# Distribution and seasonal variation of concentrations of particulate carbohydrates and uronic acids in the northern Indian Ocean

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#### Abstract:

Suspended particulate matter (SPM) samples were collected from the surface seawaters at 31 stations, and from various depths (2 to 1000 m) at 9 locations in the northern Indian Ocean during various seasons. SPM samples were analyzed for total particulate carbohydrate (TPCHO), total particulate uronic acid (TPURA) and total particulate neutral carbohydrate (TPNCHO) concentrations and composition. Strong spatial, temporal and depth related variations were evident in the distribution of these compounds. In surface waters, concentrations of TPCHO, TPNCHO, and TPURA varied from 0.57 to 3.58  $\mu$ M C, 0.11 to 2.34  $\mu$ M C, and from 0.01 to 0.31  $\mu$ M C, respectively, and accounted for 2.6 to 34.6 %, 2 to 24.5 %, and 0.2 to 6.3 % of POC, respectively, whereas the TPURA accounted for 4.7 to 22.7 % of TPCHO. Concentrations and yields of both TPNCHO and TPURA decreased rapidly in the upper 100 m of the water column suggesting their utilization by heterotrophic organisms. Glucose was the most abundant constituent of the TPNCHO. Glucose mole fraction decreased while that of other monosaccharides, especially galactose, arabinose, mannose, rhamnose and fucose increased in the upper 100 m water. Below this depth, mole fraction of glucose increased while that of other sugars decreased with the increasing water depth. Generally, high C:N ratios were associated with low yields of carbohydrates and uronic acids. Inverse correlation between the mole fractions of arabinose plus xylose and rhamnose plus fucose indicates the importance of biogenic and terrestrial organic matter input to the Bay of Bengal. TPURA are surface-active in nature and thus may play an important role in coagulation of particles and macromolecules. The observed spatial and

seasonal variations of these compounds may be due to differences in phytoplankton biomass, nutrient status, and the influence of terrestrial material.

Keywords: Total carbohydrates; Neutral carbohydrates; Uronic acids; C:N ratio; POC: Chlorophyll a; Carbohydrate yields; Monosaccharides; Northern Indian Ocean

#### 1. Introduction

In oceanic environments, particulate organic matter (POM) is mostly derived from phytoplankton (Deuser et al., 1981). Conversely, POM in the coastal and shelf waters is influenced by the inputs of terrestrial organic matter discharged by rivers and re-suspension of bottom sediments (Degens and Ittekkot, 1985). In aquatic environments, POM serve as an important source of food for the aquatic organisms. Moreover, POM is of considerable biogeochemical and oceanographic importance because it serves as a vehicle for the transport of organic matter produced in the upper sunlit surface waters of the ocean to the deep-sea sediments. During their transport from surface waters to the bottom sediments, POM is degraded or undergoes biochemical changes, thereby making the deep waters nutrient rich (Eppley and Peterson, 1979). Nature and quality of POM is influenced by availability of nutrients and the composition of phytoplankton.

Carbohydrates serve both as structural and storage components in marine and terrestrial organisms, and account for a substantial proportion of

POM (> 40 %) in marine organisms, suspended particles, sedimenting particles, dissolved organic matter, and sediments of marine environments (Parsons et al., 1984; Biersmith and Benner, 1998; Cowie and Hedges, 1992). Generally, total carbohydrates in marine systems contain monosaccharides, disaccharides, and polysaccharides (Borch and Kirchman, 1997; Skoog and Benner, 1997; Bhosle et al., 1998). During the transport of organic matter from the surface to greater depths, storage carbohydrates are preferentially utilized by in situ organisms (Handa and Tominaga, 1969; Ittekkot et al., 1982; Tanoue and Handa, 1987; Hernes et al., 1996). This results in the enrichment of structural polysaccharides in the degraded POM. Due to their relatively refractory nature, structural polysaccharides are useful for assessing the sources and degradation pathways of organic matter in aquatic environments. For example, Cowie and Hedges (1984) utilized the mannose/xylose ratio, abundance of ribose plus fucose, and arabinose plus galactose (on glucose free basis) to identify the inputs of marine and terrestrial organic matter in suspended and sedimented materials and sediment samples. Ittekkot et al. (1984) proposed the use of the arabinose/fucose ratio to identify the inputs from calcareous and siliceous material in sediment trap samples. Similarly, increase in wt % deoxy sugars (rhamnose plus fucose) associated with a concomitant decrease in wt % glucose indicates the presence of degraded organic matter in both marine and terrestrial samples (Hamilton and Hedges, 1988; Hedges, et al., 1994; Hernes et al., 1996; D'Souza and Bhosle, 2001).

In addition to the simple sugars described above, many microorganisms produce acidic polysaccharides (Costerton, 1984; Leppard, 1993, 1997). These carbohydrate polysaccharides may contain sulphate,

pyruvate, acetate, and acidic groups such as uronic acids and amino sugars (Mopper et al., 1995; Bergamaschi et al., 1999; Kaiser and Benner, 2000; Muldoon et al., 2001; Guo et al., 2002; Hung et al., 2001, 2003, 2005). These compounds are involved in several marine environmental processes including formation of humic substances, removal of toxic metals, detoxification of toxic chemicals, production of macroaggregates, enhancing or inhibiting metal corrosion, microbial adhesion and biofilm formation, and binding of extracellular enzymes (Decho, 1990; Leppard, 1993, 1997; Santschi et al., 1998; D'Souza and Bhosle, 2003; Bhaskar et al., 2005). Despite the importance of acidic polysaccharides we know little about their distribution and cycling in marine waters (Bergamaschi et al., 1999; Hung et al., 2001, 2003, 2005).

Little is known about the distribution of organic matter and its biochemical constituents such as carbohydrates, proteins and lipids in the northern Indian Ocean in general and in the Arabian Sea and the Bay of Bengal in particular (Bhosle et al., 1981,1989; France-Lanord and Derry, 1994; Schafer and Ittekkot, 1995; Sreepada et al., 1996). Only a few studies have focused their attention on the compound specific characterization of organic matter (Bhosle et al., 1992; Schafer et al., 1998; Unger et al., 2005). Such detailed biochemical characterization provides useful information on dynamics, nature, sources, and diagenetic changes in the organic matter. The aims of our study were, 1) to assess the spatial and temporal variations in the distribution of total particulate carbohydrates (TPCHO), total particulate neutral carbohydrates (TPNCHO) and total particulate uronic acids (TPURA), 2) to assess the monosaccharides composition of TPNCHO, and 3) to identify

the nature of organic matter. These objectives of the study were achieved by characterizing the organic matter of the suspended particulate matter collected at 40 stations sampled in the northern Indian Ocean (NIO), especially in the Bay of Bengal.

#### 2. Study area

The northern Indian Ocean comprises the Arabian Sea, the Laccadive Sea, the Bay of Bengal, and the Andaman Sea. Although situated at the same latitude, the Arabian Sea and the Bay of Bengal differ greatly in their physical, chemical, and biological characteristics. Arabian Sea receives relatively small amounts (0.3 X 10<sup>12</sup> m<sup>-3</sup> yr<sup>-1</sup>) of runoff from the major rivers Tapti and Narmada. The high rate of evaporation that exceeds precipitation and runoff results in the formation of high salinity water masses. In the Arabian Sea, surface circulation undergoes biannual reversal associated with the southwest monsoon (SWM) and northeast monsoon (NEM). Strong southwesterly winds blowing along the Somali and Arabian coasts cause intense coastal and open ocean upwelling during the SWM period in the Arabian Sea. Upwelling and the winter cooling, pump nutrients into the upper layers thus increasing the productivity of the Arabian Sea in SWM and winter monsoon. As compared to the SWM and winter monsoon, lowest primary production and Chl a concentration were recorded in SPIM (Bhattathiri et al., 1996). Arabian Sea thus remains productive for 8 to 9 months, except SPIM i.e. mid March to early June.

The uniqueness of the Bay of Bengal is the seasonal changes in circulation and weather due to reversing monsoon winds. Moreover, the Bay of Bengal receives large quantities of freshwater  $(1.6 \times 10^{12} \text{ m}^3 \text{ yr}^{-1})$  from the major rivers Ganges, Brahmputra, Irrawady, Godavari, Krishna, Pennar, and Cauvery (Rao, 1995). Warm sea surface temperatures (SSTs) and low salinity lead to strong stratification that prevents transport of nutrients into the surface waters. Moreover, weak winds are unable to break the thermocline. However, the frequently occurring cyclones can pump the nutrients into the surface waters, resulting in the development of the localized algal blooms (Vinaychandran and Mathew, 2003). Upwelling has been observed along the western boundary of the Bay (Shetye et al., 1991). As a result, Chl *a*, primary production, phytoplankton and zooplankton abundance are several fold lower in the Bay as compared to the Arabian Sea (Gauns et al., 2005).

The Arabian Sea was extensively studied under the aegis of the Joint Global Ocean Flux Studies (JGOFS). In contrast, few studies have evaluated physical, chemical and biological aspects of the Bay of Bengal. As a result, the Indian JGOFS studies were extended to the Bay of Bengal. One of the objectives of the Bay of Bengal Process studies (BOBPS) was to assess the spatial and seasonal variations in the distribution and cycling of organic matter.

