

## Seasonality and variability of coccolithophore fluxes in response to diverse oceanographic regimes in the Bay of Bengal: sediment trap results

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### Abstract

A study on coccolithophores from the sediment trap samples, collected over a period of one year (January 1992 - December 1992) from three trap locations in the Bay of Bengal (BOB) were used to understand their production and export processes in relation to diverse oceanographic regimes associated with the reversing monsoons. A total of 25 species of coccolithophores were identified, which include some of the ecologically important species: viz: *Gephyrocapsa oceanica*, *Umbellosphaera sibogae*, *Florisphaera profunda*, *Umbellosphaera irregularis*, *Emiliana huxleyi*, *Oolithotus antillarum*, *U. tenuis*, *Helicosphaera carteri* and *Calcidiscus leptoporus*. The total coccolithophore fluxes increased from the northern to southern Bay of Bengal where *G. oceanica*, *U. sibogae* and *E. huxleyi* were dominant species displaying seasonality with peak fluxes occurring during southwest (SW) and northeast (NE) monsoons reflecting their affinity for nutrient-rich waters brought in by river plumes, divergences and cyclonic eddies. *U. irregularis*, an indicator of oligotrophic/warm water, recorded peak abundance fluxes only during the spring intermonsoon period at all trap locations thus inferring its preference for oligotrophic conditions caused by increased Sea Surface Temperature (SST), stratification and lack of nutrient supply due to weak wind velocities. The deep dwelling species, *F. profunda* recorded high fluxes during the fall intermonsoon (October/November) in the northern and southern traps during the spring intermonsoon. The peak fluxes observed during the spring intermonsoon (April/May) in the central and southern traps indicated the prevalence of a deep nutricline when oligotrophic conditions prevailed at the surface. The interannual variability of coccolithophore assemblages between the years 1992 and 1994 may be attributed to the prevalence of ENSO (El Niño–Southern Oscillation) and negative IOD (Indian Ocean Dipole) during 1992 and moderate ENSO and positive IOD with different ocean dynamics in 1994. Interestingly, dissolution was encountered as evidenced by the presence of corroded coccoliths. Similarly, mechanical breakage of coccoliths was also observed. It is believed that the biologically mediated processes were the main factors responsible for both the dissolution and mechanical breakage of coccoliths.

## 1. Introduction

In the present study, the temporal and spatial variations of coccolithophore production and export in the Bay of Bengal were described and their implication on hydrography impacted by the reversing monsoons was discussed. Sediment trap experiments carried out hitherto in the Bay of Bengal have demonstrated that the settling particles in the water column sink from sea surface to deep ocean forming the marine bottom sediment. It was also inferred that the main sources of settling particles in the Bay of Bengal were the biological productivity in the euphotic zone such as foraminiferal fluxes (Guptha et al., 1997) and river inputs (Ittekkot et al., 1991; Unger et al., 2003, 2005).

Coccolithophores are one of the most dominant groups of phytoplankton playing an important role as primary producers, form a very important constituent of fine grained carbonate sediment in the oceans. Their effect on albedo (masses of detached coccoliths substantially reflect incoming light) and biochemical (e.g. dimethyl sulphide acts as a source molecule of cloud nucleation) properties have important roles to play in climate change (Westbroek et al., 1993). Besides, they also play a prominent role in the global carbon cycle and the functioning of biological and inorganic carbon pumps (Holligan, 1992). Understanding the role of phytoplankton in sequestering CO<sub>2</sub> has been an important component of global climate change research in recent years. Calcification by coccolithophores in the ocean is a major source of calcite sediment in the world oceans and plays a significant role in the export of calcium carbonate to the deep sea (Ziveri et al., 2000a; Ziveri et al., 2000b; Triantaphyllou et al., 2004). The knowledge on living coccolithophore assemblages and their distribution as isolated coccoliths in the sediments have potential uses in the paleoceanographic/paleoenvironmental reconstructions of marine sediments (Andruleit and Rogalla, 2002; Ivanova et al., 2003; Rogalla and Andruleit, 2005). Therefore, it is very important to understand the ecological implication of modern coccolithophore assemblages.

Although, studies on extant coccolithophores from sediment traps in the northern Indian Ocean began more than a decade ago (Zeltner, 1998, 2000; Andruleit et al., 2000; Broerse et al., 2000a; Guptha et al., 2005; Mergulhao et al., 2006) the regional focus was largely confined to the Arabian Sea. However, recently, Stoll et al. (2007) studied the seasonal cycles in biogenic production and export in the northern Bay of Bengal sediment traps, while Guptha et al. (2005) investigated coccolithophores from the euphotic zone of the equatorial Indian Ocean and reported high concentrations of coccoliths at shallow depths and *Umbellosphaera irregularis* as the most abundant species. Therefore, it is our endeavor to add to the paucity of information on coccolithophores in the Bay of Bengal. The main aim of the present study is to understand the processes of production, export and temporal variability of coccolithophores in relation to the diverse oceanographic processes resulting from reversing monsoons in the Bay of Bengal.

## 2. Oceanographic setting

The Bay of Bengal is a semi-enclosed basin in the northern Indian Ocean influenced by the seasonally reversing monsoon winds which are affecting its circulation pattern significantly (Cutler and Swallow, 1984; Hastenrath and Greischar, 1989). Contrary to the Arabian Sea, the Bay of Bengal receives enormous inputs of fresh water and suspended sediment which are largely discharged during the southwest (SW) monsoon (June – September) when the out flows of the Ganges, Brahmaputra and other major rivers in the region reach their maximum (Rao, 1979; Ittekkot et al., 1985; Ittekkot and Arain, 1986), with significant changes to the surface salinity over the entire Bay of Bengal (Wyrcki, 1973; Murty et al., 1992). Sea surface salinity (SSS) is reported to be low with a salinity change ranging from 3 – 7 psu during the SW monsoon (Ittekkot et al., 1991; Prasanna Kumar et al., 2002). This is further substantiated by the increased fluxes of *Neogloboquadrina dutertrei*, a low salinity foraminiferal indicator (Guptha et al., 1997). Due to prevailing strong halocline, the strong monsoon winds can not induce mixing and nutrient entrainment (Shenoi et al., 2002). In addition, its proximity to the equator makes the circulation highly complex. During the fall intermonsoon (October – November) and early northeast (NE) monsoon (i.e. December), an equatorward surface current is well developed along the east coast of India under the influence of the northeasterlies (Fig. 1a). This current is designated as the East India Coastal Current (EICC) (McCreary et al., 1993; Shankar et al., 1996) and continues to flow southward and eventually feeds into the westward flowing Northeast Monsoon Current (NMC) or Winter Monsoon Current (WMC) in the southern bay. The WMC carries low salinity water ( $S < 34$ ) that spreads out as a tongue into the Arabian Sea (Wyrcki, 1971). A large cyclonic circulation cell occupies the interior of the Bay of Bengal.

During the spring intermonsoon period (March-April), the EICC is well developed and flows northward along the east coast of India, whereas, during the SW monsoon it weakens and numerous eddies develop in the western Bay of Bengal (Shetye et al., 1991; Murty et al., 1992). The Southwest Monsoon Current (SMC) which is fed by the southeastward flow from the south central Arabian Sea (Shankar et al., 2002) flows eastward south of Sri Lanka (Schott et al., 1994) and in the eastern part of Sri Lanka (Fig. 1b). It then turns towards the NE and flows into the Bay of Bengal (Vinayachandran et al., 1999a).

High productivity during the spring intermonsoon has been observed along the east coast of India where upwelling is associated with the meandering northward flowing EICC forming the seasonal Western Boundary Current (Legeckis, 1987; Sanilkumar et al., 1997). Gauns et al. (2005) reported that the primary productivity in the Bay of Bengal is much lower than that of the Arabian Sea, in contrast Stoll et al. (2007) in a study based on coccolith and foraminiferal assemblages reported that the BOB is a region of high productivity, which may be attributed to the prevalence of changing oceanographic conditions believed to have been influenced by the El Niño–Southern Oscillation (ENSO) event in 1994.

In general, the environmental data such as Chlorophyll-a progressively increases from spring intermonsoon to SW monsoon, similar trend is followed by wind speed and mixed layer depths (Figs. 2a, b & d). Again, all these parameters display upward trend during NE monsoon. In contrast, SST gradually decreases from spring intermonsoon to SW monsoon (Fig. 2c).

### 3. Material and methods

The sediment traps (PARFLUX Mark VI) were deployed at three locations in the Bay of Bengal (Fig. 1a). Trap samples at northern Bay of Bengal trap (NBBT: 15° 44.62'N; 88° 58.06'E) were collected at a depth of 1156 m and water depth of 2682 m between June 29, 1992 and December 16, 1992 with a duration of each sample ranging from 10 to 27 days. Similarly, central Bay of Bengal trap (CBBT: 11° 01.66'N; 84° 26.21'E) trap samples were collected at a depth of 1588 m and water depth of 3462 m between February 03, 1992 and December 16, 1992 with a sample duration of 5 to 27 days followed by southern Bay of Bengal trap (SBBT: 5° 03.33'N; 87° 03.23'E) at 1518 m and water depth of 3997 m during 29 January – 16 December 1992 with a sample duration of 3 to 27 days under the Indo-German collaborative. These samples were studied to understand the temporal and spatial variability of coccolithophores. Prior to deployment of the traps, the sampling cups were filled with *in situ* deep sea water collected from trap locations to which 35 g/l NaCl and 3.3 g/l HgCl<sub>2</sub> was added to prevent biodegradation which also prevents swimmers. After retrieval, samples were wet sieved through a >1 mm sieve and the filtrate was split into aliquots of 1/4 to 1/16 using a precision splitter (Honjo, 1982). The filtrate from one of the aliquots of every sample was filtered through pre-weighed Millipore filters (0.45 µm) using a vacuum filtration pump. After filtration these filters were rinsed with buffered distilled water (NH<sub>4</sub>OH) to eliminate traces of salts if any and dried in a hot air oven at 50°C. A small portion of the above dried filter was cut and placed on a sample stub, coated with gold/palladium (100 A°) in a sputter coater and scanned, using a JOEL SEM Model 5800 LV. About 20 tracks of area in each filter was scanned in a transect from center to the outer edge. In each track, coccoliths and coccolithophres were counted in 20 fields of view at a magnification of X3500 depending on their availability. Total coccolithophore (coccolith and coccosphere) fluxes (×Nos m<sup>-2</sup>d<sup>-1</sup>) were calculated by extrapolating the number of specimens counted in the total sample, duration of trap deployment and aperture area as follows (Broerse et al., 2000a).

$$Flx = \frac{F C S}{A D O}$$

Flx = coccolith flux (specimens m<sup>-2</sup>d<sup>-1</sup>)

F = effective filtration area (mm<sup>2</sup>)

C = number of coccolithophores

$S$  = split factor (reciprocal of split fraction)

$A$  = investigated filter area ( $\text{mm}^2$ )

$D$  = length of sampling interval (d)

$O$  = opening area of the trap cone ( $\text{m}^2$ )

The  $\text{CaCO}_3$  flux of coccoliths was estimated following Broerse et al. (2000a) by multiplying the specific weight of each coccolith by their corresponding fluxes. Similarly, the  $\text{CaCO}_3$  flux of coccospheres was also estimated by multiplying the coccosphere fluxes by the mean number of coccoliths per coccosphere and the specific coccolith weight.

## 4. Results and discussion

### 4.1. Mass particulate flux

The average total particulate fluxes in traps at all the trap locations viz: NBBT, CBBT and SBBT were  $84 \text{ mg m}^{-2}\text{d}^{-1}$ ,  $95 \text{ mg m}^{-2}\text{d}^{-1}$  and  $133 \text{ mg m}^{-2}\text{d}^{-1}$  respectively showing a progressive increase from northern to southern bay. The NBBT trap showed a seasonality characterized by distinct peaks in the distribution pattern wherein a major peak flux was associated with the SW monsoon during August/September and a minor peak during the spring intermonsoon (April-May) (Fig. 3a). The CBBT trap also displayed a distinct seasonality with relatively higher fluxes during the SW monsoon with peak abundances observed during July/August and September (Fig. 3b) followed by SBBT trap which showed increased fluxes during SW monsoon (June – September), with an abundance peak at the end of SW monsoon (September) (Fig. 3c).

### 4.2. Total coccolithophore flux

It is evident from Figs. 3d-f that in general, the total coccolithophore fluxes displayed an increase from the northern to central bay, while least variation was noticed from central to southern bay. Total coccolithophore fluxes at NBBT, CBBT and SBBT sites showed average values of  $46.96 \times 10^5 \text{ m}^{-2}\text{d}^{-1}$ ,  $120.78 \times 10^5 \text{ m}^{-2}\text{d}^{-1}$  and  $122.06 \times 10^5 \text{ m}^{-2}\text{d}^{-1}$  respectively. Distinct seasonality was evident at NBBT with increased fluxes during the spring intermonsoon (March) and early SW monsoon (June) and a maximum peak during the late SW monsoon (September) (Fig. 3d). Similarly, the coccolithophore fluxes in the CBBT trap also displayed seasonality with a major peak associated with the spring intermonsoon (March/April) and a minor peak with the SW monsoon (July/August) followed by decreased fluxes in September (Fig. 3e). The fluxes at SBBT recorded elevated fluxes from March to August followed by a second peak from September - November (Fig. 3f), while decreased fluxes were observed during the NE monsoon and fag end of SW monsoon in September.

