



Towards understanding the paradox associated with the rise in algal blooms of *Noctiluca sp.* (*Dinoflagellate*) around the Indian continental waters

Rajdeep Roy^{a,*},¹ Aneesh Lotliker^b, C.V. Jayaram^a, Sanjiba Kumar Baliarsingh^b

^a Regional Remote Sensing Centre – East, National Remote Sensing Centre, Indian Space Research Organisation, Kolkata 700156, India

^b Indian National Centre for Ocean Information Services, Ministry of Earth Sciences Hyderabad, 500090, India

ARTICLE INFO

Keywords:

Noctiluca scintillans
algal blooms
ecosystem
fisheries, Arabian Sea

ABSTRACT

The recent intensification of harmful algal blooms of *Noctiluca sp.* in and around Indian waters has drawn global attention. India has a coastline of ~11098 km and rich in ecological diversity. Our study indicates that this increase is presumably linked to changes in silicate concentrations in continental waters. These changes are now fuelling an ecosystem shift from silicate-dependent diatom populations to more opportunistic *Noctiluca sp.* We observed low silicate values (<2 $\mu\text{mol l}^{-1}$) that covaried with these algal blooms. Further, a comparison of historical data from estuarine waters of the Bay of Bengal with recent measurements shows a marked reduction in dissolved silicate concentrations by at least one order. Our analysis is in agreement with a recently published model simulation, which predicts 17% reduction in the dissolved silicate fluxes due to the damming effect in Indian waters. Our long-term analysis of suspended sediment concentrations in major rivers also shows a statistically significant negative trend, suggesting a decrease in riverine inputs that modulate silicate fluxes. A modest positive correlation between the number of dams built and the occurrence of *Noctiluca* blooms was also observed. Our analysis therefore captures the complex interplay between socio-economic growth and the feedback response of marine ecosystems in Indian waters; however, their implications for the ocean carbon budget, Indian fisheries, and the tourism sector needs to be thoroughly evaluated.

1. Introduction

All coastal regions worldwide are showing an increase in the frequency of algal blooms compared to two decades earlier (Anderson et al., 2012). Processes such as eutrophication and climate change are considered environmental cues contributing to this increase (Hallegraeff, 1993; Anderson et al., 2012). Among all, a marine dinoflagellate *Noctiluca scintillans* (*NS*), is reported to dominate these algal blooms worldwide (Harrison et al., 2011) with numbers showing unimodal to bimodal occurrence (Piontkovski et al., 2021) each year. A long-term study from 1933 to 2020 in China reported an increasing trend in *NS* blooms (265 incidence) (Wang et al., 2023). A large number of these blooms (86.8%) occurred between March and May (Wang et al., 2023). Recent evidence also suggests that there is an increasing trend in proliferation of *NS* in Indian waters (do Rosário Gomes et al., 2014; Raj et al., 2020; Lotliker et al., 2018; Baliarsingh et al., 2016). *NS* is a heterotroph that engulfs prey, by phagocytosis, feeding on plankton, fish eggs, and bacteria (Han et al., 2013; Thomas et al., 2020). It is also

linked to bioluminescence in coastal and near-sea shore (Han et al., 2013; Hallegraeff et al., 2019). On a global scale, seasonal blooms of *NS* occur in two forms — red and green. The colour depends upon the pigments of organisms inside cell vacuoles (Hausmann et al., 2003). The red form is considered a temperate to sub-tropical species observed in the western Arabian Sea (AS), the shelf of Pakistan, and on the eastern and western coasts of India (Subrahmanyam, 1954). Whereas green strains of *NS* contain *Pedinomonas noctilucae* (a green alga) as an endosymbiont (Elbrächter and Qi, 1998; Sriwoon et al., 2008).

Globally, algal blooms are often linked to nutrient enrichment. They can cause massive fish kills and disrupt aquatic food chains (Glibert et al., 2018; Normile, 2019). Algal blooms can also affect local tourism (Anderson et al., 2012). Historically, most algal blooms in India were associated with withdrawal of the southwest monsoon, seasonal upwelling, monsoonal forcing, and increased riverine inputs (D'Silva et al., 2012). However, *NS* blooms are now more widespread (Harrison et al., 2011; Lotliker et al., 2018; Baliarsingh et al., 2016). This reflects a strong climatic shift from a diatom-dominated ecosystem to a more

* Corresponding author.

E-mail address: rajdeep_roy@nrsc.gov.in (R. Roy).

¹ ORCID iD: <https://orcid.org/0000-0001-5509-257X>

predatory, mixotrophic community (Madhupratap et al., 1996; D'Silva et al., 2012, and references therein) in this region. *NS* blooms in the northern Indian Ocean are also increasing. Earlier, anthropogenic pollution and hypoxia were proposed as probable causes (do Rosário Gomes et al., 2014; Raj et al., 2020). Now, the lack of silicate (Si) in the water column is thought to aid *NS* proliferation (Prakash et al., 2017; Xiang et al., 2019; Sarma et al., 2019). In addition, winds and temperature may influence these *NS* blooms in the AS (Sarma et al., 2022; Sarma et al., 2023). *NS* blooms are now reported throughout the year along the Indian waters. This suggests a complex interplay of biophysical factors controlling sudden outbreaks, which needs detailed investigations.

In this manuscript, we study the outbreaks of *NS* blooms between 1900 and 2025 in the Arabian Sea (AS) and the Bay of Bengal (BoB) to understand their spatial coverage and their blooming frequency. Among the few factors thought to influence the proliferation of *NS* blooms, we focus on changes in dissolved silicate (Si) concentration in Indian waters and examine their possible linkages. We also investigate decreases in suspended sediment concentrations (SSC) in a few selected Indian rivers and discuss their possible role in modulating *NS* blooms.

2. Materials and methods

2.1. Water column sampling and biogeochemical analysis in AS

In this study, we classify the seasons into three, wherein February to May we term as premonsoon, followed by June to September as monsoon and October to January as postmonsoon. Monitoring of bloom-forming green *NS* was carried out during the premonsoon of 2017 (3rd to 26th February) onboard the Indian Ministry of Earth Sciences (MoES) research vessel “Fishery Oceanographic Research Vessel (FORV) Sagar Sampada” (cruise no. 356). Annual observations suggest that the maximum proliferation of *NS* in AS occurs in March (Dwivedi et al., 2012). During our cruise, sporadic dense patches of green and yellowish-green discolouration of surface seawater were observed at latitudes 19 – 21 °N and longitudes 65 – 68 °E, which were sampled. Care was taken to collect samples both inside and outside the patches. For chemical analysis, the seawater samples were collected by Niskin bottles using a Tygon tubing connected to the spout. Inorganic nutrients (nitrate, Si, and phosphate) were determined by standard spectrophotometric methods (Grasshoff et al., 2009) using Skalar Autoanalyzer (San ++). Uncertainties based on multiple measurements of replicate samples for Si were ± 0.03 ($\mu\text{mol l}^{-1}$) and are further detailed elsewhere (Roy et al., 2024). Phytoplankton water samples were collected from the surface in a clean measured bucket. Thereafter, it was transferred to pre-cleaned plastic bottles for phytoplankton identification and enumeration after preserving with 1% Lugol's iodine–2% neutral formalin (Hötzel, and Croome, 1999). Phytoplankton were counted in the preserved samples using an inverted microscope (Labomed; Model: Lx 400) and standard identification keys (Tomas, 1997).