### 3. Materials and methods

#### 3.1. Collection of Samples

The samples were collected from various stations (Fig. 1) during different cruises of the ORV Sagar Kanya in the northern Indian Ocean (for details pl. see Table 1). Seawater samples were collected from eight discrete depths (2 to 1000 m) using Niskin water samplers (30 l) attached to the CTD rosette system at 5 offshore stations (Station 9 to 13) and 4 near-shore stations (Station 14 to 17) of the Bay of Bengal during the southwest monsoon (SWM, July 6 to August 2, 2001), fall inter-monsoon (FIM, September 14 – October 12, 2002), and spring inter monsoon (SPIM, April 12 – May 7, 2003). Only surface seawater samples were collected at 31 stations using PVC Niskin bottles (5 I) during the post tsumani multidisciplinary winter cruises (SK- 216 and SK-217) of the ORV Sagar Kanya in the northern Indian Ocean during January/February 2005. Immediately after collection, seawater was passed through a 200 µm nylon screen to remove zooplankton, and then filtered through pre-combusted (450°C for 4 hours) 47 mm GF/F filters for the analysis of chlorophyll a (chl-a), particulate organic carbon (POC), particulate nitrogen (PN), total particulate carbohydrates (TPCHO), total particulate neutral carbohydrates (TPNCHO), and particulate uronic acids (TPURA). All samples were transferred into clean vials and stored at -20 °C prior to analysis. In order to estimate total bacterial cells (TBC), seawater sample was fixed with glutaraldehyde (final concentration 2%) and stored at 4  $^{\circ}$ C until analysed.

#### 3.2. Analytical methods

Temperature and salinity were measured using CTD sensors. Salinity was also analysed using a auto analyzer. The SPM samples were decarbonated over night using fuming HCI in a desiccator (Ferrari et al., 2003), dried in an oven at 50<sup>0</sup> C, and then analysed for POC and PN using a Perkin Elmer Elemental analyzer 2400 CHN analyser. However, a few POC and PN samples were analysed using spectrophotometric methods (Parsons, et al., 1984; Raimbault and Gerd, 1991). Chl a was extracted using 90% acetone and estimated following the method of Parsons et al. (1984). In order to estimate total bacterial cells (TBC), a known volume of seawater (3 to 5 ml) was stained with acridine orange (final concentration 0.01 %) for 3 min, filtered onto 0.22 µm black stained Nucleopore filter. The filter was then mounted on glass slide using immersion oil (Botzoil, Germany). Bacterial cells were counted in at least 25 randomly selected fields using 100 X objective, and an epifluorescence microscope (Olympus BH2, Japan). Average cell number per field was calculated, and was used to estimate total bacterial cells following the procedure described by Parsons et al. (1984). TPCHO was estimated by the phenol-sulphuric acid method (Dubois et. al., 1956, D'Souza et al., 2005). In brief, the GF/F filter containing the particulate matter was treated with 72 % H<sub>2</sub>SO<sub>4</sub> at room temperature (28  $\pm$  2 <sup>0</sup>C). After 2 h, 2 ml 5 % phenol followed by 5 ml concentrated  $H_2SO_4$  were added. The samples were cooled and the absorption was measured 490 nm. Glucose was used as a standard. The unit used is µM C, and is obtained by multiplying µM values by 6 assuming 6 mole of carbon per mole of glucose. The TPURA were analyzed according to the method of Filisetti-Cozzi and Carpita (1991) as reported in Hung et al. (2003). In short, the GF/F filter containing the particulate sample

was placed into a test tube and 0.4 ml Milli-Q-UV treated distilled water followed by 40  $\mu$ l 2 M sulfamic acid was added, and the solution was stirred on a vortex mixer. Subsequently, 2.4 ml 75 mM sodium tetraborate in concentrated sulfuric acid was added to the test tube and heated at 100 <sup>o</sup>C for 10 min in a boiling water bath. After cooling, 80  $\mu$ l 0.15 % *m*-hydroxydiphenyl was added, and the absorbance was measured at 525 nm. Glucuronic acid was used as a standard. The unit used is  $\mu$ M C, and is obtained by multiplying  $\mu$ M values by 6 mole of carbon per mole of glucuronic acid Analytical reproducibility of these methods was lower than 10 %.

Total particulate neutral carbohydrate (TPNCHO) concentrations and composition in the samples were determined using the capillary gas chromatographic method (D'Souza et al., 2005). Briefly, the particulate matter was treated with 72 %  $H_2SO_4$  at room temperature for 2 h. The sample was diluted to 1.2 M  $H_2SO_4$  using cold distilled water, flushed with nitrogen, sealed and then hydrolyzed for 3 h at 100 °C. After cooling, an internal standard (inositol) was added. The sample was neutralized, treated with NaBH<sub>4</sub>, acetylated, and analyzed using a capillary gas chromatograph (Chrompack GC model CP-9002 or HP model 6890). The GC was equipped with a flame ionization detector (FID), a programmable on-column injector and a fused silica capillary column coated with CPSil-88 (25 m, id = 0.32). Both the detector and the on-column injector, were maintained at 300 °C. A sample was injected when the oven temperature was 70  $^{\circ}$ C, and rapidly raised to 150 °C at 30 °C/min and thereafter at 3 °C/min to 230 °C and maintained at this temperature for 10 min. Quantification of the components was achieved by peak area integration using the data handling system installed in the

instrument. In this study, the TPNCHO has been defined as the sum of all the identified aldoses. The contribution of individual aldose to the TPNCHO is expressed as mole %. Analytical reproducibility of the GC method was lower than 6 %, whereas it was lower than 10 % for the GC plus sample preparation method.

3.3. Statistical analysis

A simple correlation analysis was used to assess the relationships between various parameters (Sokal and Rohlf, 1981) using the Excel software program.

#### 4. Results and discussion

#### 4.1. General hydrography and biogeochemical patterns

As a part of the Bay of Bengal (BOB) process studies program, a number of physical, chemical, and biological parameters were monitored, and are discussed in detail elsewhere (e.g., Madhupratap et al., 2003; Kumar et al., 2004 a, b; Prasanna Kumar et al., 2004; Gauns et al., 2005). Some of the important aspects of these studies are summarized here. During the SWM, the winds varied from west to northwest, whereas air temperature did not vary much. SST during the FIM along the open Bay varied marginally (28.2 <sup>0</sup>C to 29 <sup>0</sup>C), whereas, for the coastal locations, SST did not show any trend (Kumar et al., 2004 a, b; Prasanna Kumar et al., 2004). Similarly, during the SPIM,

SST varied from 29 <sup>0</sup>C to 31.4 <sup>0</sup>C for the open ocean stations and decreased by ~ 2  $^{\circ}$ C between 14  $^{\circ}$  N to 15  $^{\circ}$  N and for the coastal stations it varied from 29.1 °C to 30.4 °C (Kumar et al., 2004 a, b). During the winter cruise in January/February 2005 (Cruise SK 216 and 217) in the northern Indian Ocean, SST at the sampled locations showed small variations (X=27.5  $\pm 0.6^{\circ}$ C) (Table 2), whereas, the sea surface salinity varied from 31.95 to 36.02 (X=  $33.58 \pm 1.1$ ) (Table 2). In general, the stations sampled in the Arabian Sea showed higher salinity than the stations located in the Bay of Bengal (Table 2). During the period of sampling SST showed small changes at these stations (Table 2). Between  $7^{\circ}$  N and  $15^{\circ}$  N, the salinity was high (33.5 salinity) in the south then decreased towards the north (27.6 salinity). The vertical salinity structure showed a strong gradient in the upper 100 m, indicating the influence of fresh water discharge. The vertical thermal structure in the upper 300 m showed oscillation within the thermocline (Prasanna Kumar et al., 2004). The period was characterized by the signature of a cold core eddy. Nutrients, especially nitrate, were undetected in the upper 30 m of the water column during the SWM and FIM seasons, whereas for the SPIM it was 0.2 µM. The concentration of nitrate increased with depth, especially between 40 and 60 m. The Bay of Bengal waters are well oxygenated as compared to the Arabian Sea. The Chl a generally was very low (< 0.1  $\mu$ g  $\Gamma^1$ ) in the Bay of Bengal. A subsurface Chl *a* maximum was generally seen at all the sampled locations in the Bay of Bengal (Madhupratap et al., 2003; Prasanna Kumar et al., 2004). Column-integrated primary production along 88<sup>°</sup> E varied between 90 and 220 mg cm<sup>2</sup> d<sup>1</sup>, and was higher (328 to 520 mg cm<sup>-2</sup> d<sup>-1</sup>) for the coastal stations (Fig. 1) (Gauns et al., 2005).

Phytoplankton abundance was higher towards the north. Diatoms, such as *Biddulphia, Chaetoceros, Thallasiothrix, Navicula* and *Nitzschia,* were the most abundant phytoplankton. Bacteria abundances were higher (0.02 to  $59.7 \times 10^9 \, \text{l}^1$ ) in the Bay of Bengal as compared to the Arabian Sea (Gauns et al., 2005).

#### 4.2. Chl a, POC and PN in the surface waters

Phytoplankton biomass, measured as Chl *a*, varied between 13 ng I<sup>-1</sup> and 300 ng I<sup>-1</sup> in the northern Indian Ocean (Table 3). Phytoplankton biomass was higher at the near shore stations compared to the offshore locations. POC concentrations varied between ~ 4 and 62  $\mu$ M C (Table 3). The POC concentrations were high at stations 39, 40, 32, and 33, located in the waters of the Andaman Sea and the Bay of Bengal, respectively. On the other hand, POC concentration was low at station 16. These POC concentration values are similar to those earlier reported for the northern Indian Ocean (Nandakumar et al., 1987; Bhosle et al., 1988). The PN concentration values varied between 0.6 and 2.5  $\mu$ M N. The general distribution pattern of PN was similar to that observed for POC.

