Benthic Foraminiferal Response to the Millennial-Scale Variations in Monsoon-Driven Productivity and Deep-Water Oxygenation in the Western Bay of Bengal During the Last 45 ka

Komal Verma 1, Harshit Singh 1, Arun Deo Singh 1,2*, Pradyumna Singh 1,2, Rajeev Kumar Satpathy 1 and Pothuri Divakar Naidu 3

1 Department of Geology, Banaras Hindu University, Varanasi, India, 2 Department of Science and Technology-Mahamana Centre of Excellence in Climate Change Research, Institute of Environmental and Sustainable Development, Banaras Hindu University, Varanasi, India, 3 Former Scientist Council of Scientific and Industrial Research-National Institute of Oceanography, Dona Paula, India

In this study, we presented a high-resolution benthic foraminiferal assemblage record from the western Bay of Bengal (BoB) (off Krishna–Godavari Basin) showing millennial-scale variations during the last 45 ka. We studied temporal variations in benthic foraminiferal assemblages (relative abundances of ecologically sensitive groups/species, microhabitat categories, and morphogroups) to infer past changes in sea bottom environment and to understand how monsoon induced primary productivity-driven organic matter export flux and externally sourced deep-water masses impacted the deep-sea environment at the core site. Our records reveal a strong coupling between surface productivity and benthic environment on glacial/interglacial and millennial scale in concert with Northern Hemisphere climate events. Faunal data suggest a relatively oxic environment when the organic matter flux to the sea floor was low due to low primary production during intensified summer monsoon attributing surface water stratification and less nutrient availability in the mixed layer. Furthermore, records of oxygen-sensitive benthic taxa (low-oxygen vs. high-oxygen benthics) indicate that changes in deep-water circulation combined with the primary productivity-driven organic matter flux modulated the sea bottom oxygen condition over the last 45 ka. We suggest that the bottom water at the core site was well-ventilated during the Holocene (except for the period since 3 ka) compared with the late glacial period. At the millennial timescale, our faunal proxy records suggest relatively oxygen-poor condition at the sea floor during the intervals corresponding to the cold stadials and North Atlantic Heinrich events (H1, H2, H3, and H4) compared with the Dansgaard/Oeschger (D-O) warm interstadials. The study further reveals oxygen-poor bottom waters during the last glacial maximum (LGM, 19–22 ka) which is more pronounced during 21–22 ka. A major shift in sea bottom condition from an oxygenated bottom water during the warm Bølling–Allerød (B/A) (between 13 and 15 ka) to the oxygen-depleted condition during the cold Younger Dryas (YD) period (between...
10.5 and 13 ka) is noticed. It is likely that the enhanced inflow of North Atlantic Deep Water (NADW) to BoB would have ventilated bottom waters at the core site during the Holocene, B/A event, and probably during the D-O interstadials of marine isotope stage (MIS) 3.

Keywords: oxygen minima zone, primary productivity, organic matter flux, Indian monsoon, ventilation, epifaunal and infaunal benthic foraminifera

INTRODUCTION

The potentiality of fossil benthic foraminifera in deciphering past changes in sea bottom oceanographic conditions has long been recognized. Studies have shown a strong relationship between distribution patterns of benthic foraminifera and bottom water oxygen condition coupled with surface productivity-driven organic matter flux to the sea floor (e.g., Bernhard, 1986; Gooday, 1996; Lutze et al., 1986; Corliss and Chen, 1988; Altenbach and Sarnthein, 1989; Jorissen et al., 1992; Kaiho, 1999). Benthic foraminifera strongly responds to the variation in benthic environment by showing variations in their abundances, diversity, microhabitats, and adaptive morphologies (e.g., Corliss, 1985; Corliss and Chen, 1988; Corliss and Emerson, 1990; Corliss and Fois, 1990; Kaiho, 1994; Almogi-Labín et al., 1996; Gupta and Thomas, 1999; Nigam et al., 2007; Singh et al., 2015; Verma et al., 2018; Ma et al., 2019). Therefore, temporal variations in benthic foraminiferal assemblage in terms of these faunal parameters are extensively used to reconstruct past deep-sea environments (e.g., Corliss, 1986; Schnitker, 1994; Otto et al., 1995; Thomas and Gooday, 1996; Schmiedl et al., 1998; Drinia et al., 2004; Ma et al., 2019).

Arabian Sea (AS) and Bay of Bengal (BoB) are the two basins in the northern Indian Ocean with different oceanographic features. The fossil records of deep-sea benthic foraminiferal assemblages in the AS have been extensively used to reconstruct the history of past changes in the deep-water environment (primarily oxygen and trophic conditions) and to understand its linkage with monsoon and deep-water circulation (Hermelin and Shimmield, 1990; Otto et al., 1995; den Dulk et al., 1998; Schmiedl et al., 1998; Gupta and Thomas, 1999; von Rad et al., 1999; Schmiedl and Leuschner, 2005; Arumugm et al., 2014; Sarkar and Gupta, 2014). Results of earlier studies provided deep insight into the surface ocean circulation, deep-water ventilation through externally sourced water masses impacting development of oxygen minimum zone (OMZ) and benthic environment in AS and its atmosphere–ocean teleconnections with climatic fluctuations at different timescales. In recent years, significant contributions on the oxygenation history and OMZ variability at millennial timescale were made using benthic foraminiferal records from the eastern AS, a region of an intensified OMZ (Bharti and Singh, 2013; Singh et al., 2015; Verma et al., 2018).

