# Quantitative distribution of meiobenthos in the Gulf of Martaban, Myanmar Coast, north-east Andaman Sea

Z. A. Ansari<sup>1\*</sup>, Pratik Mehta<sup>2</sup>, Ramila Furtado<sup>1</sup>, Cherry Aung <sup>3</sup> & R. S. Pandiyarajan<sup>1</sup>

<sup>1</sup>National Institute of Oceanography, Dona Paula, Goa, India.

<sup>2</sup>National Institute of Oceanography, Four Bungalows, Andheri, Mumbai, India.

<sup>3</sup>Department of Marine Science, University of Mawlamyine, Myanmar

[E-mail: zakir.ansari2008@gmail.com.]

Received 18 June 2012; revised 22 October 2012

Quantitative distribution of meiofauna in the depth range 20 to 1000 m of the Gulf of Martaban, Andaman Sea was studied from 46 stations during a synaptic survey carried out in April-May 2002 of ORV Sagar Kanya Cruise SK175. Fauna was dominated by three taxa: free living nematodes (80%) benthic copepods (5.9%) and foraminiferans (2.8%). Other groups together contributed more than copepods in total abundance. Total density ranged between 40 and 612/10 cm² and dry weight biomass from 0.21 to 0.428 mg / 10 cm² in different sediment type and depth zone. Numerical abundance of meiofauna was high in fine silty clay and low in sandy bottom. Formation of three main clusters suggests the influence of dominant sediment texture of clayey sand sand silt clay, silty-clay clayey-silt, and sandy substratum. Fauna was contagiously distributed except at few stations where the distribution was regular. Meiofauna of the present study were similar to those of Andaman Sea and Bay of Bengal and the density changes appears to be related to hydrographic condition and sediment characteristics of the region.

[Keywords: Meiofauna, Quantitative distribution, Martaban Bay, Myanmar coast]

### Introduction

It is well recognized that effective management and conservation of coastal resources necessitates understanding system structure and function at multiple spatial scale<sup>1</sup>. Soft sediment meiofauna has been the subject for intense quantitative study due to the important role it plays in the functioning of the coastal system. Knowledge on meiobenthos has increased considerably during recent decades, and attempts have been made to relate standing stocks with various environmental factors<sup>2,3</sup>. Increase of interest in meiofauna research has produced an expanding volume of literature on many aspect of this field particularly from temperate water. The understanding of mechanisms that control the abundance and biomass of meiobenthic fauna of the continental shelf and open sea in tropics has been limited by the paucity of descriptive studies of subtidal benthic communities<sup>4</sup>. Considering their role in nutrient cycle, food for higher trophic group and their use as biological indicator it is important to study the

response of meiofauna of different ecosystem<sup>5</sup>. Today majority of meiofaunal studies focusing on environmental challenges point to the urgent need of exploring potential usage of meiobenthos in environmental policy<sup>6</sup>.

Gulf of Martaban (Ayeyarwady continental Shelf), East Andaman Sea, is one of the least investigated regions of the Indian Ocean7. Ayeyarwady is the fifth largest river in terms of suspended sediment discharge and together with the Sanlween and Sittang deposits annually more than 350 million tones of sediment into the northern Andaman Sea. Freshwater and sediment discharge are highly seasonal with more than 80% of the annual discharge during the south-west monsoon. During this period the enhanced flux of labile organic material reaches to the benthic boundary that has profound impact on the distribution and abundance of benthos. This makes the present study area a complex system for oceanographers. There are few studies carried out on meiobenthos from the eastern Bay of Bengal

and Andaman Sea<sup>8-10</sup> but there is no information on the benthos of the Gulf of Martaban, Myanmar coast. Such information would be vital considering these areas for natural resources such as fisheries, minerals, oil and gas. The main objective of the present study was to examine the quantitative distribution of meiobenthos of the Gulf of Martaban, Myanmar coast, north-east Andaman Sea.

### **Materials and Methods**

Meiofauna sampling was conducted at 47 stations during April-May 2002 cruise SK 175 of Sagar Kanya (Fig. 1). One grab sample (0.1 m<sup>2</sup> area, 20 cm

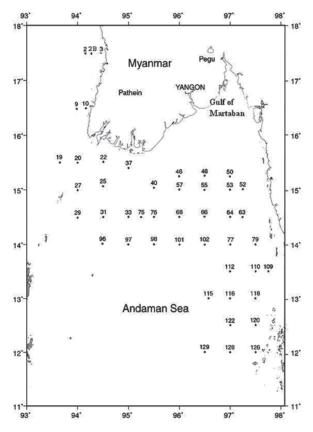


Fig. 1- Map showing station position in the study area

penetration) with undisturbed top sediment was collected for meiofaunal analysis. Three meiofaunal sub-cores (disposable syringe of 2 cm inner diameter and 10 cm length) were removed from the grab samples and preserved separately with 5% buffered formaldehyde and Rose Bengal solution, sealed and stored on board the ship for sorting. Meiofauna in all core fractions were extracted by sieving the samples with a set of two sieves, the upper one of

0.5 mm mesh size and the lower one of 0.062 mm mesh size. Animals retained on the lower mesh screen were considered for meiofauna. Meiofauna samples were examined under Stereoscopic binocular microscope and all organisms were identified to major taxa level and enumerated. Only dominant nematodes and copepods were identified up to family level. Dry weight biomass was calculated by taking representative individual biomass (average) of each group after drying in an Oven at 60°C till a constant weight was achieved.