#### 4.3. C:N and POC:Chl a ratios in surface waters

The C:N ratio is a useful tool to assess the nature of SPM. At the stations sampled in the northern Indian Ocean, the C:N ratio showed large spatial variations and ranged between 3.1 and 38.6 (Table 3). Based on the values observed for the C:N ratio, the stations can be pooled into three groups. The first group stations #25, 32, 33, 39 and 40 showed high C:N ratio

(~16 to 38). The second group, consisting of the stations # 5, 6, 7, 18, 21, and 34 gave intermediate values (>14 to 20) of the C:N ratio. Whereas, the third group, consisting of the remaining stations, exhibited relatively low (3 to < 10) C:N ratio. Marine bacteria and microalgae have a ratio of < 4 to 6 (Hamilton and Hedges, 1988; Elser et al., 2000). In contrast, the C:N ratio for the terrestrial organic matter fall in the range of 20 to 200 (Hedges et al., 1986).

Low C:N ratios (3 to <10) indicate the presence of relatively fresh organic matter derived from microalgae and bacteria. Whereas, a high (>10) C:N ratio suggests the presence of degraded organic matter. Similarly, allochthonous input could influence the SPM composition since the C:N ratios of terrestrially-derived organic matter and aerosols are generally very high (>20). Furthermore, marine plankton contains relatively low amounts of carbohydrate as compared to terrestrial plants, which are rich in cellulose (Cowie and Hedges, 1984; Opsahl, 1999). Large amounts of SPM are brought into the Bay of Bengal by the six major rivers flowing through the Indian continent. These externally supplied terrestrial particles may be responsible for the observed high C:N ratio in the Bay of Bengal. However, if the high C:N ratios of the SPM were due to the presence of terrestrial material then we would expect high relative abundance of carbohydrates in these samples. However, these samples have a relatively low % TPCHO-C, indicating that the high C:N ratios were due to the presence of degraded organic matter at these locations.

Microalgal abundance in a sample can be assessed by the POC:Chl *a* ratio. The POC:Chl *a* ratios varied between 308 and 9905 during various cruises of the ORV Sagar Kanya in the northern Indian Ocean (Table 3). The

POC:Chl a ratio of the fresh microalgae is low (< 40). POC:Chl a values recorded for these samples were very high compared to those reported for the fresh microalgae, thereby suggesting the abundance of detrital organic matter or heterotrophic microorganisms in the SPM of the study area. However, at some locations (stations # 19, 20, 22 to 24, 26, 37 and 38) the POC:Chl a ratio was relatively low. These low POC:Chl a values provide enough evidence to suggest that relatively more fresh material was present in the SPM collected at these locations.

#### 4.4. Distribution of total particulate carbohydrates (TPCHO) in surface waters

In the northern Indian Ocean, the TPCHO concentrations ranged from 0.57  $\mu$ M C to 3.58  $\mu$ M C (X= 1.4 ± 0.6  $\mu$ M C) (Table 3). Of the 31 stations sampled, 7 stations had low concentrations (<1.0  $\mu$ M C) of TPCHO, whereas, at the other stations, TPCHO values varied between >1.0 and 1.95  $\mu$ M C. In contrast, a high (3.58  $\mu$ M C) concentration was recorded at one station. TPCHO values observed for the surface waters of the northern Indian Ocean are in the range of values reported earlier for the Bay of Bengal (Bhosle et al., 1989) and the Arabian Sea (Bhosle and Wagh, 1989). For example, in the Arabian Sea, the TPCHO concentrations in the surface waters varied from 0.73  $\mu$ M C to 4.16  $\mu$ M C (*X* = 1.74 ± 0.65  $\mu$ M C) (Bhosle and Wagh, 1989). Similarly, in the central Bay of Bengal, the TPCHO varied from 1.4 to 4.76  $\mu$ M C. However, the values of TPCHO observed for the northern Indian Ocean were higher than those reported from other seas and oceans. For example, Hobson (1967) observed 0.5 to 2.23  $\mu$ M C of TPCHO in the surface waters of the Pacific off the Washington and Oregon coasts. Handa and Yanagi (1969)

reported a range of 0.33 to 0.86  $\mu$ M C TPCHO carbon for surface waters of the Kuroshio current, and slightly higher values of 0.4 to 1.30  $\mu$ M C for the Oyashio area. Similarly, in Sagami Nada off Honsyu, Japan, a average concentration of 1.6  $\mu$ M C of the TPCHO was observed (Handa, 1970). In another observation made by Romankevich (1984) in the Pacific Ocean, an average TPCHO concentration of 0.65  $\mu$ M C was recorded.

#### 4.5. Distribution of TPNCHO in surface waters

Hydrolysis using either HCl or H<sub>2</sub>SO<sub>4</sub> is routinely used for the analysis of aldoses in natural samples. We have tested both acids for their efficiency to SPM release monosaccharides from samples (D'Souza, 2004). Monosaccharide yield was higher when the SPM samples were subjected to strong hydrolysis using 72 % H2SO4 at room temperature for 2h, followed by mild hydrolysis using 1.2 M H2SO4 at 100 °C for 3 h. We used this method for the hydrolysis of SPM samples. This method has also been employed by others to assess the hydrolysable sugars in organisms, particles and sediments (Cowie and Hedges, 1984; Tanoue and Handa, 1987; D'Souza et al., 2005). There also was a good correspondence (R = 0.9469, p < 0.001) between the TPCHO concentrations estimated by the phenol-sulfuric acid method (Dubois et al., 1956) and the TPNCHO measured using the GC method. This suggests that a large proportion (63 to 93 %) of the TPCHO consisted of TPNCHO.

TPNCHO concentrations varied between 0.11 to 2.34  $\mu$ M C in the surface waters of the northern Indian Ocean (Tables 2 and 3). These values

were similar to those recorded earlier for the SPM samples collected from a few locations of the Bay of Bengal (Bhosle et al., 1992). During all sampling periods, TPNCHO showed fairly good correlation (R = 0.627, n = 151, p < 0.001) with ChI *a*, implying that live phytoplankton biomass was associated with the observed distribution of TPNCHO. In the surface waters, we also observed no north to south and/or south to north gradient in the distribution of TPNCHO in the Bay of Bengal. However, for the near-shore stations, concentrations of TPNCHO were relatively higher than those recorded for the open ocean stations.

#### 4.6. Seasonal and Depth variations in TPNCHO

Seasonal and depth-related variations in TPNCHO, Chl *a* concentration, and TBC were monitored at 9 locations in the Bay of Bengal (Table 4). Strong seasonal variations were recorded for Chl *a*, TBC, and TPNCHO in the Bay of Bengal (Table 4, Fig. 2a and c). TPNCHO showed significant positive relationships with Chl *a* (R = 0.627, n = 151, p < 0.001), and TBC (R = 0.526, n = 153, p < 0.001), indicating the importance of these microorganisms in the production of TPNCHO. For both the offshore and near-shore stations, abundances of TBC, Chl *a*, and TPNCHO decreased rapidly in the upper 100 m of the water column (Fig. 2a and c, Table 4). However, below this depth, the decrease in the TPNCHO concentrations was small. Overall, the concentrations of Chl *a*, and TPNCHO, and TBC were higher during SWM and lower in FIM and SPIM. During the SWM, the Bay of Bengal receives large amounts of river run-off that act as a source of nutrients. Moreover,

Prasanna Kumar et al. (2004) proposed eddy pumping as a possible mechanism for the vertical transfer of nutrients across the halocline to the oligotrophic euphotic zone during SWM when the upper ocean is highly stratified. This increases biological production. This enhanced production may be responsible for the relatively higher TPNCHO values during the SWM. Despite this, the measured production is much less than expected, probably due the presence of high concentrations of SPM (>12 mg l<sup>-1</sup> at station 12, data not shown) that limit sunlight required for photosynthesis.

#### 4.7. Carbohydrate yields

Carbohydrate yields decrease as organic matter becomes more refractory during microbial reworking. Therefore, carbohydrate yield is a useful tool to assess the degradation state of organic matter (Cowie and Hedges, 1994; Skoog and Benner, 1997). In surface waters, yields of TPCHO and TPNCHO, accounted for 2.6 to 34.6 % and ~ 3 to 25 %, respectively (Table, 3 and 4.). These values are higher than those recorded for the SPM samples collected from the Arabian Sea (2.7 to 15.6 %; (Bhosle et al., 1989; D'Souza and Bhosle, 2001). On the other hand, these values are in the range of values (> 30) recorded for the Pacific Ocean (Handa, 1970; Handa et al., 1972), and the Gulf of Mexico (12 to 32 %) (Hung et al., 2003).

The TPNCHO yields are higher than those recorded for other marine environments (Table 3). For example, the TPNCHO yields varied between 2.5 to 9.6 % in the Bransfield Strait (Liebezeit, 1984), and between 3 to 15 % in the North Sea (Ittekkot et al., 1982). Bhosle et al. (1992) reported that

TPNCHO-C accounted for ~15 % POC at a few locations in the Bay of Bengal. Similarly, in sedimenting particles of the Bay of Bengal, the contribution of TPNCHO-C to the POC varied between 2 to 13 % (Unger et al., 2005).

TPNCHO yields recorded for the coastal locations were relatively higher than those recorded for the deep ocean locations sampled in the northern Indian Oceans. This was due to high primary production in the coastal waters compared to oceanic waters (Madhupratap et al., 2003; Gauns, et al., 2005). High carbohydrate yields (~ 35 %) recorded at some of the stations result from predominantly autochthonous input of organic matter from *in situ* primary production (Thurman, 1985). Conversely, relatively low carbohydrate yields may indicate the contribution from extensively degraded material and/or dilution of organic matter by carbohydrate-poor organic or inorganic matter. Moreover, samples with low carbohydrate yields appear to have undergone significant biochemical degradation.

