

Seasonal variability in biological carbon biomass standing stocks and production in the surface layers of the Bay of Bengal

N Ramaiah^{1*}, V Fernandes¹, J T Paul¹, R Jyothibabu², G Mangesh¹ & E A Jayraj²

¹National Institute of Oceanography, Dona Paula, Goa 403004, India

²Regional Centre of NIO, Kochi 682 018, India

[Email: ramaiah@nio.org]

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As a part of the Bay of Bengal Process Study, several biological characteristics were investigated during summer monsoon (SuM; July-August 2001), fall intermonsoon (FIM, September-August 2002), spring intermonsoon (SpIM; April-May 2003) and northeast monsoon (NEM, Dec 2005-January 2006). Chl *a* carbon during SuM, FIM, SpIM and NEM averaged 688, 767, 1212 and 1057 mg C m⁻² in the western Bay (WB) and 518, 904, 789 and 1023 mg C m⁻² in the central Bay (CB). Primary productivity (PP) averaged 326, 281, 366 and 280 mg C m⁻²d⁻¹ in the WB and 144, 306, 241 and 375 mg C m⁻²d⁻¹ in the CB respectively. Shallow euphotic depths (~<55m) apparently are not conducive for (PP) in the 0-120 m column. Heterotrophic bacterial carbon biomass was sizable and averaged 282, 662, 95 and 288 mg C m⁻² in the WB and was 677, 227, 104 and 333 mg C m⁻² in the CB during SuM, FIM, SpIM and NEM respectively. They appear very crucial in governing the abundances of microheterotrophs in the southern and, open-ocean regions of the Bay. Microzooplankton were much poorer in abundance than those in the Arabian Sea except during SpIM. Their maximum carbon biomass (WB: 233; CB: 327 mg C m⁻² in the top 120 m was observed during SpIM. In the upper 200 m, the mesozooplankton biomass did not show much variation between the season (WB: 222, 906, 2428 and 988 mg C m⁻² and CB: 587, 1036, 821 and 808 mg C m⁻² d⁻¹ respectively during SuM, FIM, SpIM and NEM). Incidentally it was mostly decoupled with chl *a* and PP. Cold-core eddies observed during most sampled seasons seem to bear an enhancing influence on the overall biological productivity processes.

Introduction

Bay of Bengal (BoB), the eastern extent of the Indian Ocean, is a semi enclosed tropical basin. With an area of $\sim 4.08 \times 10^6$ km², it is an important region of fisheries, sustaining millions of fisher-folk in as many as six bordering nations. It is a region of positive water balance as enormous amounts of fresh water both from precipitation (~ 2 m yr⁻¹)¹ and river run off (1.63 trillion m³ yr⁻¹)² are added. These physical settings substantially decimate the entrainment of nutrients from the deeper layers to the surface, which in turn, decrease the surface productivity³. Neither summer upwelling, nor winter convection is prominent in the Bay due to which there is no effective exchange between surface and subsurface waters. While eddies are implicated to enhance nutrients diffusion in to the near surface waters⁴, the suspended terrigenous load drastically shallows the euphotic depths which in turn lower the photosynthesis. Nutrients which may be brought in by the rivers are thought to be lost to the deep waters of

the Bay because of its narrow shelf⁵⁻⁷. However, it is a cyclone-prone region and these episodic events are likely to churn-up large areas, facilitating nutrient injection to the shallow euphotic zone and thereby enhancing primary production, at least sporadically.

It was, in fact, postulated that higher surface production resulting from lower light intensities occurs in the BoB. Primary productivity values ranging from 3.0 to 8.7 g C m⁻² d⁻¹ have been reported from the inshore waters of the east coast of India during June-July⁸. Also, up to 50 mg m⁻² chlorophyll *a* concentrations were observed inshore by Bhattathiri et al.⁹ that led them to believe "the primary production of BoB is not less than that reported from the AS". Barring such unusual highs, most measurements report primary production <0.5 g m⁻² d⁻¹ and very low chlorophyll *a* (usually <0.1 mg m⁻³).

Many studies are available to understand the physical characteristics of the Bay of Bengal¹⁰⁻¹⁴, very few studies attempted to comprehend the water column chemistry^{6,15,16}. Even fewer studies exist which addressed the biogeochemical characteristics of the Bay¹⁷.

*corresponding author;

In order to recognize the seasonal variability in the biogeochemical processes, the Bay of Bengal Processes Study (BOBPS) was undertaken during 2001-2006. During the field experiments for this Study, many physical, chemical and biological parameters were measured to decipher their spatio-temporal variations with a view to understand the influences of physico-chemical factors on the biological productivity.

Materials and Methods

Sampling locations under the BOBPS Programme are shown in Fig. 1. Samples collected during July-August 2001 (Summer Monsoon SuM), September-October 2002 (Fall Intermonsoon, FIM), April-May 2003 (Spring Intermonsoon, SpIM), December 2005-January 2006 (Northeast monsoon, NEM) were analyzed for different biological parameters following JGOFS Protocols¹⁸. Five stations (C1-C5) were sampled along transect in the central Bay (CB) and four stations (W1-W4) along the other transect in the western Bay (WB). For biological parameters, water samples were collected from 0, 10, 20, 40, 60, 80, 100 and, 120 m using CTD rosette. Description of these parameters had been published earlier¹⁹⁻²⁶.

Results

Seasonal variations in chlorophyll a (chl a) and nutrient concentrations

In the surface waters along the CB, seasonal variation in chl *a* concentration was quite distinct.

During SuM, the surface chl *a* increased from south to north. It ranged from 0.06 to 0.28 mg m⁻³. Nitrate concentrations were undetectable except at C5 where it was 0.10 μM. Silicate in the surface layers was in measurable concentrations only at C1 (1 μM) and C5 (2.7 μM; for details of nutrients, refer to Sardesai *et al* in this issue).

During FIM, chl *a* exhibited a decreasing trend from south to north. It varied from 0.12 to 0.37 mg m⁻³ with the highest concentration at C1. The nitrate concentration was undetectable at C1 and varied from 0.04 to 0.11 μM at the other stations. Silicate concentration increased from 0.4 at C1 to 2.28 μM at C5. Ranging narrowly from 0.06 to 0.11 mg m⁻³, chl *a* showed a uniform distribution from south to north during SpIM. Also, nitrate concentration (0.2-0.4 μM) did not vary much. Silicate however, decreased from C1 (2.04 μM) to C5 (1.61 μM). During NEM, its concentration was 0.12-0.19 mg m⁻³. Nitrate concentration ranged from not detectable (ND) to 0.15 μM and, silicate from 0.56 to 1.57 μM.

