Diatoms: a potential tool to understand past oceanographic settings

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Diatoms are being potentially used to decipher palaeoceanography and past climatic changes. They are marine primary producers which play an important role in carbon, silica and nutrient budgets of modern oceans. Their importance lies in the role they play for the export of organic carbon to the deep sea and the efficiency of the biological pump for CO_2 exchange. They are useful as biostratigraphical zone fossils in marine deposits from high latitudes or at deeper water depths, both of which lack calcareous microfossils. The role of diatoms as tracers of past oceanographic conditions with recent perspectives in diatom research is reviewed in this article.

Keywords: Diatoms, palaeoceanography, sediment, tracers.

THE photosynthetic organisms living within the photic zone of the ocean are responsible for around one-half of the global primary productivity, even though they constitute only a small proportion of the earth's green biomass. The most successful organisms are thought to be photosynthetic prokaryotes and a class of eukaryotic unicellular algae known as diatoms[1]. On a global scale, diatoms contribute at least 20% of annual primary productivity, equivalent to the tropical rain forests[2]. Diatoms are unicellular, autotrophic microscopic algae found in almost all aquatic habitats[3], with each habitat developing its characteristic flora existing under different chemical and physical environments[4]. Being dominant marine primary producers[5], they play an important role in carbon, silica and nutrient budgets of modern oceans. Their size varies from 1 to 2000 μm, however, most species range from 10 to 100 μm. Diatoms can be broadly divided into two basic groups based on their symmetry, viz. 'centric diatoms' exhibit radial symmetry (i.e. symmetry about a point) and 'pennate diatoms' show bilateral symmetry (i.e. symmetry about an axes). The central line, a longitudinal unsilicified groove down the middle of each valve face called raphe facilitates the flow of mucus which aids in creeping motion. Electron microscopic studies and molecular sequence data have shown that diatoms belong to the heterokont algae[6]. Heterokonts are chlorophyll $a + c$ containing algae that typically have zoids with two heterodynamic flagella; one covered with tripartite mastigonemes and the other is smooth[7]. In diatoms, the flagellar apparatus is reduced or absent, only the spermatozoids of the oogamous 'centric' diatoms are flagellated and these are uniflagellate[8], lacking any traces of a smooth posterior flagellum or basal body. Instead of heterokont mastigonemes, diatoms possess plastid ultrastructure (with four bounding membranes, lamellae of three thylakoids and usually a peripheral ring nucleoid) and pigment composition similar to brown algae[9]. Diatoms largely control the cycling of silicon in the ocean[5] and conversely, diatom silica production rates can be limited by the availability of silicic acid[10]. They are biogeochemically important as they account for an estimated 75% of the primary production occurring in coastal and nutrient-replete waters[5], rising to more than 90% during ice-edge blooms such as the one which occurred in the Ross Sea, off Antarctica[11].

Diatoms are used to reconstruct productivity and marine silicon cycling as they act as potential contributors to the past oceanic biogeochemistry or climate[12]. Their role in the export of organic carbon to the deep sea[13–16] and the efficiency of the biological pump for CO_2 exchange therefore aids as a potential tool in understanding palaeoclimate and past oceanographic processes[17,18]. This has been particularly possible with the availability of deep-sea cores of Deep Sea Drilling Project and Ocean Drilling Project. As basic constituents and fossils of modern surface sediments, diatoms occur in sediments at deep depths. Diatoms form a delicate skeleton made of amorphous opaline silica ($SiO_2 \cdot nH_2O$) called frustule. Molecules of SiO_2 form network-like structures thereby increasing the melting point, boiling point and covalent bond that provide rigidity to the test and better preservation of diatoms. Preservation potential and frequent occurrence thereby result in diatoms being used as palaeoproxies in higher latitudes and coastal regions[13]. Diatom assemblages in sediment records reflect hydrographical changes determined through their relative abundance of species. They are important biostratigraphical zone fossils in marine deposits from high latitudes or at deeper water depths, both of which lack calcareous microfossils[19]. This work is built upon the original review work of Sancetta[13] to provide a brief review on the role of diatoms as tracers of

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past climate specifically with past oceanographic settings and recent perspectives in diatom research with relevance to studies carried out in India.

Application of marine diatoms

In oceanographic settings

Diatoms have been studied in consideration with past climate reconstruction and oceanographic settings from Bering Sea sediments[20], tropical and equatorial Atlantic[21], western equatorial Atlantic[22], eastern equatorial Atlantic[23], southeast Pacific Ocean[24], Central Benguela System[25], Peru-Chile Current[26], South China Sea[27], southwestern Atlantic Ocean 30–61°S[28], northern Indian Ocean[29] and southeast Pacific[30]. The environmental tolerances and distribution of diatoms in surface sediments have been successfully applied to interpret climatic changes within sedimentary cores from Scotia and Weddell Seas[31]; Ross Sea[32,33]; Southeast Atlantic Ocean[34], McMurdo Sound[35,36] and George V Coast[37].