This study has yielded a total of 25 coccolithophore species (Tables 1, 2 and 3). NBBT and CBBT recorded 21 species each, while SBBT recorded a higher diversity with 24 species of coccolithophores. Among them *Gephyrocapsa oceanica*, *Umbilicosphaera sibogae*, *Florisphaera profunda* and *U. irregularis* are the dominant species followed by a few common species such as *Emiliania huxleyi*, *Helicosphaera carteri*, *Calcidiscus leptoporus*, *Coronosphaera mediterranea*, *Discosphaera tubifera*, *Syracosphaera lamina*, *Gladiolithus flabellatus*, *Ceratolithus cristatus* and *Algirosphaera oryza*.

#### 4.3. Flux patterns of various species of coccolithophores

Figures 4a-f, 5a-f and 6a-f showed the temporal distribution patterns of some of the ecologically important species such as *G. oceanica*, *U. sibogae*, *E. huxleyi*, *U. irregularis*, *F. profunda* and *C. leptoporus*. The remaining minor species which comprise the upper photic zone were *D. tubifera* and *Rhabdosphaera clavigera*, the middle photic zone, *S. pulchra*, *S. pirus*, *S. rotula*, *S. anthos*, *S. lamina*, *C. mediterranea*, *Oolithotus antillarum*, *O. fragilis* and *U. tenuis* and the lower photic zone species *G. flabellatus* along with *H. carteri*, *Calciosolenia* spp., *Calyptrolithina multipora*, *A. oryza* and *C. cristatus* are shown in Tables 1, 2 and 3.

##### 4.3.1. *G. oceanica*

It is by far the most abundant species in the coccolithophore assemblage in the Bay of Bengal. The average fluxes of  $20.64 \times 10^5 \text{ m}^{-2}\text{d}^{-1}$ ,  $43.00 \times 10^5 \text{ m}^{-2}\text{d}^{-1}$  and  $35.48 \times 10^5 \text{ m}^{-2}\text{d}^{-1}$  were recorded at NBBT, CBBT and SBBT trap locations respectively. The fluxes at NBBT displayed seasonality with major and minor peaks coinciding with the early and late SW monsoons (June and September), October/November and also during the spring intermonsoon (March) (Fig. 4a). At CBBT, it exhibited three peaks with a major peak associated with the SW monsoon (July/August) followed by a peak during the spring intermonsoon (April) and a minor peak during the fall intermonsoon (October/November) (Fig. 4b). Fluxes at SBBT showed a distinct seasonality with major peaks associated with the SW monsoons (June/July and August/September) (Fig. 4c). A minor peak was observed during the fall intermonsoon (October/November). Decreased fluxes were also recorded during SW monsoon (September) and NE monsoon periods.

##### 4.3.2. *U. sibogae*

This was the second dominant species among the coccolithophores from the Bay of Bengal. The fluxes in the traps showed average values of  $6.74 \times 10^5 \text{ m}^{-2}\text{d}^{-1}$ ,  $18.83 \times 10^5 \text{ m}^{-2}\text{d}^{-1}$  and  $11.26 \times 10^5 \text{ m}^{-2}\text{d}^{-1}$  respectively at NBBT, CBBT and SBBT locations. The seasonal pattern at NBBT trap reflected the pattern displayed by *G. oceanica* (Fig. 4d). In contrast the fluxes at CBBT showed a major peak associated with the NE monsoon (February/March) followed by two minor peaks during the spring intermonsoon and early SW monsoon (April and May/June) with no significant variation during the SW monsoon (Fig. 4e).

The fluxes of *U. sibogae* at SBBT ranged from 1.52 to  $27.85 \times 10^5 \text{ m}^{-2}\text{d}^{-1}$  displaying a seasonality with a prominent peak occurring during the SW monsoon (August/September) (Fig. 4f), whereas, minor peak abundances were associated with fall and spring intermonsoons (September/October and April-May) (Fig. 4f).

#### 4.3.3. *E. huxleyi*

Its flux at NBBT varied from 0.36 to  $2.62 \times 10^5 \text{ m}^{-2}\text{d}^{-1}$  with an average value of  $1.16 \times 10^5 \text{ m}^{-2}\text{d}^{-1}$  showing a somewhat similar distribution pattern as seen by *G. oceanica* (Fig. 5a). The flux in the trap at CBBT varied between 0.83 and  $13.05 \times 10^5 \text{ m}^{-2}\text{d}^{-1}$  with an average of  $5.21 \times 10^5 \text{ m}^{-2}\text{d}^{-1}$  displaying a major peaks during the SW monsoon (July/August), followed by two minor peaks during the NE monsoon and spring intermonsoons (February/March and April) (Fig. 5b). At SBBT, the fluxes varied from 0.77 to  $20.09 \times 10^5 \text{ m}^{-2}\text{d}^{-1}$  with an average value of  $7.45 \times 10^5 \text{ m}^{-2}\text{d}^{-1}$  and with increased fluxes during the SW monsoon and fall intermonsoon (October/November). Minor peaks were also observed during May/June and August/September (Fig. 5c).

#### 4.3.4. *U. irregularis*

The flux at NBBT varied from 0.47 to  $4.77 \times 10^5 \text{ m}^{-2}\text{d}^{-1}$  with an average flux of  $2.48 \times 10^5 \text{ m}^{-2}\text{d}^{-1}$  showing two peaks associated with the spring intermonsoon and early SW monsoon (May and June/July) (Fig. 5d). In addition, minor peaks were also observed during the spring and fall intermonsoons (March and September/October and November/December) (Fig. 5d). The fluxes in the CBBT trap varied from 1.30 to  $41.06 \times 10^5 \text{ m}^{-2}\text{d}^{-1}$  with an average value of  $13.08 \times 10^5 \text{ m}^{-2}\text{d}^{-1}$ . The highest peak abundance was associated with the spring intermonsoon (April-May) (Fig. 5e). In the SBBT trap, the flux of *U. irregularis* varied from 0.77 to  $21.44 \times 10^5 \text{ m}^{-2}\text{d}^{-1}$  with an average value of  $8.78 \times 10^5 \text{ m}^{-2}\text{d}^{-1}$  showing increased fluxes associated with the spring intermonsoon and a peak in August/September (Fig. 5f).

#### 4.3.5. *F. profunda*

Its flux in the NBBT varied between 0.88 and  $20.34 \times 10^5 \text{ m}^{-2}\text{d}^{-1}$  with an average value of  $4.67 \times 10^5 \text{ m}^{-2}\text{d}^{-1}$  and continued to show decreased fluxes throughout the sampling period except for a prominent peak of  $20.34 \times 10^5 \text{ m}^{-2}\text{d}^{-1}$  occurring during the fall intermonsoon (October/November) (Fig. 6a). The fluxes at CBBT varied from 0.91 to  $28.70 \times 10^5 \text{ m}^{-2}\text{d}^{-1}$  with an average flux value of  $13.70 \times 10^5 \text{ m}^{-2}\text{d}^{-1}$ , displaying a bi-modal distribution pattern with abundance peaks associated with the spring intermonsoon (April) and SW monsoon (July/August) (Fig. 6b). It also showed an increased flux ( $13.70 \times 10^5 \text{ m}^{-2}\text{d}^{-1}$ ) during the NE monsoon (November/December). The fluxes at SBBT location varied between 0.39 and  $25.55 \times 10^5 \text{ m}^{-2}\text{d}^{-1}$  with an average value of  $9.43 \times 10^5 \text{ m}^{-2}\text{d}^{-1}$ , and were characterized by a bi-modal distribution pattern with major and minor peaks associated with the fall intermonsoon (October/November) and spring intermonsoons respectively (April) (Fig. 6c).

#### 4.3.6. *C. leptoporus*

It exhibited a patchy distribution at NBBT with increased fluxes observed during the SW monsoon (June/July) (Fig.6d). In the CBBT trap it showed a prominent peak during the fall intermonsoon (September/October) (Fig.6e). The fluxes in the SBBT trap were characterized by a polymodal distribution pattern with a major peak showing during the SW monsoon (August/September) followed by secondary peak abundances recorded during the spring intermonsoon and SW monsoon (April and June/July) respectively (Fig. 6f).

#### 4.4. Coccolithophore-CaCO<sub>3</sub> fluxes in the Bay of Bengal

The coccolithophore-CaCO<sub>3</sub> flux at NBBT, CBBT and SBBT traps ranged from 0.02 to 0.30 mg m<sup>-2</sup>d<sup>-1</sup> while it ranged from 0.19 to 0.44 mg m<sup>-2</sup>d<sup>-1</sup> at CBBT followed by SBBT trap showing fluxes from 0.15 to 0.68 mg m<sup>-2</sup>d<sup>-1</sup>. The fluxes in general followed the same trend as that of total coccolithophore fluxes at all the three trap locations (Figs. 7a - c).

#### 5.1. General characteristic features of coccolith species

*G. oceanica* (Plate – 1) is predominantly a low – latitude species very commonly found in tropical – subtropical waters with a temperature range of 12° to 30°C (McIntyre et al., 1970) and widely reported along ocean margins (Okada and Honjo, 1973). It is also known to preferentially thrive in high-nutrient environments, such as upwelling areas or continental shelves (Mitchell-Innes and Winter, 1987; Houghton and Guptha, 1991; Kleijne, 1993; Andruleit et al., 2000; Broerse et al., 2000a; Andruleit and Rogalla, 2002; Guptha et al., 2005; Mergulhao et al., 2006). Similarly, *U. sibogae* (Plate – 1 (2)) was considered to be a temperate to subtropical species in water temperatures between 21° and 28°C (McIntyre and Bé, 1967). It was the second dominant species which also prefers nutrient-rich water (Roth and Coulborn, 1982; Andruleit et al., 2000; Broerse et al., 2000a and Mergulhao et al., 2006). Recently Stoll et al. (2007) reported *G. oceanica* as the second most abundant species after *F. profunda* in the northern Bay of Bengal during the SW monsoons. Thus, it may be inferred that the NBBT is represented by a high nutrient environment which was also influenced by terrigenous input into the Bay of Bengal. *E. huxleyi* (Plate – 1 (3)) is the third dominant species, which is the most ubiquitous coccolithophore species in the world oceans (McIntyre and Bé 1967; Winter and Siesser 1994). It is also characterized as a cosmopolitan species of tropical and subtropical waters observed over a wide range of temperatures (2-30°C) and salinities (16-45 psu) (Okada and McIntyre, 1977; Ziveri et al., 2000a; Ziveri et al., 2000b; Triantaphyllou et al., 2004; Dimiza et al., 2008; Malinverno et al., 2009). The distribution of this species in surface waters is largely independent of water temperature and thermocline depth (Samtleben et al., 1995a, b). Increased fluxes of *E. huxleyi* was reported in nutrient-rich environments along the edges of the subtropical central gyres in upwelling areas, and along the outer continental shelves (Brand, 1994; Dimiza et al., 2008; Malinverno et al., 2009).



## 5.2. Seasonality and inter-trap comparisons

The northern trap (NBBT) recorded relatively higher fluxes of *G. oceanica* and *U. sibogae* during the late SW monsoon (September) which may be due to the availability of nutrients supplied by river discharge (Ittekkot et al., 1991) and the prevalence of a cyclonic gyre (Madhupratap et al., 2003; Kumar et al., 2004; Kumar and Ramesh, 2005) facilitating higher productivity up to  $2 \text{ gm C m}^{-2} \text{ d}^{-1}$  in the coastal areas in the northern part of the bay (Antoine et al., 1996). Similarly, *Globigerina bulloides*, an indicator of upwelling was also observed with high abundance (Guptha et al., 1997). The *G. oceanica*, and *U. sibogae* maxima observed during the spring intermonsoon (March) is largely attributed to offshoreward advection of upwelled-nutrient rich waters at the periphery of the subtropical anticyclonic gyre (Shetye et al., 1993; Sanilkumar et al., 1997; Babu et al., 2003). Similarly these species which were biased with seasonality at CBBT showed a peak abundance during February-April due to the circulation of nutrient-rich waters along the periphery of the subtropical anticyclonic circulation gyre (ACG) towards CBBT. The northward-flowing EICC begins in February and strengthens by April/May as the western boundary current of the large scale seasonal subtropical ACG. The observed higher fluxes during the spring intermonsoon at CBBT confirm the role of advection of nutrient-rich waters along the eastern branch of the ACG into the CBBT site. At the centre of the ACG, Ekman pumping causes deepening of Mixed Layer Depth (MLD) and allows formation and sinking of particles, which was evident from the observed peak fluxes of *U. irregularis* and deep-dwelling *F. profunda* by May at CBBT. *U. irregularis* displayed increased abundance from February to May, indicating the development of oligotrophic conditions in the euphotic layer as revealed by low chlorophyll-*a*, warmer SST's, low wind speeds and shallow MLD (Fig. 2). This confirmed the prevalence of stable stratification and availability of low nutrients in the euphotic layer.