Surface chl *a* concentration along the WB too varied seasonally. Similar to that in CB, the chl *a* ranging from 0.06 to 0.16 mg m⁻³ increased northwards during SuM. Nitrate and silicate were undetectable throughout the transect except for 4 μM silicate at the northernmost station. During FIM, the surface chl *a* ranged from 0.14-0.77 mg m⁻³,

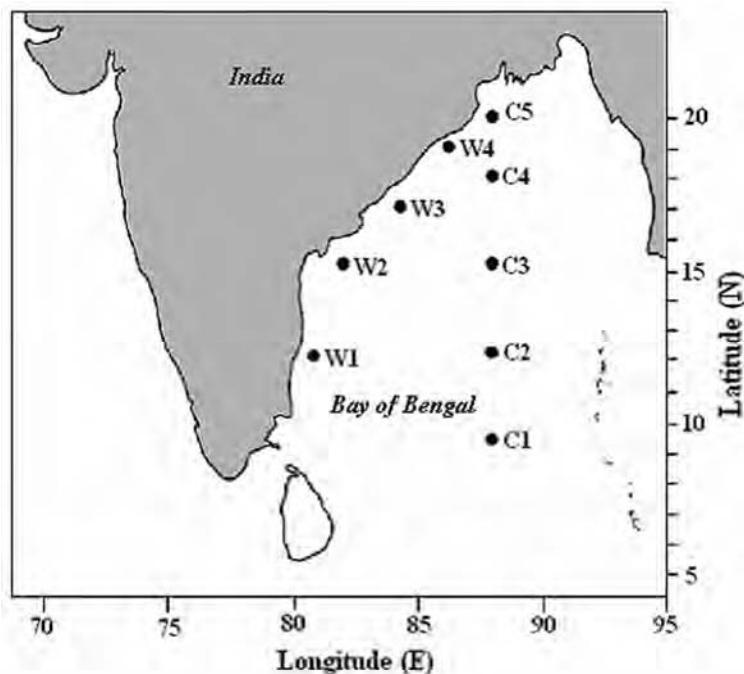


Fig. 1— Sampling locations in the Bay of Bengal during the Bay of Bengal Process Study (2001-2006)

increasing northwards. The surface nitrate and silicate ranges were 0.11-0.22 μM and 1.05- 9.69 μM respectively. Chl *a* concentration during SpIM increased from 0.06 at W1 to 0.21 mg m^{-3} at W4. Nitrate concentrations (0.2-0.8 μM) did not vary much. Silicate concentrations from W1 to W4 were 1.42-2.13 μM . During NEM, unlike during the other three seasons, the surface chl *a* values showed an oscillating pattern with highs at W2 and W4 and lows at W1 and W3. It ranged from 0.15 to 0.28 mg m^{-3} in the surface. The nitrate and silicate concentrations were 0.04-0.7 μM and, 1.28-3.07 μM respectively.

One characteristic feature of the BoB is the persistently higher concentrations of chl *a* at the base of mixed layer. In the CB, the deep chl *a* maximum (DCM) was between 40 and 60 m during SuM, FIM and NEM and at 80 m during SpIM. In the WB, the DCM was between 20 and 60 m during SuM, between 20 and 40 m during FIM, at 40 m during WM and at 80 m during SpIM.

In the CB, integrated chl *a* varied from 9 to 11.5 mg m^{-2} with its highest concentration at C1 during SuM; from 13.8 to 23.4 mg m^{-2} ; highest concentration again at C1 (and also at C2) during FIM; from 17.3 to 21.3 mg m^{-2} during NEM and from 13.4- to 18.3 mg m^{-2} during SpIM. In the WB, the integrated chl *a* varied from 12 to 18.7 mg m^{-2} , with the highest concentration observed at W4 during SuM; between

11.3 and 18.7 mg m^{-2} , with higher values at W1 and W3 during FIM; 17 and 27 mg m^{-2} during NEM and between 11 and 43 mg m^{-2} during SpIM. In terms of carbon, the column chlorophyll *a* values at different locations in the CB and WB are depicted in Fig. 2. In general, the average chl *a*-C in the CB varied between 747 and 869 mg C m^{-2} and between 750 and 1125 mg C m^{-2} in the WB. Along the CB, strong variability was seen at station C2 and in the WB; the largest variability was noticed at W3 with an unusually high SpIM value.

The integrated chl *a* carbon (mg C m^{-2}) increased from SuM (688), FIM (767), WM (1057) to SpIM (1212) in the WB. In the CB, the lowest chl *a*-C was during SUM, intermediate during SpIM and FIM and highest during NEM (Table 3).

Bacterial abundance

In the CB, the ranges of total direct counts of heterotrophic bacteria ($\text{Hbac} \times 10^9 \text{ cells l}^{-1}$) in the 0-120 m column were 0.02-1.45 from C1 to C5 during SuM, 0.04-1.00 during FIM, 0.02-0.36 during SpIM and 0.03-1.82 during WM. They varied between 0.03 and 0.88 ($\times 10^9 \text{ cells l}^{-1}$) during SuM, 0.07 and 1.85 during FIM, 0.02 and 0.25 during SpIM and 0.07 and 0.91 during WM in the WB. Unlike the chlorophyll *a*, the bacterial counts did not show subsurface maxima or a definite trend in their abundance with depth.

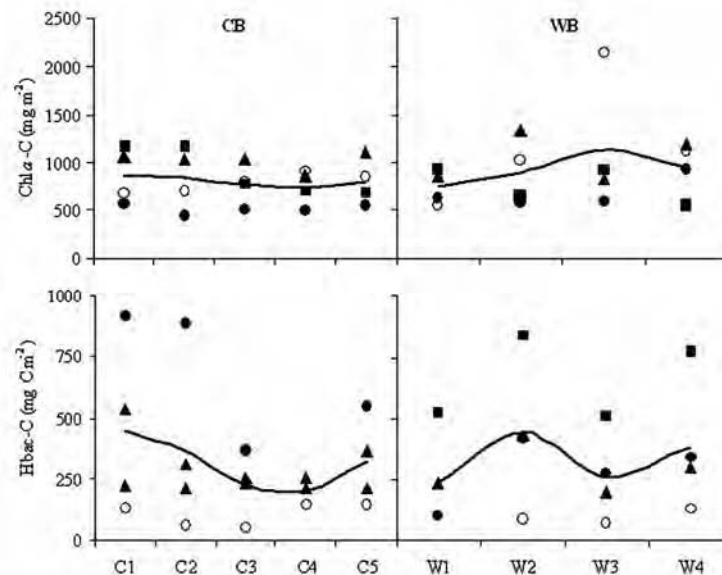


Fig. 2— Seasonal variations in chlorophyll *a* (chl *a*-C) and heterotrophic bacterial carbon (Hbac-C) at different sampling locations in the central (C1-C5) and western (W1-W4) Bay of Bengal. Symbols are: ● for Summer Monsoon, ■ for Fall Intermonsoon, ▲ for Northeast Monsoon and, ○ for Spring Intermonsoon. The line —, depicts the average value derived using the data points from corresponding locations.