In hydrological decipherment

Fossil diatom assemblages mirror surface water hydrology. *Chaetoceros* spores have been used as indicators of seasonal upwelling. Their variation in abundance has been used to understand the strength of winds[17]. Gran[38] observed *Chaetoceros* blooms, suggesting a seed population being transported from the American Coast in the Gulf Stream Extension during spring. This then becomes a bloom in open ocean when thermal stratification is established. The presence of spores in sediments reflects bloom conditions as also the lateral transport from the neighbouring shelf region. Presence of shallow water forms (especially benthic) in deep-sea sediments indicates advection of waters from the continental shelf. Shelf benthic taxa are consistently more common in sediments of glacial intervals than of interglacials, from late Pliocene of southwest Africa[39] to late Pleistocene of North Pacific[40], perhaps a result of lower sea level and erosion of shelf material directly into the deep sea. Selective preservation of upwelling indicating diatoms in sediments off Somalia, NW Indian Ocean reflects 81% of the deposition of *Thalassionema nitzschiodes* and 78% of the deposition of *Chaetoceros* occurred during the upwelling period[41].

In sedimentary and sea-ice studies

Fossil diatom assemblages are used to estimate past sea-surface temperatures (SST) by assessing relative abundance of diatom species. An individual taxon of diatoms can be used to generate an equation to predict palaeotemperature. A regression equation, along the lines of the Imbrie and Kipp[42] is used for palaeotemperature estimation. For recent and Pleistocene studies, multivariate analysis is used to perform percentage composition of entire assemblage in surface sediments from a large number of sites and correlating these results with modern overlying surface water temperature. An assemblage of warm water diatom taxa which are found in boreal settings was considered as tracers for northward extension of a western boundary current with relatively warm water, high salinity and low nutrient contents in cores from the Norwegian Sea[43]. Kanaya and Koizumi[44] looked into the ratio of warm or cold diatoms relative to either the sum of the two or to the total assemblage (Td index). This approach has its limitations. But Td index has proved useful in identifying temperature variation in the western North Pacific on varying time scales[17]. Sediment cores from Sea of Japan displayed a millennial cycle of waxing and waning of the warm Tsushima Current during the Holocene[45].

Marine diatoms have shown several periods of extinction and/or radiation since their appearance in the Mesozoic; Jouse[46] defined six stages based on turnover of diatoms at the genus and family level. Fossil records indicate that the modern pelagic diatom flora began to evolve during the late Oligocene to early Miocene, when diverse and abundant genera appeared or there occurred large radiations, including *Nitzschia* and *Thalassiosira*. But Palaeogene and Cretaceous assemblages bear no resemblance to Neogene diatoms, not even at the family level.

Diatoms are reported from the mid-Pliocene (3.2–2.8 Ma) in seas around Antarctica[47,48]. Diatom data are compared from modern surface sediments in Prydz Bay and the Kerguelen Plateau with diatom assemblages from the Sørsdal Formation, Vestfold Hills which indicates that the climate was warmer than present during early Pliocene (4.5–4.1 Ma)[49].

Sea ice affects biota by favouring diatoms over organic-walled micro-organisms[50] that export large amounts of carbon to the seabed[51]. Such diatoms can be distinguished from open ocean water diatoms found in multi-year ice. Palaeo sea-ice cover can be determined by fossil siliceous frustules of diatomaceous sea ice algae[52,53]. Sea ice diatoms inhabit the underside of first year ice at the interface with nutrient-rich seawater, where light penetration through the ice is adequate and where microscopic capillaries and brine pockets provide a unique ecological niche[52]. A distinctive community of diatoms flourishes in brine pockets at the base of sea-ice floes in both Arctic and Antarctic[54,55]. Sea-ice diatoms are released into water when ice melts, with the species adapted to the melt-water environment proliferating, making use of the low salinity, high nutrient and stable surface waters. Other sea-ice diatoms dependent on the sea-ice substrate for their habitat are lost to the ocean depth. Two species of

Fragilariopsis, viz. *F. curta* and *F. cylindrus* are often used as sea-ice proxies[56] due to their occurrence in ice and as 'seeded' forms in the ice into open water[57–61]. These two species predominate in sediments underlying sea-ice zone and are useful in identifying regions influenced by sea-ice[62,63]. *In situ* studies[64] indicate that when irradiation increases during local spring season, there is an initial bloom within ice, followed by a second bloom in open water stabilized by melting of ice. In Antarctica, *Eucampia antarctica* is commonly found at the margin of ice, but not in the ice itself[65] and can serve as an alternate tracer for the ice margin. The gradual expansion of Antarctic sea-ice during Late Pleistocene can be documented by using *Eucampia* spp.[66]. *Chaetoceros* resting spores in sediments assemblages have been widely used as an indicator for the position of the ice-edge in neritic environments. In sediments cores from Windmill Islands, *Chaetoceros* spores indicate the variability of winter sea ice presence in bays during austral summer[67].

