Evolution of productivity and monsoonal dynamics in the eastern Arabian Sea during the past 68 ka using dinoflagellate cyst records

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Abstract
For the first time here we report the dinoflagellate cyst assemblage response to the monsoon variability over the last 68 ka from the eastern Arabian Sea (EAS). Based on the cyst assemblage, five dinoflagellate cyst zones were established, corresponding to four Marine Isotopic Stages (MIS 1-4). An increased abundance of autotrophic Gonyaulacoid species (especially Spiniferites) during glacials (MIS 2 and 4) and late MIS 3 (~41.67 to 25.3 ka) reflect high productivity driven by strong winter convection during the Northeast monsoon. In contrast, their decreased abundance during MIS 1 and early MIS 3 (~58.6 to 42.87 ka) reveals decrease in productivity due to strong stratification caused by intense monsoon precipitation induced runoff from the Western Ghats and reduced light penetration driven by cloud cover. The variation in heterotrophic Protoperidinium species abundance could be related to variation in the Oxygen Minimum Zone (OMZ) intensity, with better preservation during intense OMZ in MIS 3 and the late Holocene (~3 ka onwards). Therefore, it is proposed here that the abundance of Protoperidinium can be used as an index of OMZ in the EAS.

Key words:
Eastern Arabian Sea; Monsoons; Productivity; Marine Isotopic Stages; Dinoflagellate cyst

Highlights
- Dinoflagellate cyst proxy for paleoproductivity and monsoonal dynamics in the EAS.
- Productivity increase during MIS 2, 4 and late MIS 3 controlled by winter monsoon.
- Productivity variability represented by Spiniferites species abundance.
- Protoperidinium cyst abundance characterises OMZ variability.
1. Introduction

The Asian Monsoon system has a strong bearing on the biological productivity of the Arabian Sea. The present-day climatic and oceanographic conditions predominating in the Eastern Arabian Sea (EAS) are influenced by both the South West (SW or summer) and North East (NE or winter) monsoon systems. The EAS experiences moderate upwelling and high precipitation along the entire margin during summer and winter vertical mixing in the northern part, and fresh water inflow during winter from the Bay of Bengal in the south (Banse et al., 1987; Bhattathiri et al., 1996; Prasanna Kumar et al., 2000; Gerson et al., 2014). These regional climatic and oceanographic features could also play a significant role in the evolution of productivity variation in the EAS during the Late Quaternary Period. The paleoclimatological and paleoceanographic records have provided detailed information on the late Quaternary climate variability and paleoproductivity variations in the region. Studies from the western Arabian Sea (WAS) revealed productivity was lower during the last glacial period due to a weaker SW monsoon and reduced upwelling (Naidu and Malmgren, 1996; Ivanochko et al., 2005). On the contrary, high productivity during the last glacial period was reported in the northern Arabian Sea (NAS), with an intensified NE monsoon resulting in intense deeper water mixing and increased advection of nutrient-rich subsurface water (Reichart et al., 1998; Luckge et al. 2001; Ivanova et al., 2003).

In the EAS recent studies using paleoproductivity proxies, such as abundance of planktonic foraminifera, coccolithophore, organic carbon, carbon and nitrogen isotopic records infer that productivity was higher during the Last Glacial Maximum (LGM) than in the Holocene (Ivanochko, 2004; Singh et al., 2006, 2011; Cabarcos et al., 2014; Naidu et al., 2014). In this context, present study used dinoflagellate cyst records over the last 68 ka to contribute further to the existing paleoclimatic and paleoceanographic information in the EAS.

Dinoflagellate is one of the dominant group of the primary producers in the marine ecosystem, and have a complex life cycle which includes cyst (resting stage) formation. The rigid cell wall of dinoflagellate cyst comprises of a bio-macromolecule, dinosporin (Fensome et al., 1993; Bogus et al., 2014) which enable them to resist physical, chemical and biological destruction and degradation. Thus, cyst records provide the more reliable paleoceanographic information where other calcareous and siliceous microfossil taxa, such as foraminifera, diatoms, and radiolarian, are subject to dissolution (Pospelova et al., 2006). In the recent years, various paleoceanographic studies have demonstrated the use of dinoflagellate cyst assemblages to reconstruct paleo-environmental conditions on a centennial as well as millennial time scale (Shaozhi and Harland, 1993; de Vernal and Pederson, 1997; Marret et al., 2001; Mudie et al., 2002; Matthiessen et al., 2005; Pospelova et al., 2006; Price et al., 2013). Dinoflagellates have species specific differential environmental and growth requirements, thus their cyst distribution in sediments can portray surface water conditions (Dale, 2001; Marret and Zonneveld, 2003; Zonneveld et al., 2013). Higher abundance of autotrophic species in sediments reveals stable water conditions with increased light penetration and ample nutrient supply in water column, whereas increased abundance of heterotrophic species cysts reveals availability of prey organisms and productivity changes (Zonneveld, 1997a; Marret and Zonneveld, 2003; Kim et al., 2009; Zonneveld et al., 2013). In recent surface
sediments, dinoflagellate cyst distribution patterns have shown correlation with regionally varying surface water masses, physico-chemical (temperature, salinity, dissolved oxygen, nutrients) and biological (food availability, productivity) factors (Marret and Zonneveld, 2003; Zonneveld et al., 2013).

Here we present dinoflagellate cyst abundance and assemblage records at a millennial resolution in the EAS over the last 68 ka. The focus of present study is to better understand the marine primary productivity changes and seasonal monsoonal dynamics in relation to past climatic variability in the EAS over the late Quaternary period.

2. Climatic and Oceanographic Setting

Semi-annual reversal of the SW and NE monsoon winds divides the year in the SW monsoon and NE monsoon seasons respectively, separated by the two inter-monsoonal periods (spring and fall). The environmental changes induced by the monsoonal variability strongly influence oceanographic and climatic features in the Arabian Sea. Strong SW winds develop during the SW Monsoon (May-September) as a result of differential heating of the continental and oceanic regions, leads to low atmospheric pressure above the Asian Plateau and high atmospheric pressure over the relatively cool southern Indian Ocean. In response to this, strong wind induces offshore Ekman transport, which results into intense upwelling off Somali and Oman region (Wyrtki, 1973; Clemens et al., 1991; Morrison et al., 1998). During this period the West Indian coastal current (WICC) develops in the NAS and flows towards the equatorward (Shankar et al., 2002; Fig. 1). The offshore divergence (Ekman transport) along shore wind stress component leads to moderate coastal upwelling and sea surface temperature (SST) cooling by 2.5°C along the central west coast of India (Shetye et al., 1985; Naidu and Malmgren, 1999). In the EAS, SW Monsoon precipitation from the Western Ghats drains into the Arabian Sea through rivers and streams, which develops low saline plume towards offshore (Sarkar et al., 2000). As a result, increased thermal stratification reduces mixed layer depth (MLD) and nutrient advection to the euphotic layers (Gerson et al., 2014). Along the coastal regions, the supply of nutrient from upwelled bottom water and terrestrial runoff increases the primary production (Bhattathiri et al., 1996).