Further Si measurements from coastal to offshore waters of AS in 2018 were carried out as part of the project “Marine Ecosystem Dynamics of eastern AS (MEDAS)” as detailed in Vijayan et al., 2021. Briefly, observations were conducted onboard FORV Sagar Sampada covering seven coast-offshore transects (Cape, Kochi, Mangalore, Goa, Mumbai, Veraval, and Okha) along the eastern AS during the premonsoon (January–February) of 2018. At each transect, 8–10 stations were covered with depths ranging between 10 and 2000 m. For this study, we have categorized the eastern AS in two regions: north eastern AS (NEAS) and south eastern AS (SEAS). Such that the transects up to 15°N (Cape, Kochi, Mangalore, and Goa) are grouped as SEAS, and the other three northern transects (Mumbai, Veraval, and Okha) are defined as NEAS. For the benefit of discussion, the 10–50 m depth stations are grouped as coastal stations and those beyond (up to 2000 m) as offshore stations. Water samples were collected from standard depths using 12 L Niskin samplers attached to a CTD Rosette sampler. Sub-samples for

nutrients were collected in HDPE bottles (60 and 100 ml) and poisoned with saturated HgCl_2 for analysis. Inorganic nutrients (nitrate, Si, and phosphate) were determined by standard spectrophotometric methods (Grasshoff et al., 2009) using Skalar Autoanalyzer (San ++). The analytical precisions, expressed as standard deviation based on replicate analyses, were of the same order ± 0.037 ($\mu\text{mol l}^{-1}$) (Vijayan et al., 2021). To understand the historical Si concentrations within the upper water column of the AS, data from US JGOFS cruises TT045 and TT054 were plotted along the latitudinal gradient. For this, data from US JGOFS cruise TT045 corresponds to March 1995 (representing premonsoon) and TT054, corresponding to December 1995 (representing post monsoon/active winter mixing) period were taken from the database <https://www.bco-dmo.org/dataset/>. The detailed analysis of the nutrient datasets has already been published (Morrison et al., 1998).

2.2. Water column sampling and biogeochemical analysis in BoB

Offshore Si data presented from the Bay of Bengal (BoB) was collected during the field program (BoBBLE: Bay of Bengal Boundary Layer Experiment) in the southern BoB during peak monsoon. Further details about the expedition are presented in Vinayachandran et al., 2018. Briefly, under BoBBLE, the sampling stations were along 8° N, extending from 85.3° E (hereafter referred to as TSW) to 89° E (hereafter referred to as TSE) with three more stations in between, referred to as Z1, Z2, and Z3. The transect TSW to Z3 were sampled between 24th to 3rd July, and TSE on 4th of July 2016, when the basin was under the influence of active monsoon (Roy et al., 2021). Further, the station TSE was also occupied for 10 days for a time-series study and variability of Si within the water column up to a depth of 500 m was monitored with a frequency of every 6-hr sampling. Further details about the atmospheric and physico-chemical conditions of the water column are detailed elsewhere (Vinayachandran et al., 2018; Roy et al., 2021).

For understanding the Si in the riverine system near surface water samples were collected from 22 to 25 stations from the Hooghly-Sundarban Estuarine region (BoB) during March 2023 (premonsoon) and July 2023 (Monsoon). On all occasions, nutrients (Si in this case) were analysed using an autoanalyzer (SKALAR SAN++) following Grasshoff et al. (2009) using the same machine which was used to study the bloom formation of *NS* in the AS during 2017. The analytical precisions ($\pm \sim 0.03$ $\mu\text{mol l}^{-1}$ of Si) in this case, expressed as standard deviation based on replicate analyses and further detailed in (Roy et al., 2022). Although during all the cruises mentioned above, various other parameters were also collected (temperature, salinity, dissolved oxygen, chlorophyll), for the scope of the present study, we limit our discussion to the changes in dissolved Si in AS and BoB.

2.3. Satellite data processing and analysis for *NS* bloom

In the present study, ocean colour satellite data with a spatial resolution of 9 km were acquired from NASA's Ocean Colour Web, supported by the Ocean Biology Processing Group (OBPG). The data were processed using the OC3C maximum band ratio algorithm for northern AS. This empirical algorithm uses the maximum ratio of remote sensing reflectance at 443 and 520 nm with 550 nm (http://oceancolor.gsfc.nasa.gov/cms/atbd/chlor_a#sec_2). Monthly composite from Moderate Resolution Imaging Spectroradiometer (MODIS) onboard Aqua satellite was prepared for understanding the spatial extent of the *NS* proliferation for the cruise days using an on-line visualization tool from NASA GES DISC (<http://daac.gsfc.nasa.gov/giovanni>). Past investigations suggested *Noctiluca* proliferations to be strongest within the above spatial domain, as presented here (Dwivedi et al., 2012) and these grids were considered based on long-term satellite data analysis.

2.4. Data analysis of unclassified river sediments from selected river in India

SSC data from 2002 to 2011 were obtained from the Integrated Data Hand-bBook for non-classified river basins, published in March 2012 by the Central Water Commission (<http://cwc.gov.in/>). Data for important rivers were taken from the east and west coast of India, which ultimately drain into either the AS or the BoB. Care was taken to choose a site that was closer to the coast for sediment load information. SSC was analysed by filtering a known volume of water in a pre-weighed GF/F filter paper, drying it further for moisture removal and re-weighing it and dividing by the volume filtered. Further details about the SSC analysis can be found at <http://cwc.gov.in/>.