The existing paleoceanographic reconstructions based on benthic foraminiferal assemblages in BoB are limited mainly to the longer timescales (Sharma, 1970; Singh, 1979; Srinivasan and Rajeshkhar, 1981; Gupta, 1987; Raju and Mishra, 1991). The Quaternary benthic foraminiferal assemblage records on a high-resolution timescale are very sparse from the bay (Ma et al., 2019). Most of the sea bottom paleoceanographic reconstructions made earlier were based on the stable isotope records and geochemical tracers (Ahmad and Labeyrie, 1994; Piotrowski et al., 2009; Ahmad et al., 2012; Pattan et al., 2013; Raza et al., 2014; Ma et al., 2019). Here, we present a first high-resolution benthic foraminiferal assemblage record from the western BoB (off Krishna—Godavari Basin) showing millennial-scale variation during the last 45 ka. We used temporal variations in faunal proxies (abundances of ecologically sensitive groups/species, microhabitat categories, morphgroups) to decipher past changes in the benthic environment and to understand how monsoon-induced organic matter fluxes and global deep-water circulation influenced the deep-sea environments of BoB.

MATERIALS AND METHODS

Core Location and Regional Oceanographic Settings

Gravity core SK 218/1 (8.2 m length) was collected from 3,307 m water depth in the western BoB (14°02′06″ N, 82°00′12″ E; ~204 km offshore) by ORV Sagar Kanya in 2005 (Figure 1).

BoB is a semi-enclosed basin in the eastern part of the northern Indian Ocean. Surface hydrography of BoB is driven by seasonally reversing monsoon wind circulations. During the summer season (June–September), a huge amount of freshwater and sediments are discharged into the bay through major rivers Ganga–Brahmaputra, Irrawaddy–Salween from the Himalayas and Mahanadi, Krishna–Godavari, Cauvery rivers from the Indian peninsula (Bird et al., 2008). The freshwater discharge and overhead precipitation freshen the surface layers by 3–7 psu, inducing strong stratification in the upper water column (Prasanna Kumar et al., 2002). The surface stratification restricts the wind driven mixing to a shallow depth (<20 m), thereby, inhibits the injection of nutrients from the subsurface into the euphotic zone leading to an oligotrophic condition and low primary productivity in BoB. In the winter season (December–February), surface stratification weakens and winter monsoon winds induced mixing invokes vertical transport of nutrients to the surface, enhancing primary productivity (Kay et al., 2018).

The water masses in BoB are a combination of locally and externally sourced (Schott and McCreary, 2001). The upper 100 m of the water column consists of low-saline Bay of Bengal waters (BBW) derived mainly from river discharge into the bay. The water masses at thermocline depth up to about 1,000 m are Red Sea Intermediate Water (RSIW) and Indonesian Intermediate Water (IIW). IIW is derived from North Pacific Central Water, which enters BoB via the Indonesian Throughflow.
FIGURE 1 | (A) Map showing the location of studied core (SK 218/1) in the Bay of Bengal (BoB). (B) Oxygen (ml/L, color shading) depth (m) latitude section and vertical structure of water masses in the BoB [N–S cross-section represented by black dashed line in (A)]. Map source Ocean Data View (ODV; Schlitzer, 2015). BBW, Bay of Bengal Water; RSIW, Red Sea Intermediate Water; IIW, Indonesian Intermediate Water; IDW, Indian Deep Water; AABW, Antarctic Bottom Water.

(Benthic Foraminiferal Analysis)

A total of 158 sediment samples at regular intervals of 2–4 cm were taken for benthic foraminiferal studies to obtain an average temporal resolution of ~288 years. For separation of foraminiferal tests, sediment samples were processed following the standard micropaleontological techniques (e.g., Singh et al., 2018). Census counts of benthic foraminifera were made on >125 μm size fraction. Based on census data, the relative abundances of each benthic foraminiferal species were calculated. The taxonomic classification of benthic foraminiferal species is based on Schwager (1877) revised by Srinivasan and Sharma (1980), Brady (1884) revised by Barker (1960), Loeblich and Tappan (1988, 1990), and Sen Gupta (2002).

Age Model

The age model of the core adopted in this study was established by Govil and Naidu (2011) based on 8 AMS ¹⁴C dates and δ¹⁸O record of Globigerinoides ruber correlated with δ¹⁸O global isostack curve of Martinson et al. (1987) (Table 1).
RESULTS
Temporal Variations and Environmental Preferences of Abundant Benthic Foraminifera

A total of 136 species representing 78 genera of benthic foraminifera is recorded (Appendix 1). Temporal variation in relative abundances of major benthic foraminiferal groups and their important constituent species are shown in Figures 2–4. Selected ecologically sensitive benthic species recorded in this study are illustrated in Plate 1.

The benthic foraminiferal assemblage comprises of various taxa belonging mainly to uvigerinids, buliminids, cibicidiids, miliolids, cassidulinids, and bolivinids (in decreasing order of relative abundances). Other quantitatively significant taxa of the assemblage are Gyroidinoides spp., Oridorsalis spp., Chilostomella oolina, Eggrella brady, Pullenia spp., and Fursenkoina spp.

The uvigerinid group, a major component of benthic assemblages is represented mainly by Uvigerina peregrina, U. hispida, and Neouvigerina proboscidea. The relative abundance of total uvigerinids in the core varies between 0 and 76% with maximum abundances occurring during 21–23 and 26–27 ka (Figure 4). There has been a significant reduction in the abundance of uvigerinids during 14–15, 23–24 ka, and between 38 and 40 ka. The Holocene in general is characterized by a very low abundance of the uvigerinids. The constituent species U. peregrina and U. hispida both follow a pattern similar to that of the total uvigerinids (Figures 2, 4). The uvigerinid taxa are known to be related to both the organic carbon flux and sea bottom oxygen level (Lutze et al., 1986; Hermelin and Shimmield, 1993).

### TABLE 1 | AMS $^{14}$C dates and calibrated ages (in calendar years before present) for core SK 218/1 (Govil and Naidu, 2011).

| Depth (cm) | $^{14}$C ages (years BP) | Calibrated calendar age (years) |
|-----------|--------------------------|---------------------------------|
| 68        | 1,055 ± 30               | 300                             |
| 150       | 3,840 ± 100              | 3,311                           |
| 266       | 10,400 ± 60              | 10,976                          |
| 322       | 13,940 ± 90              | 15,948                          |
| 350       | 16,410 ± 100             | 18,772                          |
| 498       | 22,100 ± 410             | 25,478                          |
| 550       | 29,300 ± 330             | 32,822                          |
| 638       | 33,060 ± 780             | 36,884                          |

The AMS radiocarbon dates measured on monospecific samples of G. ruber were converted to calendar ages by using CALIB 6.0 software (Stuiver and Reimer, 1993) and considering a reservoir age of 400 years (Southon et al., 2002).