During the NE monsoon (November-February), the wind pattern over the basin reverses to northeast due to development of high pressure gradient over the Tibetan Plateau and Central Asia, resulting into flow of cold and dry winds over the Arabian Sea. This change in wind pattern reverses the direction of the WICC northwards (Shankar et al., 2002; Fig. 1). During NE monsoon about 6 Sv of low saline water of the Bay of Bengal intrudes into the Arabian Sea (Shankar et al., 2002). The dry NE winds generally enhance the evaporation in the NAS, subsequently cooling and convective mixing injects nutrients into the surface layers from the thermocline region, which in turn increases productivity (Banse, 1987; Madhupratap et al., 1996), whereas in the EAS also, deep convective winter mixing supports moderate increase in productivity (Bhattathiri et al., 1996; Prasanna Kumar et al., 2000; Gerson et al., 2014) and biogenic particle flux (Haake et al., 1993) in the open ocean region.
3. Material and Methods

3.1. Sediment core

A 4.2 m gravity sediment core AAS 9/21 was collected from the continental slope off Goa, in the EAS (14°30.539’N, 72°39.118’E; water depth 1807) during the A.A. Sidorenko cruise 9 (Fig. 1). The sedimentary sequence consists of a mixture of terrigenous and biogenous material. The terrigenous material comprises clay and silt, whereas the biogenous material consists of planktonic and benthic foraminifera and traces of pteropods and diatoms (Govil and Naidu, 2010).

The Chronology of the core AAS 9/21 up to 310 cm depth was established based on six Accelerator Mass Spectrometry (AMS) $^{14}$C dates (Table 1). Below, the chronology was established by correlating $\delta^{18}$O of Glociberinoides ruber record with the low-latitude global isostack curve of Martinson et al. (1987) (refer Govil and Naidu, 2010). Sedimentation rate varies from 4.6 to 13.6 cm ka$^{-1}$ at the core location (Fig. 2; Govil and Naidu, 2010).

3.2. Palynological sample preparation and analysis

The core was cut into 3 cm-thick slices, out of which samples from alternative sections were used for dinoflagellate cyst analysis. Seventy five samples covering span of ~68 ka were processed using the palynological method (Matsuoka & Fukuyo, 2000) with some modifications. A known weight of dry sediment (7-8 g) was repeatedly washed with distilled water to remove salts, sonicated (30 sec.) and sieved through 120 µm and 10 µm meshes to remove coarse and fine particles. The slurry accumulated on 10 µm was treated with HCl (10%) for 10 hrs and HF (30%) for 36-48 hrs to dissolve calcareous and silicate materials. Each chemically treated sample was washed with distilled water to remove acid, sonicated for 30 sec. Later, the slurry was sieved through 10 µm to remove fine material. The residue accumulated on the 10 µm mesh was then suspended in 10 ml distilled water and kept in a vial. For observation, aliquots of processed sample were counted in duplicate or a higher number of replicates, such that a minimum of 250 cyst were counted per sample. However, in some samples (representing ages ~8.3, 1.0, 1.67, 11.11 and 11.92 ka) only 150 to 160 cysts were counted. Dinoflagellate cyst abundance was estimated per gram dry weight sediment (cysts g$^{-1}$).

Dinoflagellate cysts were identified by using inverted microscope (Olympus IX 71) at 200X and 1000X magnifications based on published morphological descriptions (Fensome et al., 1993; Zonneveld, 1997b; Lewis et al., 1999; Matsuoka and Fukuyo, 2000; Rochon et al., 2009; Radi et al., 2013) and modern dinoflagellate cyst determination key by Zonneveld and Pospelova, (in press) (online version: https://www.marum.de/en/Modern_dinoflagellate_cyst_determination_key.html). The nomenclature used for this study is in accordance with Head (1996), Zonneveld (1997b), Fensome and Williams (2004).

On the basis of morphological similarity some dinoflagellate species have been grouped together prior to statistical analysis. Spiniferites species, S. ramosus and S. bulloideus were grouped together as S.
S. ramosus because of very slight interspecific morphological variation in size and processes thickness. Similarly, S. mirabilis and S. hyperacanthus have morphological similarities with exception of the absence of crown process in S. hyperacanthus, hence grouped together as S. mirabilis (Radi and de Vernal, 2008; Rochon et al., 2009). S. quanta and cyst of P. nudum have similar morphology with some variation in size and number of process, hence considered as S. quanta. Stelladinium species, S. stellatum and S. reidii were grouped as S. stellatum. Brigantedinium spp. represent all smooth walled, spherical brown cysts. In absence of archeopyle intraspecific differentiation is difficult in these morphotypes, whereas sometimes cyst folding also hides the archeopyle structure (Pospelova et al., 2006).

3.3. Statistical analysis

The abundance of dinoflagellate cyst was further subjected to calculate species diversity (Shannon-Wiener diversity index i.e. \( H' \)), species richness and evenness using the software PRIMER (version 6).

Further multivariate statistical analysis was performed on relative abundance data of dinoflagellate cyst using CANOCO 4.5 software for Windows (ter Braak and Smilauer, 2002). Prior to statistical analysis, dinoflagellate cyst data were logarithmically transformed (\( \log(x+1) \)) to minimize the dominance of few abundant species and increase the weight of less abundant species, which could thrive in narrow ecological niche. To determine the variability within data set Detrended Correspondence Analysis (DCA) was performed. The length of the first gradient axis was 1.7 standard deviation unit (sd) indicate linear variation (ter Braak and Smilauer, 2002) in cyst assemblage within the core sections. Due to linear character of data set a Principle Component Analysis (PCA) was performed, which can reduce dimensionality of the data set and summarize it by extracting the smallest number components that account for most of the variation in the original multivariate data (Hair et al., 1992).