3. Result and discussion

3.1. Reports of NS bloom in Indian continental waters

The reported incidence of NS blooms for the past 117 years (1908–2025) is shown in Fig. 1a & b. The specific areas of manifestation along the Indian coast are detailed in Supplementary Tables 1 & 2. The data clearly show an increasing trend over the last 25 years (Fig. 1b), which is consistent with other global observations, such as those from the South China Sea (Wang et al., 2023). We found that the months (February, August, and September) have experienced the highest numbers of NS outbreaks with a clear east and west coast pattern. For example, our analysis indicates NS bloom in the BoB mostly coincided with the months of August and September (Monsoon). However, in AS, it was in February (post-monsoon). Nearly 40 reports of NS were documented between 2000 and 2025 compared to years before. In addition to these, some random outbreaks of NS were also observed in other months, excluding February, August, and September, suggesting

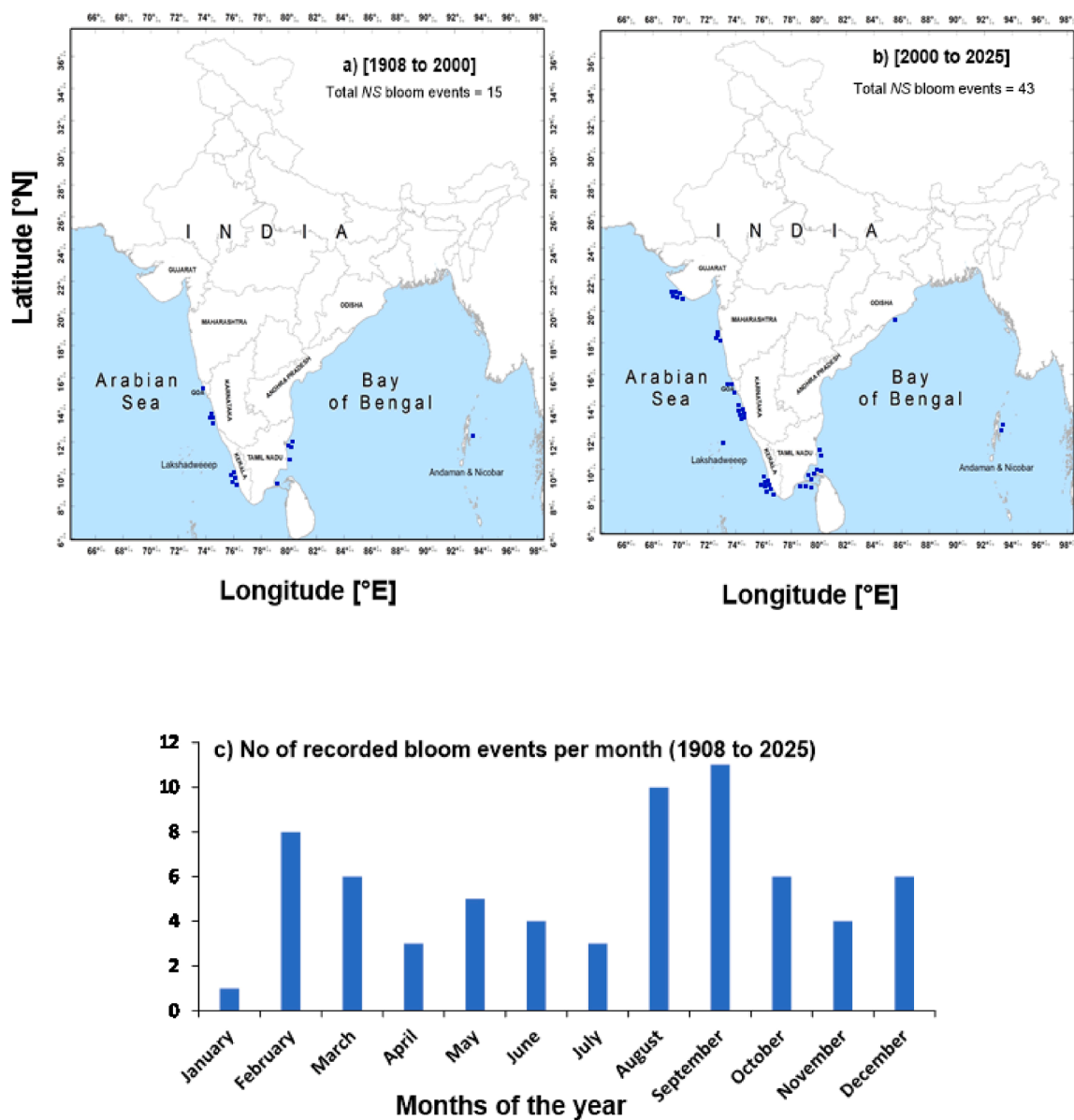


Fig. 1. Decadal trends in reports of *Noctiluca scintillans* bloom along the continental waters of India from a) 1908–2000; b) 2000–2025. c) Depicts the months they were reported with the frequency of bloom. Reports of bloom from 1910 to 2010 are reproduced from D’Silva et al., (2012). Subsequent data are compiled from peer-reviewed publication are indexed in supplementary reference material RM1.

possible changes in the ocean ecosystem. These reported incidents, therefore, warrant careful investigation, keeping a holistic approach.

3.2. Dissolved Si conditions around Indian continental waters during NS bloom and non-bloom conditions

Interestingly, most of this reported bloom coincides with very low Si in the water column (Prakash et al., 2017; Sarma et al., 2019; Roy et al., 2024). The possible prevalence of low Si and its linkages with the proliferation of NS were first proposed by Prakash et al. (2017), which prompted further investigations (Sarma et al., 2019; Xiang et al., 2019). The depth profiles of the Si concentrations from one such NS bloom studied in March 2017 are presented in Fig. 2 b, c. Fig. 2a shows that almost all of northern AS was affected by the NS bloom, albeit with varying intensity. The time series study of Si concentrations for 2–3 days within and outside the bloom is presented in Fig. 2 d to f. Irrespective of the intensity of the NS bloom, extremely low Si < 0.5–1.5 $\mu\text{mol l}^{-1}$ was observed with the top 40–50 m in northern AS during 2017, with a

marginal increase north of 20.25°N (Stn S4). The mixed layer at these stations also had low temperatures, indicating it remained under the influence of convective mixing (Roy et al., 2024). The temporal variation of surface Si concentrations alongside the cell counts of NS carried out for the time series station S3 & 4 is shown in (Supplementary Figure 1). The data suggest that most NS cells were associated with very low Si concentrations in the water column. Often, an increase in cell numbers is observed, coinciding with a dip in Si values in surface waters.

Further, in an earlier investigation (Supplementary Figure 2), a clear difference in Si concentration was noted between the bloom and non-bloom patches. The bloom-affected areas showed ~0.5–1 $\mu\text{mol l}^{-1}$ lower Si concentrations within the mixed layer than outside (Sarma et al., 2019). In general, these numbers are far below ~5 $\mu\text{mol l}^{-1}$ threshold often argued as a critical level for diatom sustenance observed during various iron fertilization experiments (see review by Yoon et al., 2018). The timing of NS blooms in the continental waters of AS is always between February and March after the withdrawal of peak convective mixing (December–January), wherein a reasonable amount of Si is found