### FIGURE 2 | Temporal variations in relative abundances of (A–C) uvigerinid species (U. peregrina, U. hispida, and N. proboscidea) and (D–G) buliminid species (B. aculeata, P. pacifica, P. pupoides, and B. tenuata) in the core SK 218/1. MIS 1–3 denotes the Marine Isotope Stages, H1–H4, Heinrich Events; YD, Younger Dryas; B/A, Bolling/Allerød; LGM, Last Glacial Maxima.

![Figure 2](https://example.com/figure2.png)
Verma et al. BoB Benthic Foraminifera and Diversity

The uvigerinids have preference for high organic carbon flux to the sea floor and low-to-moderate oxygen levels.

The buliminid group comprising genera Protoglobobulimina and Bulimina is the next important component of the benthic assemblages. The major constituent species of this group are Bulimina aculeata, Protoglobobulimina pacifica, Protoglobobulimina pupoides, and Buliminella tenuata. The buliminid group shows its high abundances during 12–13, 24–25, around 28 ka, between 30 and 37 ka and between 40 and 43 ka (Figure 4). Its abundance declines significantly during the Holocene (except for the period since 3 ka) and the last glacial maximum (LGM; 19–22 ka). However, B. aculeata, P. pacifica, and B. tenuata show an increase in their abundances during brief intervals within the Holocene (Figure 2). The tapered/cylindrical tests of the buliminids are suggestive of their preferences for infaunal habitat. Hence, their distribution pattern in the core is possibly controlled by the organic matter content in sediment and dissolved oxygen concentrations (e.g., Pfleger and Soutar, 1973; Kaiho, 1994). B. aculeata, the major constituent of the buliminid population is considered to be a tolerant species to the low-oxygen environment (den Dulk et al., 2000).

The cibicidid group, which is represented mainly by Cibicides wuellerstorfi and Cibicides robertsonianus shows large variation in its abundance down core. The total abundance of cibicidids was very low between 16 and 45 ka, as compared with the Holocene (Figure 4). There has been a rapid increase in its abundance from 11 ka, reaching to its maximum during 6–8 ka. The variation pattern of C. robertsonianus abundance appears to be almost similar to that of the total cibicidids. The pattern of C. wuellerstorfi abundance, however, is slightly different with its abundance maxima occurring between 40 and 41, 19 and 22, 13.5 and 16 ka, and during 8–9 and 1–3 ka (Figure 3). Cibicides generally prefer epifaunal habitat (Kaiho, 1994; 1999) and are known to be associated with the high-oxygen sea bottom condition (Corliss and Fois, 1990; Singh et al., 2015; Verma et al., 2018; Verma and Singh, 2019).

The miliolids are relatively abundant in the Holocene when compared with the late glacial period. Its high abundance is also recorded during 42–44 ka of MIS 3 (Figure 3). The miliolids are known to have epifaunal habitat and are considered to be associated with oxic environment and low organic carbon flux (Kaiho, 1994, 1999; Singh et al., 2015; Verma et al., 2018).

Temporal variations in abundance patterns of other important groups (cassidulinids and bolivinids) and Gyroidinoides spp., Pullenia spp., and Oridorsalis spp. all show significant changes in their abundances down-core (Figures 3, 4) and the interval of major changes (highs and lows) are associated possibly to.
variation in sea bottom condition mainly organic matter flux and oxygen level.

The cassidulinids are known to prefer infaunal habitat, moderate to high organic matter flux, and low-oxygen environment (Kaiho, 1994; Almogi-Labin et al., 2000; den Dulk et al., 2000; Singh et al., 2015). The bolivinids being infaunal species are associated with low-oxygen condition and high organic matter content in the sediment. *Pullenia* prefers infaunal microhabitat in high productive regions (Gooday, 1994), suboxic condition and is less tolerant to oxic environment. Although the environmental preferences of *Oridorsalis* are not fully known, some studies have shown its association with the low productive condition (Kuhnt et al., 1999). Nevertheless, its abundant occurrence in high productivity areas has also been reported (Woodruff, 1985). *Gyroidinoides* species have a preference for shallow infaunal habitat and suboxic condition (Kaiho, 1994; Guichard, 1997). *Fursenkoina* and *Chilostomella oolina*, both are strikingly absent or rarely present in the Holocene sediment of the examined core. The abundance patterns of these taxa indicate their peak abundances during certain time intervals of the late glacial period (Figure 3). Earlier studies have shown these taxa to be associated with very low sea bottom oxygen condition (Kaiho, 1994, 1999).

**Benthic Foraminiferal Morphotype and Microhabitat Categories**

Benthic foraminifera depending upon their adaptation capabilities to variation in sea floor environment and microhabitat preferences develop various functional morphologies (e.g., Singh et al., 2015; Verma et al., 2018). Therefore, various morphotypes shown by benthic foraminifera and their association with specific microhabitats can be potentially used in paleoenvironmental reconstructions (e.g., Nigam et al., 2007; Singh et al., 2015). Epifaunal, shallow infaunal, and deep infaunal are the broad microhabitat categories of benthic foraminifera (e.g., Corliss and Fois, 1990; Jorissen et al., 1995). The epifauna are those living on the sediment surface, shallow infauna within sediment top 2 cm, and deep infauna below 2 cm (Buzas et al., 1993). As it is difficult to distinguish clearly the shallow infauna from epifauna, generally both together are classified as epifauna (Jorissen et al., 1995). We grouped quantitatively significant benthic foraminiferal taxa into two broad categories: epifauna and infauna based on the existing knowledge of their microhabitat preferences (Figure 5).