*G. oceanica* and *U. sibogae* at SBBT also displayed a biased seasonality with higher fluxes associated with the SW monsoon (June/July and August/September) resulting from a deep MLD due to strong winds (Figs. 2b & d). The lower SST's (Fig. 2c) suggest the advection of cold upwelled waters from the SW coast of India towards SBBT wherein the surface chlorophyll-*a* was relatively high (Fig. 2a). On the contrary, Broerse et al. (2000a) have reported from off Somalia in the northwestern (NW) Indian Ocean that *U. sibogae* did not show increased abundance during the SW monsoon when the increased nutrients were available. Okada and McIntyre (1979) opined that this species prefers warm oligotrophic waters. Similarly, Kleijne (1993) reported decreasing flux in surface water samples from the western Arabian Sea in the upwelling areas. *E. huxleyi* showed relatively higher fluxes during the NE monsoon, when the WMC flows westward from the Andaman-Nicobar Islands. The observed higher fluxes during the SW and NE monsoons suggested that the southern Bay of Bengal waters may not be as oligotrophic as it was believed, which registered high productivity. Increased fluxes during the SW monsoon were related to the influence of the SMC (Murty et al., 1992; Mohan, 1997) and the

associated oceanographic processes such as advection of nutrient-rich and elevated chlorophyll-*a* waters from the upwelling region of the SW coast of India leading to high productivity and particle fluxes (Hastenrath and Lamb 1979; Unger et al. 2003, 2005; Vinayachandran et al., 2004; Joseph et al. 2005; Rao et al., 2006).

Relatively higher fluxes of *E. huxleyi* during the fall intermonsoon at SBBT may be attributed to low SST's and a deep MLD. Interestingly, decreased fluxes of *G. oceanica*, *U. sibogae* and *E. huxleyi* during the late SW monsoon may be due to intense dissolution as evidenced by corroded coccoliths believed to have resulted by biologically mediated processes Plate 2 (1-6).

The most abundant tropical water species such as *U. irregularis* (Plate -1(4)), living in waters with a temperature range of 25° to 30°C (McIntyre et al., 1970; Winter et al., 1994) is indicative of oligotrophic conditions. The *U. irregularis* fluxes recorded at NBBT were the lowest among the three trap sites. However, this species clearly showed relatively increased fluxes during the spring intermonsoon at NBBT indicating oligotrophic stratified conditions due to high SST's > 30°C (Somayajulu et al., 1987; Viswambharan and Mathew, 1992; Murty et al., 1994; Varkey et al., 1996; Unger et al., 2003) and weakened wind velocity (Kleijne et al., 1989, Kleijne, 1993; Andruleit et al., 2000; Broerse et al., 2000a; Guptha et al., 2005; Mergulhao et al., 2006). On the contrary Stoll et al. (2007) reported its total absence from the northern Bay of Bengal in 1994, reflecting the interannual variability observed in productivity pattern and associated particle fluxes (Unger et al., 2003). Similarly, increased fluxes were also observed during the spring intermonsoon at CBBT and SBBT apparently caused by oligotrophic conditions due to weak wind velocities, elevated SST's and stratified water column (Figs. 2b & c).

Okada and Honjo (1973) and Okada and McIntyre (1979) reported that in general, *F. profunda* (Plate- 1(5)) occurs abundantly in low latitude regions within the lower photic zone (100-150 m) in the Pacific and North Atlantic oceans. Similarly, Young (1994) and Beaufort et al. (1997) also reported this species from the lower photic zone in the equatorial Indian Ocean and Ziveri et al. (2000a), Dimiza et al. (2008) and Malinverno et al. (2009) from the lower photic zone of the subtropical mediterranean Sea. The variation in the abundance of *F. profunda* through time has been used as a proxy for past changes in the position of nutricline (Molfinio and McIntyre, 1990a, b; McIntyre et al., 1992). However, its occurrence may not only be related to water depth but also to various oceanographic conditions such as nutrient-content, water-transparency and/or-turbidity and also its position in the water column related to the depth of the nutricline (Ahagon et al., 1993).

At CBBT and SBBT sites *F. profunda* was well distributed, whereas' it showed relatively lower fluxes at NBBT (Figs. 6a-c) from the samples collected in 1992. However, Stoll et al. (2007) reported that the coccolithophore assemblages in the northern Bay of Bengal in 1994, an El Nino period, were dominated by *F. profunda* throughout the year with peak abundances during the SW monsoon.

Therefore, it may be assumed that the oceanographic situation during 1992 was significantly different from 1994 which is reflected by the observed variations.

A maximum peak of *F. profunda* was observed at CBBT during the SW monsoon (July/August) driven by the strong positive wind stress -curl causing a SW-NE oriented band of divergence in the central Bay of Bengal (Murty et al., 1992), which brings nutrient-rich water into the euphotic layer (Fig. 6b). Murty et al. (2000) also reported a Deep Chlorophyll Maximum (DCM) which is situated at 100 m depth in the south shoaling gradually towards the north to 65 m at 12° N under the influence of the cyclonic gyre. Similarly, it has been observed that the maximum nutrient concentrations in the mid-depths of the euphotic zone during August were related to the occurrence of subsurface chlorophyll maxima at most of the stations in the bay during summer monsoon (Gupta, 1998; Madhupratap et al., 2003) facilitating increased fluxes. Therefore, peak fluxes of *F. profunda* during this period may be mainly related to the increased nutrient concentrations at mid depths as evidenced by the presence of the DCM. The fluxes also showed a sharp peak during the spring intermonsoon (April/May) when the oligotrophic conditions prevailed with relatively low surface chlorophyll-*a* (Fig. 2a) and the development of the nutricline by increased nutrients in the subsurface waters must have facilitated increased fluxes of *F. profunda*.

At SBBT this species displayed a seasonality characterized by decreased fluxes of *F. profunda* during the SW monsoon when the MLD was deep (Fig. 2d). This was substantiated by a reported inverse relationship between surface productivity and *F. profunda* abundance (Molfinio and McIntyre, 1990a). However, Broerse et al. (2000a) reported that the deep photic zone species such as *F. profunda* and *G. flabellatus* were dominant in the early SW monsoon in the upwelling region off Somalia. Andrulleit and Rogalla (2002) reported a positive correlation between *F. profunda* and the mean annual MLD in the surface sediments from southeast Arabian Sea, which resulted from the deep thermocline. Recently, Mergulhao et al. (2006) reported increased fluxes during January, April and June when nutrient concentrations were high in the central Arabian Sea. Similarly, the present study also inferred that *F. profunda* showed its affinity for enhanced nutrients resulting in abundance during convergence followed by a deep nutricline at CBBT during the spring intermonsoon, rather than only to a specific depth (e.g. deep photic depth). Schiebel et al. (2004) reported *F. profunda* at a shallow depth of 20-60 m during May/June and assumed that *F. profunda* was showing its affinity for enhanced nutrients rather than to a specific water depth. However Stoll et al. (2007) reported *F. profunda* as the dominant species constituting about 90% of the coccolithophore flora in the northern bay, contrary to our observation. The relatively higher fluxes of *F. profunda* at CBBT and SBBT in this study and that of Stoll et al. (2007) for NBBT in 1994 suggest that the Bay of Bengal is characterized by stratified waters having a strong halocline with nutrients being occasionally present in the deeper euphotic zone.

The upper photic zone species such as *C. leptoporus* (Plate-1-(6)) (Haidar and Thierstein, 2001), was one of the most common species found in waters ranging from equatorial to polar in a wide ranging temperature (5-30°C) (McIntyre and Bé 1967; Okada and McIntyre 1979). This species displayed a relatively significant increase from north to south in the Bay of Bengal which also corresponds to the presence of nutrient rich-waters. However, it failed to compete with *G. oceanica* and *U. sibogae* which flourished at NBBT. *C. leptoporus* recorded relatively higher fluxes during early stages of the SW monsoon (June/July). Whereas at CBBT, it recorded increased fluxes during the fall intermonsoon (September/October) due to upwelling (Shetye et al., 1991, Murty et al., 1992 and 2000). At SBBT, increased fluxes were recorded during the spring intermonsoon (March/April) and SW monsoon (June/July and August/September) in the trap which may be due to the advection of nutrient-rich water from the SW coast of India, also substantiated by previous studies (Broerse et al., 2000a).

In general it can be said that although both *U. foliosa* and *U. sibogae* prefer nutrient rich waters, *U. sibogae* prefers warmer temperature than compared to *U. foliosa* with its peak abundance largely restricted to the SW monsoon. Similarly, Kleijne (1993) reported a decreasing abundance of *U. sibogae* in surface waters of the western Arabian Sea approaching the upwelling areas. Broerse (2000) reported *U. foliosa* to be associated with eutrophic, upwelling waters while *U. sibogae* associated with oligotrophic stable water (Okada and McIntyre, 1979). Broerse et al. (2000a) also reported low abundance of *U. sibogae* where it showed a positive response to the increased abundance during the onset of NE monsoon of sediment trap from the western Arabian Sea.

### 5.3. Coccolith-CaCO<sub>3</sub> fluxes inter comparisons with other oceanic areas

Coccoliths are the major contributors to the biogenic carbonate flux which are generally preserved at shallow depths (Murray and Renard, 1891; Sverdrup et al., 1942; Westbroek et al., 1993; Takahashi, 1994; Broerse, 2000; Tanaka, 2004). Calcareous organisms secrete CaCO<sub>3</sub> (both calcite and aragonite) to build their hard skeletal parts which have a tendency to dissolve in deep water layers (Broecker and Peng, 1982; Millero, 1996). They also play a prominent role in the global carbon cycle. Coccolithophores constitute a dominant component of biogenic carbonate (Honjo, 1986; Steinmetz, 1991; Neuer et al., 1997; Čeppek and Wefer, 2000; Broerse et al., 2000b). However, the estimation of Coccolithophore-CaCO<sub>3</sub> and its export to the deep sea has been a problematic until Honjo (1976) used for the first time the averaged masses of coccoliths for computation which was followed by Samtleben and Bickert (1990) and Steinmetz (1991) in their studies on the estimation of coccolithophore- CaCO<sub>3</sub> and its export to the deep sea. Later workers, Knappertsbusch and Brummer (1995) and Young and Ziveri (2000) enabled to refine and evolve a more accurate estimation of the volume and mass of individual coccoliths.

The coccolithophore-CaCO<sub>3</sub> fluxes in the Bay of Bengal showed highest occurrence at SBBT with an average flux of 0.33 mg m<sup>-2</sup>d<sup>-1</sup> followed by CBBT and NBBT trap with the average values of 0.30 mg m<sup>-2</sup>d<sup>-1</sup> and 0.12 mg m<sup>-2</sup>d<sup>-1</sup> respectively (Table 4). Similarly, annual fluxes also followed the same trend with values showing 13.6 g m<sup>-2</sup> yr<sup>-1</sup>, 12.5 g m<sup>-2</sup> yr<sup>-1</sup> and 5.0 g m<sup>-2</sup> yr<sup>-1</sup> for SBBT, CBBT and NBBT respectively. But, when compared to the reported values for same locations of different periods by Ramaswamy and Gaye (2006), only NBBT flux values were comparable with the present results. Higher coccolithophore-CaCO<sub>3</sub> flux was invariably observed during NE-SW intermonsoon periods resulted by productivity caused by Bay of Bengal Western Boundary Current (BBWBC) and ACG, whereas, decreased fluxes during the SW monsoon was attributed to dissolution. The coccolithophore-CaCO<sub>3</sub> fluxes followed the same trend as that of total fluxes at all locations (Figs. 3d-f & 7).

Ramaswamy & Gaye (2006) reported that the coccolithophorid carbonate fluxes ranged between 4 and 24 gm<sup>-2</sup> yr<sup>-1</sup> from the Arabian Sea. In the western Arabian Sea, coccolithophorids were the major contributors to biogenic flux during periods of low nutrient concentrations and coccolithophorid carbonate fluxes decreased. While in the oligotrophic eastern Arabian Sea, coccolithophorid carbonate fluxes were high throughout the year. Similarly, in the northern and central Bay of Bengal, when surface salinity values drop sharply during the SW monsoon coccolithophorid carbonate and diatom opal fluxes continued to increase.

Tanaka and Kawahata (2001) reported that the calculated coccolith- CaCO<sub>3</sub> fluxes ranged between 6.8 and 49.6 mg m<sup>-2</sup>day<sup>-1</sup> and contributed 23.3% of total CaCO<sub>3</sub> flux in the west Caroline Basin in the equatorial Pacific. While, according to Tanaka (2004), the calculated coccolith- CaCO<sub>3</sub> flux in the central north Pacific was highest in the transition zone. The average calculated coccolith carbonate flux in the northeast Atlantic Ocean was 47% of the total carbonate flux (Broerse et al., 2000b) and 33.4% of the total carbonate flux (Sprengel et al., 2000). These results from the north Pacific and the northeast Atlantic (Broerse et al., 2000b) suggested that the estimated coccolith-CaCO<sub>3</sub> fluxes and their contribution to the total carbonate fluxes were higher in the northeast Atlantic region. Furthermore, Broerse et al. (2000b) reported that the relative contribution of coccolith-CaCO<sub>3</sub> to total carbonate in the Atlantic Ocean was high in the subtropical region and low in the temperate region. And, in the northwest and central Pacific Ocean, the relative contribution of coccolith-CaCO<sub>3</sub> to total carbonate was highest in the sub arctic region, and low in the equatorial region.

#### *5.4. Influence of IOD/ENSO events on coccolithophore fluxes at NBBT*

In this study, the observations made on samples collected in the year 1992 for NBBT represented the NBBT-S of Stoll et al. (2007) who reported coccolithophores for the period during 1994-95 from NBBT-N and NBBT-S locations. These two locations were separated by about 400 km. Coccolithophore flux during the above period at NBBT-N and NBBT-S has displayed a very significant

anomaly as compared to 1992 samples. The samples collected in 1992 from NBBT distinctly displayed with increased fluxes of *G. oceanica* as a predominant species throughout the year, while increased fluxes of *F. profunda* were observed during October/November only.