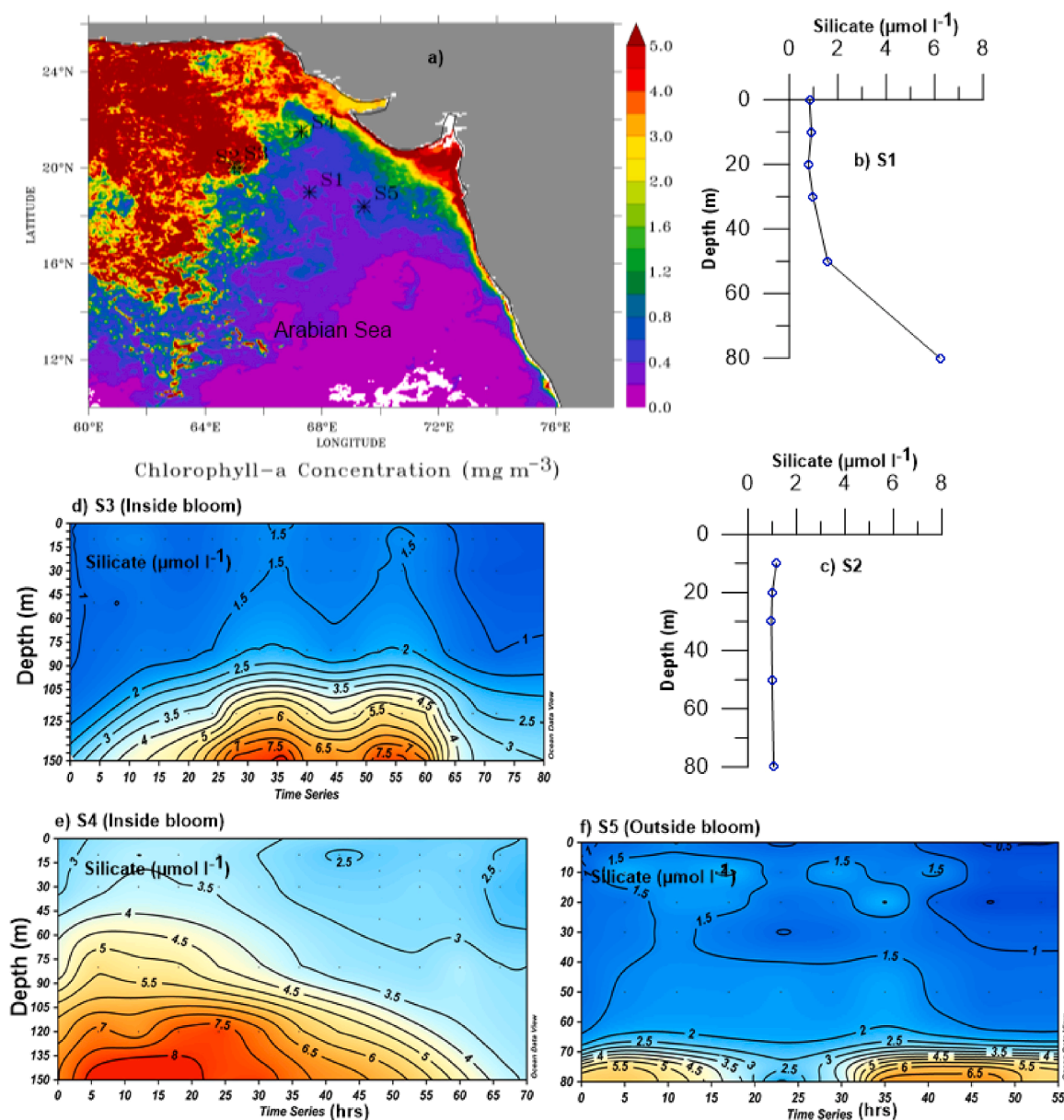


Fig. 2. a) shows the increase in satellite chlorophyll, which mimics the spread of NS blooms in 2017. a & b show the Si depth profiles ($\mu\text{mol l}^{-1}$) from within and outside the NS bloom. The time series data on Si ($\mu\text{mol l}^{-1}$) from stations within (d & e) and outside (f) is shown.

to be in the water column (Madhupratap et al., 1996). This is thought to sustain the strong diatom blooms (Madhupratap et al., 1996). More recent measurements of water column Si from November–December (a period of convective mixing) are shown in Fig. 3a, and concentrations during February–March, coinciding with the season of NS bloom are illustrated in Fig. 3c. The corresponding variations of N to Si ratios in Fig. 3b & d. Our data from November–December shows a fairly deep mixed layer (50–70 m) with a significant amount of silicate ($\sim 4 \mu\text{mol l}^{-1}$) and reaching up to $18 \mu\text{mol l}^{-1}$ within 100 m of the water column (Roy et al., 2015). This presumably enables a sustained supply of Si to the mixed layer until it becomes shallow during February–March, thereby restricting any further proliferation of the diatoms due to less Si recharge from below. It is reported that silicicline resides much deeper compared to nitricline and phosphocline in this region (Madhupratap et al., 1996; Naqvi et al., 2002), with shallow mixed layer post convective mixing recharge becoming limited. A clear depletion of at least $\sim 2 \mu\text{mol l}^{-1}$ within the upper water column is noted during February–March (Fig. 3c) with a gradual increase in the N/Si ratios compared to November–December. This is also reflected in the historical data. The latitudinal variation from 10°N to 20°N from data collected during US JGOFS in AS is shown in Supplementary Figure 3. The $4 \mu\text{mol l}^{-1}$ isolines of Si modulate close to 60 m during November–December and show upward propagation beyond 20°N with high concentrations below ($\sim 10 \mu\text{mol l}^{-1}$). In contrast, it lay much below 80 m during February–March of 1995. This makes it evident that during February–March, the region is affected by low Si in the water column, thereby helping the bloom of NS to proliferate as there are fewer diatoms. This gradual change in the concentrations of mixed-layer Si is due to its response to physical forcing. It is observed that during February, the fresh water carried by the West India Coastal Current forms a barrier layer, making the mixed layer shallower beyond 20°N , below which the slow AS (High Salinity) waters flow south (Shankar et al., 2016). This water is much saltier and leads to weaker mixing in this region, thereby restricting Si recharge from below. It is also proposed that this stronger stratification observed during February–March weakens the impact of the diurnal cycle of temperature, and the mixed layer does not respond to daytime heat and nighttime cooling and remains a stable shallow mixed layer (Sarma et al., 2019). Although this sufficiently explains the reason for proliferations of the NS in northern AS, it falls short of elucidating the reasons for the widespread manifestation observed in the last two decades (Fig. 1) in and around Indian coastlines. This possibly indicates impaired Si budget in the Indian continental waters, leading to fewer diatoms and more NS bloom due to its heterotrophic nature. Recent measurements suggest consistent low Si (within the top 15 m) in both coastal and open ocean transects in AS (Supplementary Figure 4) (Vijayan et al., 2021). Similarly, open ocean measurements of Si during peak monsoon (July) showed concentrations as low as $1 \mu\text{mol l}^{-1}$ within the top 100 m in BoB. In addition to this, 10-day time series measurements conducted during the same cruise showed no increase in Si concentrations within the top 100 m (Figs. 4 and 5). Further, data collected along India's largest estuarine system from the BoB showed an average concentration of $3.7 \mu\text{mol l}^{-1}$ during non-monsoon and $5.0 \mu\text{mol l}^{-1}$ during monsoon (Fig. 4). Data from the same location from the 6th of July 1983 show up to $56 \mu\text{mol l}^{-1}$ in surface, $77 \mu\text{mol l}^{-1}$ at 5 m, and $81 \mu\text{mol l}^{-1}$ in bottom waters, suggesting a decrease in Si input. Studies suggest that Si cycle in the coastal zone is highly sensitive to human-induced changes, for example, dams, resulting in a decrease in dissolved Si fluxes (see review by Tréguer and De La Rocha, 2013), which is explicitly derived from chemical weathering of continental rocks and discharged into the coastal zone by rivers and groundwaters (Tréguer and De La Rocha, 2013). Si has also been proposed as a regulating nutrient during phytoplankton competition (Egge and Aksnes, 1992).