---

1 Verma, K., Singh, A. D., Singh, P., Singh, H., Satpathy, R. K., Uddandam, P. R., et al. (under revision). Monsoon-related changes in surface hydrography and productivity in the Bay of Bengal over the last 45 kyr. Palaeogeogr. Palaeoclimatol. Palaeoecol.
Plate 1 | The benthic foraminiferal species were recorded from the western Bay of Bengal (SK 218/1). 1. *Eggerella bradyi* (Cushman) Apertural view: 458–460 cm, 23.67 ka; 2. *Textularia lythostrota* (Schwager) Agglutinated form: 282–284 cm, 12.40 ka; 3. *Textularia laxata* (Schwager) Front view: 282–284 cm, 12.40 ka; 4. *Textularia agglutinans* d’Orbigny Agglutinated form: 290–292 cm, 13.11 ka; 5. *Siphotextularia bengalensis* n. sp. Oblique front view: 458–460 cm, 23.67 ka; 6. *Quinqueloculina seminulum* (Linné) Front view: 278–280 cm, 12.04 ka; 7. *Quinqueloculina oblonga* (Montagu) Front view: 262–264 cm, 10.71 ka; 8. *Quinqueloculina lamarckiana* d’Orbigny Front view: 144–146 cm, 3.09 ka; 9. *Ceratobulimina pacifica* Cushman and Harris Side view: 702–704 cm, 39.84 ka; 10. *Hoeglundina elegans* (d’Orbigny) Front view: 702–704 cm, 39.84 ka; 11. *Bolivina robusta* Brady Front view: 278–280 cm, 12.04 ka; 12. *Bolivina spathulata* (Williamson) Front view: 188–190 cm, 5.82 ka; 13. *Brizalina pygmaea* Brady Front view: 730–731 cm, 41.13 ka; 14. *Brizalina pseudobeyrichi* Cushman Front view: 514–516 cm, 27.74 ka; 15. (Continued)
Down core variation in abundance patterns of these two groups reflects prominent changes on glacial/interglacial scale and also on the millennial scale. The Holocene period is characterized by a high abundance of epifaunal taxa and corresponding low abundances of infaunal taxa except for the late Holocene showing an opposite pattern since 3 ka. The abundance of infaunal taxa was generally high during the late glacial period between 21 and 45 ka. At the millennial timescale, the faunal record shows a conspicuous decline in infaunal taxa during 38–38.5, 28–29, 23.5–25, and 19–21 ka. During these time intervals, the abundances of epifaunal taxa increased. Additionally, there have been periods of a major increase in epifauna and corresponding decline in infauna between 13 and 15, 40 and 41, and 43 and 44 ka. The period between 10.5 and 13 ka is characterized by a conspicuous reduction of epifauna taxa and corresponding increased abundance of infauna (Figure 5).

Epifaunal taxa generally show varying morphologies such as plano-convex, biconvex, milioline, and rounded trochospiral. The infaunal species commonly prefer to have tapered/cylindrical, flattened ovoid, spherical, or rounded plani-spiral tests (Singh et al., 2015). Singh et al. (2015) in their recent study from the AS OMZ suggested benthic foraminifera with plano-convex tests (epifaunal) and tapered/cylindrical (infaunal) to be more sensitive to changes in bottom oxygen level coupled with organic matter flux. The relative abundance profiles of these two ecologically sensitive benthic morphotype categories in the examined core are shown in Figure 5. Abundance records of these morphogroups reveal that the pattern of variation in tapered/cylindrical category is broadly opposite to the plano-convex record. The variation pattern of tapered/cylindrical category mirrors to the pattern of infaunal abundance record both on glacial/interglacial and millennial scales. The abundance of tapered/ cylindrical forms was high during the late glacial, whereas, plano-convex tests were more abundant during the Holocene (Figure 5).
**DISCUSSION**

**Impact of Surface Productivity Variation on Benthic Environment**

The benthic foraminiferal distribution in deep sea is primarily controlled by primary productivity-related organic matter flux to the sea floor and dissolved oxygen level (Otto et al., 1995; den Dulk et al., 1998, 2000; von Rad et al., 1999; Schmiedl and Leuschner, 2005; Bharti and Singh, 2013; Singh et al., 2015). In this study, we evaluate the benthic foraminiferal response to the past changes in surface productivity in western BoB. We compared the abundance records of major benthic foraminiferal groups (uvigerinids, buliminids, bolivinids, and cassidulinids) with the record of mixed layer eutrophic planktic foraminiferal assemblage (relative abundances of *Globigerina bulloides*, *Globigerinita glutinata*, and *Globigerina falconensis*), which has been suggested to be linked to the surface primary productivity (Singh et al., 2011, 2018; Verma et al. under revision); Figure 4). From the faunal abundance records, it is evident that the intervals of increased abundances of these benthic groups broadly correspond to the peak abundances of eutrophic planktic species. It is to be noted that the abundance of eutrophic planktic species is high during the late glacial period as compared with the Holocene. The millennial-scale variations in both the planktonic and benthic assemblage records broadly correspond to the Northern Hemisphere cold stadials and warm interstadials (Figure 5). However, the temporal variation in abundance of uvigerinid and buliminid groups appears to be governed by the surface primary productivity-driven organic carbon flux to the sea floor. The primary productivity in BoB is mainly modulated by the summer monsoon-induced precipitation and continental runoff. Earlier studies have shown low primary productivity and thus low export flux of organic carbon to the sea floor, during the periods of intensified summer monsoon when sea surface was more stratified due to increased fluvial discharge into the bay (e.g., Narvekar and Prasanna Kumar, 2006; Da Silva et al., 2017). In contrast, the surface productivity-induced organic flux enhanced during the periods of weakened summer monsoon resulting in less stratified surface waters coupled with winter monsoon intensification invoking vertical advection of nutrient-rich waters to the surface mixed layer.