Seasonal and depth-related changes in the TPNCHO yields were observed (Table 4). The TPNCHO yields generally decreased rapidly in the upper 100 m of the water column of the offshore and near-shore stations of the Bay of Bengal (Fig. 2b and d). However, below this depth, the decrease in the TPNCHO yields was small. De and Ramaiah (2006) reported that at these stations, viable cell count of bacteria generally increased with depth in the Bay of Bengal during SWM (De and Ramaiah, 2006). A simple correlation analysis was carried out to assess the effect of total viable bacterial cell count on the abundance of TPNCHO in the Bay of Bengal. There was a significant inverse relationship (R = 0.732, n = 22, p < 0.001) between TPNCHO, and total viable

cell count. Therefore, the rapid decrease with depth in the upper 100 m (Fig. 2b and d) indicates preferential removal of neutral sugars from particulate organic matter by heterotrophic organisms. However, observed decrease in TPNCHO also may be due to dilution by lithogenic material or material poor in TPNCHO brought in by the rivers flowing into the Bay of Bengal.

Carbohydrate production by microorganisms is influenced by several factors, including phase of growth, nutrient status, phytoplankton species, and/or bacterial activity (Morris, 1981; Sakugawa and Handa, 1985). Therefore, it is possible that observed changes in the TPCHO and TPNCHO may be associated with the variations in these parameters. Generally, during the different periods of sampling, diatoms were the most abundant phytoplankton in the Bay of Bengal. Diatoms are known to produce large amounts of carbohydrates in culture (Handa, 1969; Myklestad et al., 1989), and in natural waters (Ittekkot et al., 1981; Tanoue and Handa, 1987; Bhosle et al., 1989, 1998). For example, laboratory grown diatom cultures, bacteria, and natural phytoplankton populations are known to produce lower amounts of carbohydrates during the early logarithmic growth, and higher amounts of carbohydrates during the stationary growth phase (Myklestad et al., 1977; Hitchcock, 1978; D'Souza and Bhosle, 2001). Therefore, the observed variations in the concentration and yield of carbohydrates may reflect the effect of the growth phase of microorganisms.

Nutrient concentrations, particularly, nitrate and phosphate, in the growth medium affect the production of carbohydrates by microorganisms (Myklestad, 1977; Myklestad et al., 1989, D'Souza and Bhosle, 2001). It appears that microorganisms, especially diatoms, generally produce higher

amounts of carbohydrates under nutrient deficient conditions. During the sampling period nutrients generally could not be detected in the surface waters and/or were present in very low amounts at most of the stations sampled (Madhupratap et al., 2003; Kumar et al., 2004a, b; Gauns, et al., 2005). These nutrient deficient conditions may have influenced the abundance of carbohydrates at the stations sampled in the northern Indian Ocean.

Carbohydrate content is also influenced by the phytoplankton species composition (Hecky et al., 1973; Sakugawa and Handa, 1985). Diatoms such as *Biddulphia, Chaetoceros, Thallasiothrix, Navicula, Nitzschia, Coscinodiscus, Rhizosolenia* were generally present at the stations sampled in the northern Indian Ocean. However, their relative abundance, varied over the period of observation. For example, diatoms *Nitzschia, Rhizosolenia and Navicula* were most abundant in SWM, FIM and SPIM, respectively (Ramaiah, personal correspondence). It is thus likely that observed variations in the carbohydrate concentrations and yields were due the changes in the diatom species composition.

#### 4.8. Aldose Composition of the surface SPM

Arabinose, fucose, galactose, glucose, mannose, rhamnose, ribose, and xylose were detected in the SPM samples collected from surface waters of the different locations in the northern Indian Ocean (Fig. 3). Of these, glucose (15 to 75 %) was generally the most abundant followed by galactose (7 to 17 %), mannose (4 to 11 %), rhamnose (2.3 to 45 %), fucose (1.4 to 25

%), xylose (3 to 9 %), ribose (1.5 to 8 %), and arabinose (1 to 5.6 %). This aldose composition compares well with that of marine and terrestrial sources. The monosaccharide composition varied from station to station. The observed variations in the monosaccharide composition may be due to changes in the sources of organic matter, phytoplankton abundance and composition, growth phase of algae, light conditions, and nutrient concentrations. Moreover, many sugars serve as an important source of carbon and energy, and thus are rapidly removed by heterotrophic microorganisms. Some of these processes may be responsible for the observed spatial and temporal variation in monosaccharides composition.

Though abundance of glucose was not surprising, as it is the most abundant monosaccharide of terrestrial and marine sources. A glucose contribution ranging from 20 to 80 % of the total TPNCHO has been reported for the SPM collected from other environments, particularly during phytoplankton blooms or for laboratory grown stationary phase diatom cultures (Handa and Yanagi, 1969; Ittekkot et al, 1982, Tanoue and Handa, 1987, D'Souza and Bhosle, 2001). Under nutrient-limited conditions the diatom cultures or natural phytoplankton populations accumulate glucose-rich storage polymer  $\beta$ -1,3 glucan (Handa, 1969; Handa and Yanagi, 1969). For example, low levels of nitrate and phosphate induced the production of glucose-rich polysaccharides by the *Navicula* sp dominated natural phytoplankton populations in the surface waters of the Dona Paula Bay, the west coast of India and by the *Navicula* sp grown in the laboratory (Bhosle et al., 1995; D'Souza and Bhosle, 2001). These glucose-rich storage polysaccharides are easily degraded by the *in situ* aquatic organisms and/or

metabolized during diatom cell sinking (Handa, 1969, Liebezeit, 1986, Tanoue and Handa, 1987; and Goes et al., 1996). Cowie and Hedges (1996) have reported the rapid utilization of glucose-rich storage polysaccharides by herbivorous copepod zooplankton *Calanus pacificus* when fed *Thalassisora weissflogii* under laboratory conditions. Lower abundance of glucose was recorded at some stations, which may indicate the preferential or selective removal of glucose-rich polymers and/or dilution by glucose-poor material.

The decrease in mole fraction of glucose was associated with increase in mole fractions of galactose, mannose, rhamnose, fucose, ribose, arabinose and xylose. These sugars are associated with the structural polysaccharides of the microorganisms, especially diatom (Hecky et al., 1973; Haug and Myklestad, 1976). These structural polysaccharides degrade less rapidly than the glucose-rich storage polysaccharides in the ocean (Handa and Yanagi, 1969: Ittekkot et al., 1982). Furthermore, adsorption of structural polysaccharides by clay minerals may make them less available for microbial utilization which may result in the accumulation of these sugars. Based on field and laboratory studies, it was apparent that galactose, mannose, xylose, arabinose and rhamnose are more resistant to biodegradation than glucose (Cowie and Hedges, 1996; Hamilton and Hedges, 1988; Tanoue and Handa, 1987). Therefore, the relative abundance of these sugars in our samples indicates the relative stability of these compounds during the initial period of decomposition.

Fucose accounted for 1.4 % to 25 % of the TPNCHO. In some of the diatoms, glucose-rich storage polymers are replaced by fucose-rich polysaccharides (Percival, 1970). Moreover, this monosaccharide is also one

of the abundant constituents of cell wall polysaccharides of some diatoms, especially *Navicula* sp and *Nitzschia* sp. Both these diatoms were abundant at the stations sampled (Madhupratap et al., 2003; N. Ramaiah, personal communication). High contribution of this aldose to the TPNCHO at stations 8, 9, and 14 may indicate greater contribution of such organisms to the SPM of these stations.

Rhamnose, fucose, and ribose are abundant in bacteria. For example, *Pseudomonas* sp and *Azotobacter* sp are enriched in rhamnose (Hicks, et al 1994). Similarly, ribose is also abundant in some unindentified bacteria (Cowie and Hdeges, 1984; D'Souza, 2004). Furthermore, both rhamnose and fucose are part of storage polysaccharides of fungi, bacteria, and phytoplankton (Cowie and Hedges, 1984; Moers et al., 1989). High abundance of these sugars may indicate the contribution from microbial biomass, especially bacteria. High contribution from rhamnose plus fucose plus ribose at station 8 and 9 were associated with very low yields of TPCHO and TPNCHO. For sedimenting particles, Unger et al. (2005) observed high abundance of rhamnose plus ribose that was associated with low % TPNCHO-C. Similarly, high abundance of ribose in sediment samples was associated with enhanced microbial activity (Jennerjahn and Ittekkot, 1999).

Arabinose plus xylose together accounted for ~7 to 34 % of TPNCHO (on glucose-free basis). Neither of these sugars contribute significantly to whole cell or cell wall material of diatoms. However, they are abundant in terrestrial plants as constituents of arabinoxylan and arabino glucuronoxylan (Cowie and Hedges, 1984). If arabinose and xylose represent terrestrial organic matter and rhamnose and fucose biogenic organic matter then we

should expect inverse trends between these sugars (Fig. 4a). The mole % of arabinose plus xylose (on glucose free basis) showed significant negative relationship (R = 0.791, n = 32; p < 0.001) with mole % of rhamnose plus fucose, suggesting the interplay between the terrestrial and marine organic matter sources. Moreover, a ratio of rhamnose plus fucose to arabinose plus xylose of 0.5 or less has been proposed to indicate the presence of terrestrial organic matter (Biersmith and Benner, 1998; Guggenberger et al., 1994). Values of the ratio were generally > 0.5 for our samples (data not shown) with some exceptions, suggesting low contribution, if any, of terrestrial organic matter. We also observed low  $^{15}\text{N}$  values (2 to 3  $^{0}\text{/}_{00}\text{)}$  for the SPM samples collected at locations with low salinity (<32 psu). Low <sup>15</sup>N values also indicate the influence of terrestrial material at these stations (Kumar et al., 2004a). The rivers draining into the Bay of Bengal bring terrestrial organic matter as well as detritus material (Unger, et al., 2003; Kumar et al., 2004a). Therefore, it is possible that the terrestrial material brought in by the rivers might have diluted the overall <sup>15</sup>N signal of the PN. However, the abundance of terrestrial material appears to be small as shown by small changes in <sup>15</sup>N values at these stations. Further support for low fractions of terrestrial organic matter was found by Reemtsma et al. (1993) who observed that fatty acids of terrestrial origin accounted for < 10 % of the total fatty acids in particulate matter of the Bay of Bengal.