4. Results

4.1. Dinoflagellate cyst assemblage and abundance

A total of 29 dinoflagellate cyst species were identified from 75 sediment sample intervals analysed in the core AAS 9/21, covering a time span of ~68 ka (MIS 1-4) (Table 2). The number of species varied from 4 to 17. Cysts of autotrophic Gonyaulacoid species were the most dominant and mainly represented by Spiniferites group, Spiniferites ramosus (up to 54%), S. membranaceus (up to 45%), S. bentori (up to 40%), S. mirabilis (up to 38%), Impagidinium sphaericum (up to 37%) and Spiniferites sp. 1 (up to 21%) (Fig. 2). Other dominant autotrophic species were S. pachydermus (up to 17%) and Operculodinium centrocarpum (up to 8%). Among heterotrophic species, Selenopemphix nephroides (up to 13%), Brigantedinium spp. (up to 8%) and Trinovantedinium applanatum (up to 7%) were dominant.

Dinoflagellate cyst abundance varied down-core from ~140 to 26000 cysts g\(^{-1}\), averaging 3000 cysts g\(^{-1}\) (Fig.3a). Cyst abundance was higher (~260 to 3390 cysts g\(^{-1}\), avg. 1470 cysts g\(^{-1}\)) in MIS 4 than in early MIS 3 (~222 to 2081 cysts g\(^{-1}\), avg. 987 cysts g\(^{-1}\)), whereas approximately two fold increase was
observed in late MIS 3 (~41.67 to 25.3 ka) (~1030 to 6350 cysts g⁻¹, avg. 3210 cysts g⁻¹). The cyst abundance was two folds higher during MIS 2 (~1500 to 26000 cysts g⁻¹, avg. 5450 cysts g⁻¹), including the LGM (19 to 21 ka), than in MIS 3. In the Holocene, cyst abundance decreased about three folds than the preceding LGM (Fig. 3a). Over the last 68 ka autotrophic Gonyaulacoid species were dominant (avg. 2400 cysts g⁻¹), than heterotrophic Protoperidinoid species (avg. 80 cysts g⁻¹) (Fig. 3b and d). Although, absolute abundance of heterotrophic cyst taxa was less, their relative abundance was comparatively more during MIS 3 and in the late Holocene (from ~3 ka onwards) (Fig. 3d). The heterotrophic (H) and autotrophic (A) dinoflagellate cyst ratio (H/A) decreased during MIS 4, MIS 2 and the early Holocene (Fig. 3e). An abrupt increase in H/A ratio towards the late Holocene and large variation during MIS 3 was due to contribution of Protoperidinoid species (Fig. 3d and e).

The Shannon-Wiener, a species diversity index (H’) varied from 1.05 to 2.39. It was highest from ~35 to 25 ka and since ~3 ka, and the lowest was observed during the LGM to early Holocene (Fig. 3f). Species richness also followed similar trends as that of species diversity index (Fig. 3g). However, species evenness varied from 0.59 to 0.95, cyst assemblage was more even in MIS 1 (avg. 0.86) (Fig. 3h).

4.2. Statistical analysis and dinoflagellate cyst zones

A PCA performed on the logarithmically transformed relative abundance data of dinoflagellate cyst, reveals four principal components axis (1-4 PCs) accounting 28.4%, 11.5%, 8.8% and 7.3% of variances respectively, with total cumulative variance of 56%. Graphical representation of the same, a PCA biplot, shows ordination of each species and samples along first two most dominant PCs, PCA1 and PCA2 (Fig. 4). Samples similar in species composition are located close to each other in the PCA biplot. Based on sample score for PCA1, PCA2 and relative abundance of dinoflagellate cyst, five dinoflagellate cyst zones (DZ1-5) were established. All dinoflagellate cyst zones were characterized by dominance of Spiniferites species. Apart from this, the characteristic species composition of each zone are presented below.

4.2.1. DZ1 (~67.5 to 58.67 ka)

This zone was dominated by autotrophic Spiniferites species, S. membranaceus (avg. ~23.2%), S. mirabilis (avg. 23.4%), S. ramosus (avg. 16.8%) and S. bentorii (avg. 13.9%), and relatively less contribution of Protoperidinoid species (avg. 0.03%), which results into lesser Shannon-Wiener diversity index, species richness and evenness (Fig. 2 and 3e, f, g). This zone corresponds to MIS 4 and is characterised by fluctuating values of PCA1 and negative values of PCA2 (Fig. 3i and j).

4.2.2. DZ2 (~58.60 to 42.87 ka)

Approximately two fold decrease in absolute cyst and Gonyaulacoid cyst abundance was observed in DZ2 than the preceding DZ1 (Fig. 3a and b). Increased relative abundance of Protoperidinoid species, Brigantedinium spp., S. nephroides, S. stellatum, Q. concreta, cyst of P. latissimum and T. applanatum
was observed during this period, which could also be responsible for increase in the H/A ratio and Shannon-Wiener diversity index (Fig. 2 and 3e, f).

4.2.3. DZ3 (~41.67 to 25.30 ka)

DZ3 extend from mid to late MIS 3 and is distinguished by mostly positive PCA1 and PCA2 values (Fig. 3i and j). Relative abundance of *S. miribilis* (avg. 21.91%), *S. membranaceus* (avg. 21.3%), *S. ramosus* (avg. 16.6%) and *S. bentorii* (avg. 12.09%) increased during this period, whereas heterotrophic taxa *S. quanta* (avg. ~0.8%) appeared during ~34.09 to 29.04 ka (Fig. 2).

4.2.4. DZ4 (~24.6 to 13.17 ka)

DZ4 coincides with MIS 2, including the LGM. Absolute cyst and autotrophic species abundance showed large fluctuation with numerous spikes (Fig. 3a and b), whereas heterotrophic species abundance was highest during the LGM. An abrupt decrease in absolute cyst, autotrophic and *Spiniferites* species abundance was observed during early MIS2 (23.54 and 20.39 ka) and from 17.03 to 16.45 ka (Fig 3a, b and c). Changes in cyst assemblage and abundance were also reflected in fluctuating values of PCA1, whereas most of the PCA2 values were negative (Fig. 3i and j). Relative abundance of *S. membranaceus* (avg. ~22%), *S. ramosus* (avg. 21.54%) and *S. mirabilis* (avg. 21.36%) reached to its maximum during the LGM whereas it was declined in case of heterotrophic taxa *Brigantedinium* spp. (avg. ~0.7%), *Selenopemphix quanta* (avg. ~0.02%), *Quinquecuspis concreta* (avg. ~0.2%) and *Trinovantedinium applanatum* (avg. ~0.4%) (Fig. 2). Absolute abundance of heterotrophic species was lowest during this period than preceding MIS 3 which negatively influenced H/A ratio (Fig. 3e). Fluctuating values of species indices also support the variability in cyst assemblage during this period. Overall decreasing trend in Protoperinidinoid taxa reflected in decreased Shannon-Wiener index, species richness whereas increasing species evenness could be supported by increased abundance of Gonyaulacoid species (Fig. 3).