On the contrary, Stoll et al. (2007) reported during 1994-1995, the year of positive Indian Ocean Dipole (IOD) that *F. profunda* unusually dominated during (NBBT-N: May – September, 1994 and NBBT-S: July-October 1994) followed by a lesser dominant *G. oceanica*. Furthermore, Stoll et al. (2007) reported the total absence of upper photic zone species such as *U. irregularis* and *U. tenuis*, whereas these two species were observed with increased abundances in 1992 as observed in the present study (Figs. 5d-f). These significant variations between 1992 and 1994 may be attributed to the prevalence of different oceanic conditions associated with the negative IOD in 1992 and the moderate ENSO and positive IOD in 1994. This is further substantiated by Somayajulu et al. (2003) who have reported that during 1994, there has been a change in seasonal cycle of surface circulation in response to the moderate ENSO warm event of the equatorial Pacific.

The Indian Ocean, particularly, the equatorial region experienced the negative IOD in 1992 and positive IOD in 1994 (Vinayachandran et al., 1999b; Meyers et al., 2007). Strong westerlies over the equatorial Indian Ocean and anomalously warmer SST's off Sumatra coast characterize the negative IOD, while anomalous easterlies and colder SST's in the eastern equatorial Indian Ocean characterize the positive IOD. In general, the IOD which begins in May continues to strengthen during July through October/ November. Associated with these IOD events, the wind field over the Bay of Bengal would also exhibit variability affecting thermocline depth variation leading nutricline variations. In order to understand the depth of thermocline variations during 1992 and 1994 IOD events, we have examined the Ocean General Circulation Model (OGCM) simulated D20 anomaly (long-term (1992-2006) D20 seasonal cycle removed) variations (Murtugudde et al., 2000) in 1992 and 1994 at NBBT-S location (referred to as NBBT in the present study) shown in Fig. 8. It shows an interesting feature with an opposite variation in D20 anomalies of 1992 and 1994 from June to December owing to the influence of IOD events. Thus, shoaling of D20 (negative anomaly) suggests the occurrence of upwelling in June 1992 and September-October 1992 and deepening of D20 (positive anomaly) indicating sinking in 1994 for the same period. It may be assumed that these D20 variations in the thermocline would in turn affect the nutricline depth variations. Interestingly, the coccolithophore variation (Fig. 3d) would correspond to the D20 anomaly variation in 1992. The peak total flux of coccolithophore in September (Fig. 3d), the peak abundance of *G. oceanica* (Fig. 4a) and *U. sibogae* during September/October (Fig. 4d) coincide with the peak upwelling in the region (compare Figs. 3d, 4a & 4d with the Fig. 8). Furthermore, the shift in the peak flux of *F. profunda* (Fig. 6a) towards November 1992 also coincides with the deepening trend of D20 implying the deepening of nutricline.

Thus, the interannual variability of coccolithophore assemblages between the years 1992 and 1994 may be attributed to a moderate ENSO and positive IOD wherein the eastern equatorial Indian Ocean cools below normal SST's with different ocean dynamics in 1994 and the prevalence of ENSO and negative IOD during 1992.

#### 5.5. *Dissolution and mechanical breakage of coccolithophores*

In the course of our investigation, dissolution of coccolithophores was encountered in the waters above lysocline depths as evidenced by the presence of corroded coccoliths of *G. oceanica*, *U. sibogae*, *H. carteri* and *C. leptoporus* at all the three trap sites (Plate 2 (1-6)). Furthermore, this assemblage was comprised of an admixture of both pristine (intact) and corroded coccoliths which possibly may be due to diverse source. No signs of coccolith dissolution was observed at the end of January to mid July at NBBT, while it was conspicuous during mid July to mid December, which may be due to the fact that the NBBT falls under the influence of divergence in the cyclonic gyre which lead to high productivity and degradation of the resultant organic matter causing reduction in pH of the waters eventually leading to dissolution (George et al., 1994; Sarma et al., 2000).

At CBBT, coccolithophore fluxes showed dissolution throughout the year which may be due to high productivity resulted by upwelling, except during the spring intermonsoon (April – June) when the productivity was relatively low. Similarly, at SBBT, dissolution was observed throughout the sampling period except during the early NE monsoon (February - March), which may be attributed to high biological productivity or bottom water circulation. Besides, it has been reported that the Arabian Sea is affected by ocean acidification and seasonal upwelling evidenced by the thinning of a foraminiferal species *G. bulloides* (de Moel et al., 2009).

Broerse et al. (2000b) showed that the preservation of coccoliths strongly depends on rapid transport for protection from corrosive water masses. When the sinking rate is high they can resist dissolution by getting incorporated into fecal pellets and other oceanic macroaggregates that are responsible for the rapid vertical transport to the sea floor. Samtleben and Bickert (1990) reported similar findings in the sediment trap samples from the subarctic Atlantic Lofoten Basin. Andruseit (2000) reported dissolution of *Coccolithus pelagicus*, while other species in the same samples do not show dissolution. From these observations he concluded that dissolution did not take place during or after entrapment of the coccolith assemblages, hence they must have originated from different source areas or have experienced different settling conditions. Owing to the differential dissolution of coccolithophores, the possibility of advection in supplying corroded forms cannot be ruled out. Milliman et al. (1999) documented an increasing evidence to support considerable dissolution of calcium carbonate well above the chemical lysocline and concluded that biological processes as well as biologically mediated processes could be responsible for dissolution. He further elaborates that one of the biologically mediated mechanisms of

dissolution is with the guts and feces of grazers and the microbial oxidation of organic matter produced in microenvironment causing dissolution.

In addition to dissolution, mechanical breakage or fragmentation of coccoliths mainly exhibited by *G. oceanica*, *U. sibogae*, *H. carteri*, *C. leptoporus* and *E. huxleyi*. (Plate 2 (7 & 8)), was also observed. The intense fragmentation of both coccoliths and coccospheres was largely attributed to zooplankton grazing substantiated by the presence of a large quantity of copepods and fecal pellets in the trap samples. Similarly, Broerse et al. (2000b) reported the fragmentation of coccoliths and disintegration of coccospheres and defined fragmentation as mechanical breakage where parts of the distal and/or proximal shields are lost. They also reported that fragmentation was encountered in both well-preserved and etched coccoliths. Etching starts normally in the central area of a coccolith, which is most susceptible to dissolution, while fragmentation is largely encountered at the outer parts of a coccolith (Plate 2 (7 & 8)). Fragmentation of coccoliths due to zooplankton grazing was observed in feeding experiments and field observations (Harris, 1994; Andruleit, 1997). Samtleben and Bickert (1990) also reported that zooplankton activity affecting coccolith fluxes, where more fragile holococcoliths were broken up by zooplankton grazing and digestion forming the unidentifiable fragments in fine fractions. Thus, both the dissolution and mechanical breakdown of coccoliths could largely be attributed to biologically mediated processes.

## **6. Conclusion**

The total particulate and coccolithophore fluxes increased from the northern to the central bays, while it exhibited uniform distribution from the central to southern bays. Coccolithophore assemblage inferred that the Bay of Bengal experienced increased biological productivity during SW monsoon. Besides it also experienced oligotrophic conditions during the peak summer period, i.e. May. The dominance of photic zone species like *G. oceanica*, *U. sibogae* and *E. huxleyi* which displayed seasonality with peak fluxes associated with the SW and NE monsoons, reflecting their affinity to nutrient-rich waters. *U. irregularis* recorded its peak abundance during the spring intermonsoon periods at all the three trap locations reflecting its preference for oligotrophic conditions. Increased fluxes of the deep photic species *F. profunda* and also *O. antillarum* indicated the presence of deep nutricline in the Bay of Bengal which was very distinct during the fall intermonsoon (October/November) in the northern trap and spring intermonsoon in the central and southern traps when oligotrophic conditions prevailed. Furthermore, it is believed that *F. profunda* and *O. antillarum* may be more dependent on depth of the nutricline rather than a specific depth of the deep photic zone. The interannual variability of coccolithophore assemblages between the years 1992 and 1994 may be attributed to the prevalence of ENSO and negative IOD during 1992 and moderate ENSO and positive IOD with different ocean dynamics in 1994. Dissolution and mechanical breakage of coccoliths encountered may be largely related to biologically mediated processes.



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Northern Bay of Bengal Trap (NBBT 06)														
	Flux (x 10 <sup>5</sup> m <sup>-2</sup> d <sup>-1</sup> )													
Interval	29/1/92-8/2/92	8/2/92-5/3/92	5/3/92-31/3/92	31/3/92-26/4/92	26/4/92-22/5/92	22/5/92-17/6/92	17/6/92-13/7/92	13/7/92-8/8/92	8/8/92-3/9/92	3/9/92-29/9/92	29/9/92-25/10/92	25/10/92-20/11/92	25/10/92-20/11/92	Average
Station No. Species	1	2	3	4	5	6	7	8	9	10	11	12	13	
<i>G. oceanica</i>	6.84	10.87	28.76	7.75	15.32	28.29	14.16	20.92	14.46	44.35	35.71	27.38	13.52	<b>20.64</b>
<i>E. huxleyi</i>	0.47	1.30	2.29	1.38	1.30	1.74	0.47	1.13	0.77	2.62	0.39	0.83	0.36	<b>1.16</b>
<i>C. mediterranea</i>			1.38	0.91	1.30	1.74	0.47	0.39		0.44	1.60	0.83		<b>1.01</b>
<i>S. pulchra</i>					0.44		0.47	0.39		0.88	0.39			<b>0.51</b>
<i>U. sibogae</i>	1.82	3.04	9.13	2.73	2.62	6.95	7.31	2.65	6.46	19.12	13.49	7.89	4.39	<b>6.74</b>
<i>U. irregularis</i>	0.47	1.74	3.64	1.38	4.77	3.04	4.55	3.04	1.52	3.04	2.79	0.83	1.46	<b>2.48</b>
<i>U. tenuis</i>												0.41		<b>0.41</b>
<i>H. carteri</i>			1.82			0.88	0.47	0.77	0.77	2.18	1.99	2.48		<b>1.42</b>
<i>C. leptopora</i>		0.44		0.47	0.88	1.32	2.35	0.77		0.88	0.80	1.24		<b>1.02</b>
<i>F. profunda</i>	1.41	1.30	2.73	1.82	0.88	1.74	1.41	1.52	1.90	4.77	14.68	20.34	6.21	<b>4.67</b>
<i>Calcosolenids</i> sp.			0.47			0.88		0.39		0.88	0.80		0.72	<b>0.69</b>
<i>D. tubifera</i>	0.94		0.47		0.88			0.39			0.39	0.41		<b>0.58</b>
<i>R. clavigera</i>				0.47	0.44								0.36	<b>0.42</b>
<i>O. antillarum</i>					0.44	0.44			0.39	1.32	0.80	0.83	0.36	<b>0.65</b>
<i>S. pulchra</i>			0.47											<b>0.47</b>
<i>S. pirus</i>							0.47	0.77						<b>0.62</b>
<i>S. lamina</i>	0.94	1.74	1.82			0.44			0.39	0.88	1.99	0.41	0.72	<b>1.04</b>
<i>Syracosphaera</i> sp.			0.47		0.88		0.47	0.39		0.88				<b>0.62</b>
<i>N. coccolithomorpha</i>			0.94	0.47	1.30	0.44	0.47	1.52		0.88	0.80			<b>0.85</b>
<i>A. oryza</i>				0.47		0.88								<b>0.68</b>
<i>C. cristatus</i>					0.44		0.47			0.44	0.39			<b>0.43</b>
Total coccolith flux	12.89	20.42	54.39	17.86	31.90	48.79	33.53	35.02	26.66	83.59	77.00	63.88	28.09	<b>41.08</b>
Total coccosphere flux		0.44				0.44		0.77		1.76	0.78	1.24	0.72	<b>0.47</b>
<b>Total coccolithophore flux</b>	<b>12.89</b>	<b>20.86</b>	<b>54.39</b>	<b>17.86</b>	<b>31.90</b>	<b>49.23</b>	<b>33.53</b>	<b>35.79</b>	<b>26.66</b>	<b>85.35</b>	<b>77.78</b>	<b>65.12</b>	<b>28.81</b>	<b>41.55</b>

**Table 1.** Seasonal variation of different coccolithophore species and coccosphere fluxes with their average fluxes recorded in the Northern Bay of Bengal Trap (NBBT) for the period 29 January - 16 December 1992.