Abundances of uvigerinids and buliminids are generally low during the Holocene and warm B/A periods when summer monsoon was intensified leading to the low primary production and reduced export flux of organic matter. Conversely, the group cibicidids show its maximum abundances during the periods of low primary productivity. It is also noticed that the patterns of temporal variation in benthic foraminiferal groups individually vary and do not always match each other. These differences in the individual pattern may be related to their differential responses to the surface productivity-related organic fluxes. Additionally, it is plausible that changes in deep-water oxygenation/ventilation through externally sourced water masses might have influenced their distribution patterns.

**Changes in Deep-Water Oxygenation**

Benthic foraminifera are sensitive to changes in dissolved oxygen concentration over the sea floor. They show different microhabitat preferences in response to changes in ocean-bottom oxygen level and adapt distinct morphological features (Corliss, 1985; Corliss and Chen, 1988; Corliss and Emerson, 1990). Previous studies have indicated a good correlation between microhabitat preferences and morphological characteristics of benthic foraminifera and sea bottom oxygen condition (e.g., Corliss and Fois, 1990; Kahl, 1994). Therefore, the abundance records of different microhabitat categories and morphgroups are the potential proxies to reconstruct the deep-sea oxygenation history (Figure 5). This approach has been applied to the late Quaternary benthic foraminiferal assemblages of the AS to decipher temporal changes of the OMZ intensity in the eastern AS (e.g., Nigam et al., 2007; Mazumder and Nigam, 2014; Singh et al., 2015; Verma et al., 2018). In this study, the relative abundance records of two broad groups of microhabitat categories (epifauna and infauna) in combination with the two predominant morphgroups (tapered/cylindrical and plano-convex) (Tables 2, 3) show major changes on glacial/interglacial and millennial scales. Epifaunal taxa have a preference for high-oxygen condition over the sea floor, whereas infaunal taxa prefer a low-oxygen habitat associated with a decrease in dissolved oxygen content within the sediment (e.g., Corliss and Chen, 1988; Kahl, 1994). High abundances of tapered/cylindrical benthic foraminiferal tests in sediment are suggestive of low bottom oxygen condition, whereas increased abundances of plano-convex tests indicate the presence of an oxygenated environment at the sea floor (Corliss and Fois, 1990; Gooday, 1994; Verma et al., 2018). The predominance of epifaunal taxa and benthic foraminifera with plano-convex tests during the Holocene suggests an oxygenated sea bottom environment compared with the late glacial period between 21 and 45 ka characterized by a general increase in abundances of infauna, tapered/cylindrical tests, and very low abundances of plano-convex tests. A rapid increase in epifaunal taxa corresponding to a significant decline of infaunal and tapered/cylindrical tests between 13 and 15 ka (equivalent to the warm B/A event) reflects a major shift in the benthic environment from a low-oxygen to the oxygenated condition. From the faunal record, it is clearly evident that the oxygenated benthic environment rapidly switched to a low-oxygen condition again during 10.5–13 ka, a period corresponding to the cold Younger Dryas (YD) event. Further, the relative abundance records of benthic microhabitat and morphotype categories for late glacial period depicts millennial-scale oscillations in the late glacial period, apparently in concert with the Northern Hemisphere Heinrich and Dansgaard–Oeschger (D-O) events (Figure 5). These short-term fluctuations in benthic records are obviously related to the changes in bottom water oxygen condition, which seems to be more pronounced between 40 and 45 ka.

In order to have a better reconstruction of past changes in bottom oxygen condition, we used oxygen-sensitive benthic species of assemblages and classified them into low-oxygen and high-oxygen groups based on their association with changing dissolved oxygen levels (e.g., Douglas, 1981; Hermelin and...
Climate events. The bottom water was relatively oxygen-poor during the LGM (19 - 22 ka). However, it appears that the bottom water during 19–21 ka was more oxygenated than during 21–22 ka suggesting two-step changes in sea floor environment within the LGM. The other most striking feature of major fluctuation in oxygen condition was more pronounced than H1–H3. Furthermore, the benthic environment at the core site during the cold YD event is also characterized by low-oxygen condition. Prior to YD, the bottom water was oxygenated during the period corresponding to the warm B/A. It is also evident from the faunal record that the sea bottom oxygen condition in the BoB B/A, and Halimeda was more pronounced than H1–H3.

Our study reveals that the sea bottom oxygen condition in the western BoB oscillated in concert with the Northern Hemisphere climate events. The bottom water was relatively oxygen-poor during the time intervals corresponding broadly to the North Atlantic Heinrich events H1, H2, H3, and H4 and D-O cold stadials as compared with the warm interstadials. Apparently, the change in bottom water oxygen condition during the H4 event was more pronounced than H1–H3. Furthermore, the benthic environment at the core site during the cold YD event is also characterized by low-oxygen condition. Prior to YD, the bottom water was oxygenated during the period corresponding to the warm B/A. It is also evident from the faunal record that the bottom water was relatively oxygen-poor during the LGM (19–22 ka). However, it appears that the bottom water during 19–21 ka was more oxygenated than during 21–22 ka suggesting two-step changes in sea floor environment within the LGM. The other most striking feature of major fluctuation in oxygen condition during MIS 3 is noticed between 35 and 45 ka. The faunal data reveal a high oxygenated environment at around 38, 40, and 42.5 ka which broadly corresponds to the D-O interstadials 8, 9, and 11, respectively (Figure 6).

