bloom period was characterised by a more diverse and heterogenous phytoplankton community (Fig. 6). The PERMANOVA results revealed significant monthly differences in the phytoplankton community composition (pseudo-F = 4.53, p=0.001). PERMDISP analysis indicated no significant differences in multivariate dispersion among months (F=0.79, p=0.08), confirming that the observed temporal variation was due to changes in community composition.

Diversity indices

The phytoplankton diversity indices exhibited marked variation between the bloom and non-bloom periods. The Simpson dominance index (D), Simpson's diversity index, Shannon–Wiener diversity index and Margalef's richness index were were used to assess changes in community structure.

The Margalef richness index ranged from 0 to 2.638 with an average value of 0.697±0.555. A drastic decline in the index was observed during the bloom period, reflecting the reduction in species richness associated with the dominance of *G. spinifera*. This reduction in richness is likely attributable to competitive exclusion and intense resource utilisation by the bloom forming species, which suppress the occurrence of other phytoplankton taxa. The Simpson dominance index, which measures the degree of species dominance ranged from 0.0712—1.0, with a mean value of 0.432±0.361. The highest value (D=1) was recorded during the bloom period, indicating the absolute dominance of *G. spinifera*. Simpson's diversity index takes a value between 0 and 1, with values near 0 indicate that the species are least evenly distributed, and values near 1 imply that the species are the most evenly distributed, indicating maximum diversity (Thakur *et al*., 2013). The Simpson's diversity index was highest during the pre-bloom and post-bloom periods, indicating greater species diversity and evenness. The index had a mean value of 0.568 ± 0.361 and and declined to 0 during the bloom period, indicating the development of a monospecific bloom of the bioluminescent dinoflagellate *G. spinifera*.

The Shannon–Wiener index for phytoplankton community of the Cochin Estuary has been reported to be lower during pre-monsoon period (H'=1.7) than during the monsoon period (H' = 2.5) (Paul *et al.*, 2021). The Shannon–Wiener diversity index of the Kumbalangi bloom area exhibited a similar seasonal pattern, ranging between 0 and 2.859, with a mean value of 1.379±0.11. The minimum value (H=0) was recorded during the pre-monsoon bloom period. The decline in Shannon diversity index during bloom conditions indicates a reduction in both species' richness and evenness, a characteristic feature of monospecific phytoplankton blooms (Manna *et al*., 2010).

A negative correlation was observed between the Shannon–Wiener diversity index and the Chl a concentration (r=-0.385, p=0.063), with Chl a values ranging from 7.34--38.20 mg m^{-3}). Relatively high Chl a value coincided periods when the phytoplankton community was dominated by the dinoflagellate *G. spinifera* (>95% of the total abundance). This shows that the increase in phytoplankton biomass during the bloom was caused primarily by the proliferation of a single bloom-forming species rather than by an overall increase in phytoplankton productivity (Duarte *et al*., 2006). Previous studies have reported high phytoplankton diversity, richness, and evenness in the coastal waters of Cochin during pre-monsoon season, excluding bloom events (Soumya *et al*., 2019). In the present study, the simultaneous decline in richness, diversity, and evenness