4.2.4. DZ5 (~12.80 to 0.79 ka)

An abrupt increase in cyst of autotrophic taxa, *Bitectatodinium spongium*, *S. pachydermus* and *O. centrocarpum* were the characteristic feature of this zone (Fig. 2). *S. bentorii*, *S. membranaceus* and *S. mirabilis* relatively dominate cyst assemblage especially during 12.36, 9.4, 6.07 and 3.1 ka, in the Holocene (Fig. 2). Relative abundance of heterotrophic species, *S. stellatun*, *S. robustum* and *V. calvum* and *S. nephroides* increased during the late Holocene (~3 ka), which in turn increases H/A ratio, species richness and evenness (Fig. 2 and 3e, f, g). Shannon-Wiener diversity index was lowest during the entire Holocene, and increased since ~3 ka due to appearance of heterotrophic species. PCA1 values were positive whereas PCA2 values were negative in DZ5 (Fig. 3i and j).
5. Discussion

Dinoflagellate cyst production in the marine environment is mainly influenced by physico-chemical factors such as SST, sea surface salinity (SSS) and nutrients, thus cyst abundance and assemblages in sediments have been used to reconstruct climatic and oceanographic variability in the geological past (de Vernal et al., 2001; Dale, 2001; Mudie et al., 2002; Morquecho and Lechuga-Deveze, 2004; Pospelova et al., 2008; Zonneveld et al., 2013). Recent sediment trap and cyst distribution studies in the Arabian Sea revealed the monsoon influence on cyst production and assemblage (Zonneveld, 1997a; Zonneveld and Brummer, 2000; D’Costa et al., 2008). Here, we demonstrate the use of dinoflagellate cyst abundance as a paleoceanographic proxy to understand the monsoonal productivity and OMZ variations in the EAS (Table 3).

5.1. Dinoflagellate cyst preservation and OMZ intensity

Dinoflagellate cyst can be affected by oxidative degradation similar to the organic matter, especially cysts of Protoperidinium species, which appears to be more sensitive to oxidative degradation than Spiniferites species (Zonneveld et al., 1997a). Poor preservation of Protoperidinium in sediment can be linked to aerobic decay in oxygenated bottom water and weak intensity of the OMZ (Zonneveld et al., 1997a, 2007; Reichart and Brinkhuis, 2003), therefore high abundance of Protoperidinium species could indicate the increased productivity and good preservation state in the OMZ sediments (Reichart and Brinkhuis, 2003; Zonneveld et al., 2007; Zonneveld et al., 2013). Reichart and Brinkhuis (2003) used Protoperidinium cyst as proxy for paleoproductivity in the NAS, where comparison of Protoperidinium cyst abundance within and outside the OMZ settings highlighted their degradation during paleo-climatic events where bottom waters were oxic. In the core AAS 9/21, absolute abundance of Protoperidinium varies over last 68 ka with maximum abundance in MIS 3 and late Holocene (Fig. 3e). This increase in Protoperidinium cyst abundance could be facilitated by their better preservation due to reduced oxygen supply and increased denitrification resultant of intense OMZ, an inference supported by several line of evidences. First, higher \(^{15}\text{N}\) and \(C_{\text{org}}\) value during MIS 3 and late Holocene reveals the increased denitrification and better organic matter preservation in the Core AAS 9/21 sediments (Goddad, 2014). Second, increased Mo concentration highlights the low oxygen condition and intensified OMZ during this period (Goddad, 2014). Since Protoperidinium cysts can be used as productivity proxy, we could expect higher Protoperidinium cyst abundance during MIS 4 than in MIS 3, because in the EAS productivity was higher during glacials than interglacials (Ivanchko, 2004; Banakar et al. 2005; Kessarkar et al., 2010; Singh et al., 2011). The sedimentary \(^{15}\text{N}\) and Mo records in the core AAS 9/21 reveals weak OMZ due to less denitrification and oxic conditions during the glacial MIS 4 and MIS 2 (Goddad, 2014). This is further supported by other studies in the EAS, which reveals OMZ was less intense and water column denitrification declined during the glacial periods (Ivanchko et al., 2005; Kessarkar et al., 2010). In this context, the variation in Protoperidinium cyst abundance can be used as a biological proxy to reconstruct the OMZ variation (Table 3), similar to other geochemical proxies in the late Quaternary sediments along the EAS, in particular species like Q. concreta, S. stellatum, S. nephroides, T. applanatum and Brigantedinium sp. which are more susceptible for oxidative degradation.
and observed in higher concentrations in anoxic or hypoxic sediments (Zonneveld et al., 1997a, 2007; Zonneveld et al., 2013).

Cyst produced by Gonyaulacoid species, *L. machaerophorum*, *O. centrocarpum* and *Spiniferites* species including *S. bentori*, *S. mirabilis*, *S. pachydermus* and *S. ramosus* are proven to be moderately sensitive, whereas *Impagidinium* species (*I. aculeatum* and *I. paradoxum*) and *N. labyrinthus* are resistant to the oxidative degradation (Zonneveld et al., 1997a, 2007). Reichart and Brinkhuis (2003) reported that in surface sediments within and outside the OMZ in the WAS, where fluxes in the productive sea-surface layer were identical, concentrations of most Gonyaulacoid species were similar in all sediments, whereas the OMZ samples were relatively enriched in *Protoperidinium* cysts. The effect of post-depositional species-selective oxidative degradation was minimal on preservation of Gonyaulacoid species than *Protoperidinium* (Reichart and Brinkhuis, 2003). In the core AAS 9/21, autotrophic Gonyaulacoid species dominated cyst assemblage, with peaks in MIS 4, late MIS 3 and MIS 2 (Fig. 3b). Increased absolute abundance of Gonyaulacoid species, in particular *Spiniferites* species during these periods reflects the variability in the primary productivity and monsoon in the EAS (Table 3).