Central Bay of Bengal Trap (CBBT 06)														
	Flux (x 10 <sup>5</sup> m <sup>-2</sup> d <sup>-1</sup> )													
Interval	3/2/92-8/2/92	8/2/92-5/3/92	5/3/92-31/3/92	31/3/92-26/4/92	26/4/92-22/5/92	22/5/92-17/6/92	17/6/92-13/7/92	13/7/92-8/8/92	8/8/92-3/9/92	3/9/92-29/9/92	29/9/92-25/10/92	25/10/92-20/11/92	20/11/92-16/12/92	Average
Station No.	1	2	3	4	5	6	7	8	9	10	11	12	13	
Species														
<i>G. oceanica</i>	43.35	41.06	42.00	59.80	37.42	46.09	32.87	61.73	46.09	24.78	37.75	46.89	39.13	<b>43.00</b>
<i>E. huxleyi</i>	4.11	7.75	1.82	7.75	6.84	3.64	5.93	13.05	8.22	2.18	0.83	2.48	3.04	<b>5.21</b>
<i>C. mediterranea</i>	0.91	1.82	0.91	0.91	1.38	3.64	1.38	0.44	0.91	0.88	0.83	2.07	1.30	<b>1.34</b>
<i>S. pulchra</i>	0.47	0.91	1.82		1.38	1.38		0.44	0.47	0.44	1.24	0.41	0.44	<b>0.86</b>
<i>U. sibogae</i>	19.18	31.05	15.98	25.55	19.18	22.82	14.16	13.47	15.51	15.21	18.68	17.41	16.53	<b>18.83</b>
<i>U. irregularis</i>	1.82	8.67	18.74	23.26	41.06	21.44	13.25	5.22	7.75	1.30	6.24	8.72	12.61	<b>13.08</b>
<i>U. tenuis</i>		2.29	0.91	0.47	0.91				0.91				0.44	<b>0.99</b>
<i>H. carteri</i>	1.38	4.55	4.11	3.20	5.46	3.64	1.82	2.62	2.73	0.44	1.66	0.83	1.74	<b>2.63</b>
<i>C. leptopora</i>	0.91	2.29	4.11	2.73	2.73	2.73	2.73	2.18	4.11	7.40	14.10	4.14	6.95	<b>4.39</b>
<i>F. profunda</i>	0.91	6.84	4.55	16.89	25.11	19.18	10.05	28.70	15.51	6.95	4.97	13.69	24.78	<b>13.70</b>
<i>Calciosoleniodes</i> sp.	0.47	2.29	1.82	2.73	0.91	2.29			1.38		0.83	1.24	0.88	<b>1.48</b>
<i>D. tubifera</i>	0.47	0.91	1.38	1.38		1.38								<b>1.10</b>
<i>A. oryza</i>		0.91		0.91										<b>0.91</b>
<i>R. clavigera</i>	0.47		1.82	2.73	1.82	1.38			1.88					<b>1.68</b>
<i>O. antillarum</i>	0.47	1.38	2.73	2.29	0.91	3.64	1.82	2.18	1.38	0.88	2.48	5.80	2.62	<b>2.20</b>
<i>S. pirus</i>	5.52	0.91	0.47	0.47		2.29					0.41	1.24	1.74	<b>1.63</b>
<i>S. lamina</i>	1.38	0.91	0.91	4.11	1.82	2.73	0.47	1.32	0.91		0.83	2.90	1.74	<b>1.67</b>
<i>Syracosphaera</i> sp.		0.91		0.91			1.82							<b>1.21</b>
<i>N. coccolithomorpha</i>	1.38	1.82	2.73	5.93	4.11	3.64	3.20	2.18	2.29	1.30	1.66	1.66	0.88	<b>2.52</b>
<i>C. cristatus</i>		0.47	0.91		0.47		0.47	0.44	0.47		0.41	0.41	0.44	<b>0.50</b>
<i>G. flabellatus</i>				1.82	1.82		0.47							<b>1.37</b>
Total Coccolith flux	83.21	117.76	107.74	163.87	153.36	141.93	90.44	133.98	110.53	61.76	92.92	109.89	115.27	<b>114.05</b>
Total Cocosphere flux	0.94	1.85	0.47	0.47	0.91	0.47	0.91	0.44	0.47	0.44	0.41		0.44	<b>0.63</b>
<b>Total Coccolithophore Flux</b>	<b>84.15</b>	<b>119.61</b>	<b>108.21</b>	<b>164.34</b>	<b>154.27</b>	<b>142.40</b>	<b>91.35</b>	<b>134.42</b>	<b>111.00</b>	<b>62.20</b>	<b>93.33</b>	<b>109.89</b>	<b>115.71</b>	<b>114.68</b>

**Table 2.** Seasonal variation of different coccolithophore species and cocosphere fluxes with their average fluxes recorded in the Central Bay of Bengal Trap (CBBT) for the period 3 February - 16 December 1992.

Southern Bay of Bengal Trap (SBBT 06)														
( x 10 <sup>5</sup> m <sup>-2</sup> d <sup>-1</sup> )														Average
Interval	5/2/92-8/2/92	8/2/92-5/3/92	5/3/92-31/3/92	31/3/92-26/4/92	26/4/92-22/5/92	22/5/92-17/6/92	17/6/92-13/7/92	13/7/92-8/8/92	8/8/92-3/9/92	3/9/92-29/9/92	29/9/92-25/10/92	25/10/92-20/11/92	20/11/92-16/12/92	
Station No.	1	2	3	4	5	6	7	8	9	10	11	12	13	
Species														
<i>G. oceanica</i>	5.71	26.02	37.42	31.05	37.42	26.02	63.45	45.65	73.02	18.68	33.78	46.56	16.42	<b>35.48</b>
<i>E. huxleyi</i>	0.77	5.93	3.20	5.46	3.20	12.34	8.67	6.84	11.40	1.66	16.42	20.09	0.91	<b>7.45</b>
<i>C. mediterranea</i>	0.39	2.29	2.29	1.38	0.91		0.91	1.82	0.47		0.91	0.91	2.29	<b>1.32</b>
<i>S. pulchra</i>					0.91	0.91	1.38	1.38	0.91	0.41	0.91	0.91	1.82	<b>1.06</b>
<i>U. sibogae</i>	3.04	1.52	13.25	14.60	15.07	10.96	11.40	10.05	27.85	5.80	14.60	7.75	10.49	<b>11.26</b>
<i>U. irregularis</i>	0.77	7.31	7.75	21.44	18.71	21.44	3.20	7.31	5.93	3.31	6.84	7.75	2.29	<b>8.78</b>
<i>U. tenuis</i>				2.29	4.58	1.38	0.47	0.47	0.91			0.91	0.91	<b>1.49</b>
<i>H. carteri</i>	0.77	1.38	3.20	18.27	2.76	3.64	4.11	1.82	1.38	0.83	1.38	0.91	1.82	<b>3.25</b>
<i>C. leptopora</i>		2.76	5.46	18.27	2.76	3.64	11.40	1.38	20.53	4.97	7.31	5.93	2.29	<b>7.23</b>
<i>F. profunda</i>	0.39	2.76	6.40	13.25	12.78	8.67	2.29	6.84	2.73	6.24	19.18	25.55	15.51	<b>9.43</b>
<i>Calciosolenids</i> sp.	0.77	1.82	1.82	0.91	1.38	1.38	0.91	1.38	0.91	0.83	0.47	0.47	0.91	<b>1.07</b>
<i>D. tubifera</i>		1.38	2.29	0.91	3.20	0.47	0.47	1.82	0.47	0.41	0.91	0.47		<b>1.16</b>
<i>R. clavigera</i>		1.38	1.82	1.38			0.91	1.38	1.82	0.83	1.38	1.82		<b>1.41</b>
<i>O. antillarum</i>	0.39	8.67	10.05	11.40	15.51	14.16	6.84	12.34	1.82	2.48	30.58	33.78	8.67	<b>12.05</b>
<i>S. pirus</i>	0.39					0.91	0.91	1.38				0.91		<b>0.90</b>
<i>S. lamina</i>	0.77	1.38	3.20	3.64	2.29	2.35	1.82	1.82	0.91	0.41	3.20	1.82		<b>1.97</b>
<i>Syracosphaera</i> sp.								3.64						<b>3.64</b>
<i>N. coccolithomorpha</i>		0.47	1.38	2.76	1.82	3.20	0.91	1.38		1.24	0.91	0.91	1.82	<b>1.53</b>
<i>C. cristatus</i>		0.47	0.47		1.38	0.47	0.47			0.83	0.47			<b>0.65</b>
<i>G. flabellatus</i>				1.38		0.91						1.38	2.29	<b>1.49</b>
<i>S. rotula</i>				0.47				0.47					0.47	<b>0.47</b>
<i>A. oryza</i>		0.91	2.76	2.29	1.82	1.82	1.38	1.38		1.24	8.67	2.29	0.91	<b>2.32</b>
<i>S. anthos</i>													4.55	<b>4.55</b>
<i>C. multipora</i>											0.47			<b>0.47</b>
Total Coccolith flux	14.16	66.45	102.77	151.15	126.50	114.67	121.90	110.55	151.07	50.17	148.39	161.14	74.37	<b>107.18</b>
Total Cocosphere flux		0.91		3.23	0.94	0.94		2.32		2.46	10.95	4.64	1.88	<b>2.17</b>
<b>Total Coccolithophore Flux</b>	<b>14.16</b>	<b>67.36</b>	<b>102.77</b>	<b>154.38</b>	<b>127.44</b>	<b>115.61</b>	<b>121.90</b>	<b>112.87</b>	<b>151.07</b>	<b>52.63</b>	<b>159.34</b>	<b>165.78</b>	<b>76.25</b>	<b>109.35</b>

**Table 3.** Seasonal variation of different coccolithophore species and cocosphere fluxes with their average fluxes recorded in the Southern Bay of Bengal Trap (SBBT) for the period 5 February - 16 December 1992.

Northern Bay of Bengal Trap (NBBT 06)														
Interval	29/1/92-8/2/92	8/2/92-5/3/92	5/3/92-31/3/92	31/3/92-26/4/92	26/4/92-22/5/92	22/5/92-17/6/92	17/6/92-13/7/92	13/7/92-8/8/92	8/8/92-3/9/92	3/9/92-29/9/92	29/9/92-25/10/92	25/10/92-20/11/92	25/10/92-20/11/92	Average
Station No.	1	2	3	4	5	6	7	8	9	10	11	12	13	
Average Coccolithophore-CaCO <sub>3</sub> (mg m <sup>-2</sup> d <sup>-1</sup> )	0.02	0.06	0.13	0.04	0.07	0.26	0.09	0.10	0.06	0.30	0.18	0.17	0.07	0.12

Central Bay of Bengal Trap (CBBT 06)														
Interval	3/2/92-8/2/92	8/2/92-5/3/92	5/3/92-31/3/92	31/3/92-26/4/92	26/4/92-22/5/92	22/5/92-17/6/92	17/6/92-13/7/92	13/7/92-8/8/92	8/8/92-3/9/92	3/9/92-29/9/92	29/9/92-25/10/92	25/10/92-20/11/92	20/11/92-16/12/92	Average
Station No.	1	2	3	4	5	6	7	8	9	10	11	12	13	
Average Coccolithophore-CaCO <sub>3</sub> (mg m <sup>-2</sup> d <sup>-1</sup> )	0.21	0.37	0.32	0.40	0.44	0.35	0.24	0.25	0.27	0.19	0.31	0.23	0.28	0.30

Southern Bay of Bengal Trap (SBBT 06)														
Interval	3/2/92-8/2/92	8/2/92-5/3/92	5/3/92-31/3/92	31/3/92-26/4/92	26/4/92-22/5/92	22/5/92-17/6/92	17/6/92-13/7/92	13/7/92-8/8/92	8/8/92-3/9/92	3/9/92-29/9/92	29/9/92-25/10/92	25/10/92-20/11/92	20/11/92-16/12/92	Average
Station No.	1	2	3	4	5	6	7	8	9	10	11	12	13	
Average Coccolithophore-CaCO <sub>3</sub> (mg m <sup>-2</sup> d <sup>-1</sup> )	0.15	0.17	0.25	0.68	0.29	0.27	0.33	0.3	0.43	0.28	0.45	0.47	0.22	0.33

**Table 4.** Monthly variation of average Coccolith-CaCO<sub>3</sub> fluxes (calculated) in mg m<sup>-2</sup> d<sup>-1</sup> recorded in the Northern, Central and Southern Bay of Bengal.

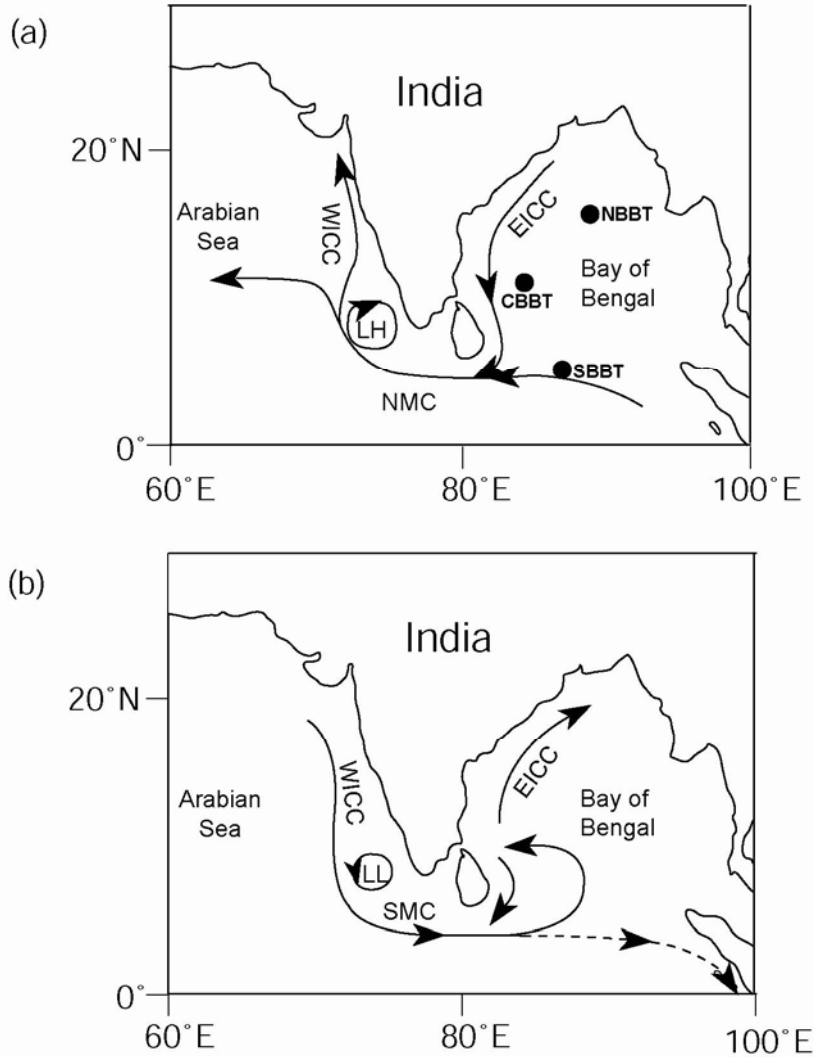


Fig. 1. A schematic representation of current patterns of the Indian Ocean during (a) Northeast monsoon and (b) Southwest monsoon. Abbreviations for the different currents indicated are: Southwest and Northeast Monsoon Current (SMC and NMC), West Indian Coastal Current (WICC) and East Indian Coastal Current (EICC). Locations of sediments trap moorings (shown as black circle) in the Bay of Bengal (*after* Schott and McCreary, 2001).