The Hbac-C varied widely between the seasons in both transects with the highest variability at C1 and C2 in CB and at W2 and W4 in the WB (Fig. 2). The seasonal average bacterial biomass varied from 203 to 450 mg C m⁻² in the CB and 239 to 443 mg C m⁻² in the WB. While the highest biomass in the CB was found during SuM (677 mg C m⁻²), it was far more during FIM (662 mg C m⁻²) in the WB (Table 3). The lowest biomass was recorded during SpIM in both transects.

Microzooplankton (MCZP)

Since the MCZP data collection was carried out during one season (FIM) under the BOBPS programme, MCZP data collected from one other program (MRLR) for SuM, SpIM and NEM is included here (Table 3) for a comprehension of MCZP living biomass carbon in the Bay. As the station positions were not exactly the same during these programmes, the data considered here are for 11°N 84°E (A3 of Jyothibabu 2004²⁷), 13°N 84°E (A6), 15°N 84°E (A9), 17°N 87°E (A12) and 19°N 89°E (A15) from the CB and, 11°N 80.5°E (A1), 15°N

82°E (A8), 17°N 83°E (A10) and 19°N 85°E (A13) from the WB. More details are available in Jyothibabu 2004²⁷. In the CB, the MCZP carbon biomass ranged from 201 to 753 mg C m⁻² during SpIM. Similarly, it varied from 113 to 493 mg C m⁻², 19 to 28 mg C m⁻² and 23 to 159 mg C m⁻² during SuM, FIM and NEM respectively (Fig. 3). In the WB, it varied from 17 to 124 mg C m⁻² in the WB. Higher values were found at the northernmost station C5 in the CB and at the southernmost station W1 in the WB. The MCZP biomass varied seasonally with its lowest values during FIM and the highest during SpIM along both transects (Table 3). Its range was 22-327 mg C m⁻² in the CB and 30 to 233 mg C m⁻² in the WB.

Mesozooplankton (MZP)

The MZP abundance in the mixed layer of the CB ranged from 5.2 to 35.8 (mean: 26 × 10³ ind. 100 m⁻³) during SuM, 48 to 356 (128 × 10³ ind. 100 m⁻³) during FIM, 16 to 308 (78 × 10³ ind. 100 m⁻³) during NEM and 3.8 to 248 (102 × 10³ ind. 100 m⁻³) during SpIM. In the WB, it was 1.7 to 462 (mean: 157 × 10³ ind. 100 m⁻³) during SuM, 99 to 136.3 (124 × 10³ ind. 100 m⁻³) during

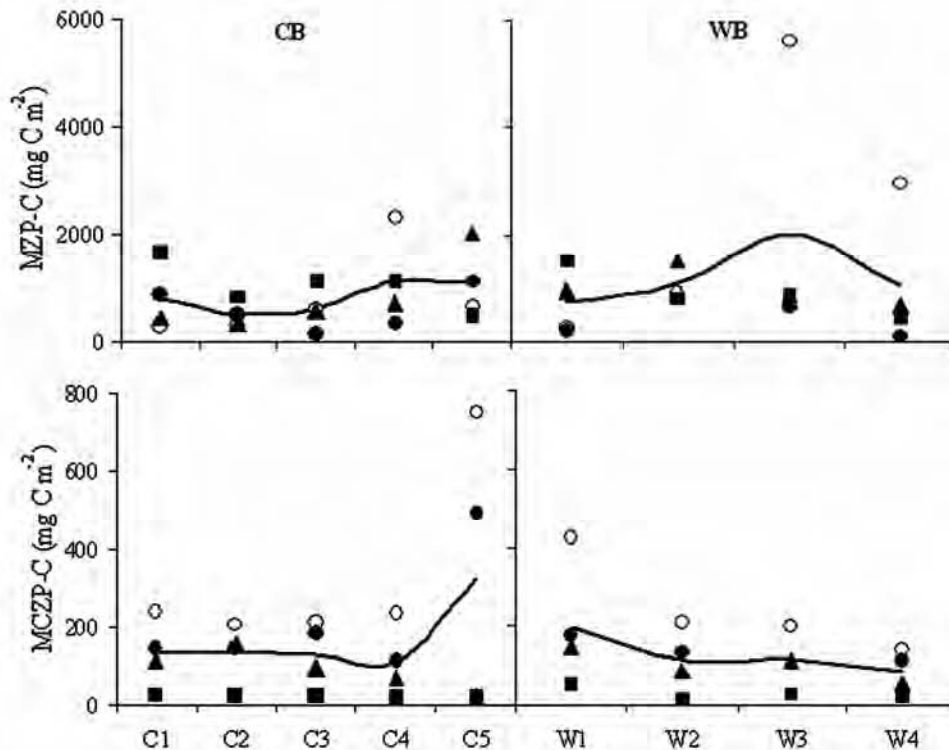


Fig. 3— Seasonal variations in mesozooplankton (MZP) and microzooplankton (MCZP) carbon at different sampling locations in the central (C1-C5) and western (W1-W4) Bay of Bengal. Symbols are: ● for Summer Monsoon, ■ for Fall Intermonsoon, ▲ for Northeast Monsoon and, ○ for Spring Intermonsoon. The line —, depicts the average value derived using the data points from corresponding locations.

FIM, 73 to 161.8 (102×10^3 ind. 100 m^{-3}) during NEM and 31 to 533.8 (163×10^3 ind. 100 m^{-3}) during SpIM. Contrary to the seasonal distribution of biomass, the abundance in the CB was the lowest during SuM and highest during FIM. In the WB, it was lower during NEM and FIM and higher during SpIM and SuM. Higher abundances were also observed in the vicinities of cold core eddies.

The MZP-C biomass averaged 481-1115 mg C m^{-2} along stations in the CB. In the WB, it varied from 722 to 1993 mg C m^{-2} with a generally increasing trend from south to north (Fig. 3). The MZP biomass varied between seasons with its lowest during SuM and the highest during FIM in the CB. The variation in the MZP-C was far wider in the WB ranging from 222 mg C m^{-2} during SuM to 2428 mg C m^{-2} during SpIM (Table 3). Copepods were the dominant component of the mesozooplankton among a total of 37 taxonomic groups identified in the Bay. The other major groups comprising over 2% of the total abundance were chaetognaths, ostracods, euphausiids, siphonophores, polychaetes and appendicularians²⁶.

Primary production (PP)

The ranges of PP in the 0-120 m column at different sampling locations during different sampling seasons are provided in Table 1. Seasonal variability in the primary productivity (PP) is depicted in Fig. 4. The largest seasonal variability was at station C1, where the FIM recorded the highest and during SpIM, the lowest rates of PP. While the average column PP varied narrowly between 208 and 318 $\text{mg C m}^{-2} \text{ d}^{-1}$ among stations in the CB, it ranged from 125 to 396 $\text{mg C m}^{-2} \text{ d}^{-1}$ in the WB.