5.2. Productivity variations in the EAS

Dinoflagellate cyst assemblage composition reflect surface productivity and their fossil assemblages were used for the reconstruction of the paleoproductivity during the Late Quaternary period in the Santa Barbara Basin (Pospelova et al., 2006), Guaymas Basin (Price at al., 2013), Gulf of Alaska (de Vernal and Pederson, 1997; Marret et al., 2001), Arctic region (Matthiessen et al., 2005), Black sea (Mudie et al., 2002) and south China Sea (Shaozhi and Harland, 1993). In the WAS, relative abundance of dinoflagellate cyst was used for the reconstruction of the SW monsoon variability during the Late Quaternary (Zonneveld, et al., 1997b), whereas in the Bay of Bengal variation in cyst abundance and species assemblage was implicated to study the Late Quaternary productivity and climatic variability (Naidu et al., 2012). In Core AAS 9/21, temporal variation observed in Gonyaulacoid species, *Spiniferites* species in particular, provide valuable information about the millennial time scale productivity variations in the EAS region and is discussed below.

High absolute abundance of Gonyaulacoid species, *Spiniferites* species in particular, during MIS 2 and MIS 4, indicate biological productivity increase during the glacialis (Fig. 3c,d and 5). *Spiniferites* cysts belongs to autotrophic *Gonyaulax* species, which can sustain in wide range of environmental variables (mainly salinity, temperature and nutrients) (Zonneveld et al., 2013). Higher abundance of *Spiniferites* species during the glacialis suggest nutrient supply from deeper waters due to vertical winter convection resultant of the strong NE Monsoons, whereas reduced strength of the SW Monsoon decreases cloud cover and supply of low saline terrestrial runoff. This reduces turbidity and increases light penetration into euhphotic layers which in turn favours growth of *Spiniferites* species. Zonneveld and Brummer (2000), also observed high flux of *Spiniferites* species in the sediment trap along the Somalian region during the end of the SW monsoon when water conditions were relatively stable with high nutrient concentrations and reduced turbulence. Furthermore, our interpretation of the NE monsoonal control on
glacial productivity in the EAS gets support from CaCO$_3$ data in the present core (Godad, 2014) and recent planktonic foraminifera, coccolithophore and geochemical productivity proxy data from other core studies in the region (Rostek et al., 1997; Ivanochko, 2004; Singh et al., 2006, 2011; Cabarcos et al., 2014). The planktonic foraminiferal species and geochemical proxy records in the core MD76-131 and SK 17 increased two fold during the glacial and has been attributed to productivity increase due to nutrient enrichment resultant of the NE Monsoon induced winter mixing (Singh et al., 2006, 2011; Naidu et al., 2014). The strong, cold and dry NE winds during the glacial would have resulted in enhanced evaporation, resulting increase of SSS (Govil and Naidu, 2010) and convective upward winter mixing in the EAS (Singh et al., 2011; Rostek et al., 1997; Cabarcos et al., 2014). Above mentioned cores (MD76-131 and SK 17) were from the present OMZ regions. Thus, comparison of cyst abundance records in the core AAS 9/21 with the productivity trends observed in OMZ cores support that *Spiniferites* species abundance in the present core can be a good indicator of productivity changes during the glacial and interglacial periods in the EAS.

In glacial, *Spiniferites* species abundance was comparatively lower during the MIS 4 than MIS 2 (Fig. 3b), which could reveal the productivity variability during the MIS 4 and MIS 2. This could attributed to comparatively decreased strength of the NE Monsoon during the MIS 4 than MIS 2 as observed in salinity proxy ($\delta^{18}$Ow) records in the core AAS/9-21 (Govil and Naidu, 2010). Furthermore, geochemical paleoproductivity proxy records in OMZ also suggest higher productivity during the MIS 2 than MIS 4 due to the strongest NE monsoon (Banakar et al., 2005).

5.3. Relationship between dinoflagellate cyst assemblage and monsoon variability

The MIS 4 was dominated by *Spiniferites* species, mainly *S. bentorii*, *S. ramosus*, *S. membranaceus* and *S. mirabilis* (Fig. 2 and 3b). In modern sediments, these *Spiniferites* species can found in the eutrophic to oligotrophic waters, whereas their high relative abundance can be observed in the nutrient elevated waters within well-mixed surface waters as well as outside the upwelling cells (Zonneveld et al., 2013). *S. bentorii*, *S. membranaceus* and *S. mirabilis* are warm-water species. In addition *S. bentorii* and *S. mirabilis* can tolerate high SSS as well (Marret and Zonneveld, 2003; Zonneveld et al., 2013). Higher proportion of *Spiniferites* taxa have also been suggested to reflect the warmer water in the southern Californian region (Prauss, 2002). In the EAS increased abundance of *Spiniferites* species during MIS 4 could be attributed to comparatively warm, hypersaline (Fig. 1, 2) and stable water mass. This interpretation could be supported by previous paleo-salinity reconstructions on this Core AAS 9/21 (Govil and Naidu, 2010), which reveals that during MIS 4, variation in SST and SSS was higher (Fig. 3k and l), indicating the warmer and saline water as a result of increased evaporation and decreased precipitation due to the relatively stronger NE monsoon.

Absolute cyst abundance decreased from MIS 4 to early MIS 3 (~58.61 to 42.87 ka). Similar shift has been observed in *Spiniferites* species, whereas *Protoperidinium* cyst abundance increased in MIS 3 compared to MIS 4 (Fig. 3c and d). This interval characterised by *Q. concreta*, *S. nephroides*, cyst of *P. latissimum*, *T. applanatum* and *Brigantedinium* spp. (Fig. 2). This increase in *Protoperidinium* species
abundance could be due to their better preservation in the anoxic sediments as discussed in section 5.1. During most of the deglaciation, the winter monsoon winds were weak, resulting in reduced vertical mixing. However, the strong SW monsoon and associated river discharge in to the EAS enhances nutrients supply in surface layers, which fuel the growth of primary producers, mainly diatoms. However, reduced light penetration due to increased turbidity and cloud cover during the prevalent SW monsoon as well as competition with diatom for nutrients could be the reasons for the suppressed growth of Spiniferites species during early MIS 3.

The upper section of MIS 3 (~41.67 to 25.3 ka) was characterised by increased abundance of autotrophic Spiniferites species (Fig. 3b). In the Santa Barbara Basin, elevated relative abundance of Spiniferites species was related to the enhanced input of nutrient enriched water (Pospelova et al., 2006). In core AAS 9/21, increasing relative abundance of Spiniferites species, especially S. membranaceus, S. miribilis and S. remosus during late MIS 3 could be due to elevated nutrient concentrations resultant of the strong winter convection and more availability of light due to less cloud cover, especially from ~34.09 to 26.62 ka. Cysts of other autotrophic species like I. sphaericum and Spiniferites sp. 1 increased greatly during this period, which highlights elevated SSS (Fig. 2 and 3k), resultant of increased evaporation due to the strong NE monsoon dry and cold winds. This conclusion is in part supported by the increasing SSS due to lower precipitation during late MIS 3 (Fig. 3l). Increasing abundance of Protoperidinium species, especially S. quanta reveals decrease in oxidative degradation due to intense OMZ (refer section 5.1).