4.9. Influence of depth on the aldose composition

The aldose composition varied with depth (Fig. 5). Glucose was the most abundant monosaccharide at all depths (2 to 1000 m) sampled. Diatoms most abundant phytoplankton (N. Ramaiah, were the personal communications). Carbohydrates of diatoms are classified as storage and structural (Tanoue and Handa, 1987). The former compounds are preferentially removed by heterotrophic organisms. If so, we would expect two different patterns for SPM glucose distribution with depth. For the first pattern, we would expect mole fraction of glucose to decrease while that of other sugars to increase until the storage polysaccharides were removed in the upper water column. Whereas in the second pattern, if the organic matter has already undergone some degradation of storage polysaccharides then we would expect the glucose mole fraction to increase while that of other sugars to decrease with depth. We did observe both patterns, however, with some difference. The second pattern occurred during the SWM suggesting that the organic matter had undergone some degradation with respect to storage polysaccharides at the sampling locations. On the other hand, during FIM and SPIM, glucose mole fraction decreased in the upper 60 m to 100 m. This decrease in glucose was associated with the increase in other sugars. The observed pattern probably suggests the removal of easily utilizable, glucoserich storage polysaccharides. Below 100 m, mole fraction of glucose increased while those of other sugars decreased with the depth for all the three sampling seasons. This indicates the utilization of structural hetero polysaccharides by the in situ organisms.

During all sampling periods, the glucose mole fraction increased with depth, and at greater depth (1000 m) glucose was the single most abundant

monosaccharide (~70 % of the total monosaccharides). The observed abundance of glucose may also be due to the presence of terrestrial organic matter brought in by the six major rivers flowing through the Indian subcontinent. Increase in the glucose mole fraction with depth also has been observed in the North Pacific and the equatorial Pacific (Tanoue and Handa, 1987; Skoog and Benner, 1997). This selective retention of glucose relative to other sugars indicates the association of this sugar with refractory material. This is inconsistent with the general belief that glucose is the biologically most reactive molecule. However, it appears that lability of glucose-rich polymers depends on their origin as storage or structural polysaccharides. As mentioned above, storage polysaccharides are degraded faster than structural polysaccharides. Structural polysaccharides are further classified as either alkali soluble or insoluble (Tanoue and Handa, 1987). As compared to alkali-soluble heteropolysaccharides, the alkali-insoluble, glucose-rich structural polysaccharides are resistant to degradation (Tanoue and Handa, 1987). The abundance of dissolved structural polysaccharides increased with depth in the Bay of Bengal (Bhosle et al., 1998). Therefore, increasing mole fraction of glucose with depth may be due to the accumulation of alkaliinsoluble structural polysaccharides.

4.10. Distribution, seasonal and depth related variation of particulate uronic acids (TPURA)

TPURA are carboxylated acidic polysaccharides. They are surfaceactive scavengers of heavy metal pollutants, and play important roles in the

detoxification, immobilization and removal of toxic substances, production of macroaggregates, and the development of biofilm in aquatic environments (Tang et al., 2001; Ndung et al., 2003). However, not much is known about the distribution and cycling of uronic acids in the marine environments.

In the northern Indian Ocean, TPURA concentrations in surface waters showed strong spatial variation (0.04  $\mu$ M C to 0.31  $\mu$ M C) and accounted for 4.7 to 22.7 wt % of TPCHO (Table 3). Although somewhat higher, these values are in the range of values reported for other environments. For example, using a spectrophotometric method, Hung et al. (2003) reported that TPURA accounted for ~3 to 9% of the TPCHO in the Gulf of Mexico. Whereas, in Galveston Bay, the dissolved uronic acids accounted for 10.2% of dissolved total carbohydrates (Hung et al. 2001). Our values are also higher than those recorded using the GC method for sedimenting particles (9.89 %) collected from the Dabob Bay (Bergamaschi et al., 1999).

For the surface waters of the northern Indian Ocean, TPURA yields varied from 0.2 % to 2.6 % (Table 3). The average TPURA yield in the SPM collected from the Gulf of Mexico was 0.64 and 0.7 % in 2000 and 2001, respectively (Hung et al., 2003). For the sedimenting particles, TPURA yield was 0.7 % for the Sagami Bay, Japan (Hamanaka et al., 2002), while it varied from 0.3 to 1.2 % for the Dabob Bay (Bergamaschi et al., 1999). From this, it was evident that despite the differences in the sampling locations and depth, our values of TPURA, normalized to POC are comparable to those earlier reported from other marine environments. The average TPURA concentration (~ 0.12  $\mu$ M C) in both the Arabian Sea and the Bay of Bengal was similar. However, their contribution to POC was relatively greater in the Bay (1.28 %)

compared to the Arabian Sea (0.79 %). This was probably due to the observed higher abundance of bacteria in the Bay of Bengal. (Gauns et al., 2005).

Vertical distribution of TPURA in the upper 1000 m was studied at 5 offshore and 4 near-shore locations in the Bay of Bengal during FIM and SPIM (Table 4). The average vertical profiles of TPURA are shown in Fig. 6. TPURA showed three peaks, one was at 2 m, the second was located at 60 or 100 m, and the third was located at 500 m. The concentrations of TPURA and the TPURA yields rapidly declined in the upper 300 m of the water column. This decrease probably indicates utilization of these compounds by *in situ* organisms and/or dilution by TPURA-poor lithogenic material. During both the FIM and SPIM, concentration of the TPURA and its contribution to POC increased at 500 m depth. Higher TPURA yield at 500 m depth suggests additional inputs and/or the production of these compounds at depth. The concentration and the TPURA yield were generally higher during FIM as compared to SPIM, probably due to higher abundance of phytoplankton and bacteria during FIM (Gauns et al., 2005).

Uronic acids are produced by both micro-algae and bacteria (Decho, 1990). Uronic acids showed fairly good significant positive relationships with Chl *a* (R = 0.487, n = 119, p < 0.001), and TBC (as Log10) (R = 0.453, n = 117, p < 0.001). This suggests the importance of these microorganisms in the production of uronic acids in the Bay of Bengal. Furthermore, production of uronic acids by bacteria and microalgae is also influenced by nutrient concentrations in the growth medium or in natural waters (Leppard et al., 1993). At most of the sampling stations, nutrients could not be detected in the

surface waters of the northern Indian Ocean. Therefore, higher TPURA content in the northern Indian Ocean may reflect the effect of nutrient concentrations. The nutrient effect was also evident in the seasonal distribution of TPURA. The concentrations of TPURA were higher during the FIM compared to SPIM. This compares well with the distribution of nutrients in the Bay. In general, the surface nitrate concentration was very low (< 0.1  $\mu$ M) during FIM whereas it was higher (0.20  $\mu$ M) in SPIM (Kumar et al., 2004a,b). This implies that low nutrient concentrations may have induced the production of TPURA.

TPURA concentrations are not only controlled by phytoplankton production, but are also regulated by bacterial assimilation and degradation (Leppard, 1997; Hung et al., 2001). Furthermore, uronic acids are surfaceactive compounds and adsorption by particles is another factor that is likely to influence the concentrations of TPURA in the water column. This was supported by higher content of TPURA in the sinking particles (Bergamaschi et al., 1999; Hung et al., 2003). Moreover, it appears that uronic acid concentrations also are controlled by metal concentrations. For example, uronic acids showed significant positive correlations with the concentrations of copper in the Galveston Bay, and with lead concentrations in the Trinity river (Hung et al., 2001, 2005). Based on these studies, they suggested that uronic acids are induced by elevated trace metal concentrations. Yet another factor that is likely to influence the production of uronic acids is the composition of microorganisms. For particulate matter in Gulf of Mexico, Hung et al. (2003) observed that acidic polysaccharides showed good correlations with

cyanobacterial abundance in 2000, and with prymnesiophyte abundance in 2001.

#### 4.11. Indicators of diagenetic changes in the carbohydrates

The relative reactivity of individual components of organic matter can be estimated by determining the yield or a fraction of carbon as specific molecules. Yields of reactive molecules decrease with increasing decomposition. Carbohydrate yield is a useful indicator of diagenetic state of organic matter (Cowie and Hedges, 1994; Skoog and Benner, 1997; Amon and Benner, 2003). Low and high yields of carbohydrates indicate degraded and fresh organic material, respectively (Cowie and Hedges, 1994; Skoog and Benner, 1997; Amon and Benner, 2003). Carbohydrate yields varied spatially and decreased with depth in the water column, indicating that carbohydrates are reactive components that are selectively removed from organic matter as it undergoes degradation in near-shore and oceanic waters (Table 4, Fig. 2). Organic materials of the surface SPM at many stations as well as those collected from greater depths have low carbohydrate yields (Tables 3 and 4). The observed yields of TPCHO and the TPNCHO in the SPM samples were much lower than those recorded for fresh marine (40 % POC), and terrestrial (75 %) organic matter (Cowie and Hedges, 1984; Opsahl and Benner, 1999), indicating degraded organic material at these stations.