The PP varied from as low as 144 $\text{mg C m}^{-2} \text{ d}^{-1}$ (SuM) to 375 $\text{mg C m}^{-2} \text{ d}^{-1}$ (NEM) in the CB (Table 3). In general, it was higher in the WB ranging from 280 $\text{mg C m}^{-2} \text{ d}^{-1}$ (FIM) to 366 $\text{mg C m}^{-2} \text{ d}^{-1}$ (SpIM).

Bacterial production (BP)

The 0-120 m column ranges of BP during different sampling seasons at different sampling locations are provided in Table 2. Unlike the PP, the BP did not decrease with increasing depth and, fluctuated rather independent of depth at most locations. In addition, it often did not co-vary with the bacterial abundance. Nor was it coupled to chl *a* concentrations. BP showed the largest seasonal variability at C1 in the CB and on an average varied between 131 and 191 $\text{mg C m}^{-2} \text{ d}^{-1}$ between stations. In the WB, the largest

variability was observed at W3 with a high NEM value and the average BP ranged from 119 to 151 $\text{mg C m}^{-2} \text{ d}^{-1}$. BP contributed to the bulk of the primary production in particular during SuM and NEM in the CB as well as WB (Table 3). It was the least during SpIM and FIM along both the tracks.

Discussion

Krey and Babenard²⁸ pointed out that during the International Indian Ocean Expedition the Bay of Bengal was very poorly sampled. As far as biological investigations are concerned, this fact remained quite true until the late 1980s. The investigations of Bhattathiri *et al* 1980²⁹, Gomes (2000)³⁰ and Vinaychandran *et al* (2003)³¹ have provided information on the variations in chl *a* concentrations and primary production. A comprehensive account of different biotic components (viz phyto-, microzoo- and mesozoo-plankton and heterotrophic bacteria is made available by the BOBPS.

Table 1—Primary production ($\text{mg C m}^{-3} \text{ d}^{-1}$) at different sampling stations in the BOB during different seasons. Ranges are for surface to 120 m column

Station	Seasons			
	Summer Monsoon	Fall Intermonsoon	Northeast Monsoon	Spring Intermonsoon
C1	0.07- 5.20	0.06-17.83	0.01- 5.87	0*- 3.80
C2	0.06- 1.97	0.07- 5.34	0*-10.04	0.03- 3.23
C3	0.23- 2.44	0*- 9.87	0.06- 4.93	0*- 3.97
C4	0.09- 5.75	0*- 5.70	0.09- 5.86	0.06- 2.94
C5	0.01- 6.04	0*- 8.54	0*- 6.22	0*- 8.28
W1	0.37-12.66	0*- 6.72	0*- 6.96	0.05- 4.35
W2	0.10- 0.75	0*- 5.16	0.02- 0.37	0.56- 3.82
W3	0.03- 8.65	0*-25.41	0.23- 5.70	0*-13.09
W4	0.18-15.80	0*-45.15	0.13- 6.94	0*-10.48

Table 2—Bacterial production ($\text{mg C m}^{-3} \text{ d}^{-1}$) at different sampling stations in the BOB during different seasons. Ranges are for surface to 120 m column

Station	Seasons			
	Summer Monsoon	Fall Intermonsoon	Northeast Monsoon	Spring Intermonsoon
C1	0.84-5.75	0.16-4.19	0.65- 2.49	0.10-1.33
C2	0.45-3.19	0.09-1.24	0.49- 2.61	0.17-2.49
C3	0.44-4.34	0.09-2.28	0.42- 2.47	0.22-1.94
C4	0.20-4.36	0.07-0.94	0.78- 2.37	0.01-0.83
C5	0.24-6.75	0.01-2.15	0.62- 3.28	0.10-1.74
W1	0.46-3.81	0.07-2.53	0.77- 3.34	0.40-0.66
W2	0.21-1.53	0.19-3.73	0.35- 3.55	0.30-0.64
W3	0.34-1.40	0.10-1.86	0.56-18.56	0.16-1.40
W4	0.18-4.75	0.07-0.94	0.60- 2.98	0.13-1.60

From the earlier studies, it is understood that there is low-salinity surface layer during SuM (29 psu) and FIM (25 psu), than during SpIM (33 psu). The warm surface waters and thermal stratification is a well-known feature of the BoB during SpIM. Along the WB, the SST during SpIM did not differ much from that of FIM. Shetye *et al*³² observed several warm water recirculation zones in the northwestern Bay in association with the pole-ward flow of the east India coastal current (EICC) north of 10°N during SpIM. This EICC carries nutrient poor warm water from the south.

For any oceanic/marine region to be biologically stable, diverse and productive, the microalgal photosynthetic activity is of paramount importance. A reliable measure of microalgal abundance is through the determination of chlorophyll. Higher the chlorophyll concentration, higher would be the possible biological activity. While there were a few higher concentrations of chl *a* at some locations, there was no drastic difference in its concentration in the BoB during different seasons. The 0-120 m column integrated chl *a* did not show significant seasonal differences although its subsurface maxima deepened

Table 3—Living carbon biomass standing stocks and production during different seasons in the Bay of Bengal. Figures are averages from five locations in the central and, four in the western Bay.

	Season			
	Summer Monsoon	Fall Intermonsoon	Northeast Monsoon	Spring Intermonsoon
Chlorophyll <i>a</i> carbon biomass (mg C m ⁻²)				
Central Bay	518	904	1023	789
Western Bay	688	767	1057	1212
Heterotrophic bacterial carbon biomass (mg C m ⁻²)				
Central Bay	677	227	333	104
Western Bay	282	662	288	95
Microzooplankton carbon biomass (mg C m ⁻²)				
Central Bay	215	22	92	327
Western Bay	143	30	93	233
Mesozooplankton carbon biomass (mg C m ⁻²)				
Central Bay	587	1036	808	821
Western Bay	222	906	988	2428
Primary production (mg C m ⁻² d ⁻¹)				
Central Bay	144	306	375	241
Western Bay	326	281	280	366
Bacterial Production (mg C m ⁻² d ⁻¹)				
Central Bay	248	85	196	70
Western Bay	161	76	220	78
Mesozooplankton Production (mg C m ⁻² d ⁻¹)				
Central Bay	127	133	94	225
Western Bay	76	70	113	247

down to 80m during SpIM. Detailed analyses of phytoplankton composition in the BoB are now available^{33,34}. Major and very preponderant genera/species are listed in Table 4.