Down core study on Antarctic Sea ice has provided sufficient insight into past sea ice dynamics due to a short span of time period[68,69]. Diatom assemblages from Lallemand Fjord, Antarctic Peninsula were compared statistically to sedimentary and geochemical variables which reflect presence of seasonal and loose sea ice. The mid-Holocene is characterized by more open water diatoms and higher primary production. The Late Holocene underwent climatic cooling and increased sea ice cover, in the form of compact pack ice, multi-year ice, fast ice and/or closer proximity of Muller Ice Shelf[70].

Diatom assemblages preserved in Late Quaternary marine sediments from Prydz Bay, East Antarctica, were compared to modern assemblages to reconstruct depositional environments over the last ca. 21,000 years. During this stage, diatom frustules are abundant and well preserved with *Thalassiosira antarctica* resting spores and *Fragilariopsis curta* dominating the assemblage that suggests open marine deposition in an environment where the spatial and temporal distribution of sea ice is less than present[71].

T. antarctica is an open water species, occupying habitats in near-shore regions with SST ranging from –2°C to 1°C (ref. 61). This species is also found in ice-edge regions[72,73], sea-ice samples[74], platelet ice that gathers under true coastal pack and fast ice[74,75,60]. Krebs *et al.*[74] considered *T. antarctica* resting spores to be truly cryophilic, based on a study of microflora collected from a variety of sea-ice types from Antarctic Peninsula.

Diatom data provides evidence for two interstadials and one episode of glacial ice advance in Prydz Bay during the last ca. 22.0 Ma (ref. 76) which supports sedimentological and palaeoecological studies in Prydz Channel[77–79].

Late Quaternary sea ice history in the Indian sector of Southern Ocean was deciphered by using a Modern Analogue Technique and applied to fossil diatom assemblages to provide down core estimates of February SST and sea ice duration over the past 220,000 years at 56°40′S, 160°14′E (ref. 80). Studies carried out on the surface sediments from the Southern Ocean represent modern circumscription of tropical/subtropical diatoms regarding their relationship with SST and sea-ice cover in the form of distribution maps of eight tropical/subtropical diatom species[81]. Diatoms are useful tracers for analysing the complex glacigenic marine sediment facies of the Antarctic continental shelf. Analyses of fossil assemblages provide an important addition to traditional litho-stratigraphic description for distinguishing glacial sedimentary packets and interpreting past ice sheet processes[82].

All these studies indicate sea ice variation in the past at a given location and not sea-ice seasonality. Recently, Antarctic coastal areas with the demonstration of potential diatom species to document climate change at seasonal scale have been utilized to describe relative abundance of four diatom species and species groups, viz. *F. curta* group as a proxy for yearly sea ice cover, *F. kerguelensis* as a proxy for summer SST, *Chaetoceros* and *Hyalochaete* resting spores as a proxy for spring sea ice melting and *T. antarctica* group as a proxy for autumn sea-ice formation in Adélie Land on the Antarctic continental shelf. *F curta* group consists of *F. curta*, *F. cylindrus* and *F. vanheurckii* in which *F. curta* is the main species of this group. *Chaetoceros*, *Hyalochaete* resting spores and *T. antarctica* group are used to document the seasonal cycle of sea-ice in Antarctic coastal environments[83]. Modern Southern Ocean diatom studies provide sediment based biogeography that refers to many separate and local reports on sediment distributions of diatom taxa documented since the work of Kozlova[84]. Sedimentary distributions of 14 sea-ice related diatom species or groups of species with relative abundances greater than 2% in core-top surface sediment samples from the Southern Ocean documents abundance relationship of each of these species to three physical parameters (sea ice duration, sea ice concentration and SST). Their geographical distribution provides useful details on previous sedimentary and plankton reports and glimpses of their environments of preference[85]. In addition to the biogeographic distribution, abundance of diatom species or taxa from the core has been compared to both sea ice and SST data, indicating the environmental pressures that affect diatom distributions at sea surface. Sea ice related species are confined southward of the Polar Front generally observed within the sea ice zone[86].