Stations occupied in the northern Indian Ocean were grouped into different areas, and the average yield of TPCHO, TPNCHO and TPURA was calculated for each area. Higher yields of TPCHO, TPNCHO, and TPURA

were recorded for stations sampled in the Bay of Bengal, followed by the eastern Arabian Sea, southern tip of India, and the Andaman Sea (Fig. 7). From this data it was evident that SPM samples collected from the Bay of Bengal had higher yields of TPCHO, TPNCHO, and TPURA, indicating the presence of fresher organic matter as compared to other areas. Conversely, the Andaman Sea was characterized by highly degraded organic matter.

The mole fraction of deoxy sugars (rhamnose plus fucose) is yet another useful parameter to assess the degradative state of organic matter in both marine plankton and vascular plant materials (Cowie and Hedges, 1984, 1994; Hedges et al., 1994; Opsahl and Benner, 1999). The rationale is that the deoxy sugar mole fraction typically increase during the degradation process while glucose is selectively lost (Hedges et al, 1994; Opsahl and Benner 1999). Degradation of non-living organic matter usually gave a negative correlation between these two parameters. We observed high mole fraction of deoxy sugars in surface SPM samples at many stations (Fig. 4b). Moreover, high mole fractions of deoxy sugars were associated with low mole fractions of glucose in the surface SPM samples (Fig. 4b). This also was evident from the significant inverse relationship between the mole % glucose and the mole % deoxy sugars in our surface SPM samples (R = 0.871, n = 32, p < 0.001). We also observed a negative trend between mole % deoxy sugars and mole % glucose for the SPM samples collected from various depths (surface to 1000 m). However, the relationship was not significant, suggesting that deoxy sugars were not very robust indicators of POM degradation of SPM samples collected from various depths of the northern Indian Ocean.

At present, we do not know if glucose is a labile sugar or not because this monosaccharide appears to be a dominant sugar in highly degraded material as well as fresh and labile organic matter (Hama and Yanagi, 2001; Amon and Benner, 2003). Based on preferential degradation of glucose from POM of plankton to sediments, Hernes et al. (1996) proposed that relative mole % glucose in the POM could be used as a diagenetic indicator for organic material in the equatorial Pacific region. Similarly, mole % glucose in fresh vascular plant tissues was consistently high (> 54 to 58 mole %) relative to degraded plant tissues (Opsahl and Benner, 1999). Conversely, Skoog and Benner (1997) did not find a similar relationship for dissolved and suspended particulate matter. They recorded increase in glucose contribution to total carbohydrates with the increase in the water column depth. Similarly, for the SPM samples collected from the deep waters of the northern North Pacific Ocean glucose abundance increased with depth, and accounted for > 70 % of TPNCHO (Tanoue and Handa, 1987). During all the cruises in the northern Indian Ocean, we observed increase in the concentrations of glucose (>70 mole %) with depth (Fig. 5). It was also surprising that at many stations high mole % glucose was associated with high C/N ratio (Table 3 & Fig. 4b). It could be argued that such a trend is possible due to the presence of terrestrially derived organic matter. If this was the case we would expect high yields of TPCHO and TPNCHO associated with high mole % glucose. However, this was not the case. For many of our SPM samples, high values of mole % glucose were associated with lower yields of TPCHO and/or TPNCHO. From our study, it appears that high mole % glucose in some of the

SPM samples of the northern Indian Ocean was associated with degraded organic matter.

#### Acknowledgements

The authors are grateful to Dr Satish R. Shetye, the Director NIO for encouragement and facilities. We thank the Department of Ocean Development, Govt. of India, New Delhi for the financial support to carry out these studies under the Bay of Bengal Process Studies Program. Mr. Vishwas Khodse is grateful to the INCOIS for financial support. We also thank Dr S.Prasanna Kumar, Dr Sugndha Sardesai, Dr N. Ramaiah, Dr Ramesh and the other BOBPS team members for their help on board the research vessel. We also appreciate very much the help given by the Captains and the crew during various cruises of the ORV Sagar Kanya in the northern Indian Ocean. We thank Mr A. P. Selvam for his help in running the GC samples. Authors are grateful to Dr James Bauer, the Associate Editor, and the two anonymous referees for their constructive and helpful comments. This is NIO contribution number 4194.

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## Table 1

Sampling area, period, season, stations, type of samples and sampling depth during various cruises in the northern Indian Ocean

Study region	Cruise no.	Sampling period	Season	Stations	Samples	Sampling Depth (m)
BOB	Sk-166	6 July – 2 August 2001	SWM	9 to 17	SPM	8 (2 to 1000 m)
	Sk-182	14 September – 12 October 2002	FIM	9 to 17	SPM	8 (2 to 1000 m)
	Sk-191	9 April – 11 May 2003	SPIM	9 to 17	SPM	8 (2 to 1000 m)
	Sk-216	9 January – 14 January2005	Winter	18 to 21	SPM	Surface (2 m)
	Sk-217	16 January – 2 February 2005	Winter	22 to 31	SPM	Surface (2 m)
		12 February – 20 February 2005		32 to 38	SPM	Surface (2 m
ANS	Sk-217	3 February – 4 February 2005	Winter	39 to 40	SPM	Surface (2 m)
EAS	Sk-216	5 February – 7 February 2005	Winter	1 to 5	SPM	Surface (2 m)
STI	Sk-216	7 February – 8 February 2005	Winter	6 to 8	SPM	Surface (2 m)

BOB = Bay of Bengal; ANS = Andaman Sea; EAS = Eastern Arabian Sea; STI = Southern Tip of India. SWM = Southwest monsoon; FIM = fall intermonsoon; SPIM = Spring intermonsoon.

# Table 2

Sample locations, water depth (m), surface water temperature, and salinity in the northern Indian Ocean

Station no.	Latitude	Longitude	Depth (m)	Temperature °C	Salinity
EAS					
1	15.00' N	72.53' E	560	28.42	35.50
2	13.34' N	73.53' E	500	28.74	36.02
3	12.00' N	74.17' E	800	28.83	35.31
4	09.56' N	75.31' E	513	28.04	35.59
5	08.52' N	75.56' E	342	28.88	33.45
STI					
6	07.23' N	77.48' E	203	26.90	33.36
7	06.26' N	78.06' E	2780	27.24	33.08
8	05.27' N	78.23' E	3800	27.10	33.23
BOB					
9*	09.00' N	88.00' E	3520	29.30	33.36
10*	12.00' N	88.00' E	2320	33.50	33.30
11*	15.00' N	88.00' E	2835	28.80	32.80
12*	17.00' N	88.00' E	2200	29.10	30.30
13*	20.00' N	88.00' E	1045	28.90	30.30
14*	19.00' N	85.00' E	600	29.20	28.50
15*	16.00' N	83.00' E	1500	29.60	28.60
16*	15.00' N	81.00' E	2700	30.10	33.00
17*	12.00 <sup>°</sup> N	81.00' E	3290	29.80	33.60
18	08.18 N	81.40°E	352	26.84	32.54
19	11.14 N 11.44' N	80.00 E	500	20.84	33.83
20	11.44 IN 12.20' N	00.41 E	550	21.22	33.09
27	12.29 N	80.59 E	333	20.03	33.09
23	10.07' N	83 12' E	3630	27 50	33 91
20	10.00' N	84 00' E	3595	27.80	34 04
25	10.00' N	85.00' E	3548	27.60	33.94
26	09.59' N	86.00' E	3518	27.04	33.85
27	09.59' N	87.59' E	3427	27.72	34.11
28	10.00' N	89.00' E	3369	27.68	34.11
29	09.59' N	90.00' E	3308	27.39	33.59
30	09.59' N	90.58' E	3459	27.82	33.87
31	10.00' N	92.00' E	1890	27.79	32.03
32	10.58' N	90.59' E	3309	27.50	32.77
33	11.59' N	90.59' E	3300	27.50	32.56
34	12.59' N	90.59' E	2988	26.31	31.81
35	13.00' N	89.00' E	3015	27.73	32.43
36	13.00′ N	85.00' E	3192	26.95	33.22
31 20	13.00 <sup>°</sup> N	83.00 E	3337	20.07	33.09
১০	13.00 N	01.00 E	341Z	20./1	JJ.45

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ANS					
39	10.39' N	94.21' E	3477	27.70	32.04
40	10.17' N	94.14' E	3120	28.05	31.95

Area abbreviations used are same as in Table 1.

\* = Values are the averages of three different samples.