A swift from relatively stable to largely fluctuating dinoflagellate cyst abundance characterizes a shift from MIS 3 to MIS 2 (Fig. 3a). Abrupt change in total cyst abundance is the characteristic feature of the MIS 2, including LGM period. Samples from DZ4 are more dispersed in the PCA biplot, demonstrating greater variation in cyst assemblages during MIS 2. Since dinoflagellates respond to their surrounding environmental conditions, high variation in cyst abundance during MIS 2 indicate variability in the climatic and oceanographic conditions was more complex. Absolute abundance of autotrophic species indicate higher productivity, but largely fluctuating cyst abundance values emphasizes the productivity changes were not constant throughout MIS 2. This fluctuation in the cyst abundance could be due to the varying cyst flux, which can be influenced by variation in sedimentation rate during MIS 2 in the present core (Fig. 3). The increased abundance of Gonyaulacoid species, especially S. ramosus, S. membranaceus, S. mirabilis, S. pachydermus and Spiniferites sp. 1 during this period suggest strong winter mixing due to prevalence of the strong NE monsoon winds. Reduced stratification and deeper MLD facilitate vertical advection of nutrients in to upper photic layers, which in turn supports growth of autotrophic dinoflagellates.

Our dinoflagellate records showed the sudden decrease in total cyst abundance, Spiniferites specie abundance and relative abundance of all dominant species during stadial periods (Northern hemisphere cold periods), the Heinrich events (HE2 and HE1) and Younger Dryas (YD) (Fig. 2 and 3a). The reduction in the NE monsoon wind-flow could leads to reduce the winter deep convective mixing and/or upwelling along the EAS, leading to the higher SST (Govil and Naidu, 2010) and decreased production.
(Anand et al., 2008; Singh et al., 2011). Although the Spiniferites species well responds to the warmer SST, a rapid switch to stratified, oligotrophic water due to decreased strength of the NE monsoon control their growth in the EAS region. Similar, drastic fluctuations in cyst abundance during the deglaciation caused due to rapid SST fluctuations (Govil and Naidu, 2010).

The dinoflagellate cyst abundance and assemblages document an abrupt change during the transition from MIS 2 to MIS 1 (Fig. 2 and 3a). Absolute cyst abundance declined from about 12.8 to 10 ka, could be resultant of decreased winter mixing due to the weak NE monsoon winds during deglaciation period. This result coincides with the sharp decrease in foraminiferal records in the Core SK 17, which suggest low productivity during deglaciation in the EAS (Singh et al., 2011). The most important change in cyst assemblage during this period was the presence of O. centrocarpum, B. spongium and S. pachydermus (from about ~11 ka). O. centrocarpum reached its maximum abundance during MIS 1 (Fig. 2). This autotrophic cosmopolitan species tolerate wide range of salinity and temperature (Zonneveld et al., 2013), and commonly associated with unstable waters at the coastal-oceanic boundary (Dale et al., 2002). In recent sediment, B. spongium are typical to warmer tropical-subtropical marine settings with salinity range 31.9 to 38.3 psu, whereas higher abundance can be observer in regions where SST >20°C (Zonneveld et al., 2013). S. pachydermus are strictly restricted to temperate to equatorial regions (Zonneveld et al., 2013) and able to tolerates SSS 27.8 to 39 psu (Zonneveld et al., 2013). This shift in species assemblage along with increased species diversity could support the increased SST and moderate SSS during the early Holocene (Fig. 3k and l). In the WAS, B. spongium and S. pachydermus are typically dominant during the SW monsoon upwelling (Zonneveld, 1997a; Zonneveld and Brummer, 2000). The presence of these species during the early Holocene in AAS 9/21 strengthens the belief that the SW monsoon evolved during this period in the Holocene. Furthermore, increase in SST and decreased trend of δ¹⁸Ow values and SSS represents increased strength of the SW monsoon during ~10.5 to 3 ka in the present core (Fig. 3; Govil and Naidu, 2010).

Since 3 ka, a major shift in the cyst assemblage was observed. Cyst assemblage was characterised by the appearance of Protoperidinium species, S. stellatum, S. robustum, S. nephroides and V. calvum (Fig. 2). In modern sediments, high relative abundance of S. robustum and S. stellatum can found in warm, hypersaline waters in mesotrophic to eutrophic regions. Among these S. robustum is endemic to the Indian Ocean (Zonneveld et al., 2013). Occurrence of these species suggests increase in SSS and SST around 3 ka (Fig. 3k and l), which could be due to the weak SW monsoon (Govil and Naidu, 2010). Increased abundance of Protoperidinoid species could be due to, better preservation state in sediment with less oxidative stress and increased denitrification (Godad, 2014). However, moderate increase in productivity has been observed in the fertile foraminiferal species records between ~3-1 ka in the core SK 17 (Singh et al., 2011; Cabarcos et al., 2014) which also reveals presence of food material and organic matter, whereas this increase in productivity was not evidenced in autotrophic coccolithophore (productivity factor) records in the same core (Cabarcos et al., 2014). In our study, productivity increase during this period was not evidenced by autotrophic Gonyaulacoid species. Thus an inference can be drawn that change in the environmental conditions (elevated SST) during the late Holocene period were not optimal to support the growth of these autotrophic species (Fig. 3b). Furthermore, most of the
Spiniferites species can grow in temperature up to 29°C (Zonneveld et al., 2013), whereas in the WAS their maximum flux was reported at the end of summer monsoon when temperature ranges from 23 to 27°C (Zonneveld and Brummer, 2000), which could be the optimum range for their proliferation in the Arabian Sea region. Thus, increased SST (28.5 to 29°C) in the EAS from ~3 to 1 ka (Govil and Naidu, 2010) could be responsible for decline in abundance of Spiniferites species.

Recent modern dinoflagellate cyst distribution studies in the EAS reveals dominance of Protoperidinium species in surface sediments (Godhe et al., 2000; D’Costa et al., 2008; D’Silva et al., 2011). The relative shift in dinoflagellate cyst assemblage during ~3-0.7 ka suggests that the increased trend in Protoperidinium abundance incited during this time and could be due to changing environment conditions initiated by increased SST and SSS. Thus, it can be predicted that the increase in SST due to global warming would lead to different dinoflagellate assemblages which will be dominated by heterotrophic species in future.