Deciphering fluvial discharge

Freshwater diatoms are found in marine sediments deposited onto the continents as reflected from the close relationship of diatoms to the major rivers from the continental shelf of Portugal[87]. Freshwater diatoms have been used to track changes in direction of a river plume determined by shifting oceanic circulation. Pliocene freshwater diatoms found in late glacial section off the west coast of North America reflect that winter season is characterized by strong easterly winds which is also confirmed from predictions of global climate model for the Last Glacial Maximum[39].

Palaeoproductivity

Ocean productivity involves uptake of dissolved inorganic carbon and its sequestration into organic compounds by marine primary producer diatoms. Thus, they play a major role in controlling the partitioning of carbon between the ocean and atmosphere. Productivity fluctuation can in turn influence climate by altering the atmospheric concentrations of the greenhouse carbon dioxide[88,89]. Presence of diatom species in marine sediments indicates relatively high rates of production under conditions of moderate to high nutrient availability. Diatoms produce mono-specific oozes in extreme cases which frequently reflect the occurrence of bloom conditions (e.g. Chain forming genera such as *Phaeoceran*, *Chaetoceros* and *Skeletonema*)[17]. An individual taxon can be used to generate an equation to predict productivity (usually as carbon mass/area/time) using distribution of taxa in surface sediments. The statistically defined taxonomic assemblage is used with its highest correlation with known surface productivity.

Phaeoceran spores are dominant members of the diatom assemblages in North Atlantic in a broad zone centred at 60°N (ref. 90) whereas they are essentially absent from surface waters and modern sediments of the subarctic North Pacific[91,92]. This is a high nutrient–low chlorophyll (HNLC) region where rates of production and biomass are relatively low and seasonally invariant[93]. Extinct taxa consistently found only in sediments are known to be derived from continental margins, considered as high productivity indicators whereas those found at sites formerly located in high latitudes are indicators of cold conditions.

Usefulness in isotopic studies

Isotopes of diatoms are useful for estimating the palaeoclimate (both oxygen and silicon). The chemical make up of diatom shells reflect water chemistry at the time of shell formation. Stable oxygen isotope ratios contained in the shell can be used to infer past water temperatures. It is an emerging field in diatom research as it requires high level of expertise and sophisticated instrumentation. Hodell *et al.*[68] have estimated SST and sea-ice cover through diatom transfer functions as also carbon and nitrogen isotopes of diatom-intrinsic organic matter which provide evidence for a rapid change in surface water properties about 5000 years BP. De La Rocha *et al.*[12] have used ratio of ^{30}Si to ^{28}Si in sedimentary opal to provide information on past silicon cycles.

Silicon stable isotope measurements suggest that the percentage utilization of silicic acid by diatoms in the Southern Ocean during the last glacial period was a strongly diminished relative to the present interglacial. Frifiat *et al.*[94] have measured the silicon-isotopic composition $\delta^{29}Si$ of dissolved silicon and biogenic silica collected by sequential melting from spring Antarctic pack ice collected near 117°E–64.5°S. They investigated the use of Si isotopes to quantify the activity of sea-ice diatoms in the different brine structures and the influence of sea-ice diatoms on the spring ice edge blooms. Cardinal *et al.*[95] have described Southern Ocean diatom silicon isotopic signatures and compared them with the previously published data for dissolved silicic acid from the same locations. They compared $\delta^{29}Si_{BSi}$ within and below the mixed layer and identified a two-step history of the Polar Front and Inter-Polar Front Zones (PFZ–IPFZ) bloom in contrast to the newly formed diatom bloom in the Sea Ice Zone (SIZ). Shemesh *et al.*[96,97] have observed lowering in $\delta^{18}O$ of diatom through the Holocene in Atlantic sector of Southern Ocean. Three cores of Atlantic and Indian Sector of Southern Ocean south of Polar Front have indicated periodic decrease in $\delta^{18}O$ of diatom up to 2–3% during the last glacial[98].