### Table 2 | Morphotype classification of benthic foraminifera from the examined core SK 218/1.

| Plano-Convex | Tapered/cylindrical |
|--------------|---------------------|
| Anomalinaeoids spp. | Angulogerina sp. |
| Anomalina colligera | Bulimina spp. |
| Cibicides spp. | Buliminella tenuata |
| Gavelinopsis lobatulus | Chilostomella oolina |
| **Milioline** | Dentalina spp. |
| Biloculina murhina | Ehrenbergina sp. |
| Nummuloculina spp. | Fursenkoinea spp. |
| Quinqueloculina spp. | Marginulina spp. |
| Sigmoilina spp. | Nodosaria spp. |
| Sigmoilopsis spp. | Reussella atlantica |
| Spiroloculina depressa | Trifarina bradyi |
| Triloculina spp. | Uvigerina sp. |

### Table 3 | Microhabitat preferences for quantitatively significant benthic foraminifera recorded from the core SK 218/1.

| Epifauna | Infauna |
|----------|---------|
| Anomalinaeoids sp. | Angulogerina sp. |
| Anomalina colligera | Bulimina spp. |
| Ceratobulimina pacifica | Buliminella tenuata |
| Cibicides spp. | Chilostomella oolina |
| Ehrenbergina pacifica | Dentalina spp. |
| Gavelinopsis lobatulus | Ehrenbergina sp. |
| Globocassidulina spp. | Fursenkoinea spp. |
| Gyroidinoides spp. | Marginulina spp. |
| Hyalinea bathica | Nodosaria spp. |
| Hoeglundina elegans | Reussella atlantica |
| Milolites | Trifarina bradyi |
| Orbulina spp. | Uvigerina sp. |
| Osangularia bengalensis | Nonion spp. |
| Sphaerooidina bulboides | Onidorsalis spp. |
| Osangularia bengalensis | Osangularia bengalensis |
| Sphaerooidina bulboides | Protoglobobulimina spp. |
| Buliminella tenuata | Pullenia spp. |
| Triloculina spp. | Trifarina bradyi |
| Uvigerina sp. | Uvigerina sp. |

### Table 4 | Constituent species of low O$_2$ (<0.5 ml/L O$_2$) and high O$_2$ (>0.5 ml/L O$_2$) benthic foraminiferal assemblages.

| Low Oxic (O$_2 < 0.5$ ml/l) | High Oxic (O$_2 > 0.5$ ml/l) |
|-----------------------------|-----------------------------|
| Bolivina quadrilatera | Buloculina spp. |
| Bolivina spp. | Cibicides spp. |
| Brizaina spp. | Gavelinopsis lobatulus |
| Bulimina spp. | Quinqueloculina spp. |
| Buliminella tenuata | Triloculina spp. |
| Cancris indicus | **Note:** Oxygenation categories of species are based on: Harman (1964), Smith (1964), Douglas and Heftman (1979), Quinteno and Gardner (1987), Mackensen and Douglas (1989), Corliss and Fois (1990), Bernhard (1992), Kaiho (1994, 1999), Jannink et al. (1998), Jorissen et al. (2007), Ohkushi et al. (2013), Singh et al. (2015). |
The bottom water oxygen condition is driven mainly by two factors: (1) amount of organic matter to the sea floor and magnitude of its degradation and (2) deep-water circulation (Joos et al., 2003; Rathburn et al., 2018). By comparison of benthic foraminiferal record with the surface productivity record (mixed layer eutrophic planktic foraminifera abundance), it can be inferred that the bottom oxygen condition at the core site is governed primarily by the surface productivity-related export flux of organic carbon to the sea floor. The respiration of sinking organic matter and the release of CO$_2$ lead to a low-oxygen condition on the sea floor. The benthic environment was more oxygenated (as evident by high abundances of high-oxygen taxa) when surface productivity and export flux of organic carbon was low, a condition associated with the intensified SW summer monsoon precipitation resulting in high fluvial discharge and stratified surface waters in BoB. On the other hand, the export flux of organic carbon was enhanced during the intensified NE winter monsoon wind-induced vertical mixing, coupled with a weakened summer monsoon. Additionally, the deep-water circulation might have also influenced the oxygen level of bottom water mass at the core site. Previous studies have shown that the relative proportions of NADW and southern sourced AAIW and AABW modulated the bottom water oxygen condition in the northern Indian Ocean both on the glacial/interglacial and millennial scales (e.g., Ahmad and Labeyrie, 1994; Piotrowski et al., 2009; Ma et al., 2019 and references therein). A significant reduction in NADW export to the Indian Ocean during the cold North Atlantic events (Heinrich and YD events) has been suggested (Naqvi et al., 1994; Piotrowski et al., 2009). These studies provided ample evidences of increased propagation of
NADW to BoB during the Holocene (Piotrowski et al., 2009; Ma et al., 2019) compared with the late glacial period. It is plausible, therefore, that the deep water at the core site was more ventilated by NADW during the Holocene. We also suggest that the high-oxygen condition during the warm D-O interstadials of MIS 3 is most likely related to the effective propagation of NADW to the BoB. This is in line with the previous results indicating an enhanced influence of NADW during the warm B/A event (Piotrowski et al., 2009). However, more research on high-resolution timescale is required to better understand the relative contributions of NADW and AAIW/AABW flow in modulating the deep ocean oxygenation history in BoB in concert with the D-O oscillations.

**CONCLUSION**

A high-resolution deep-sea benthic foraminiferal assemblage record obtained from a sediment core in the western BoB reveals millennial-scale variations during the last 45 ka. Temporal variations in faunal proxy records suggest a strong influence of surface primary productivity-related organic matter flux on the bottom water oxygen condition at the core site. Our records indicate oxygenated sea bottom condition during the Holocene, when primary productivity was significantly low as compared with the late glacial period between 21 and 45 ka, due to intensified summer monsoon resulting in high fluvial discharge to BoB. In addition to the surface productivity factor, changes in deep-water circulation at the millennial timescale might have also strongly influenced the benthic environment.

The relative abundance records of two broad groups of microhabitat categories (epifauna and infauna) and morphogroups (tapered/cylindrical and plano-convex) show major changes on glacial/interglacial and millennial timescales. We also used oxygen-sensitive benthic foraminiferal groups (low-oxygen and high-oxygen taxa) to better understand past changes in bottom water oxygen conditions. Our records reveal that the sea bottom oxygen condition in the western BoB varied in concert with the Northern Hemisphere Heinrich and D-O events. The benthic environment was oxygen depleted during the North Atlantic cold events (YD and Heinrich events) and the LGM (19–22 ka). We suggest that the bottom water was more ventilated by NADW during the warm B/A event, D-O interstadials (8, 9, and 11) of MIS 3, and during the Holocene.