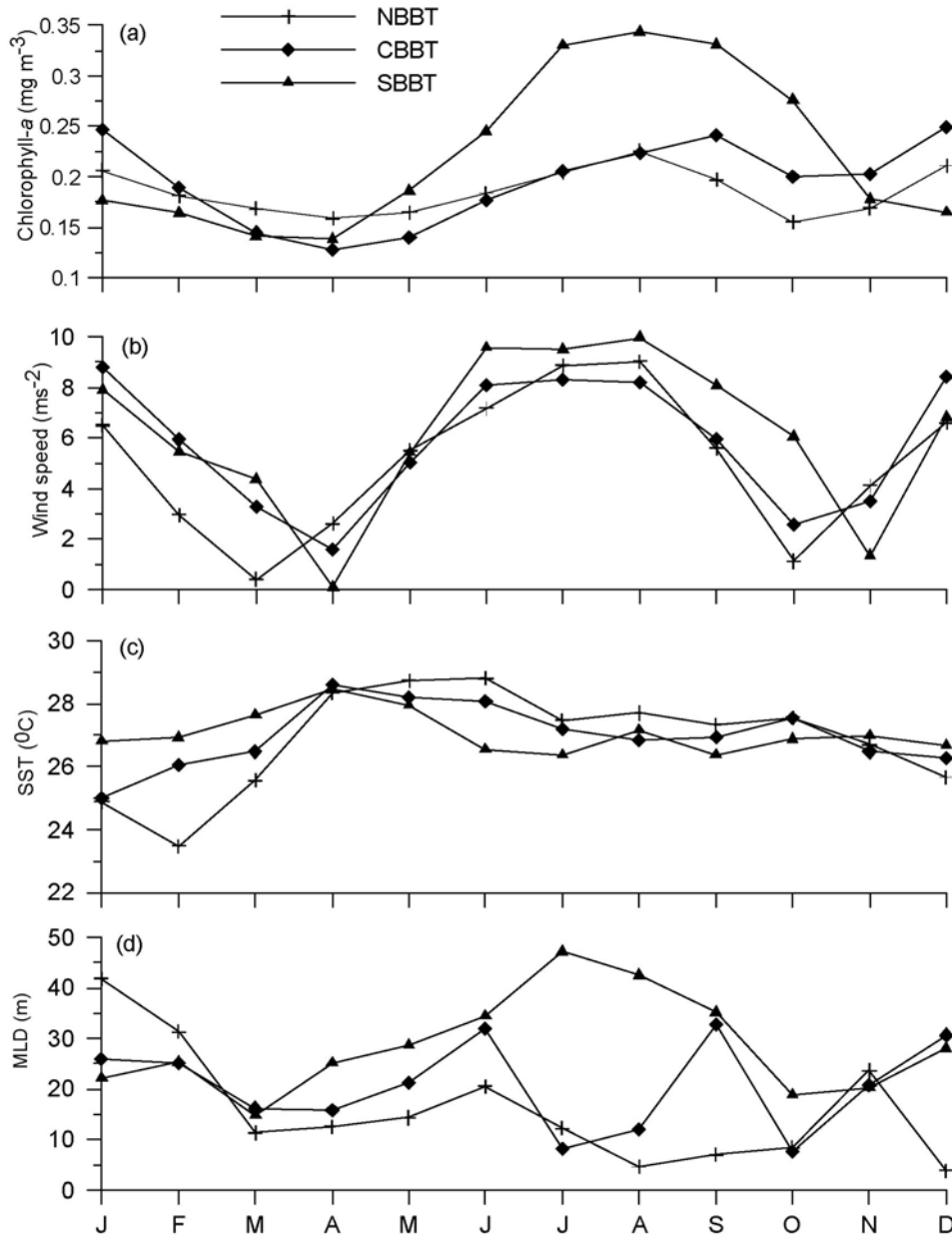


Fig. 2. Monthly variation of (a) chlorophyll-a, (b) wind speed, (c) SST and (d) MLD at NBBT, CBBT and SBBT trap locations in the Bay of Bengal.

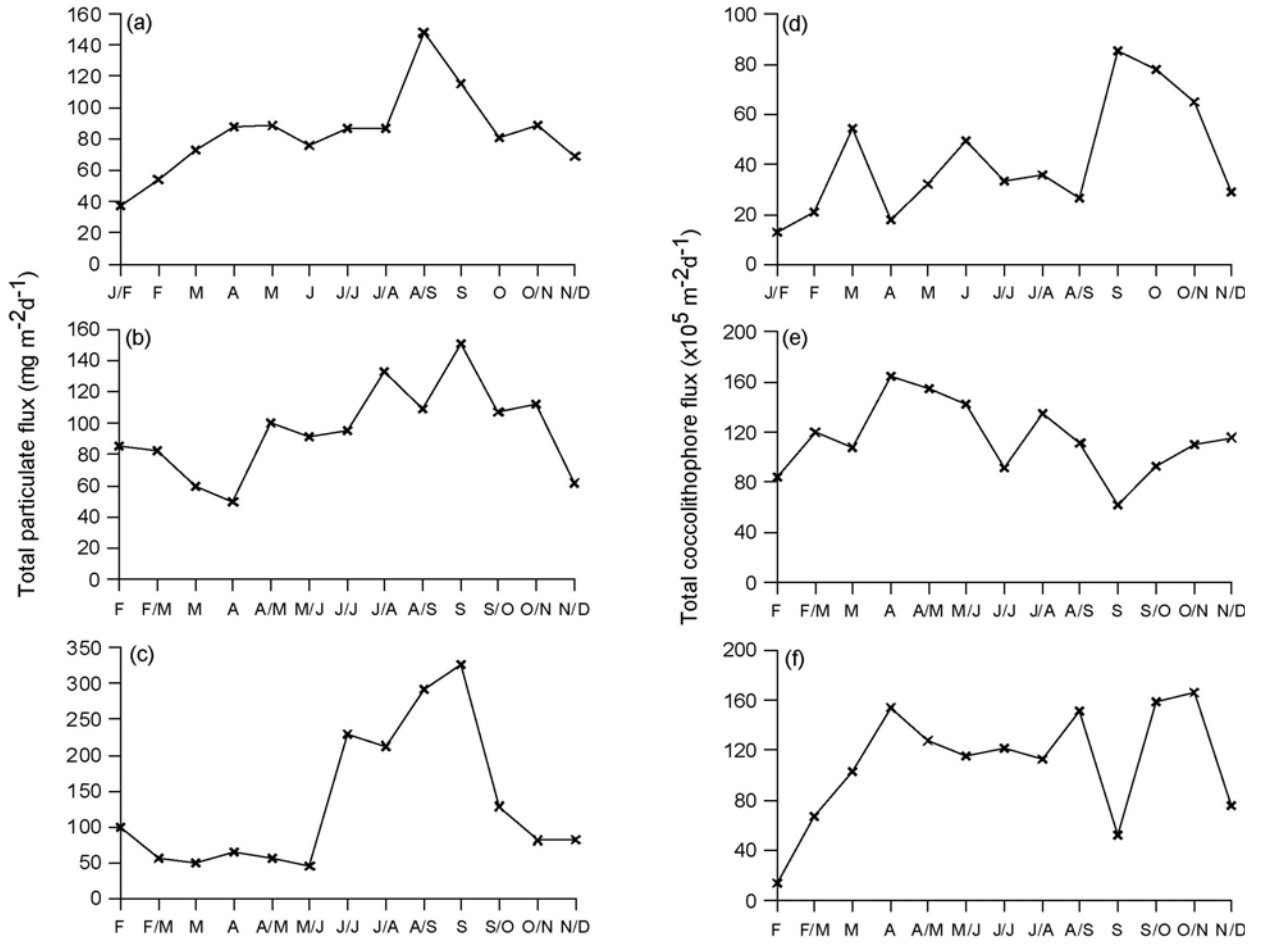


Fig. 3. Seasonal variation of total particulate fluxes (a-c) and total coccolithophore fluxes (d-f) from the northern Bay of Bengal (NBBT) (a & d), central Bay of Bengal (CBBT) (b & e) and southern Bay of Bengal (SBBT) (c & f) traps.

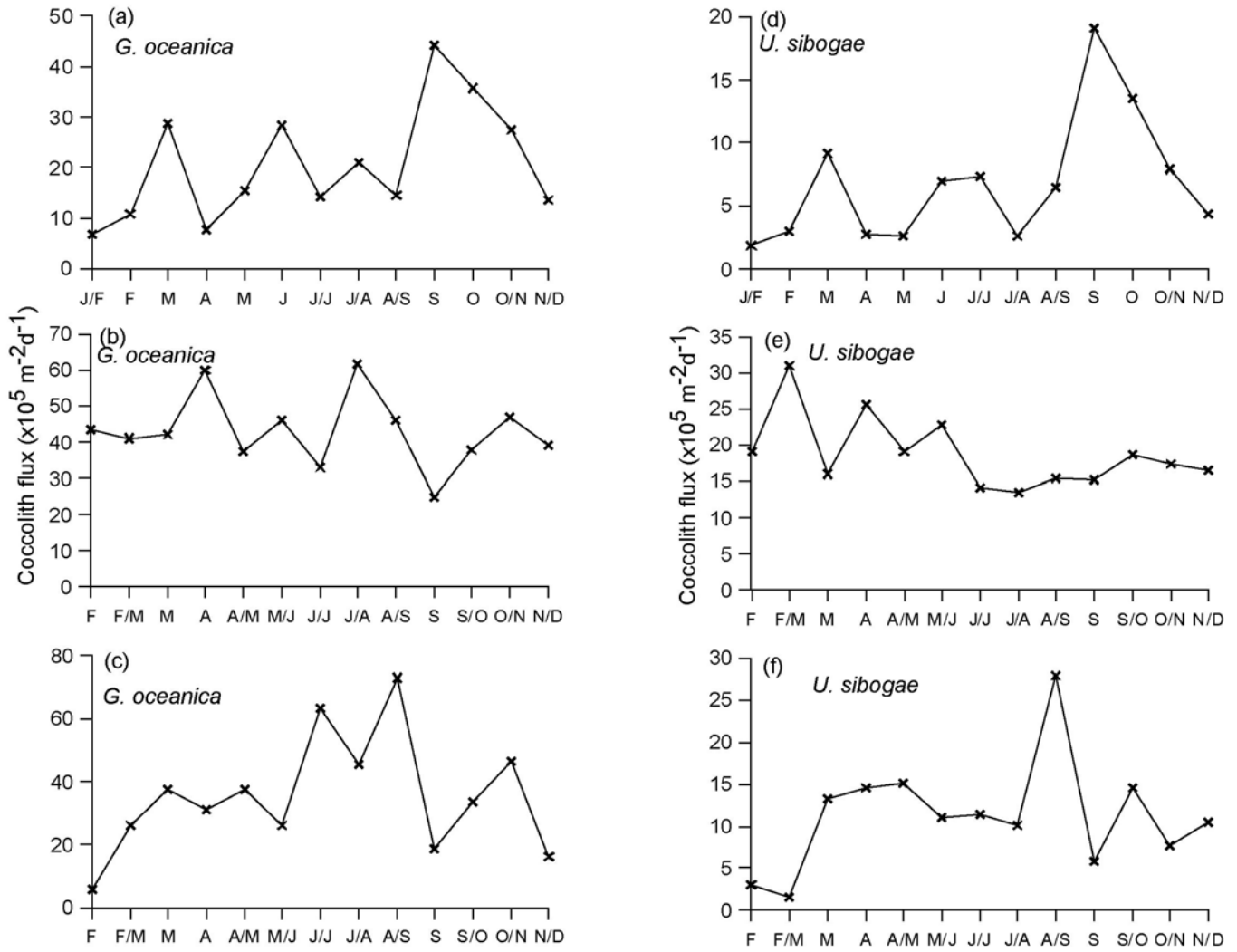


Fig. 4. Seasonal variation of coccolith fluxes of *G. oceanica* (a-c) and *U. sibogae* (d-f) from the northern Bay of Bengal (NBBT) (a & d), central Bay of Bengal (CBBT) (b & e) and southern Bay of Bengal (SBBT) (c & f) in the shallow trap.