3.3. Dams and sediment discharge by Indian Rivers and its relations with NS bloom and associated Si concentrations

Dams are often a source of water for drinking, industrial, irrigation, and power generation; therefore, their increase directly reflects a country's socioeconomic growth. Till 2020, India reported the presence of 5745 large dams (height > 15 m) (<http://cwc.gov.in/>). The correlation between growth in India's GDP and large dams is found to be 0.92 (Shi et al., 2019), which highlights its strong dependence. A list of the major dams used in this study is illustrated in Supplementary Table 3. The analysis for suspended SSC of major rivers of the Indian subcontinent, for which data is available from <http://cwc.gov.in/> is presented in Fig. 4. The approximate locations of these dams, after which the sediment data were collected, are illustrated in Supplementary Figure 4. Excluding one, a statistically significant, strong decline in the major rivers studied is reflected in SSC over the last few decades (Supplementary Figure 4). In the Indian west coast, 60–80% of sediment load reaching AS has decreased due to the Sardar Sarovar Dam traps on the Narmada basin (Gupta and Chakrapani, 2005). Further construction of irrigation barrage in the Indus River has led to 80% reduction in sediment load in the northern AS (Milliman and Farnsworth, 2013). Studies suggest that major hot spots of dissolved Si release are located in Southeast Asia, wherein the Ganges and its neighbouring small rivers contribute 23.32 Mt SiO_2 to BoB (Bernard et al., 2011). A comparative account of the historical Si data from a few major rivers in India is presented in Table 1. The numbers clearly indicate a reduction in the Si values compared to 4 decades earlier. This further corroborates the recent model results, which suggest a strong reduction in Si input, particularly in BoB, presumably due to the damming effect (Bernard et al., 2010; 2011). In BoB, a reduction of 17% in Si input is projected due to the damming effect, amounting to $50 \text{ mmol m}^{-2} \text{ yr}^{-1}$ (Bernard et al., 2010). We also made an attempt to understand the relationships between the number of dams built per two decades and the reported numbers of NS bloom for the same time line. This is depicted in Supplementary Figure 5a. The list of dams used for this purpose, along with the year of completion, is presented in Supplementary Table 3. A modest linear positive correlation ($r = 0.31$, $n = 6$) was observed, suggesting that more dams may potentially contribute to more proliferation of NS blooms. Similarly, we investigated the relationship between NS cell numbers and the associated Si concentrations reported from the region affected by these blooms, and the relationships observed are shown in Supplementary Figure 5b. A significant positive correlation ($r = 0.43$, $n = 32$) is observed for a small range of Si concentrations. This range presumably indicates the optimum level that supports the NS proliferations much better than the diatoms' cell growth. In contrast, low cell numbers were associated with high Si ($9.75 \mu\text{mol l}^{-1}$ of Si vs 1000 NS cells l^{-1} , $28.28 \mu\text{mol l}^{-1}$ of Si vs 1000 NS cells l^{-1}) during two separate studies from the coastal waters of India (Mishra et al., 2022; Haridevi et al., 2022). All these data indicate a possible association between decreased sediment input and depleting Si concentrations in oceanic waters compared to historical observations (Madhupratap et al., 2003; Sardessai et al., 2007) & (Table 1). Investigation suggests sediment retention by dams potentially contributes to low SSC downstream (Vörösmarty and Sahagian, 2000; Ittekkot et al., 2000). Tréguer and De La Rocha, 2013, highlighted that by trapping biogenic and other forms of particulate, easily soluble Si, dams can starve the downstream area, thereby significantly reducing flux to the ocean. Meanwhile, the doubling of phosphate and nitrate inputs to the coastal ocean from agriculture can increase biogenic silica production by diatoms (further leading towards Si limitation). This may potentially reduce the relative importance of diatoms in coastal ecosystems (Tréguer and De La Rocha, 2013). This is presumably reflected in Indian waters. Diatoms are an integral part of ocean new production and carbon cycling, whose growth rates are limited by Si (Dugdale and Wilkerson, 1998; Nature; Smetacek, 1998; Falkowski et al., 1998).