Status of current research

Polar regions

Diatoms are sensitive environmental indicators of change and are a valuable tool in Antarctic palaeoclimate reconstruction[70,99–102]. Diatom assemblages from Antarctica have been used to estimate Quaternary oceanographic conditions[99,102], with interest in particular to water mass distribution[103], SST reconstruction[62,73,104–106], water depth[107], salinity[108,109] and sea-ice extent[110–114]. Planktic diatoms in surface sediments of Prydz Bay have been identified and correlated to environmental variables such as sea-ice cover and ocean currents by using multivariate analysis[115]. Four diatom assemblages have been identified from surface sediments of Prydz Bay and the Mc Robertson Shelf which are represented by coastal assemblage (characterized by sea-ice diatoms), shelf assemblage (characterized by sea-ice and ice-edge diatoms), oceanic assemblage (characterized by open-water diatoms) and Cape Darnley assemblage (characterized by heavily silicified, large diatoms typical of both sea-ice and open-water communities). The surface assemblages have been identified and correlated to latitude and sea-ice cover[115]. Diatom assemblages in association with modern environment suggest that upper water column of Fram Bank shelf waters of Prydz Bay is probably stratified due to the presence of low-salinity melt water and a very shallow mixed layer, protected from storms, with sea-ice cover for less than 10 months per year. This was attributed to changes in sea-ice patterns and oceanographic conditions which may have been linked to regional and global climate changes that occurred over the past 8000 yr BP (ref. 116). Description of modern geographic distribution of 10 major open ocean species and species groups in Atlantic and Indian sectors of Southern Ocean reveal the presence of *Rhizosolenia* pointed group, *Thalassiosira gracilis* group and *Trichotoxon reinboldii* with maximum relative abundances occurring within the maximum winter sea-ice edge. *Fragilariopsis kerguelensis*, *Thalassiosira lentiginosa*, *Thalassiosira oliverana* and *Thalassiothrix* spp. group are the maximum occurrences at the Antarctic Polar Front. A warm open ocean grouping with maximum abundances is observed within the PFZ primarily composed of *Rhizosolenia* rounded group, *Thalassionema nitzschoides* var. *nitzschiodes* group and *Thalassionema nitzschiodes* var. *lanceolata*[117]. Pelagic and sedimentary processes from Norwegian Sea have been described for better understanding of different hydrographical conditions with seasonal ice coverage reflected in seasonal variations of total diatom flux and species composition[118]. Surface sediment diatom assemblages in depth profiles along the southeastern Beaufort Sea, Arctic Ocean (Canada) were analysed to describe the relationship between species composition and water depth of deposition[119]. Diatom studies with respect to paleoceanographic reconstruction in Arctic Ocean have been carried out by various workers[90,120–130].

Indian Ocean

Cenozoic marine planktic diatom stratigraphy of the tropical Indian Ocean has been described by Schrader[131]. The first attempt to construct a continuous record of past sea-ice concentration is from two sediment cores from the southeast Indian Ocean along the 145°E meridian at 54°S and 56°S (ref. 63). Diatom data sets have been recently compiled for both the South Atlantic and Indian Oceans, and applied on transfer functions[62,76]. Diatom species composition in sediments of Somalia, NW Indian Ocean indicate the applicability of biogenic silica as an indicator for changes in palaeo-upwelling intensities[132]. Mass fluxes of diatom opal with other proxies have been measured with time-series sediment trap at six sites in the Arabian Sea, Bay of Bengal and Equatorial Indian Ocean[29].

Indian context and future prospects

Marine diatoms studies in India were initiated by Desikachary[133] which includes studies from the Arabian Sea and Indian Ocean; Indian Ocean region. These studies included taxonomic approach of fossil and plankton diatoms. Mohan *et al.*[134] documented spatial distribution of diatoms in surface sediments of Indian sector of Southern Ocean and correlated it to frontal changes and nutrient availability. There have been sparse studies on diatoms with respect to palaeoclimatology and palaeoceanography from Indian Ocean. As northern Indian Ocean is considered as a carbonate ocean but monsoon processes push it towards a silica ocean therefore, it is imperative to carry out diatom studies for improved understanding of the monsoonal processes. This necessitates a group working on marine diatoms of open ocean which is being developed at NCAOR (National Centre for Antarctic of Ocean Research), Goa.

Conclusion

Knowledge of diatoms has been known to exist since the last century but only in the last few decades it has been applied more to understand the palaeoceanography and palaeoclimatology. This article describes the applicability of diatoms in palaeoceanography but there are still huge gaps in our knowledge of fossil diatoms because we do not have living representatives of many of the fossil genera. Though we can identify some species of fossil diatoms and interpret the past oceanographic conditions, we lack basic information on the morphology, protoplast structure, cytology and life cycle of many extant diatom genera[135]. Their omnipresence and versatility to generate a hydrated siliceous covering leads to better preservation than their counterparts, thereby aiding decipherment of past SSTs, water masses, surface water hydrology, palaeoproductivity as also palaeo sea-ice cover and sea-ice extent. Diatomists believe that there are approximately one million species yet to be identified[136]. As we have only selected identified fossil diatom species to infer palaeocenography, we need to improve our knowledge in identifying more diatom species and their particular habitats.

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