# Table 3

Distribution of particulate organic carbon (POC), particulate total nitrogen (PN), C/N ratio, chlorophyll a (Chl a), POC/Chl a ratio, total particulate carbohydrates (TPCHO), %TPCHO-C/POC, total particulate neutral carbohydrates (TPNCHO), %TPNCHO-C/POC, particulate uronic acids (TPURA), %TPURA-C/POC and %TPURA/TPCHO in the surface seawater collected at various locations of the northern Indian Ocean

St.	POC	PN	C/N	Chl a	POC/	TPCHO	TPCHO-C/	TPNCHO	TPNCHO-C/	TPURA	TPURA-C/	TPURA/
no.	µM C	μΜ Ν	ratio	ng l⁻¹	Chl a	μM C	POC	µM C	POC	µM C	POC	ТРСНО
					ratio		%		%		%	%
EAS												
1	11.6	NS	NS	120	1162	$1.22 \pm 0.16$	10.5	NS	NS	$0.13 \pm 0.01$	1.0	11.4
2	28.0	NS	NS	262	1283	$1.60 \pm 0.03$	5.7	1.36	4.9	$0.13 \pm 0.02$	0.4	8.7
3	17.8	1.7	9.2	171	1249	0.85 ±0.11	4.7	0.72	4.1	$0.10 \pm 0.01$	0.5	12.4
4	6.3	0.7	7.7	67	1135	1.08 ±0.13	17.0	0.93	14.7	$0.10 \pm 0.01$	1.4	9.7
5	20.6	1.1	16.0	67	3687	$1.65 \pm 0.06$	8.0	1.17	5.7	$0.16 \pm 0.02$	0.7	10.7
STI												
6	43.1	1.9	19.8	100	5176	$1.75 \pm 0.10$	4.0	1.49	3.4	$0.21 \pm 0.03$	0.4	12.8
7	24.4	1.5	13.6	167	1756	$0.84 \pm 0.08$	3.5	NS	NS	$0.10 \pm 0.01$	0.4	12.9
8	9.8	0.9	9.5	167	707	$0.57 \pm 0.08$	5.8	0.46	4.7	$0.12 \pm 0.02$	1.1	22.7
BOB												
9*	8.9	1.0	9.7	20	5459	NS	NS	0.65	7.3	$0.13 \pm 0.02$	1.3	NS
10*	5.4	1.0	6.8	23	2802	NS	NS	0.37	6.8	$0.08 \pm 0.05$	1.3	NS
11*	5.4	0.7	9.7	19	3444	NS	NS	0.28	5.3	$0.04 \pm 0.04$	0.6	NS
12*	6.9	0.9	7.8	35	2346	NS	NS	0.62	9.0	$0.08 \pm 0.02$	1.0	NS
13*	4.3	0.8	6.4	64	807	NS	NS	0.50	11.6	$0.05 \pm 0.05$	1.1	NS
14*	6.8	0.8	7.2	24	3356	NS	NS	0.56	8.3	$0.10 \pm 0.08$	1.3	NS
15*	6.3	0.8	7.7	28	2696	NS	NS	0.66	10.4	0.11 ±0.01	1.6	NS
16*	4.1	0.6	9.2	13	3811	NS	NS	0.51	12.4	$0.06 \pm 000$	1.3	NS

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17*	5.3	0.9	7.5	13	4792	NS	NS	0.22	4.1	0.08 ±0.06	1.4	NS
18	22.0	1.0	18.3	234	1129	$0.85 \pm 0.05$	3.9	0.69	3.1	0.11 ±0.01	0.5	14.2
19	11.0	1.2	7.8	300	440	1.00 ±0.15	9.1	NS	NS	$0.18 \pm 000$	1.5	19.7
20	4.9	1.0	4.3	167	352	0.76 ±0.03	15.5	NS	NS	$0.09 \pm 0.01$	1.7	13.1
21	18.9	0.9	19.1	100	2270	$1.33 \pm 0.07$	7.0	0.95	5.0	$0.18 \pm 0.01$	0.9	14.9
22	5.2	0.7	6.9	149	421	1.45 ±0.08	27.7	1.15	22.0	$0.06 \pm 0.01$	1.1	4.7
23	5.2	1.0	4.5	130	483	1.54 ±0.12	29.3	1.25	23.8	0.14 ±0.02	2.5	10.1
24	4.5	0.7	5.2	145	370	1.15 ±0.04	25.8	1.03	23.1	$0.09 \pm 0.01$	1.7	8.1
25	22.3	0.7	29.3	176	1520	$0.96 \pm 0.04$	4.3	0.83	3.7	$0.09 \pm 000$	0.4	9.9
26	5.1	0.7	6.4	200	309	1.02 ±0.11	19.9	NS	NS	$0.05 \pm 0.01$	0.9	5.5
27	5.9	0.9	5.7	150	469	1.21 ±0.12	20.7	NS	NS	$0.13 \pm 0.01$	2.0	11.9
28	9.7	1.0	8.3	118	987	1.60 ±0.20	16.5	1.01	10.4	$0.13 \pm 0.01$	1.2	9.0
29	4.8	0.7	5.6	95	602	$0.89 \pm 0.03$	17.3	0.76	16.0	0.14 ±0.01	2.6	18.0
30	8.2	0.8	8.8	134	734	1.21 ±0.03	14.7	1.10	13.4	0.11 ±0.01	1.2	9.8
31	8.7	1.1	6.7	72	1442	$1.39 \pm 0.18$	16.1	1.03	11.9	$0.13 \pm 0.01$	1.4	10.4
32	46.1	2.5	15.9	95	5824	1.79 ±0.21	3.9	1.43	3.1	$0.31 \pm 0.04$	0.6	18.5
33	61.9	2.1	25.4	75	9906	1.61 ±0.07	2.6	1.50	2.4	0.14 ±0.01	0.2	9.4
34	30.4	1.8	14.5	83	4398	1.71 ±0.15	5.6	1.54	5.1	0.14 ±0.01	0.4	9.0
35	7.4	1.5	4.2	69	1294	1.47 ±0.08	19.7	NS	NS	$0.19 \pm 0.01$	2.2	13.6
36	5.2	1.4	3.1	91	691	$1.12 \pm 0.08$	21.4	0.91	17.3	$0.08 \pm 0.01$	1.4	7.7
37	8.4	1.5	5.0	182	557	$1.70 \pm 0.05$	20.2	NS	NS	$0.10 \pm 0.02$	1.1	6.5
38	10.4	1.3	7.0	230	540	$3.58 \pm 0.04$	34.6	2.34	22.6	$0.22 \pm 0.02$	1.9	6.5
ANS												
39	39.2	1.6	21.6	91	5165	1.77 ±0.08	4.5	1.54	3.9	$0.08 \pm 0.01$	0.2	4.9
40	51.1	1.1	38.6	91	6740	$1.95 \pm 0.19$	3.8	1.65	3.2	$0.19\pm\!\!0.03$	0.3	10.3

NS = no sample. \* = Values are the averages of three different samples. Area abbreviations used are same as in Table 1.

# Table 4

Seasonal and depth related changes in the concentrations of chlorophyll a (Chl a), total bacterial count cell no. (TBC), total particulate neutral carbohydrates (TPNCHO) and total particulate uronic acids (TPURA) and their contribution as carbon (TPNCHO-C OR TPURA-C) to POC (as %) in the northern Indian Ocean

			Sk-166			Sk-182						Sk-191					
St.	Depth (m)	Chla	TBC X10 <sup>5</sup> ml <sup>-1</sup>	TPN	CHO %POC	Chl a	la TBC <u>TPNCHO</u> <u>TPURA</u> C		Chl a	Chla TBC <u>TPNCHO</u> ng l <sup>-1</sup> X10 <sup>5</sup> m <sup>[-1</sup> uM C %POC		TPURA					
	()	iig i		μινιο	<i>x</i> i 00	''g '		μιίι Ο	/// 00	μιιο	/// 00			μιιο		μιιο	/01 00
Off-sho	ore statior	าร															
#9	2	27	266.7	0.65	9.3	31	3.01	0.60	5.5	0.12	1.0	1	2.09	0.71	7.9	0.15	1.5
	10	50	126.9	0.92	18.6	39	1.54	0.60	4.2	0.16	1.0	3	0.82	0.57	7.6	0.05	0.6
	30	80	786.6	1.15	19.7	1	0.87	0.53	3.4	0.11	0.6	3	0.80	0.45	7.7	0.12	1.8
	60	56	14.5	0.55	12.9	8	2.29	0.42	9.3	0.05	1.0	7	0.98	0.40	5.7	0.12	1.5
	100	7		0.29	7.1	1	0.83	0.45	19.5	0.10	3.8	4	0.30	0.35	5.8	0.01	0.1
	300	3	3.7	0.19	3.7	ND	0.73	0.31	3.2	0.12	1.1	ND	1.03	0.27	6.4	0.01	0.2
	500	3	1.8	0.31	6.9	ND	1.00	0.46	9.7	0.11	2.2	ND	0.40	0.20	5.4	0.07	1.6
	1000	ND	5.1	0.26	3.3	ND	0.44	0.42	7.8	0.10	1.7	ND	0.70	0.24	7.0	0.04	1.0
# 10	2	56	5.0	0.51	7.4	11	1.53	0.17	3.5	0.12	2.3	3	0.88	0.43	NS	0.04	8.0
	10	43	59.9	0.82	14.5	10	1.78	0.16	8.0	0.08	0.3	5	0.40	0.39	5.6	0.04	0.5
	30	34	NS	0.66	11.6	11	2.90	0.14	0.6	0.18	0.7	4	0.40	0.35	7.1	0.10	1.8
	60	49	76.9	0.75	15.6	28	2.02	0.13	2.9	0.05	1.0	16	0.39	0.42	8.7	0.12	2.3
	100	40	7.6	0.24	3.8	ND	0.58	0.09	3.2	0.04	1.4	7	0.25	0.31	6.2	0.04	0.7
	300	1	NS	0.36	5.5	ND	NS	0.12	0.6	0.04	0.2	ND	NS	0.22	6.4	0.05	1.2
	500	ND	NS	0.41	6.8	ND	NS	0.10	3.7	0.06	1.9	ND	NS	0.16	3.9	0.07	1.5
	1000	ND	NS	0.47	6.2	ND	NS	0.11	4.4	0.05	1.7	ND	NS	0.16	5.0	0.02	0.4
#11	2	40	4.2	0.37	5.7	15	1.67	0.11	2.5	0.06	1.3	1	0.52	0.37	7.1	0.01	0.2
	10	55	2.8	0.24	3.8	33	1.41	0.12	1.5	0.02	0.2	1	0.82	0.38	9.9	0.02	0.4
	30	23	1.2	0.43	6.5	60	0.59	0.12	1.3	0.02	0.2	5	0.24	0.42	8.4	0.04	0.7
	60	121	0.2	0.27	3.7	10	1.36	0.13	2.7	0.10	1.8	8	0.40	0.37	6.8	0.06	0.9
	100	16	2.4	0.22	3.3	2	2.02	0.09	4.0	0.05	1.9	5	0.25	0.21	3.6	0.10	1.6
	300	ND	2.8	0.29	4.4	ND	2.83	0.13	1.7	0.03	0.3	ND	0.23	0.15	4.7	0.01	0.2