Earlier studies^{7,9} reported surface chl *a* in the ranges of 0.08-1.67 and 0.01-1.01 mg m⁻³ in the WB during summer. Similar to ranges observed during this study, recently Madhu *et al*³⁵ reported <0.1 mg m⁻³ chl *a* in surface waters during SuM. Availability of higher nitrate (1 μM) and phosphate (<0.4 μM) in the top 20 m might have led to such concentrations of chl *a* in the well-lit surface layers. However, they did not

Table 4—Major species of phytoplankton (contributing ≥ 2 % of total counts) in the Central Bay during different seasons

Season	Phytoplankton species	cells × 10 ³ l ⁻¹	%
Summer Monsoon	<i>Thalassiothrix longissima</i>	18.65	20.29
	<i>Thalassiothrix fauelfeldii</i>	14.90	16.21
	<i>Nitzschia angularis</i>	7.86	8.55
	<i>Skeletonema costatum</i>	3.69	4.42
	<i>Thalassionema nitzschioides</i>	4.06	4.01
	<i>Chaetoceros coarctatus</i>	3.6	3.92
	<i>Coscinodiscus radiatus</i>	3.32	3.62
	<i>Coscinodiscus concinnus</i>	2.71	2.95
	<i>Chaetoceros eibonii</i>	2.18	2.37
	<i>Rhizosolenia styliformis</i>	2.04	2.22
	<i>Thalassionema nitzschioides</i>	3.56	12.01
	<i>Navicula</i> spp	2.76	9.30
Fall Intermonsoon	<i>Rhizosolenia styliformis</i>	2.2	7.41
	<i>Rhizosolenia shrubsolei</i>	1.44	4.85
	<i>Synedra hennadyana</i>	1.44	4.85
	<i>Rhizosolenia</i> spp	0.88	2.96
	<i>Chaetoceros didymus</i>	0.84	2.83
	<i>Pseudo-nitzschia</i> spp	0.76	2.56
	<i>Thalassiothrix fauelfeldii</i>	0.68	2.29
	<i>Thalassiosira</i> spp	0.6	2.02
	<i>Navicula</i> spp	2.19	9.85
	<i>Coscinodiscus</i> spp	1.74	7.85
	<i>Cyanobacteria</i>	1.62	7.28
	<i>Navicula distans</i>	1.56	7.04
Northeast Monsoon	<i>Fragilariopsis doliolus</i>	1.45	6.52
	<i>Thalassionema nitzschioides</i>	1.34	6.05
	<i>Chaetoceros didymus</i>	1.26	5.67
	<i>Thalassiosira</i> spp	1.08	4.88
	<i>Peridinium</i> sp	1.00	4.50
	<i>Ceratium furca</i>	0.69	3.10
	<i>Eucampia zodiacus</i>	0.56	2.56
	<i>Thalassiothrix fauelfeldii</i>	0.46	2.05
	<i>Navicula</i> spp	3.40	31.14
	<i>Trichodesmium</i> spp	2.36	21.61
	<i>Coscinodiscus</i> spp	0.64	5.86
	<i>Pseudo-nitzschia</i> spp	0.56	5.13
Spring Intermonsoon	<i>Leptocylindrus mediterraneus</i>	0.44	4.03
	<i>Navicula distans</i>	0.36	3.3
	<i>Rhizosolenia cylindrus</i>	0.32	2.93
	<i>Thalassionema nitzschioides</i>	0.32	2.93
	<i>Fragilariopsis doliolus</i>	0.24	2.2

observe any DCM as observed during SM of this study. Frequent DCM observed in this study are attributable to: (a) lack of nutrients in the top 10-30 m but, (b) their availability in excess of $0.5 \mu\text{M}$ below 30 m. The phytoplankton in the BoB appear to have adapted to low light conditions as the SCM were often deep seated and, chl *a* was often far more than that recorded from surface samples from the same location.

The average surface (0.09 mg m^{-3}) and column integrated (15.79 mg m^{-2}) chl *a* reported in this study during SpIM are lower than previously reported ($<0.3 \text{ mg m}^{-3}$ ⁴²; 18 mg m^{-2} ³⁷). Sengupta *et al*⁶ reported that rivers did not contribute to the inorganic nutrient pool of the western BoB during SpIM. Such a situation might be forcing the phytoplankton to depend on 'ideal concentrations' persisting in nitracline of ~30-70 m layer. As also observed in this study, deep-seated DCM ~50 to 80 m is apparently a common SpIM feature^{35,30}. Further, the DCM occurring in the nitracline are essential features of the typical tropical structure in the Atlantic³⁶ and in the Arabian Sea²⁴. Riverine influx and eddies^{3,4,37} and/or Ekman pumping seem to affect availability of nutrients to the phytoplankton. Distribution of phytoplankton in terms of biomass (chl *a*) along both transects, thus, appear to be governed by nutrient inputs.

It was postulated that higher surface production resulting from lower light intensities occurs in the BOB although the column production is much higher in the AS⁷. Primary productivity values ranging from 3.0 to $8.7 \text{ g C m}^{-2} \text{ d}^{-1}$ have been reported from the *inshore* waters of the east coast of India in June-July⁸. Based on measurements during August-September 1978 chl *a* up to 50 mg m^{-2} was reported inshore⁹ and was concluded that "the primary production of BOB is not less than that reported from the AS"³⁸. Most measurements during this study that covered different seasons are in effect less than $0.5 \text{ g m}^{-2} \text{ d}^{-1}$ along with very low chlorophyll *a* (usually $<0.1 \text{ mg m}^{-3}$ or $<20 \text{ mg m}^{-2}$).

While the influence of nitrate and silicate concentrations on the primary production (PP) was implicit, cold-core eddies at 9°N 88°E and 17°N 85°E enhanced chlorophyll and primary production implying their strong influence on biological productivity. Our observations suggest that the primary production in the Bay is somewhat higher during FIM, NEM followed by SuM and SpIM (Table 3). Aside from strong stratification as a

consequence of freshwater capping, rapidly diminishing euphotic depth (from about 40-50m in open ocean to $<6\text{m}$ inshore) along with the lack of major upwelling regions (unlike the Arabian Sea) may be the plausible reasons for the low primary production in the BoB. Lower primary production as a consequence of unfavorable physical, atmospheric and turbidity regimens is leading, apparently, to consequent low BP and, secondary production.

Ubiquitous and abundant heterotrophic bacteria are key players in ocean biology and, are important components of marine biomass³⁹. They form food for protozoa, invertebrate larvae and many large zooplankton. Further, they regenerate dissolved nutrients required for marine photosynthesis and formation of newer organic biomass. In addition, they are pivotal in remineralizing the dead organic matter releasing many inorganic dissolved nutrients such as NO_3 , PO_4 , SiO_3 , CO_2 , H_2S etc. which govern the marine chemosynthesis and fuel the biogeochemistry of the oceans⁴⁰. In general, Bacterial biomasses in the BoB are higher than those reported from the Arabian Sea. Seasonal differences in bacterial numbers and production rates at different sampling locations are depicted in Fig. 2 and Fig. 4. Abundance of bacterioplankton in the BoB are generally comparable to ranges reported from different regions of tropical oceanic waters. Although the observed bacterial production (BP) rates are lower than those in the productive Arabian Sea, it is quite intriguing that the bacterial abundances are higher. In the Bay, bacterioplankton [quite abundant with $3 \times 10^8 \text{ cells l}^{-1}$] attained maximum numbers usually at the upper boundary of the thermocline where higher biomasses of mesozooplankton were recorded.