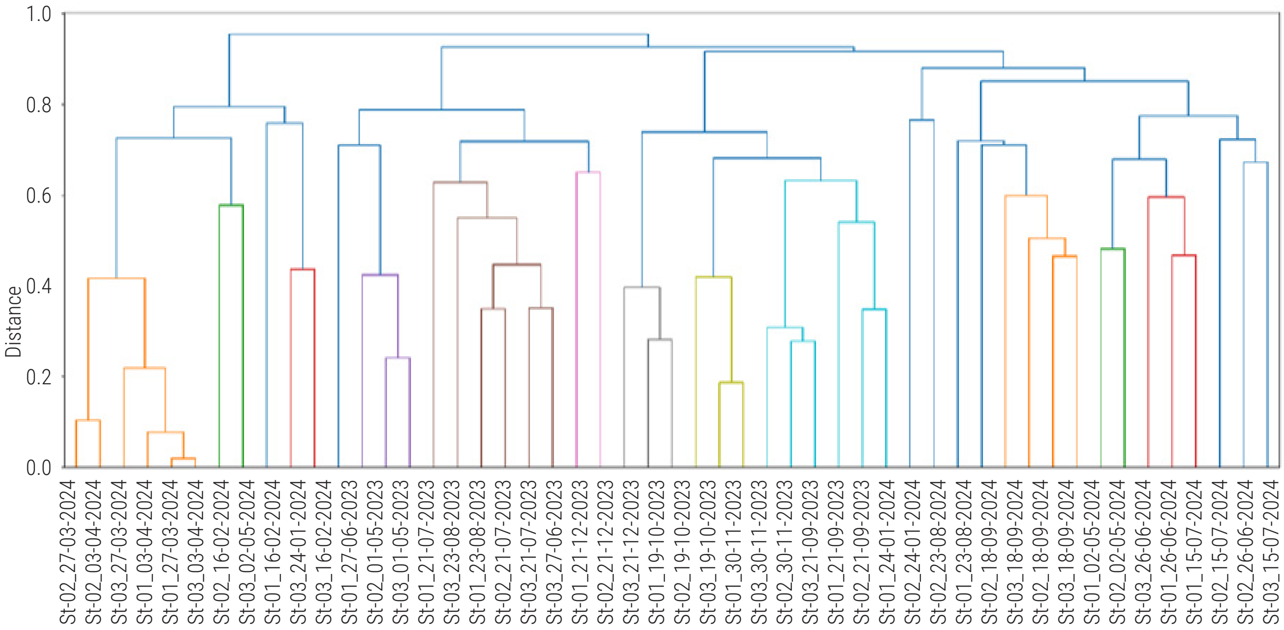


Fig. 6. Cluster analysis of the phytoplankton composition based on Bray–Curtis dissimilarity

indices during the bloom period, clearly demonstrates a marked shift in the phytoplankton community from a relatively diverse assemblage during non-bloom periods to one dominated by a single species, *G. spinifera*. Such monospecific blooms have the potential to alter trophic interactions, nutrient cycling, and energy transfer within estuarine ecosystems.

Pattern of phytoplankton occurrence in the study area

The succession of diatoms and dinoflagellates under bloom conditions reflects their differential responses to changing environmental conditions (Vineis *et al*., 2025). Both groups respond strongly to changes in nutrient availability, whereas the intensity of the response is largely controlled by temperature (Bi *et al*., 2021). Similar findings have been reported by Morse (2013); Jiang *et al*. (2015) and Xie *et al*. (2015), who demonstrated that a rise in water temperature favours the relative abundance of dinoflagellates, enabling them to codominate or become the only dominating taxon. A similar successional pattern was observed in the present study. The competitive superiority of diatoms at high silicate concentrations shifted to dinoflagellates at conditions of high temperature, salinity and low nutrient concentration particularly silicate levels (SiO_3-Si).

The seasonal succession of phytoplankton in the Kumbalangi bloom area followed a distinct and repeatable pattern. During periods of active water column mixing, long-celled diatoms dominated the phytoplankton community. With the onset of stratification, these were replaced by a more diverse assemblage of phytoplankton representing different taxonomic groups, which were later replaced by stress-tolerant large dinoflagellates under prolonged stratification. Continued stratification led to the formation of monospecific blooms with reduced diversity (Reynolds (1980) suggested that such bloom development may be interrupted by intermittent mixing that promotes the regrowth of diatoms, gradually leading to a more diverse phytoplankton population. A similar succession pattern of phytoplankton community was observed in the Kumbalangi bloom area during the present study (Fig. 7). Diatoms dominated during the active mixing period of heavy monsoon precipitation, which resulted in a copious supply of silicates. A gradual increase in temperature supported a more diverse phytoplankton population during the post-monsoon period. High salinity, high temperature, and low nutrient conditions during the following pre-monsoon period provided a favourable environmental setting for the proliferation of *G. spinifera* leading to bioluminescent bloom. The onset of the following monsoon, accompanied by heavy precipitation along with a drastic declinein salinity and renewed mixing of the water column, disrupted the bloom and v=facilitated the reestablishment of more diverse phytoplankton community. during the monsoon season.