6. Conclusion

This study presents the first detailed investigation of dinoflagellate cyst records over the late Quaternary period in the EAS. The variation observed in dinoflagellate cyst abundance and assemblages suggests that productivity changes over the past 68 ka in the EAS were influenced by seasonal monsoon circulation. The main dinoflagellate cyst signals recorded in the EAS are as follows;

1. The productivity in the EAS was higher during the glacial than interglacial periods, mainly controlled by nutrient supply from subsurface water due to winter convection driven by the NE monsoonal wind. The productivity change was mainly highlighted by increased abundance of Gonyaulacoid species (especially Spiniferites). Within the glacials, productivity was higher during MIS 2 than in MIS 4 and characterised by two fold increase in cyst abundance. During the interglacials, reduction in the primary productivity during early MIS 3 (~67.5 to 58.67 ka) and in MIS 1 was highlighted by less abundance of Gonyaulacoid cyst, which could be due to strong summer monsoon, resulting intense stratification and reduced light penetration.

2. Dinoflagellate cyst abundance and assemblage difference reveals that productivity was higher during the LGM than Holocene. The LGM was more dynamic with larger fluctuations in cyst abundance and assemblages. This reveals the winter mixing was not consistent throughout the LGM.

3. Variation in Protoperidinium species abundance over the past 68 ka represents variation in the OMZ intensity. Increased Protoperidinium abundance during MIS 3 and late MIS 1 (~3 ka onwards) highlighted their good preservation in sediments due to strong OMZ.

4. SST increased during the Holocene was characterised by increased abundance of B. spongium, S. pachydermus and O. centrocarpum.
Present study supports the use of dinoflagellate cyst abundance and assemblages as a proxy of paleoproductivity and paleoceanographic variability in the EAS. Our dinoflagellate cyst proxy demonstrate that, the EAS responds to both regional and global scale climatic variations.

**Acknowledgements**

We are grateful to the Director, CSIR-National Institute of Oceanography (NIO), India for his support. We thank Dr. Paropakari, CSIR-NIO, India for sharing the core samples; Dr. Kenneth Neil Mertens, Ghent University, Belgium and Dr. Malte Elbrachter, AWI, Germany for dinoflagellate cyst identification training course and providing taxonomic literature. D.D.N. is grateful to CSIR for awarding the Senior Research Fellowship (SRF) and DST-SERB for International Travel Support Scheme. This is an NIO contribution (No. ####).

**References**


Fig. 1: Core AAS 9/21 sampling site and schematic representation of the ocean circulation (black lines) and dominant wind directions (red lines) in the Arabian Sea during the monsoons (Shankar et al., 2002; Schott et al., 2009). Map indicates chlorophyll concentration (source NASA/ SeaWiFS) during a) the South West monsoon and b) the North East monsoons. WICC=West Indian Coastal Current.
Fig. 2: Relative abundances (%) of selected dinoflagellate cyst taxa and a plot of age-depth along with sedimentation rates (cm ka$^{-1}$) corresponding between two tie points. AMS $^{14}$C dates calibrated to calendar age (filled circles) and isotope stage boundary of MIS 3 and 4 (unfilled circle) [Govil and Naidu, 2010]. For cyst abbreviation please refer Table 2. Dinoflagellate cyst zones (DZ) are separate by dashed lines. The Holocene and LGM are shown by grey shaded horizontal bars. Heinrich events (HE 2 and HE1) and the Younger Dryas (YD) are highlighted in grey.
Fig. 3: (a) Total cyst abundance along with (b) Autotrophic (c) Spiniferites (dark line) and (d) Heterotrophic cyst species; (e) Ratio of autotrophic to heterotrophic cysts (A/H); diversity indices (f) Shannon-Wiener diversity index, (g) Species richness, (h) Species evenness; sample score for (i) PCAs 1, (j) PCA 2 and (k) Sea surface temperature (SST) and (l) Salinity (SSS) estimated using Mg/Ca and δ¹⁸Ow of Globigerinoides ruber respectively (Govil and Naidu, 2010), (m) Plot of age-depth along with sedimentation rates (cm ka⁻¹) corresponding between two tie points. AMS ¹⁴C dates calibrated to calendar age (filled circles) and isotope stage boundary of MIS 3 and 4 (unfilled circle) [Govil and Naidu, 2010]. Dinoflagellate cyst zones (DZ) are separate by dashed lines. The Holocene and LGM are shown by grey shaded horizontal bars. Heinrich events (HE 2 and HE1) and the Younger Dryas (YD) are highlighted in grey.
**Fig. 4:** Principle Component Analysis (PCA) biplot diagram indicate dinoflagellate cyst species (grey arrows) in relation with sediment sample ordination (coloured symbols; diamond, triangle, star, circle, square). Species abbreviations are as given in Table 2.
Table 1: Age model for core AAS 9/21

<table>
<thead>
<tr>
<th>Depth (cm)</th>
<th>Radiocarbon age*</th>
<th>Calibrated Calendar years BP**</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>850±25</td>
<td>512±9</td>
</tr>
<tr>
<td>53</td>
<td>9540±80</td>
<td>10343±326</td>
</tr>
<tr>
<td>110</td>
<td>12770±80</td>
<td>14529±326</td>
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<tr>
<td>148</td>
<td>16070±115</td>
<td>18965±240</td>
</tr>
<tr>
<td>213</td>
<td>21290±180</td>
<td>24980±458</td>
</tr>
<tr>
<td>310</td>
<td>42660±2500</td>
<td>46282±2283</td>
</tr>
</tbody>
</table>

*AMS 14C dating was performed on monospecific samples of the planktonic foraminifera *G. ruber* using the Tandem Accelerator at Leibniz Labor für Altersbestimmung und Isotopenforschung, Christian-Albrechts-Universität, Kiel, Germany. **Measured 14C ages were converted to sediment ages using the online CalPal version QuickCal 2005 version 1.4 (Weninger et al., 2006) [adopted from Govil and Naidu, 2010].
Table 2: List of dinoflagellate cyst species identified in sediment samples from the Core AAS 9/21 with abbreviations and thecate dinoflagellate affinity.