In the Bay, heterotrophic bacteria are prominent contributors to this biomass almost throughout the year. The bacterial abundance was higher mostly in the central region during SuM compared to other seasons. In the overall, they are comparable to those recorded from the Arabian Sea^{21,22,41} and higher than in the Equatorial Indian Ocean⁴². A comparative account of seasonal stocks of Hbac carbon calculated using $11 \text{ fg C cell}^{-1}$ implies the standing stocks of bacterial carbon to be higher during SuM in CB and during FIM in the WB. They are of moderate quantity during NEM and, the lowest during SpIM. In WB, the annual bacterial carbon averaged 0.332 g C m^{-2} and in the CB, 0.335 g C m^{-2} in the 0-120 m column. The average bacterial biomass equaled 41% of

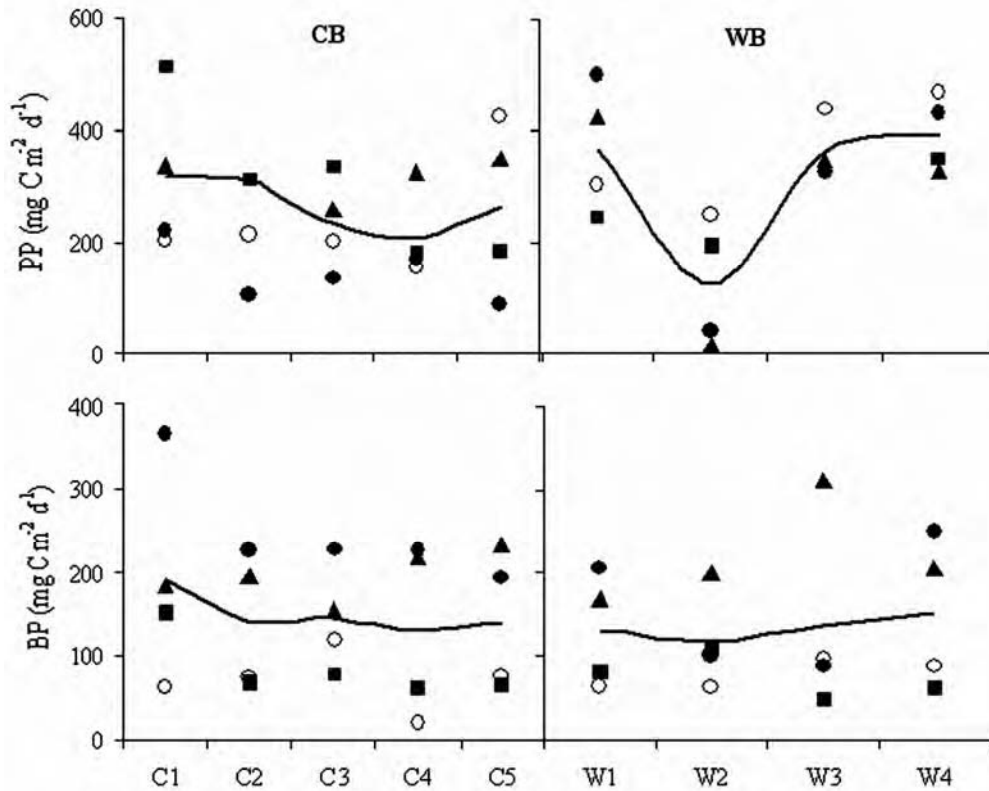


Fig. 4— Seasonal variations in primary (PP) and bacterial production (BP) at different sampling locations in the central (C1-C5) and western (W1-W4) Bay of Bengal. Symbols are: ● for Summer Monsoon, ■ for Fall intermonsoon, ▲ for Northeast Monsoon and, ○ for Spring Intermonsoon. The line—, depicts the average value derived using the data points from corresponding locations.

phytoplankton biomass in the CB and as high as 36% in the WB. Though puzzlingly slower in growth rates, this high biomass in the WB implies that the heterotrophic bacteria are efficient in assimilating the allochthonous organics and, are far more important in the food web dynamics of the coastal BoB.

The water column microfauna in the size range of 20-200 μm , the microzooplankton, can be called operators of microbial loop in the marine environment. All protozoa, invertebrate larvae, early stages of mesozooplankton <200 μm fall in this category. They also form food of many mesozooplankters and fish larvae⁴³. Together with heterotrophic bacteria, microzooplankton are pivotal in extending and sustaining deep-sea fauna⁴⁴. Microzooplankton biomass was low and did not indicate drastic spatial variations. But there were temporal variations. Tintinnid ciliates and heterotrophic dinoflagellates were the predominant fauna.

Strong seasonal shifts in mesozooplankton composition were also evidenced. They were

specifically evident with SuM and SpIM supporting higher biomass compared to the other two seasons in the CB. *Pyrosoma* swarms and scyphomedusae contributed to the higher biovolumes during SuM and SpIM respectively. The biomass in the mixed layer increased from SuM, FIM, NEM to SpIM. Higher biomasses were recorded at locations in the vicinities of cold-core eddies⁴⁵.

In general, the chl *a*, PP, BP, and MCZP abundance were more in the south of 15°N along 88°E. In the WB, northward increases in these parameters were common during most seasons. A number of subsurface maxima in bacterial abundance were observed and, their abundances increased with depth in the WB. This could be possibly due to the higher amounts of carbon fluxes in to deeper regions in the coasts. From such abundances and their subsurface maxima, it can be suggested that higher bacterial abundances in the deep BoB are unique. Bacteria are primarily responsible for assimilating the dissolved organic matter even in the deeper layers.

Via microbial loop, they are forage to deep-sea fauna, which are not only diverse but noticeably numerous²¹. Thus, it is important to understand their relationship with other microheterotrophs. With MCZP abundances being more in the southern region of the BoB, it is quite likely that the heterotrophic bacteria respond to grazing pressures and have a relatively rapid turnover. This can be indirectly evidenced from the high bacterial biomass as well as faster BP south of 15°N²¹. Aloricate ciliates and heterotrophic flagellates were discerned as the predominant groups that are main bacterivores among the microzooplankton. Grazing by these groups on bacteria appears to be an important event in the trophodynamics of the BoB. In addition, the sizable biomass of mesozooplankton [*vis a vis* Arabian Sea] in the epipelagic zone can be ascribed to their possibility of 'engulfing/phagocitizing' bacterial cells along with other food particles. Thus, heterotrophic pathway of energy transfer apparently is more prominent in the low chlorophyll productivity regions of the Bay.