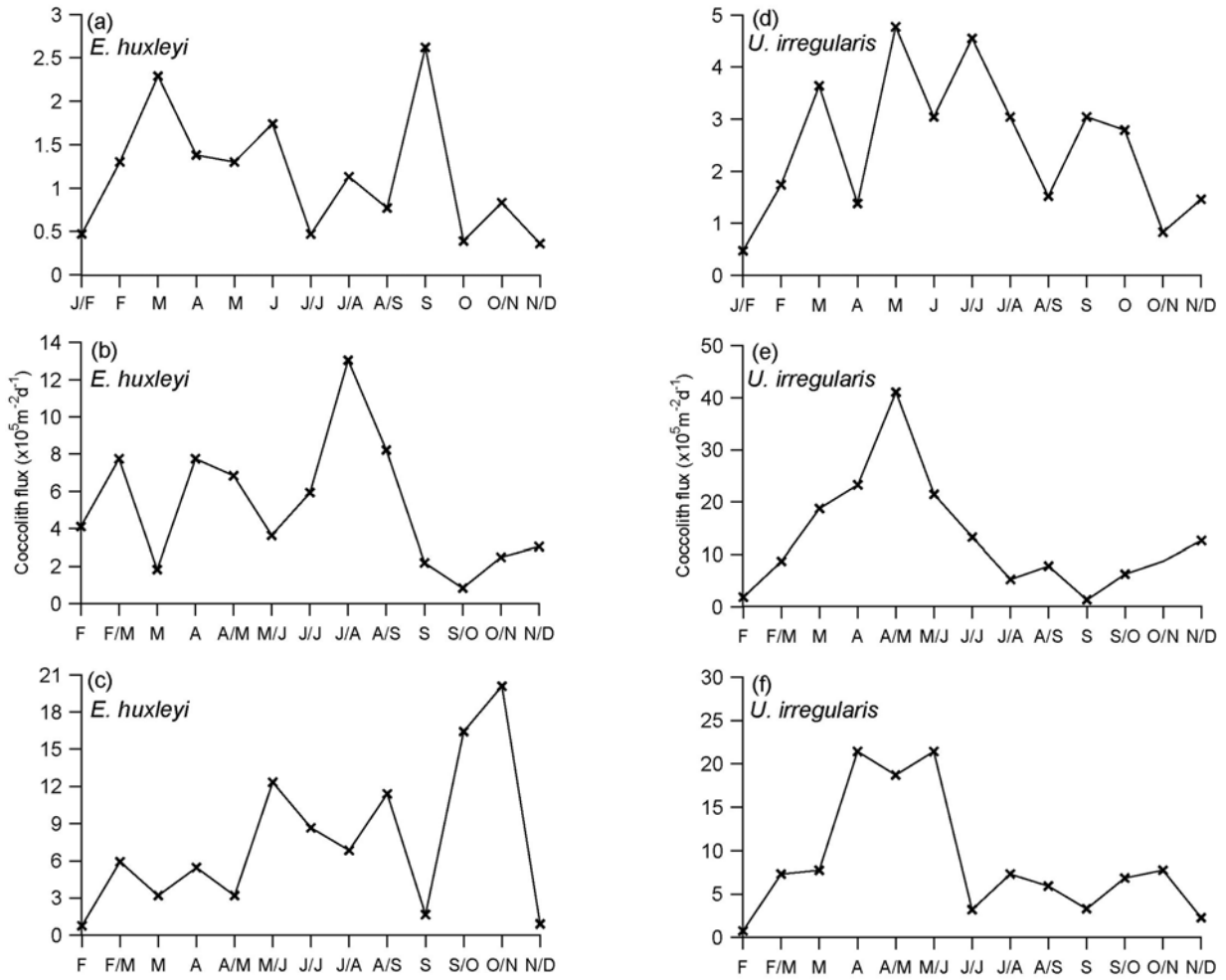


Fig. 5. Seasonal variation of coccolith fluxes of *E. huxleyi* (a-c) and *U. irregularis* (d-f) from the northern Bay of Bengal (NBBT) (a & d), central Bay of Bengal (CBBT) (b & e) and southern Bay of Bengal (SBBT) (c & f) in the shallow trap.

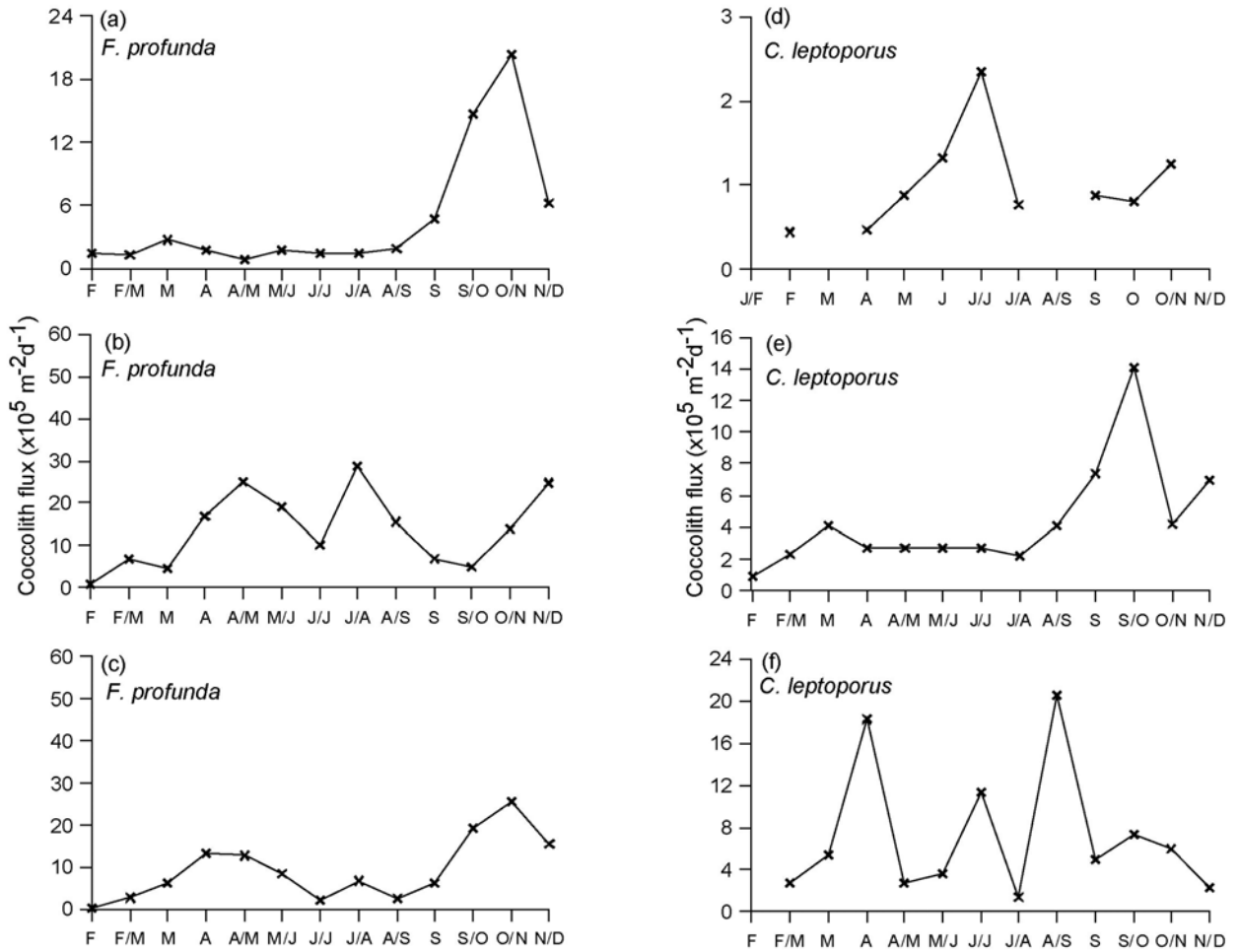


Fig. 6. Seasonal variation of coccolith fluxes of *F. profunda* (a-c) and *C. leptopus* (d-f) from the northern Bay of Bengal (NBBT) (a & d), central Bay of Bengal (CBBT) (b & e) and southern Bay of Bengal (SBBT) (c & f) traps.

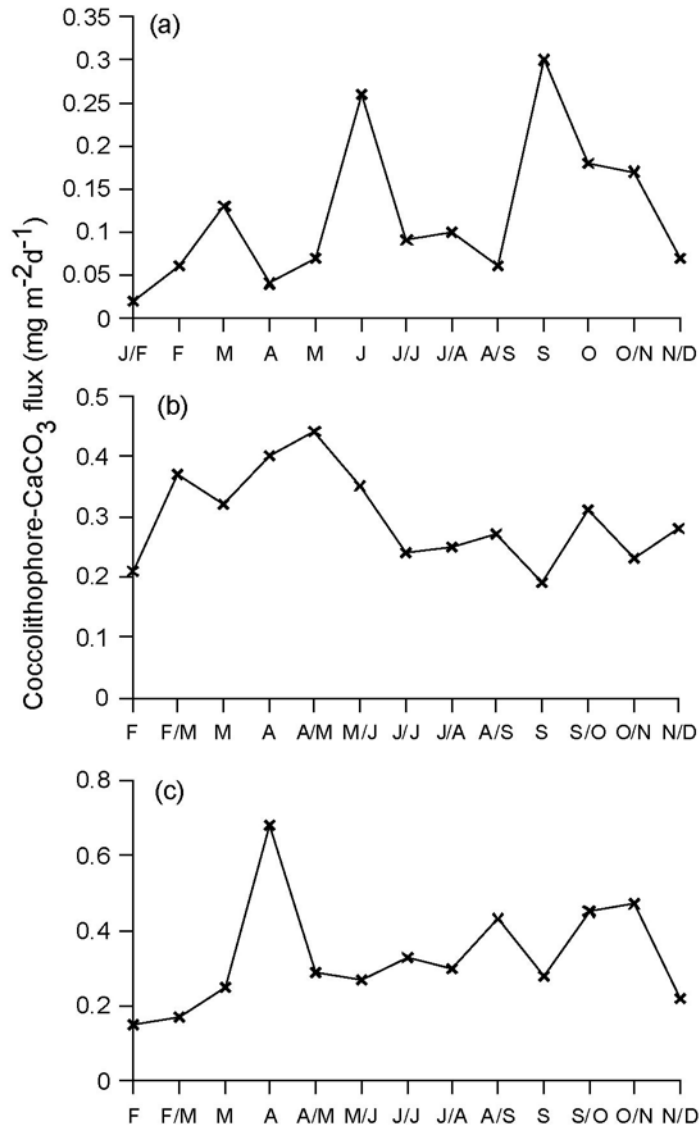


Fig. 7. Seasonal variation of Coccolithophore-CaCO<sub>3</sub> flux (mg m<sup>-2</sup>d<sup>-1</sup>) (a-c) from the northern Bay of Bengal (NBBT) (a), central Bay of Bengal (CBBT) (b) and southern Bay of Bengal (SBBT) (c) in the shallow trap.

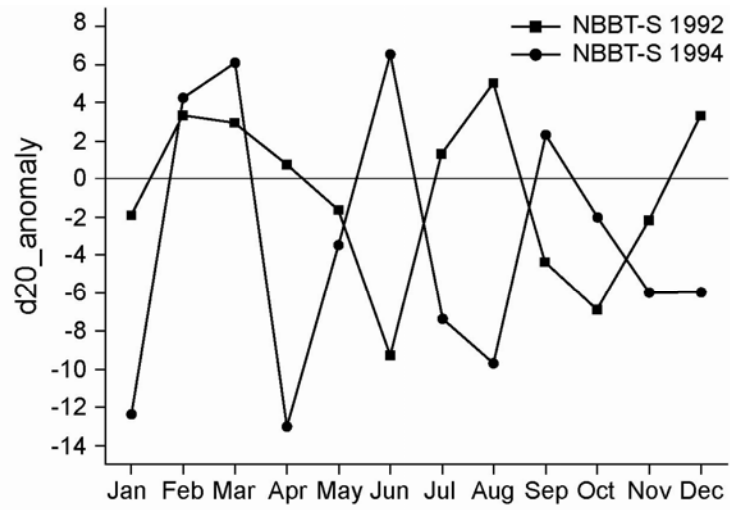
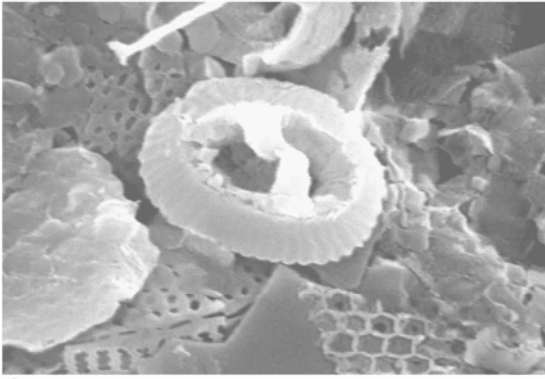


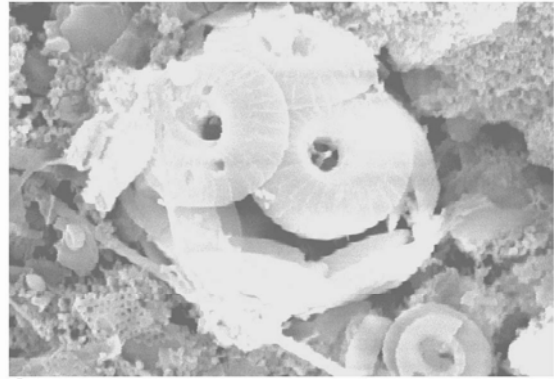
Fig. 8. Seasonal variation of D20 anomaly (long term D20 seasonal cycle is removed) in 1992 and 1994, based on the Indo-Pacific run simulations from an Ocean General Circulation Model (OGCM) (Murtugudde et al., 2000).