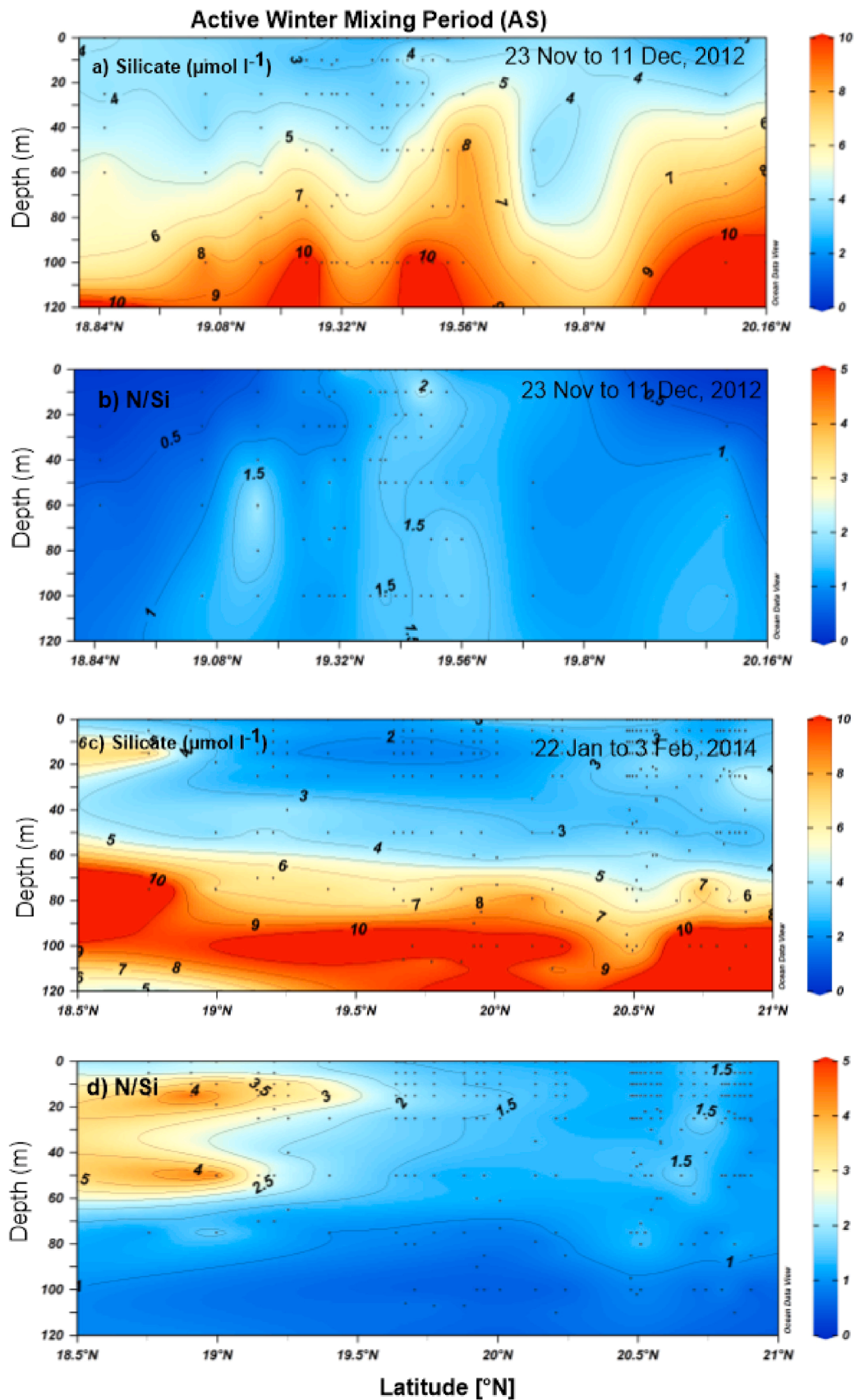


Fig. 3. Latitudinal variation in the water column Si concentrations and N/Si ratios a) during post monsoon covarying with the period of convective mixing and corresponding N/Si in ($\mu\text{mol l}^{-1}$) b) during early premonsoon associated with the beginning time frame of NS bloom. Note Si concentrations when compared between both the season shows at least a reduction of $2 \mu\text{mol l}^{-1}$ within the upper water column.

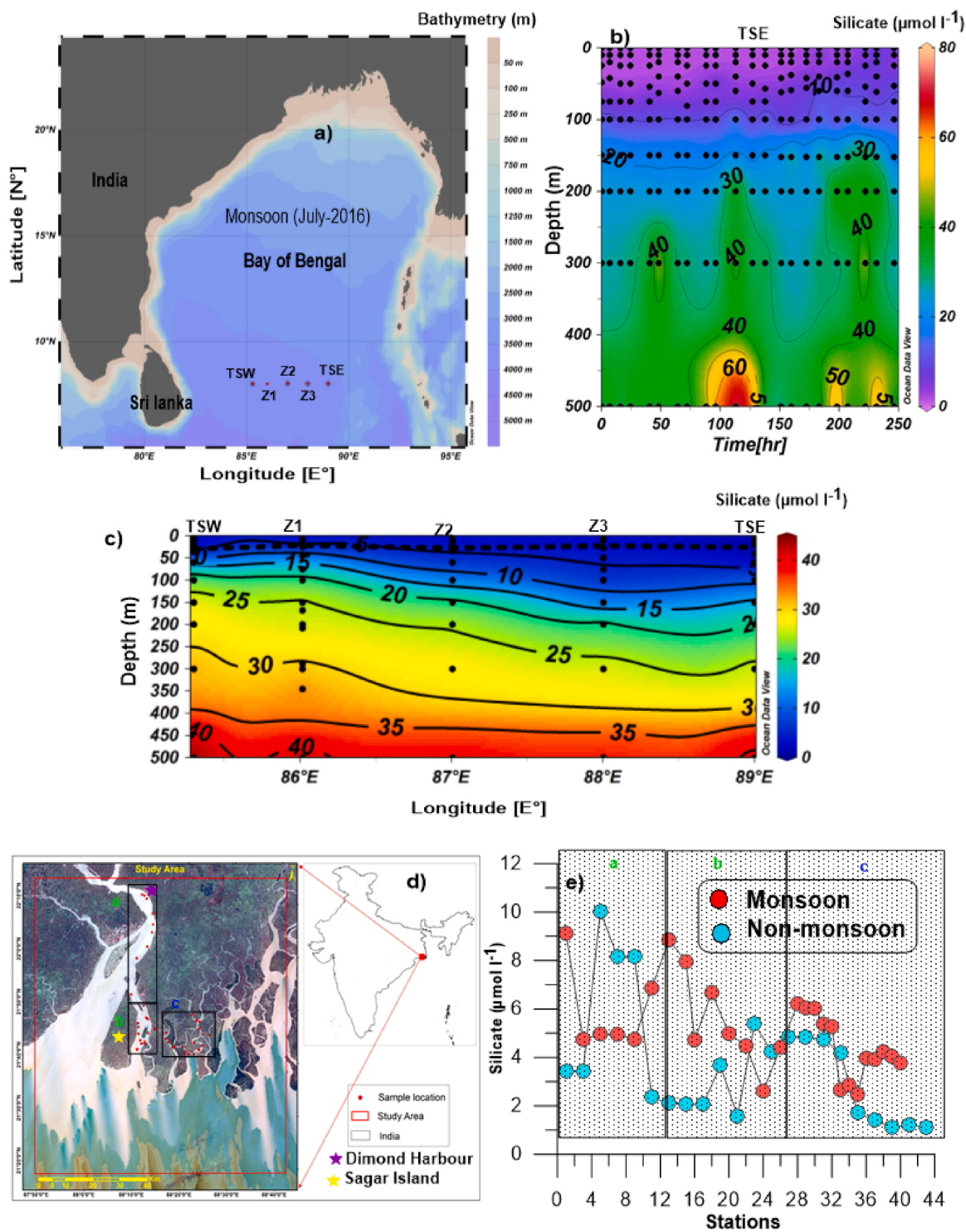


Fig. 4. a) shows the sampling locations in BoB b) corresponding silicate time series data for 10 days for the water column up to a depth of 500 m. c) Shows the longitudinal distribution of Si in the BoB for the upper water column till 500 m. d) shows the sampling stations within the Gangetic estuary with near-surface water (1 m) sampled during the monsoon and non-monsoon season. The three boxes a, b, and c represent the freshwater, brackish and estuarine zone based on the salinity b and c represent the freshwater, brackish and estuarine zone based on the salinity distribution. e) shows the spatial variability of Si between the monsoon and non-monsoon seasons.