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	500	ND	2.1	0.32	5.0	ND	0.73	0.08	2.7	0.05	1.3	ND	0.34	0.22	6.5	0.01	0.2
	1000	NS	INS .	N9	NS	ND	N5	0.08	3.3	0.02	0.9	ND	0.20	0.18	C.C	0.03	0.8
#12	2	84	NS	1.13	10.2	19	0.67	0.35	7.8	0.09	1.8	2	1.72	0.37	7.2	0.06	1.1
	10	72	NS	0.98	7.3	19	0.65	0.43	3.6	0.02	0.1	6	1.25	0.42	7.7	0.09	1.4
	30	76	NS	0.61	4.5	61	2.12	0.29	1.0	0.08	0.3	5	1.53	0.35	6.8	0.04	0.7
	60	52	NS	0.34	3.0	11	0.56	0.17	5.6	0.10	2.9	14	0.40	0.36	7.8	0.05	0.9
	200	9	NS NC	0.13	1.4	1		0.10	8.3 1.2	0.03	1.3	9 ND	0.99	0.31	9.8	0.04	1.2
	500	ے 1	NS	0.27	1.9 2.1		NS	0.11	T.Z 7 0	0.00	1.0		NS	0.25	0.3 1 0	0.05	0.0
	1000	5	NS	0.20	4.6	ND	NS	0.13	7.9 7.2	0.02	0.9	ND	NS	0.10	4.2	0.05	1.4
	-	-															
# 13	2	1//	21.2	0.63	NS	9	10.0	0.46	11.6	0.09	1.9	6	NS	0.42	9.0	0.02	0.4
	10	60	34.1	0.46	3.1	19	0.81	0.45	5.1	0.10	1.0	12	0.56	0.41	7.4 0.0	0.08	1.2
	30 60	28		0.33	3.U 2.1	37 13	0.59	0.30	3.0 3.0	0.10	1.1	ວ 14	1.00	0.30	0.0 1 Q	0.07	1.2
	100	20 5	NS	0.19	2.1	2	1.83	0.12	3.5	0.03	0.0 6.3	5	0.92	0.20	4.0	0.03	0.7
	300	4	19.9	0.34	3.5		1.86	0.07	1.3	0.03	0.0	ND	1.05	0.10	47	0.00	0.3
	500	6	NS	0.13	1.5	ND	1.10	0.09	3.9	0.06	2.4	ND	0.75	0.15	3.6	0.12	2.5
	1000	8	NS	0.52	4.6	ND	1.44	0.06	2.7	0.04	1.7	ND		0.13	4.2	0.01	0.4
Near-s	hore stati	ons															
# 14	2	29	1.3	0.93	14.2	39	8.91	0.67	8.7	0.16	2.0	6	1.18	0.13	2.0	0.04	0.6
	10	51	8.8	1.02	16.3	77	18.5	0.37	2.5	0.12	8.0	8	0.47	0.14	2.0	0.09	1.1
	30	77	2.1	0.99	23.7	47	4.39	0.20	1.9	0.14	1.3	10	2.46	0.13	2.1	0.06	0.9
	60	51	1.0	0.74	21.2	7	NS	0.12	1.9	0.03	0.5	9	1.24	0.11	1.3	0.10	1.0
	100	11	7.4	0.32	8.1	1	0.86	0.13	3.7	0.13	3.6	4	0.51	0.10	2.7	0.01	0.3
	300	1	NS	0.15	4.4	1	1.20	0.08	1.0	0.03	0.4	ND	0.40	0.07	2.3	0.06	1.8
	500	2	NS	0.12	3.8	ND	NS	0.09	2.3	0.02	0.5	ND	0.35	0.06	2.0	0.03	1.0
# 15	2	45	4.2	0.48	11.2	33	5.89	1.40	16.2	0.12	1.3	7	0.59	0.20	3.0	0.10	1.3
	10	35	5.8	0.53	14.2	28	7.13	0.90	7.1	0.10	0.8	9	1.00	0.24	4.8	0.08	1.5
	30	86	NS	0.50	9.2	19	2.31	0.42	3.5	0.04	0.3	24	0.60	0.32	4.7	0.07	1.0
	60	21	NS	0.32	6.6	13	2.13	0.22	5.7	0.02	0.5	107	0.30	0.22	2.9	80.0	1.0
	100	1	2.4 NO	0.30	0./	1	5.03	0.22	1.1	0.12	4.1	6	0.39	0.09	2.2	0.01	0.2
	300 500	1 2		0.24	5./ 0.2	1	NS NS	0.18	2.9	0.08	1.3		0.30	0.08 0.09	2.3 1.0	0.02	0.4
	1000	2 0		0.43	9.3 5.0			0.12	0.3	0.00	ა. <i>լ</i> 11		0.39	0.00	1.9	0.01	0.Z
	1000	ฮ	GNI	0.30	5.0	ND	00	0.07	1.9	0.04	1.1	IND	0.00	0.04	0.9	0.00	1.2
# 16	2	24	20.5	1.20	24.5	11	9.85	0.13	3.8	0.22	6.3	3	1.05	0.20	4.7	0.06	1.3

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1	10	21	68.0	0.86	16.2	18	NS	0.10	1.3	0.04	0.5	4	0.60	0.19	3.7	0.01	0.1
3	30	18	NS	1.07	25.5	28	NS	0.10	2.0	0.02	0.4	3	0.50	0.23	4.6	0.02	0.4
6	60	19	NS	0.98	23.0	19	5.26	0.05	2.4	0.06	2.6	12	0.70	0.22	4.9	0.05	1.0
1	100	19	1.3	0.68	17.0	3	NS	0.03	1.7	0.05	2.2	18	0.57	0.19	3.4	0.06	1.0
3	300	ND	7.3	0.51	13.4	ND	NS	0.03	0.9	0.04	1.1	ND	0.41	0.11	4.5	0.02	0.8
5	500	ND	22.2	0.59	15.2	ND	NS	0.04	2.5	0.01	0.3	ND	0.30	0.08	2.7	0.04	1.1
1	1000	ND	8.5	0.42	17.3	ND	NS	0.04	2.8	0.02	1.4	ND	0.32	0.09	2.6	0.02	0.6
#17 2	2	25	NS	NS	NS	10	3.80	0.12	2.0	0.12	1.9	5	0.60	0.33	6.6	0.04	0.7
1	10	30	NS	NS	NS	22	3.18	0.11	1.5	0.03	0.4	3	0.41	0.27	5.8	0.07	1.3
3	30	36	NS	NS	NS	36	1.41	0.15	1.7	0.15	1.7	5	0.77	0.19	4.4	0.06	1.3
6	60	79	NS	NS	NS	11	3.16	0.10	2.5	0.03	8.0	6	0.73	0.29	5.6	0.08	1.3
1	100	2	NS	NS	NS	1	0.92	0.06	2.5	0.03	1.1	2	0.57	0.15	3.1	0.07	1.4
3	300	ND	NS	NS	NS	ND	4.63	0.05	0.5	0.16	1.5	ND	0.30	0.02	0.7	0.02	0.7
5	500	ND	NS	NS	NS	ND	0.94	0.04	1.5	0.14	4.8	ND	0.39	0.01	0.3	0.09	1.9
1	1000	ND	NS	NS	NS	ND	5.63	0.03	1.3	0.07	2.9	ND	0.66	0.15	5.2	0.03	0.9

NS = no samples. ND = not detected.



Fig. 1. Locations of the stations sampled during various cruises of ORV Sagar Kanya in the northern Indian Ocean.



Fig. 2. Vertical distribution of average TPNCHO concentrations (a and c) and % TPNCHO-C/ POC (b and d) in the off-shore (#9 to #13) and near-shore (#14 to #17) stations respectively, during the SK-166, Sk-182 and SK-191 cruises in the Bay of Bengal. Bar represents + SD, for clarity SD of some points is not shown.



Fig. 3. Variation in the average mole% monosaccharide composition (Rham, rhamnose; Fuc, fucose; Rib, ribose; Arb, arabinose; Xyl, xylose; Man, mannose; Gal, galactose; Glu, glucose) of the suspended particulate matter of surface seawaters collected from various stations of the northern Indian Ocean. Area abbreviations used are same as in Table 1.



Fig. 4. Spatial variations in glucose (Glu) free mole % (Rham + Fuc)a and (Arb + Xyl)a (a), and mole % (Rham + Fuc) and Glu (b) of the suspended particulate matter of the surface water collected from various stations in the northern Indian Ocean.



Fig. 5. Variation in the monosaccharide composition of the suspended particulate matter (SPM) collected at various sampling depths of various stations sampled during Sk-166, Sk-182 and Sk-191 cruises of ORV Sagar Kanya in the Bay of Bengal. Bar indicates mean ± SD.



Fig. 6. Vertical distribution of average TPURA concentrations (a and c) and % of TPURA-C/POC (b and d) in the off-shore (#9 to #13) and near -shore (#14 to #17) stations respectively, during the SK-182 and SK-191 cruises in the Bay of Bengal. Bar represents +SD, for clarity SD of some points is not shown.



Fig. 7. The average Yields of TPCHO, TPNCHO, and TPURA as percentages of POC in various sampling regions. BOB = Bay of Bengal, EAS = Eastern Arabian Sea, STI = Southern Tip of India, ANS = Andaman Sea.