Plate 1



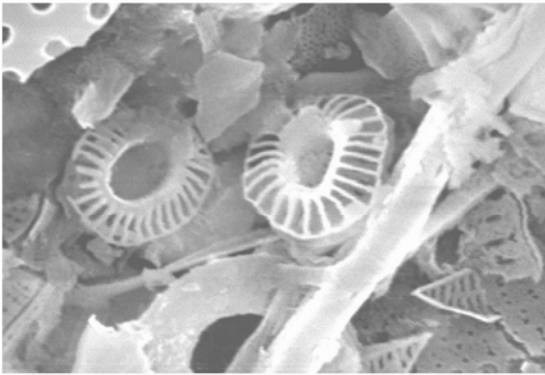
1

1 μm



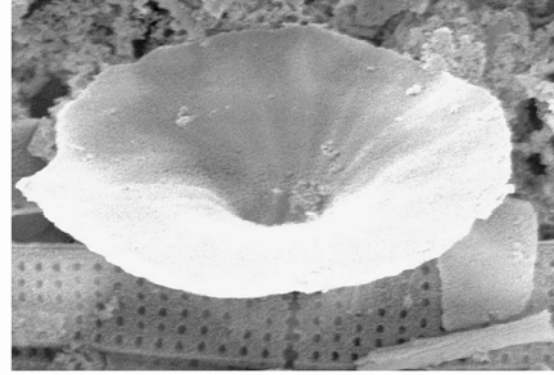
2

2 μm



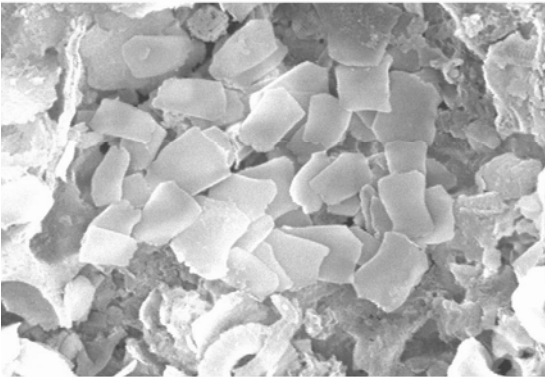
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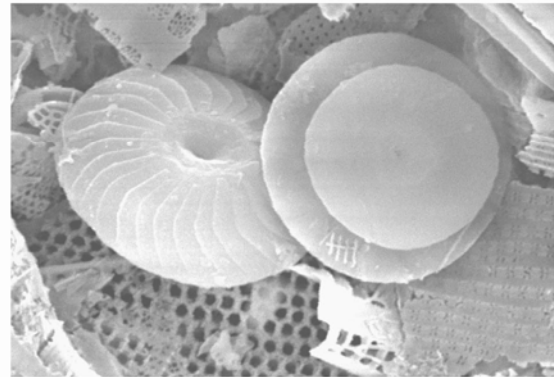
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1 μm



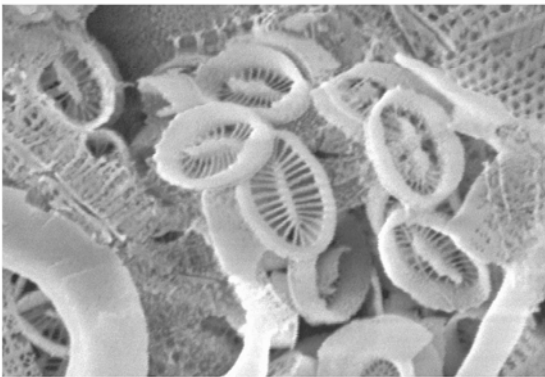
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2 μm



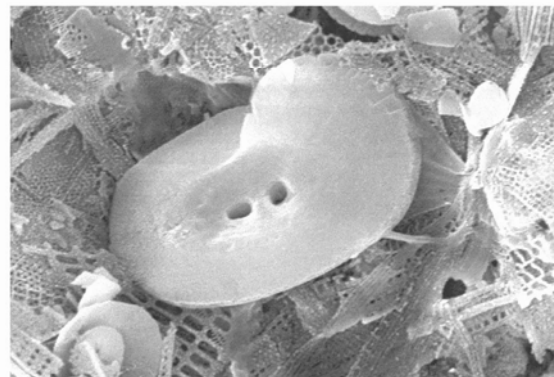
6

2 μm



7

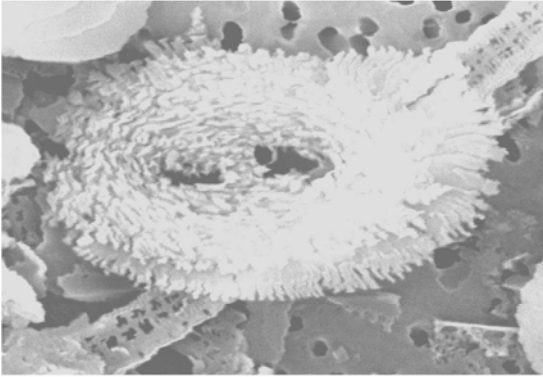
1 μm



8

2 μm

Plate 2



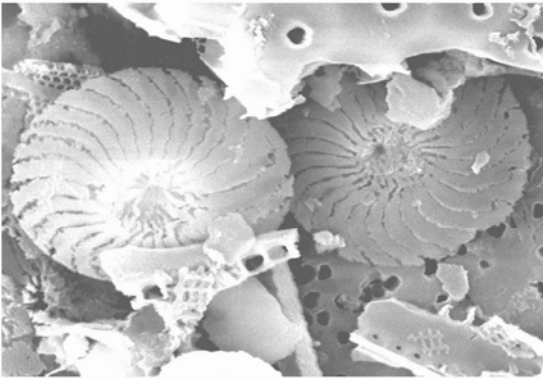
1

1  $\mu\text{m}$



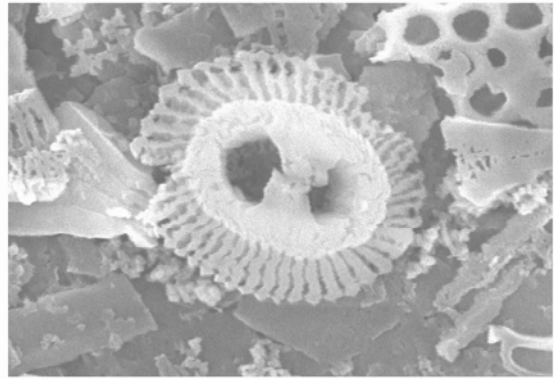
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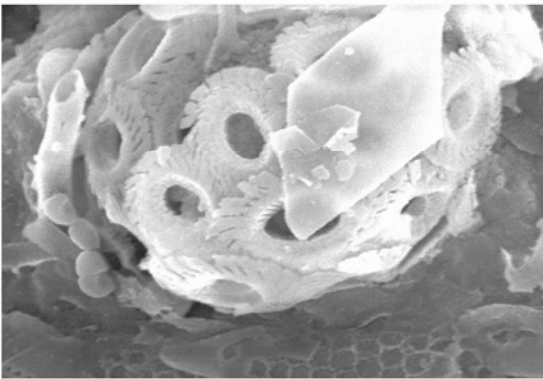
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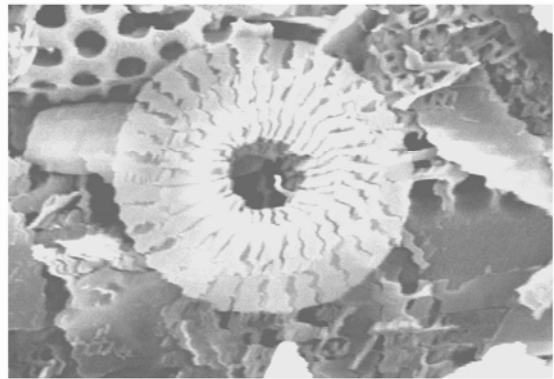
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1  $\mu\text{m}$



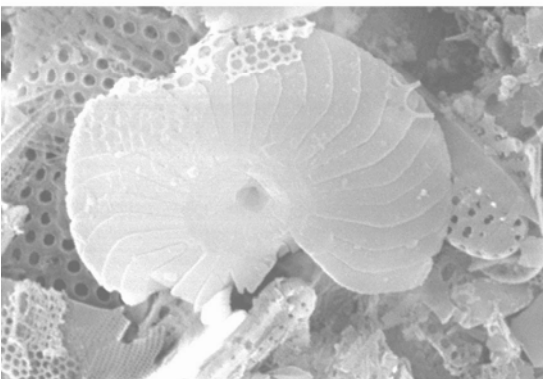
5

1  $\mu\text{m}$



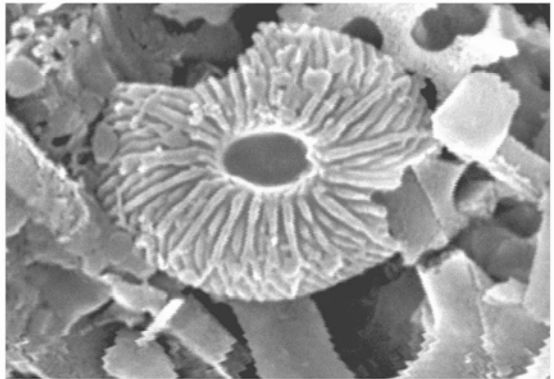
6

1  $\mu\text{m}$



7

1  $\mu\text{m}$



8

2  $\mu\text{m}$

## Legend to plates

### Plate 1

1. *Gephyrocapsa oceanica*, distal view (x14,000; 8 February – 5 March 1992; CBBT trap)
2. *Umbilicosphaera sibogae*, coccosphere showing signs of dissolution (x8,000; 25 October – 20 November 1992; SBBT trap)
3. *Emiliana huxleyi*, distal view (x15,000; 8 February – 5 March 1992; CBBT trap)
4. *Umbellosphaera irregularis*, distal view (x13,000; 8 August – 3 September 1992; SBBT trap)
5. *Florisphaera profunda*, collapsed coccosphere (x8,500; 29 September – 25 October 1992; NBBT trap)
6. *Calcidiscus leptopora*, distal and proximal views (x8,000; 29 September – 25 October 1992; CBBT trap)
7. *Syracosphaera lamina*, collapsed coccosphere (x13,000; 13 July – 8 August 1992; SBBT trap)
8. *Helicosphaera carteri*, distal view (x7,500; 13 July – 8 August 1992; CBBT trap)

### Plate 2

1. *Helicosphaera carteri*, distal view showing intense dissolution (x13,000; 17 June – 13 July 1992; SBBT trap)
2. *Calcidiscus leptopora*, coccolith well preserved and showing intense dissolution (x8,000; 8 August – 3 September 1992; SBBT trap)
3. *Calcidiscus leptopora*, distal view of coccolith showing intense dissolution (x9,000; 8 August – 3 September 1992; SBBT trap)
4. *Gephyrocapsa oceanica*, coccoliths showing intense dissolution (x16,000; 8 August – 3 September 1992; SBBT trap)
5. *Umbilicosphaera sibogae*, coccosphere showing intense dissolution (x12,000; August – 3 September 1992; SBBT trap)
6. *Umbilicosphaera sibogae*, coccolith showing intense dissolution (x15,000; 8 August – 3 September 1992; SBBT trap)
7. *Calcidiscus leptopora*, distal view showing mechanical breakdown (x11,000; 29 September – 25 October 1992; CBBT trap)
8. *Umbellosphaera tenuis*, distal view showing mechanical breakdown (x17,000; 20 November – 16 September 1992; CBBT trap)

## Appendix A. Taxonomic appendix

The taxonomic list includes all taxa identified during the present study. Identification followed Winter et al. (1994), Nishida (1979) and Kleijne (1990, 1991, 1992, 1993) in which full references can be found.

*Anoplosolenia brasiliensis* Lohmann (1919).  
*Algirosphaera oryza* Schlauder (1945)  
*Calcidiscus leptopora* (Murray and Blackman, 1898)  
*Calciosolenia murrayi* Gran (1912)  
*Calyptrolithina multipora* Norris (1985)  
*Ceratolithus cristatus* Kamptner (1950)  
*Coronosphaera mediterranea* Lohmann (1902)  
*Discosphaera tubifera* (Murray and Blackman, 1898)  
*Emiliana huxleyi* Lohmann (1902)  
*Florisphaera profunda* Okada and Honjo (1973)  
*Gladiolithus flabellatus* (Halldal and Markali, 1955)  
*Gephyrocapsa oceanica* Kamptner (1943)  
*Helicosphaera carteri* Wallich (1877)  
*Neosphaera coccolithomorpha* Lecal-Schlauder (1950)  
*Oolithotus antillarum* Cohen (1964)  
*Oolithotus fragilis* Lohmann (1912)  
*Rhabdosphaera clavigera* (Murray and Blackman, 1898)  
*Umbellosphaera irregularis* Paasche in Markali and Paasche (1955)  
*Umbellosphaera tenuis* Kamptner (1937)  
*Umbilicosphaera sibogae* Kamptner (1963)  
*Syracosphaera anthos* Lohmann (1912)  
*Syracosphaera lamina* Lecal-Schlauder 1951  
*Syracosphaera pirus* (Halldal and Markali, 1955)  
*Syracosphaera pulchra* Lohmann (1902)  
*Syracosphaera rotula* (Okada and McIntyre, 1977)