3.4. Possible implication of NS bloom on carbon budget and Si fluxes

In NS, the presence of large cell vacuoles filled with ammonium ions assists them with their buoyancy (Tiselius and Kiørboe, 1998). Accumulation of buoyant cells is suggested as one of the factors leading NS to bloom in surface waters (do Rosário Gomes et al., 2014; Tada et al.,

2000., Tiselius and Kiørboe, 1998). The presence of NS in surface waters therefore decreases the effectiveness of the biological pump, which potentially controls the ocean CO₂ cycle and the carbon budget through export fluxes. In the northern Indian Ocean, the concentration of *Nocutiluca* cells could exceed 10⁶ cells L⁻¹ (Piontkovski et al., 2021). Interestingly, the vertical flux of organic matter into the ocean interior is

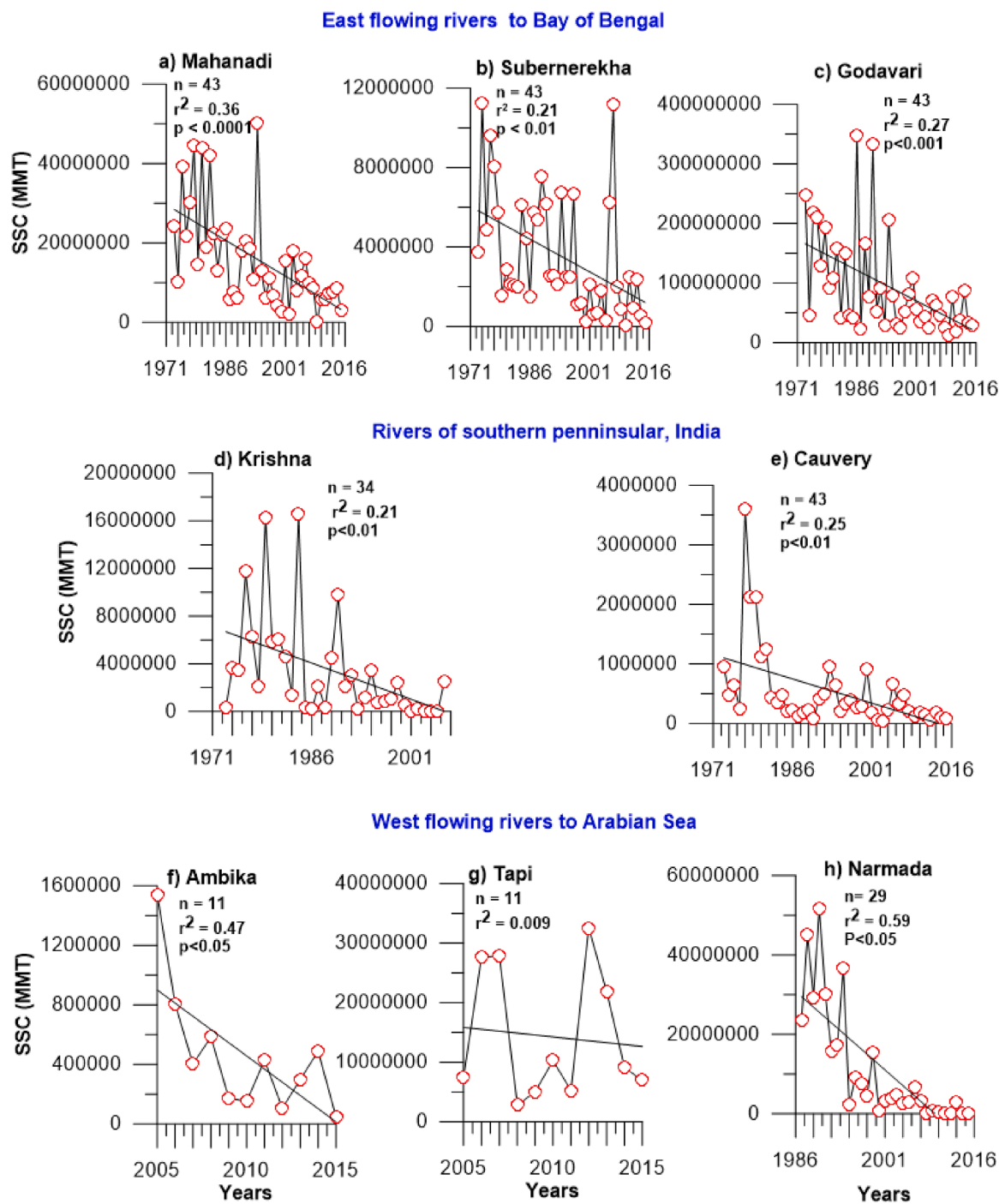


Fig. 5. Annual trends in the SSC (in million metric tonnes) of major Indian rivers draining in the BoB and AS. All major rivers show a decreasing trend suggesting changes in sedimentation pattern over the years in the Indian Ocean region. The corresponding coefficient of determination and the p values are given alongside. Note the river Tapi shows no significant trend presumably due less data points.

greatly enhanced by the higher sinking rates associated with larger, heavier cells, especially diatoms (Falkowski et al., 1998). In the contemporary ocean, the biogeochemical cycle of silicon is perceived to be dominated by the activity of the diatoms (Tréguer et al., 2018). This group is estimated to contribute up to 45% of total oceanic primary production (Tréguer et al., 2018), making them major players in the cycling of all biological elements. Silicon, the seventh-most-abundant element in the universe, is a key nutrient element in the ocean. Silica supply, essential for diatom blooms, is primarily dependent on riverine fluxes and upwelling from the ocean interior (Falkowski et al., 1998). Taking the approach of box modelling and stoichiometric conversion of

net primary production to silica production, the gross production of biogenic silica in the ocean is estimated to be $FP(\text{gross}) = 240 \pm 40 \text{ Tmol Si year}^{-1}$ (Tera mol), or $0.67 \pm 11 \text{ mol Si m}^{-2} \text{ year}^{-1}$ (see review by Tréguer and De La Rocha, 2013). This production was attributed mainly to diatoms occurring in the photic zone. Part of this flux is directly recycled in the surface ocean, and part is exported to the deep ocean. The exported biogenic silica continues to dissolve as it sinks through the deep ocean, regenerating silicic acid there within deeper layers.

The biogenic opal, which survives generally, accumulates at the sediment-water interface, wherein further dissolution may occur

Table 1

Shows the temporal variability in historical silicate data from major river flowing in (BoB) and (AS). Note few historical data was measured in mg l^{-1} which was converted to $\mu\text{mol l}^{-1}$.