Supply of energy and carbon from preponderant diatoms and, microheterotrophic communities however, are of greater significance for zooplankton in the Bay. The daily photosynthesis, phytoplankton exudates and cellular materials released from sloppy feeding of zooplankton, viral lysis, faunal excreta, carcass fragmentation and decomposition, and natural mortality of phytoplankton are of great importance in the trophodynamics. A combination of bacteria and other microheterotrophs being 'more complete and highly nutritious' and ingesting them even indirectly via aggregates or, directly would be a more efficient means for zooplankton and, macrofaunal growth and sustenance. Mostly never considered in the classical food webs, these small sized microheterotrophic assemblages with very high carbon standing stocks may be playing a major role. With sizable biomass equaling (41% in CB) or (36% in WB) of chlorophyll carbon, bacteria, and consequent heterotrophic food chain, appear important in sustaining MCZP as well as MZP. In addition to remineralizing most of the inorganic nutrients essential for autotrophic production in the euphotic zone of the Bay, the capacity of microheterotrophs, heterotrophic bacteria in particular, in assimilating DOM and POM in the deep might certainly be far more important than we have so far realized. Increased flux of organic carbon to the subsurface in the northern latitudes due to

ballast effect⁴⁶ from the river derived mineral particles settling onto organic aggregates may accelerate particle sedimentation in the water column and in turn help heterotrophic bacterial abundance.

Traditionally, the BoB is considered poorer in biological productivity *vis a vis* its western counterpart, the AS. Although the riverine flux is expected to bring-in large amount of nutrients, they are thought to be lost either within the river mouths or, to the deep because of Bay's narrow shelf. Heavier cloud cover may be another reason. Episodic cyclonic events are likely to churn-up and break the stratification and help inject nutrients to the usually shallow euphotic zone (due to turbidity arising from sediment influx), enhancing photosynthetic production at least for a short while. While surface stratification and higher suspended loads are greater hindrances to the general productivity and overall biology of the Bay, persistent cold core eddies in the central Bay around 9 °N and in the northwestern Bay are apparently important in enhancing the biological productivity at least during some period of the year, in some pockets. Thus, more understanding through ecological modelling efforts and through further investigation on important physical as well as chemical characteristics of the Bay seem to hold answers to the apparently lower photosynthetic productivity.

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References

- 1 Prasad, T. G., Annual and seasonal mean buoyancy fluxes for the tropical Indian Ocean, *Curr. Sci.*, 73 (1997) 667-674.
- 2 Subramanian, V., Sediment load of Indian rivers, *Curr. Sci.*, 64(1993) 928-930.
- 3 Prasanna Kumar, S., Muraleedharan, P. M., Prasad, T. G., Gauns, M., Ramaiah, N., De Souza, S. N., Sardessai, S. & Madhupratap, M., Why is the Bay of Bengal less productive during summer monsoon compared to the Arabian Sea?, *Geophys. Res. Lett.*, 29 No. 24(2002) doi: 10.1029/2002GL016013.
- 4 Prasanna Kumar, S., Nuncio, M., Narvekar, J., Kumar, A., Sardessai, S., De Souza, S. N., Gauns, M., Ramaiah, N. & Madhupratap, M., Are eddies nature's trigger to enhance biological productivity in the Bay of Bengal?, *Geophys. Res. Lett.*, 31 L07309(2004) doi: 10.1029/2003GL019274.
- 5 Qasim, S. Z., Biological productivity of the Indian Ocean, *Indian J. Mar. Sci.*, 6(1977) 122-137.