<table>
<thead>
<tr>
<th>Dinoflagellate cyst (Paleontological Name)</th>
<th>Abbreviations</th>
<th>Thecate dinoflagellate affinity (Biological Name)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Autotrophic</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Autotrophic</em></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Bitectatodinium spongium</em></td>
<td>Bspo</td>
<td>–</td>
</tr>
<tr>
<td><em>Impagidinium aculeatum</em></td>
<td>Iacu</td>
<td><em>Gonyaulax sp.</em></td>
</tr>
<tr>
<td><em>Impagidinium paradoxum</em></td>
<td>Ipar</td>
<td><em>Gonyaulax sp.</em></td>
</tr>
<tr>
<td><em>Impagidinium sphaericum</em></td>
<td>Isph</td>
<td><em>Gonyaulax sp.</em></td>
</tr>
<tr>
<td><em>Lingulodinium machaerophorum</em></td>
<td>Lmac</td>
<td><em>Lingulodinium polyedra</em></td>
</tr>
<tr>
<td><em>Nematosphaeropsis labyrinthus</em></td>
<td>Nlab</td>
<td><em>Gonyaulax spinifera complex</em></td>
</tr>
<tr>
<td><em>Operculodinium centrocarpum</em></td>
<td>Ocen</td>
<td><em>Protoceratium reticulatum</em></td>
</tr>
<tr>
<td><em>Polysphaeridinium zoharyi</em></td>
<td>Pzoh</td>
<td><em>Pyrodinium bahamense</em></td>
</tr>
<tr>
<td><em>Spiniferites benti</em></td>
<td>Sben</td>
<td><em>Gonyaulax digitalis, G. spinifera complex</em></td>
</tr>
<tr>
<td><em>Spiniferites bulloideus</em></td>
<td>–</td>
<td><em>Gonyaulax scrippsae, G. spinifera complex</em></td>
</tr>
<tr>
<td><em>Spiniferites hyperacanthus</em></td>
<td>–</td>
<td><em>Gonyaulax spinifera complex</em></td>
</tr>
<tr>
<td><em>Spiniferites membranaceus</em></td>
<td>Smem</td>
<td><em>Gonyaulax spinifera complex</em></td>
</tr>
<tr>
<td><em>Spiniferites mirabilis</em></td>
<td>Smir</td>
<td><em>Gonyaulax spinifera complex</em></td>
</tr>
<tr>
<td><em>Spiniferites pachydermus</em></td>
<td>Spac</td>
<td><em>Gonyaulax spinifera complex</em></td>
</tr>
<tr>
<td><em>Spiniferites ramosus</em></td>
<td>Sram</td>
<td><em>Gonyaulax scrippsae, G. spinifera complex</em></td>
</tr>
<tr>
<td><em>Spiniferites sp. 1</em></td>
<td>Ssp.1</td>
<td><em>Gonyaulax sp. complex</em></td>
</tr>
<tr>
<td><strong>Heterotrophic</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Brigantedinium spp.</em></td>
<td>Bsp.</td>
<td><em>Protoperidinium spp.</em></td>
</tr>
<tr>
<td>–</td>
<td>Pkof</td>
<td><em>Polykrikos kofoidii</em></td>
</tr>
<tr>
<td>–</td>
<td>Plat</td>
<td><em>Protoperidinium latissimum</em></td>
</tr>
<tr>
<td><em>Echinidinium transparantum</em></td>
<td>Etra</td>
<td><em>Protoperidinium sp.</em></td>
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<td><em>Quinquecuspis concreta</em></td>
<td>Qcon</td>
<td><em>Protoperidinium leonis</em></td>
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<td><em>Selenopemphix nephroides</em></td>
<td>Snep</td>
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<td><em>Selenopemphix quanta</em></td>
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<td>–</td>
<td>–</td>
<td><em>Protoperidinium nudum</em></td>
</tr>
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<td>Srob</td>
<td><em>Protoperidinium sp.</em></td>
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<tr>
<td><em>Stelladinium stellatum</em></td>
<td>Sste</td>
<td><em>Protoperidinium stellatum</em></td>
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<tr>
<td><em>Stelladinium reidii</em></td>
<td>–</td>
<td><em>Protoperidinium sp.</em></td>
</tr>
<tr>
<td><em>Trinovantedinium applanatum</em></td>
<td>Tapp</td>
<td><em>Protoperidinium pentagonum</em></td>
</tr>
<tr>
<td><em>Votadinium calvum</em></td>
<td>Vcal</td>
<td><em>Protoperidinium oblongum</em></td>
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**Table 3**: Schematic presentation of variation in productivity, OMZ, monsoon and dinoflagellate cyst assemblage in the eastern Arabian Sea during the four Marine Isotopic Stages (MIS 1-4).

<table>
<thead>
<tr>
<th>MIS 1</th>
<th>DZ5 (~12.8 to 0.79 ka)</th>
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<tbody>
<tr>
<td>Strong summer Monsoon</td>
<td>Total cyst abundance (ψ)</td>
</tr>
<tr>
<td>Increased rainfall</td>
<td>Gonyaulacoid species (ψ)</td>
</tr>
<tr>
<td>Increased SST + decreased SSS</td>
<td>Protoperidinoid species (ψ)</td>
</tr>
<tr>
<td>Stratified water</td>
<td>Reduced productivity</td>
</tr>
<tr>
<td>Cloud cover + low light penetration</td>
<td></td>
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</table>

<table>
<thead>
<tr>
<th>MIS 2</th>
<th>DZ4 (~24.6 to 13.17 ka)</th>
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<tbody>
<tr>
<td>Strong winter monsoon</td>
<td>Abrupt changes in total cyst abundance</td>
</tr>
<tr>
<td>Reduced SST + fluctuating SSS</td>
<td>Fluctuation in Gonyaulacoid and</td>
</tr>
<tr>
<td>Less turbulence + deeper light penetration</td>
<td>Protoperidinoid abundance</td>
</tr>
<tr>
<td></td>
<td>High productivity</td>
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<table>
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<tr>
<th>MIS 3</th>
<th>DZ3 (~41.67 to 25.3 ka)</th>
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<tr>
<td>Increased strength of winter monsoon</td>
<td>Total cyst abundance (↑)</td>
</tr>
<tr>
<td>Decreasing SST + increasing SSS</td>
<td>Gonyaulacoid species (↑)</td>
</tr>
<tr>
<td>Increased winter convection</td>
<td>Protoperidinoid species (↑)</td>
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<tr>
<td>Increased light penetration</td>
<td>Increase in productivity</td>
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**Intense OMZ**

<table>
<thead>
<tr>
<th>MIS 4</th>
<th>DZ1 (~67.5 to 58.67 ka)</th>
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<tr>
<td>Winter monsoon convection</td>
<td>Total cyst abundance (ψ)</td>
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<tr>
<td>High SST + SSS</td>
<td>Gonyaulacoid species (ψ)</td>
</tr>
<tr>
<td>Less turbulence + deeper light penetration</td>
<td>Protoperidinoid species (ψ)</td>
</tr>
<tr>
<td></td>
<td>Increased productivity</td>
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