Sl no	River Name	Drainage Basin	Sampling Year	Month/ Seasons	Sampling Area	Depth (m)	DSI ($\mu\text{mol l}^{-1}$)	References		
1	Ganga	BoB	1983	PRM M POM	Sagar Island	1	56.79	Sengupta et al., (1989)		
			1998–1990	PRM M POM	Sagar Island	1	79.86	De et al., (1994)		
			1999–2001	PRM M POM	Sagar Island	1	65.48 85.43 77.75	Mukhopadhyay et al. (2006)		
			2014–2016	Total Average	Frazer Gunj (Sagar Island)	0.5	42.32	Gogoi et al., (2021)		
			2014–2015	PRM M POM	Sagar Island	0.5	81.58 129.70 64.21	Mitra et al., 2018		
			2023–2024	PRM M	Sagar Island	1	3.39 6.93	This study		
			2	Mahanadi	BoB	1983	PRM M POM	Paradeep	1	13.8 23.8 41.4
2004–2005	PRM M POM	Paradeep	1			2.70 4.28 3.82	Naik et al., (2009)			
2005–2006	PRM M POM	Paradeep	1			3.43 7.48 3.99	Naik et al., (2009)			
2006–2007	PRM M POM	Paradeep	1			4.66 8.22 5.21	Naik et al., (2009)			
2007–2009	PRM M POM	Paradeep	1			6.09 9.01 7.65	Naik et al., (2020)			
2014–2015	PRM M POM	Paradeep	1			50.9 103.7 60.8	Mishra et al., (2018)			
3	Godavari	BoB	1989–1990			POM	Lower estuary	1	63.48	Sarma et al., (1993)
			1993–1995			PRM M POM	Lower estuary	1	90 170 120	Padmavathi and Satyanarayana, (1999)
			2007–2008			PRM M POM	Lower estuary	1	18.9 92.2 41.9	Sarma et al., (2010)
			2012			PRM	Lower estuary	1	15.0	Bharathi et al., (2022)
			2015	PRM M	Lower estuary (Kakinada Bay)	1	72.15 173.75	Rao and Sarma, (2017)		
			2011	M	Lower estuary	1	26.54	Krishna et al., (2016)		
			2004	M POM	Lower estuary (Bharuch)	1	208 219	Sharma and Subramanian, (2008)		
	Narmada	AS	2005	POM	Lower estuary (Bharuch)	1	0.32	Sonal et al., (2014)		
			2007	POM	Lower estuary (Bharuch)	1	0.34	Sonal et al., (2014)		
			2010	POM	Lower estuary (Bharuch)	1	0.26	Sonal et al., (2014)		
			2011	M	Lower estuary	1	13.08	Krishna et al., (2016)		
			2021		Lower estuary	1	1	Patel et al., (2023)		

(Tréguer and De La Rocha, 2013). Further average silica production has been estimated at $6 \text{ Tmol Si year}^{-1}$ in the major upwelling zones of the ocean and at $74 \text{ Tmol Si year}^{-1}$ for eastern boundary coastal regions outside of the major upwelling zones (Shipe and Brzezinski, 2001). The importance of diatoms to the transport of carbon, coupled with their utilization of silicic acid, has led to the proposal of the “silica pump” hypothesis (Dugdale and Wilkerson, 1998). In this hypothesis, the export of biogenic material (i.e., carbon, nitrogen, and phosphorus) from the mixed layer is tightly coupled to silica export due to the activity of diatoms. For example, the export continues until silicic acid becomes limiting, after which biological activity in the mixed layer is dominated by the microbial loop, which regenerates nutrients more efficiently and exports at a much-reduced rate. All these numbers reinforce the fact that gradual transitions from a diatom-based ecosystem to a more mixotrophic NS will not only have a profound impact on carbon export but will also complicate the biogenic silica cycle further. However, from the

viewpoint of marine ecology, the production, accumulation, and export of phytoplankton may also influence the world’s fisheries through complex food web dynamics, which therefore warrant detailed investigation and global focus.

3.5. Role of factors other than Si in modulating NS blooms

Algal blooms are complex environmental incidents and have been often linked to eutrophication (Anderson et al., 2009; Anderson et al., 2012). In general, it is believed that in case of any algal bloom, once the population is established its range and biomass are influenced by physical controls such as currents, temperature, nutrients & irradiance (Anderson et al., 2012). However, the presence of NS in Indian waters has generally been associated with low nutrient conditions (Sarma et al., 2019; Xiang et al., 2019; Roy et al., 2024), making it more difficult to discern the underlying causes. In this manuscript, although we focused

on how limiting Si conditions in the water column may favor the proliferation of *NS* blooms by outcompeting Si-dependent diatoms, physical factors such as ocean currents and warm temperatures and even hypoxia have also been proposed to aid the dispersal and abundance of *NS* in Indian waters (Mishra et al., 2022; Sathish et al., 2023; Sarma et al., 2023; do Rosário Gomes et al., 2014). A long-term study (1933–2020) along the Chinese coast suggested that the spatial–temporal distribution of *NS* blooms was mainly associated with precipitation, hydrodynamics, water temperature & food availability (Wang et al., 2023). All these suggest that the development and sustenance of *NS* blooms in oceans is a mixture of complex interactions of physical forcing and phytoplankton itself, and for understanding the resultant impact, more usage of ecological models is necessary.

4. Conclusion and the way forward

Virtually every country is now experiencing a worrisome trend in algal blooms (Anderson, 2009) and the coastal ecosystem seems vulnerable (Anderson et al., 2012). In this study, we showed the possible linkages between dissolved Si and the recent increase of *NS* bloom in Indian continental waters. It is possible that riverine fluxes of Si are getting modulated due to the decrease in sediment discharge in recent years due to anthropogenic changes. This is further corroborated by the modelling studies, which show, a, reduction of 17% in Si input is projected due to the damming effect, amounting to 50 mmol m⁻² yr⁻¹ (Bernard et al., 2010). Apart from the role of Si, the role of wind forcing in regulating the intensity of *NS* proliferation in the northern AS has also been proposed. We believe the interplay of wind forcing, shallow mixing and the role of Si needs further investigation. In the modern era of operational oceanography, putting up biogeochemical sensors with buoys in regions experiencing *NS* bloom may prove useful in providing real-time information on water column characteristics and can help us to track any changes in the marine ecosystem and can provide large volume of high-resolution data.

CRedit authorship contribution statement

Sanjiba Kumar Baliarsingh: Writing – review & editing, Data curation, Conceptualization. **C V Jayaram:** Writing – review & editing, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Aneesh Lotliker:** Writing – review & editing, Supervision, Resources. **Rajdeep Roy:** Writing – review & editing, Writing – original draft, Visualization, Validation, Supervision, Software, Resources, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgement

RR and CVJ acknowledge the Director, NRSC CGM RC's and DGM RRSC-EAST for his constant encouragement. AL and SKB are thankful to Director, Indian National Centre for Ocean Information Services (INCOIS), Ministry of Earth Sciences, Hyderabad, India, for the encouragement. The authors sincerely thank the Captain, crew, and scientific team of FORV Sagar Sampada (Cruise No. 356) for their excellent support and assistance in the collection of samples and field data during the cruise. This is an INCOIS publication contribution number 717.

Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.gecadv.2026.100034.

Data availability

Data will be made available on request.

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