- 6 Sen Gupta R., De Sousa S. N. & Reddy C. V. G., On nitrogen and phosphorous in the western Bay of Bengal, *Indian J. Mar. Sci.*, 6(1977) 107-110.
- 7 Radhakrishna, K., Devassy, V. P., Bhargava, R. M. S. & Bhattathiri, P. M. A., Primary production in the Northern Arabian Sea, *Indian J. Mar. Sci.*, 7(1978) 271-275.
- 8 Nair, K. K. C., Jacob, P. G. & Kumaran, S., Distribution and abundance of planktonic amphipods in the Indian Ocean, in: *The biology of the Indian Ocean*, edited by B. Zeitzschel & S.A. Gerlach (Springer-Verlag, Berlin) (1973), pp. 349-356.
- 9 Bhattathiri, P. M. A., Devassy, V. P. & Radhakrishna, K., Primary production in the Bay of Bengal during Southwest monsoon of 1978, *Mahasagar-Bulletin of the National Institute of Oceanography* 13(1980) 315-323.
- 10 La Fond, E. C., Oceanographic studies in the Bay of Bengal. Proceedings of the Indian Academic Sciences (Earth and Planetary Sciences) 46B(1957) 1-46.
- 11 Suryanarayana, A., Murty, V. S. N., Sarma, Y. V. B., Babu, M. T., Rao, D. P. & Sastry, J. S., Hydrographic features of the western Bay of Bengal in the upper 500 m under the influence of NE and SW monsoons, in: *Oceanography of the Indian Ocean*, edited by B. N. Desai (Oxford & IBH Publishing Co. Pvt. Ltd., New Delhi) (1991), pp. 595-604.
- 12 Murty, V. S. N., Sarma, Y. V. B., Rao, D. P. & Murty, C. S., Water characteristics, mixing and circulation in the Bay of Bengal during Southwest monsoon, *J. Mar. Res.*, 50(1992) 207-228.
- 13 Varkey, M. J., Murty, V. S. N. & Suryanarayana, A., Physical oceanography of Bay of Bengal and Andaman Sea, in: *Oceanography and marine biology: an annual review*, edited by A. D. Ansell, R. N. Gibson & M. Barnes (UCL Press.) Vol 34(1996) pp. 1-70.
- 14 Schott, F. & McCreary, Jr. J. P., The monsoon circulation of the Indian Ocean, *Prog. Oceanogr.*, 51(2001) 1-123.
- 15 De Sousa, S. N., Naqvi, S. W. A. & Reddy, C. V. G., Distribution of nutrients in the western Bay of Bengal, *Indian J. Mar. Sci.*, 10(1981) 327-331.
- 16 Rao, C. K., Naqvi, S. W. A., Kumar, M. D., Varaprasad, S. J. D., Jayakumar, D. A., George, M. D. & Singbal, S. Y. S., Hydrochemistry of the Bay of Bengal: possible reasons for a different water-column cycling of carbon and nitrogen from the Arabian Sea, *Mar. Chem.*, 47(1994) 279-290.
- 17 Madhupratap, M., Gauns, M., Ramaiah, N., Prasanna Kumar, S., Muraleedharan, P. M., De Sousa, S. N., Sardessai, S. & Muraleedharan, U., Biogeochemistry of the Bay of Bengal: physical, chemical and primary productivity characteristics of the central and western Bay of Bengal during summer monsoon 2001, *Deep-Sea Res. II*, 50(2003) 881-896.
- 18 UNESCO Protocols for the Joint Global Ocean Flux Study (JGOFS), *Manual and Guides* 29(1994) pp. 170.
- 19 Ramaiah, N., Raghukumar, S. & Gauns, M., Bacterial abundance and production in the central and eastern Arabian Sea, *Curr. Sci.*, 71(1996) 888-893.
- 20 Ramaiah, N., Sarma, V. V. S. S., Gauns, M., Dileep Kumar, M. & Madhupratap, M., Abundance and relationship of bacteria with transparent exopolymer particles during the 1996 summer monsoon in the Arabian Sea, *Proc. Indian Acad. Sci., (Earth Planet Sci)*, 109(2000) 443-451.
- 21 Fernandes, V., Ramaiah, N., Paul, J. T., Sardessai, S., Jyothibabu, R. & Gauns, M., Strong variability in bacterioplankton abundance and production in central and western Bay of Bengal, *Mar Biol* 153(2008) 975-985. DOI 10.1007/s00227-007-0873-z.
- 22 Gauns, M., Mohanraju, R. & Madhupratap, M., Studies on the microzooplankton from the central and eastern Arabian Sea, *Curr. Sci.*, 71(1996) 874-877.
- 23 Gauns, M., *Role of microzooplankton in the food chain dynamics of some tropical marine environments*, Ph. D. Thesis, Goa University, India, (2000).
- 24 Madhupratap M., Gopalakrishnan T. C., Haridas P., Nair K. K. C., Aravindakshan P. N., Padmavati G. & Shiney P., Lack of seasonal and geographical variation in mesozooplankton biomass in the Arabian Sea and its structure in the mixed layer, *Curr. Sci.*, 71(1996) 863-868.
- 25 Fernandes, V. & Ramaiah, N., Mesozooplankton community in the Bay of Bengal (India): spatial variability during the summer monsoon, *Aquat. Ecol.*, (in press) DOI 10.1007/s10452-008-9209-4.
- 26 Fernandes, V., *Mesozooplankton community structure: Its seasonal shifts, grazing and growth potential in the Bay of Bengal*, Ph. D. Thesis, Goa University, India, (2008).
- 27 Jyothibabu, R., *Ecobiogeography, spatial and temporal variations of microzooplankton along the east coast of India*, Ph.D thesis, Cochin University of Science and Technology, Kochi, India, (2004).
- 28 Krey, J. & Babener, B., Environmental conditions, in: *Phytoplankton production Atlas of the International Indian Ocean Expedition*, (1976) pp 15-16.
- 29 Bhattathiri, P. M. A., Devassy, V. P. & Radhakrishna, K., Primary production in the Bay of Bengal during Southwest monsoon of 1978. *Mahasagar-Bulletin of the National Institute of Oceanography* 13(1980) 315-323.
- 30 Gomes, H. R., Goes, J. I., Saino, T., Influence of physical processes and freshwater discharge on the seasonality of phytoplankton regime in the Bay of Bengal. *Cont. Shelf Res.*, 20 (2000) 313-330.
- 31 Vinayachandran, P. N., Matthew, S., Phytoplankton bloom in the Bay of Bengal during the northeast monsoon and its intensification by cyclones. *Geophys. Res. Letts.*, 30(2003) 1572, doi:10.1029/2002GL016717.
- 32 Shetye, S. R., Gouveia, A. D., Shenoi, S. S. C., Sunder, D., Michael, G. S. & Nampoothiri, G., The western boundary current of the seasonal subtropical gyre in the Bay of Bengal. *J. Geophys. Res.*, 98 CI(1993) 945-954.
- 33 Paul, J. T., *Ecological and experimental analyses of phytoplankton dynamics in the Bay of Bengal*, PhD thesis, Goa University, India, (2007).
- 34 Paul, J. T., Ramaiah, N., Gauns, M. & Fernandes, V., Preponderance of a few diatom species among the highly diverse microphytoplankton assemblages in the Bay of Bengal. *Mar. Biol.*, 152(2007) 63-75 DOI 10.1007/s00227-007-0657-5.
- 35 Madhu, N. V., Jyothibabu, R., Maheswaran, P. A., Gerson, V. J., Gopalakrishnan, T. C. & Nair K. K. C., Lack of seasonality in phytoplankton standing stock (chlorophyll *a*) and production in the western Bay of Bengal, *Cont. Shelf Res.*, 26(2006) 1868-1883.
- 36 Herbland, A. & Voituriez, B., Hydrological structure analysis for estimating the primary production in the tropical Atlantic Ocean, *J. Mar. Res.*, 37(1979) 87-101.
- 37 Prasanna Kumar, S., Nuncio, M., Ramaiah, N., Sardessai, S., Narvekar, J., Fernandes, V. & Paul, J. T., Eddy-

- mediated biological productivity in the Bay of Bengal during fall and spring intermonsoons, *Deep-Sea Res. I*, 54(2007) 619–1640.
- 38 Pant, A., Primary productivity in coastal and off-shore waters of India during two southwest monsoons, 1987 and 1989, in: *Oceanography of the Indian Ocean*, edited by B.N. Desai (Oxford and IBH, New Delhi) (1992), pp. 81-90.
- 39 Ducklow, H. W., Smith, D. C., Campbell, L., Landry, M. R., Quinby, H. L., Steward, G. F. & Azam F., Heterotrophic bacterioplankton in the Arabian Sea: basinwide response to year-round high primary productivity, *Deep-Sea Res. II*, 48 (2001) 1303–1323.
- 40 Ramaiah, N., Role of Heterotrophic Bacteria in Marine Ecological Processes, in: *Marine Microbiology: Facets and Opportunities*, edited by N. Ramaiah (National Institute of Oceanography, Goa) (2004), 27-38 pp.
- 41 Raghukumar, S., Ramaiah, N., Raghukumar, C., Dynamics of thraustochytrid protista in the water column of the Arabian Sea. *Aquat. Microb. Ecol.*, 24(2001) 175–186.
- 42 Fernandes, V., Rodrigues, V., Ramaiah, N. & Paul, J. T., Relevance of bacterioplankton abundance and production in the oligotrophic equatorial Indian Ocean, *Aquat. Ecol.* 42(2008) 511-519, DOI 10.1007/s10452-007-9142-y.
- 43 Landry, M. R., et al., Biological response to iron fertilization in the eastern equatorial Pacific (IronEx II). III. Dynamics of phytoplankton growth and microzooplankton grazing, *Mar. Ecol. Prog. Ser.*, 201(2000) 57–72.
- 44 Ramaiah, N., Raghukumar, S., Gauns, M. & Madhupratap, M., Seasonal variations in carbon biomass of bacteria, thraustochytrids and microzooplankton in the Northern Arabian Sea, *Deep-Sea Res. II*, 52(2005) 1910–1921.
- 45 Fernandes, V., The effect of semi-permanent eddies on the distribution of mesozooplankton in the central Bay of Bengal, *J. Mar. Res.*, 66(2008) 465-488.
- 46 Ittekkot, V., Nair, R. R., Honjo, S., Ramaswamy, V., Bartsch, M., Manganini, S., Desai, B. N., Enhanced particle fluxes in Bay of Bengal induced by injection of fresh water. *Nature* 351(1991) 385-387.