**DATA AVAILABILITY STATEMENT**

The original contributions presented in the study are included in the article/Supplementary Materials, further inquiries can be directed to the corresponding author/s.

**AUTHOR CONTRIBUTIONS**

AS and PN conceptualized the study. KV carried out the sample analysis. AS supervised the study. AS and KV prepared the original draft of the manuscript with contributions from HS, PS, RS, and PN. All authors participated in reviewing, editing, and preparation of final draft of the manuscript.

**FUNDING**

AS acknowledges the financial support by the ISRO-GBP sponsored project (P-32-14) and IoE Incentive Grant BHU and KV for IOE Seed Grant (R/Dev/IOE/Seed grant/2020-21). HS acknowledges UGC for Senior Research Fellowship [419/(CSIR-UGC NET JUNE 2018)]. PS acknowledges the Climate Change Programme of DST (DST/CCP/CoE/80/2017-G) for Junior Research Fellowship. RS acknowledges the CSIR for Senior Research Fellowship.

**ACKNOWLEDGMENTS**

The present study is part of the unpublished doctoral thesis of KV entitled Late quaternary oceanographic changes in the Bay of Bengal based on foraminiferal records, submitted to Banaras Hindu University and archived at http://hdl.handle.net/10603/268142. We thank the scientific party and crew of ORV Sagar Kanya for coring the samples in western BOB. We also thank two referees and editors for their constructive reviews that have helped to improve the manuscript.

**SUPPLEMENTARY MATERIAL**

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fmars.2021.733365/full#supplementary-material
the South China sea. *Mar. Geol.* 156, 123–157. doi: 10.1016/S0025-3227(98)00176-5

Loeblich, A. R., and Tappan, H. (1988). *Foraminiferal Genera and Their Classification*. New York, NY: Van Nostrand Reinhold. 715. doi: 10.1007/978-1-4899-5760-3

Loeblich, A. R., and Tappan, H. (1990). "Present status of foraminiferal classification in Studies in Benthic foraminifera," in *Proceedings of the Fourth Symposium on benthic foraminifera, Sendai*, eds Y. Takayanagi, and T. Saito. Tokyo, Tokai University Press, 93–102.

Lutze, G. F., Pflaumann, U., and Weinholz, P. (1986). Jungquartäre fluktuationen der benthischen foraminiferen faunen in tiefsee-sedimentenov nw-afrika – eine reaktion auf produktivitätsänderungern in oberflächenwasser. *Meteor Forsch. Ergebn.* C40, 163–180.

Lynch-Stieglitz, J., Fairbanks, R. G., and Charles, C. D. (1994). Glacial-interglacial history of Antarctic intermediate water: relative strengths of antarctic versus Indian ocean sources. *Paleoceanography* 9, 7–29. doi: 10.1029/93PA02446

Ma, R., Sépulcre, S., Ligari, L., Bassinot, F., Liu, Z., and Tisnérat-Laborde, N. (2019). Changes in intermediate circulation in the Bay of Bengal since the last glacial maximum as inferred from benthic foraminifera assemblages and geochemical proxies. *Geochem. Geophys. Geosyst.* 20, 1592–1608. doi: 10.1029/2018GC008179

Mackensen, A., and Douglas, R. G. (1989). Down-core distribution of live and dead foraminiferal species in the Western Equatorial Pacific. *Geochemistry, Geophysics, Geosystems* 14, 2246–2266. doi: 10.1029/93GC02327

Rathburn, A. E., and Corliss, B. H. (1994). The ecology of living (stained) deep-sea benthic foraminifera from the Sulu sea. *Paleoceanography* 9, 87–150. doi: 10.1029/93PA02327

Rathburn, A. E., Corliss, B. H., Tappa, K. D., and Lohmann, K. C. (1996). Comparison of the ecology and stable isotopic composition of living (stained) benthic foraminifera from the Sulu and South China Seas. *Deep Sea Res. Part I* 43, 1617–1646.

Rathburn, A. E., Willingham, J., Ziebis, W., Burkett, A. M., and Corliss, B. H. (2018). A new biological proxy for deep-sea paleo-oxygen: pores of epifaunal benthic foraminifera. *Sci. Rep.* 8:9456. doi: 10.1038/s41598-018-27793-4

Raza, T., Ahmad, S. M., Sahoo, M., Banerjee, B., Bari, I., Dash, S., et al. (2014). Hydrographic changes in the southern Bay of Bengal during the last ~65,000 y inferred from carbon and oxygen isotopes of foraminiferal fossils shells. *Q. Int.* 333, 77–85. doi: 10.1016/j.qint.2014.02.010

Sarkar, S., and Gupta, A. K. (2014). Late quaternary productivity changes in the equatorial Indian ocean (ODP Hole 716A). *Paleoceanog.* *Paleooclimatol.* *Paleoocסר.* 397, 7–19. doi: 10.1016/j.palaeo.2013.12.002

Schlitzer, R. (2015). *Ocean Data View*. Available online at: http://odv.awi.de

Schmiedl, G., Hemleben, C., Keller, J., and Segl, M. (1998). Impact of climatic changes on the benthic foraminiferal fauna in the Ionian sea during the last 330,000 years. *Paleoceanography* 13, 447–458. doi: 10.1029/98PA1864

Schmiedl, G., and Leuschner, D. C. (2005). Oxygenation changes in the deep western Arabian sea during the last 190,000 years: productivity versus deepwater circulation. *Paleoceanography* 20:PA2008. doi: 10.1029/2004PA001044

Schmiedl, G., and Mackensen, A. (1997). Late quaternary paleoproduction and deep water circulation in the eastern South Atlantic Ocean: Evidence from benthic foraminifera. *Paleoceanog.* *Paleooclimatol.* *Paleoocسكر.* 130, 43–80.