Adverse environmental conditions, such as nutrient limitation, salinity, or temperature fluctuations, can lead to the encystation of *G. spinifera* (Rodrigues *et al*., 2019). Species of the genus *Gonyaulax* produce temporary cysts in response to sudden environmental changes. Unlike resting cysts, they lack distinctive morphological features, but are more transitory in nature and are sometimes associated with motile stages of plankton rather than accumulation in bottom sediments (Dale,1983). Large numbers of *G. polygramma* cysts have been observed along with active cells along the Tuticorin coast, south-east coast of India (Bharathi *et al*., 2023). During the present study, dinocysts were observed in the water samples collected during non-bloom period and were identified as temporary cysts of *G. spinifera* (Fig. 8) based on standard taxonomic descriptions (Tian *et al*., 2018; Mertens *et al*., 2020). Molecular identification could not be performed for dinocyst identification, as sufficient samples could not be gathered for DNA analyses. Temporary cysts were observed from September

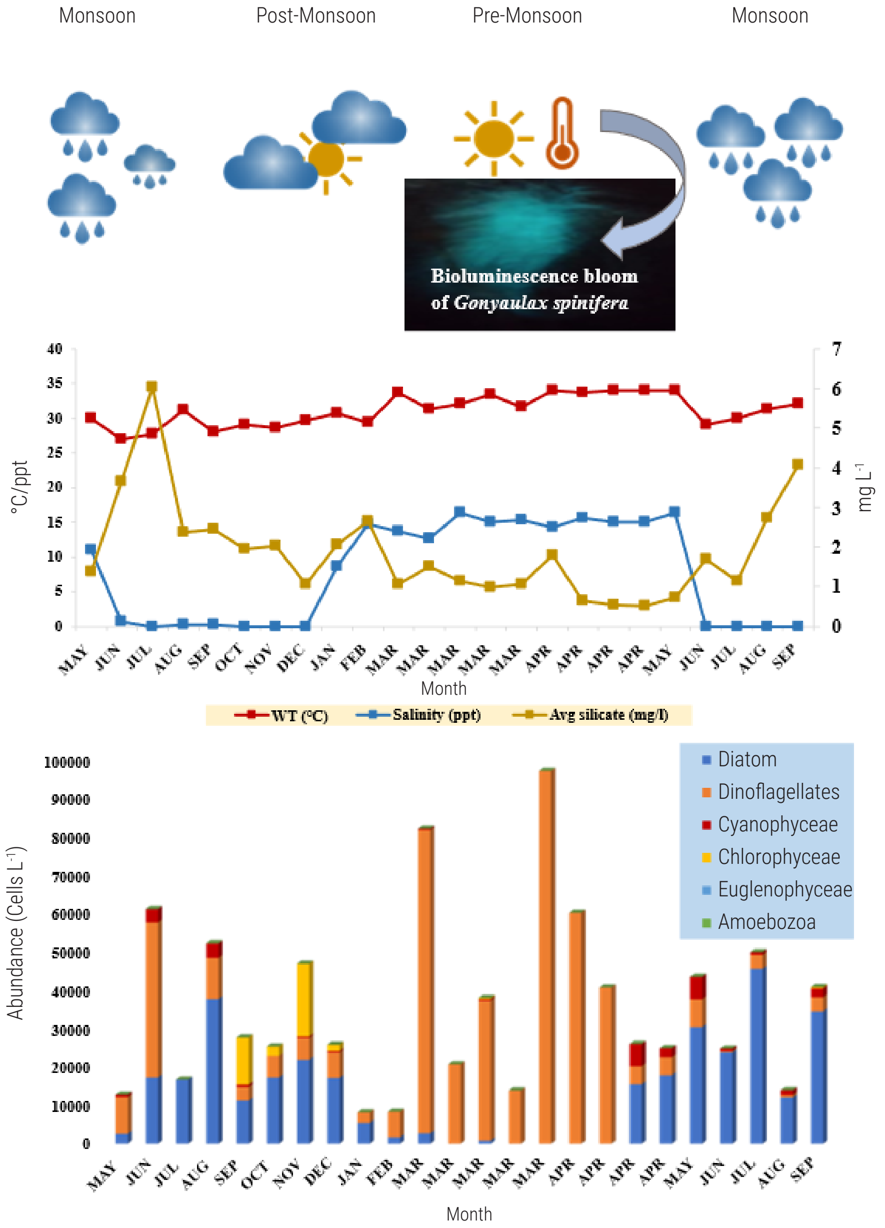


Fig. 7. Seasonal succession of diatoms and dinoflagellates in the Kumbalangi bloom area

to December 2023. Nitrate limitation has been reported as an important trigger for dinoflagellate cyst formation (Anderson *et al.*,1983; Figueroa *et al.*, 2008). However, in the present study, only a weak negative correlation (r=-0.05, p>0.05) was observed between nitrate concentration and *G. spinifera* cyst abundance, indicating that nitrate may not be a limiting factor regulating cyst formation in the study area. The occurrence of temporary cysts indicates the existence of a potential seed bank mechanism that might contribute to the recurrent bioluminescent blooms observed in the in the area, over the past several years. However, direct evidence from studies on cyst germination and viability is needed to confirm this association.