Schnitker, D. (1994). "Deep-sea benthic foraminifers: food and bottom water masses," in *Carbon Cycling in the Glacial Ocean: Constraints on the Ocean's Role in Global Change*. Berlin: Springer, 539–554. doi: 10.1007/978-3-642-78737-9_23

Schott, F., and McCreary, J. P. (2001). The monsoon circulation of the Indian ocean. *Prog. Oceanogr.* 51, 1–123. doi: 10.1016/S0079-6611(01)00083-0

Schwager, C. (1877). *Quadro del proposto sistema di classificazione del Foraminiferi*, ed B. K. Sen Gupta (Dordrecht: Kluwer Academic Publishers), 1–55.

Singh, D. N. (1979). *Japanese Palaeoecol. 16, 123–157.*

Singh, A. D., Jung, S. J. A., Darling, K., Ganeshram, R., Ivanovich, T., and Kroon, D. S. N., et al. (2002). Why is the Bay of Bengal less productive during summer monsoon compared to the Arabian sea? *Geophys. Res. Lett.* 29, 22–35. doi: 10.1029/2002GL016013

Sen Gupta, B. K. (2002). "Systematics of Modern Foraminifera," in *Studies in Late Tertiary Smaller Foraminifera of Car Nicobar Island, Bay of Bengal*. (Ph.D. Thesis), Banaras Hindu University, Varanasi (India).

Singh, A. D., Jung, S. J. A., Anand, P., Kroon, D., and Ganeshram, R. S. (2018). Rapid switch in monsoon-wind induced surface hydrographic conditions of the eastern Arabian sea during the last deglaciation. *Q. Int.* 479, 3–11. doi: 10.1016/j.quaint.2018.03.027

Singh, A. D., Jung, S. J. A., Darlín, K., Ganeshram, R., Ivanochko, T., and Kroon, D. (2011). Productivity collapses in the Arabian Sea during glacial cold phases. *Paleoceanography* 26(3), doi: 10.1029/2010PA001923

Singh, A. D., Rai, A. K., Verma, K., Das, S., and Bharti, S. K. (2015). Benthic foraminiferal diversity response to the climate induced changes in the eastern Arabian Sea oxygen minimum zone during the last 30 ka BP. *Qu. Int.* 374, 118–125. doi: 10.1016/j.quaint.2014.11.052

Singh, D. N. (1979). *Studies in Neogene Smaller Foraminifera of Little Andaman Island, Bay of Bengal*. Ph. D. Thesis, Banaras Hindu University, Varanasi (India).

Smith, C. R. (1964). Ecology of benthonic species. *U. S. Geol. Surv. Prof. Pap.* 429, 1–55.
Southon, J., Kashgarian, M., Fontugne, M., Metivier, B., and Yim, W. W.-S. (2002). Marine reservoir corrections for the Indian Ocean and Southeast Asia. *Radiocarbon* 44, 167–180.

Srinivasan, M. S., and Rajeshkhar, C. (1981). New benthic foraminifera from the late cenozoic of ritchie’s archipelago, Andaman Sea. *Biovigyanam* 7, 1–8.

Srinivasan, M. S., and Sharma, V. (1980). *Schwager’s Car Nicobar foraminifera in the Reports of the Novara Expedition a Revision*. New Delhi: Today and Tomorrows Printers and Publishers.

Stuiver, M., and Reimer, P. J. (1993). Extended 14C data base and revised CALIB 3.0 14C age calibration program. *Radiocarbon* 35, 215–230.

Thomas, E., and Gooday, A. J. (1996). Cenozoic deep-sea benthic foraminifers: tracers for changes in oceanic productivity? *Geology* 24, 355–358. doi: 10.1130/0091-7613(1996)024<0355:CDSFIB>2.3.CO;2

Tomczak, M., and Godfrey, J. S. (2003). *Regional Oceanography: An Introduction*, 2nd Edn. Delhi: Daya Publishing House.

Verma, K., Bharti, S. K., and Singh, A. D. (2018). Late Glacial–Holocene record of benthic foraminiferal morphogroups from the eastern Arabian Sea OMZ: paleoenvironmental implications. *J. Earth Syst. Sci.* 127:21. doi: 10.1007/s12040-018-0920-9

Verma, K., and Singh, A. D. (2019). Genus cibicides from the western Bay of Bengal: relationship to deep sea changes. *J. Palaeontol. Soc. India* 64, 1–10.

von Rad, U., Schulz, H., Riech, V., den Dulk, M., Berner, U., and Stroock, F. (1999). Multiple monsoon-controlled breakdown of oxygen-minimum conditions during the past 30,000 years documented in laminated sediments off Pakistan. *Palaeogeogr., Palaeoclimatol., Palaeoecol.* 152, 129–161. doi: 10.1016/S0031-0182(99)00425-W

Woodruff, F. (1985). Changes in Miocene deep sea benthic foraminiferal distribution in the miocene ocean: paleoceanography and biogeography. *Geol. Soc. Am. 163, 131–176. doi: 10.1130/MEM163-p131

You, Y. (1998). Intermediate water circulation and ventilation of the Indian Ocean derived from water-mass contributions. *J. Mar. Res.* 56, 1029–1067. doi: 10.1357/002224098765173455

You, Y., and Tomczak, M. (1993). Thermocline circulation and ventilation in the Indian ocean derived from water mass analysis. *Deep Sea Res. Part I* 40, 13–56. doi: 10.1016/0967-0637(93)90052-5

**Conflict of Interest:** The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

**Publisher’s Note:** All claims expressed in this article are solely those of the authors and do not necessarily represent those of their affiliated organizations, or those of the publisher, the editors and the reviewers. Any product that may be evaluated in this article, or claim that may be made by its manufacturer, is not guaranteed or endorsed by the publisher.

*Copyright © 2021 Verma, Singh, Singh, Satpathy and Naidu. This is an open-access article distributed under the terms of the Creative Commons Attribution License (CC BY). The use, distribution or reproduction in other forums is permitted, provided the original author(s) and the copyright owner(s) are credited and that the original publication in this journal is cited, in accordance with accepted academic practice. No use, distribution or reproduction is permitted which does not comply with these terms.*