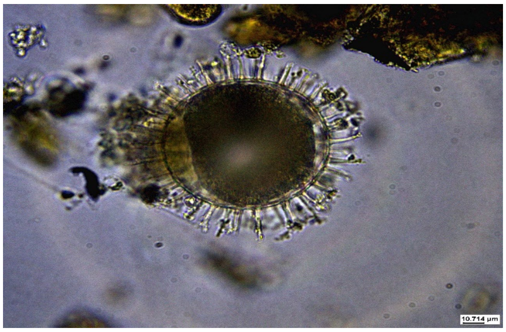


Fig. 8. Dinocyst of *G. spinifera* identified from Kumbalangi bloom area

The exchange of coastal waters through the Cochin estuarine inlet may represent a potential source of vegetative cells and/ or cysts of *G. spinifera* in the Kumbalangi bloom area. The south-west monsoon season (June--September) is characterised by the highest freshwater runoff, whereas the dry season (January–May) experiences relatively low runoff (Vinita *et al*., 2015). The Cochin Estuary has an average water residence time of 7.5 days, which increases during the pre-monsoon period, owing to low river discharge and enhanced tidal incursion. The resulting low water exchange, prolonged residence time and limited flushing create favourable conditions for the accumulation and proliferation of *G. spinifera*, thereby promoting bioluminescent bloom formation (John *et al*.,2020).

In addition to nutrient limitation, the presence of fine silty-clayey sediments, rich in organic matter can also facilitate dinocyst abundance. Previous studies have reported that dinocysts abundance in positively associated with fine silty sediments and salinity (Prabhudessai and Rivonker, 2020). In the present study, the mean sediment salinity recorded at Kumbalangi bloom area was 3.3±0.4 ppt. However, *G. spinifera* cyst abundance exhibited a significant negative correlation ($r=-0.37$, $p<0.05$) with sediment salinity, indicating that the cystformation was favoured during periods of reduced salinity associated with south-west monsoon. The similarity in the hydrodynamic behaviour of fine silt particles and cysts promotes their co-deposition, resulting in higher abundance of cysts in sediments with higher mud content (Dale, 1983). Although the soils of the Kumbalangi area are predominantly alluvial and sandy, (Kamarudheen *et al*., 2025), sediment textural analysis revealed that the sediment texture of Kumbalangi bloom area was predominantly sandy in nature (sand: 89±0.8%, silt: 3±0.3%, clay: 12±0.6%) throughout the study period, with approximately 15% comprised of fine (silt+clay) particles. These fine-grained fractions may provide favourable microhabitats for the accumulation and preservation of *G. spinifera* cysts. However, the role of sediment characteristics on bloom recurrence requires further investigations, through targeted sediment core analyses and cyst viability and germination studies.

The photosynthetic eukaryotic dinoflagellate *G. spinifera* was identified as the causative organism responsible for the recurrent bioluminescent blooms in the Kumbalangi bloom area. The occurrence and proliferation of this dinoflagellate are strongly influenced by environmental variables, particularly temperature, and salinity. Elevated temperature and salinity may during the pre-monsoon period facilitated favourable conditions for bloom formation in the area. The seasonal succession of phytoplankton followed a distinct and repeatable pattern in Kumbalangi. Diatoms dominated during the nutrient-rich monsoon season, under conditions of high silicate availability, while the warmer, more saline and nutrient depleted conditions during the pre-monsoon season, favoured proliferation of the stress-tolerant dinoflagellate *G. spinifera*. This resulted in the formation of monospecific bioluminescent bloom episodes, characterised by intense blue-green light emissions regulated by the species' circadian rhythm, offering a spectacular view in the dark during night hours. The occurrence of temporary cysts suggests the existence of a potential seed-bank mechanism that may contribute to the recurrent nature of these blooms.

This study provides the first comprehensive assessment of the environmental drivers, phytoplankton succession, and cyst dynamics associated with recurrent *G. spinifera* blooms in the Kumbalangi bloom area, thereby establishing an important baseline for future ecological monitoring and bloom prediction in the Cochin estuarine ecosystem.

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