# Data analysis

For total density average of three replicate was taken and the mean valve per was calculated. The data were subjected to statistical analysis using PRIMER. Green's index of dispersion<sup>11</sup> was calculated for total meiofauna by the following equation:

$$ID = (S^2/x - 1) ("x - 1)^{-1} ... (1)$$

where,  $S^2$  = variance, x = mean number of animals, x=number of animals in each replicate. The index value of 0, +1 and -1 indicate maximized random distribution, clumped distribution and uniform distribution, respectively. Shepard's<sup>12</sup> sediment classification, based on proportions of sand, silt and clay size particles was used for the description of sediment type. The correlation coefficient between density/biomass and depth was performed using best fit regression.

## Results

# Distribution of sediment

The distribution of sediment is related to the bottom topography and prevailing currents in the area. Present area falls under Gulf of Martaban of the Ayeyarwady continental shelf which has complex sedimentary system. A detail report on the sediment distribution of the present study area is given in Rao *et.al*<sup>13</sup>. Sediment transport and the movement of suspended matter is a seasonal feature and plays critical role in the in the biogeochemistry of the area<sup>14</sup>. Sediment distribution reveals three distinct areas in terms of sediment texture (i) a near-shore mud belt (ii) outer shelf relict sand and (iii) mixed sediment with varying proportion of sand, silt and clay at intermediate depth.

# Faunal composition and abundance

The total meiofaunal density (No/10 cm² surface area) enumerated in the samples from different depth and station is given in Table 1 and Fig. 2. Density

was moderate to high, suggesting that the present study with the fine and medium sediment types were capable of supporting good meiofauna population. There were however, some qualitative differences in the occurrence of major meiofauna taxa among the

Table 1	Table 1–Distribution of meiofaunal density (No./10cm²) and dry weight biomass (mg/10cm²) in the study			
St. No.	Sediment type	Depth (m)	Biomass	Density
2	sand,silt,clay	137	0.28	409
2B	Silty- clay	71	0.33	475
3	Silty-clay	49	0.36	525
9	Silty- clay	132	0.21	301
10	clayey,silt	31	0.38	544
19	Silty- clay	282	0.28	406
20	sandy	33	0.30	440
22	Sand silt clay	37	0.38	551
25	Clayey-sand	47	0.35	509
29	Sandy	90	0.33	481
31	sandy	90	0.31	448
33	sand,silt,clay	88	0.29	428
35	Silty- clay	50	0.29	419
37	Clayey-silt	23	0.38	544
40	Clayey silt	63	0.28	411
46	Sand, silt clay	20	0.39	569
48	Silty- clay	22	0.42	612
50	Silty- clay	20	0.42	606
52	Sand Silt clay	28	0.38	553
53	Silty- clay	27	0.38	543
55	Sand silt, clay	31	0.40	572
57	Silty- clay	68	0.32	470
63	Sandy	35	0.41	590
64	sandy	52	0.37	531
66	sandy	97	0.29	422
68	sandy	103	0.29	425
75	sandy	73	0.32	468
76	Silty-clay	94	0.31	44
77	sandy	78	0.29	428
79	sandy	57	0.30	430
96	clayey,silt	550	0.25	368
97	Clayey-silt	600	0.24	346

98	sand,silt,clay	230	0.32	464
101	Sand-silt-clay	225	0.24	353
102	sandy	110	0.25	359
109	Silty-clay	51	0.25	365
110	sand,silt,clay	72	0.29	425
112	Sand silt clay	85	0.28	402
115	sandy	124	0.22	475
116	sandy	96	0.23	335
118	sand	83	0.27	393
120	sand	80	0.28	406
122	sandy	198	0.28	401
126	sandy	75	0.29	427
128	sandy	232	0.32	444
129	Clayey-silt	946	0.28	329

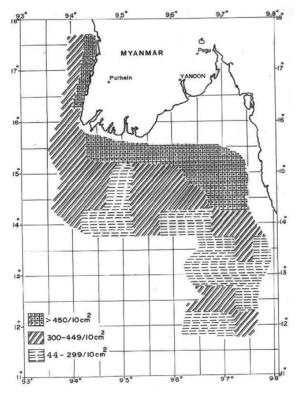


Fig. 2–Distribution of mean meiofaunal density in the study

stations. Ten taxonomic groups and crustacean nauplii were identified. They include Nematodes, Nemertines, Foraminiferans, Harpacticoid Copepods, Turbellarian, Polychaetes, Kinorhyncha, Ostracoda, and Tardigrada. Nematodes were always nearly the

dominant group in the meiobenthos, comprising more than 80% of the total fauna. Harpacticoida was next in the order of abundance (5.39%) followed by foraminiferans, and turbellarians. Other group showed higher percentage than copepods but in reality this group was represented by polychaeta, ostracoda, tardigrada, kinorhyncha, gastritricha and crustacean nauplii which were insignificant in their numerical abundance. Total faunal density ranged between 44/ 10 cm<sup>2</sup> (Station 76) and 612/10 cm<sup>2</sup> (Station 46) with an average value of 460/10 cm<sup>2</sup>. The numerical abundance of meiofauna was generally high in the shallower depth and decreased progressively with increasing depth. Nematodes were the only group that showed 100% prevalence while benthic copepods recorded from all but one station (#76). The other groups were inconsistent in the occurrence.

Meiobenthic biomass (mg/10 cm²) distribution showed wide variation and the values ranged between 0.21 and 0.428 (Fig.3). Presence of larger foraminiferans increased the dry weight biomass. Near-shore areas (<50 m) mainly contribute the high biomass production and the standing crop decreased with the increasing depth as was seen in the case of density distribution.

An attempt was made to study the dominant families of two major taxa, the nematode and benthic copepod. Dominant nematode families were

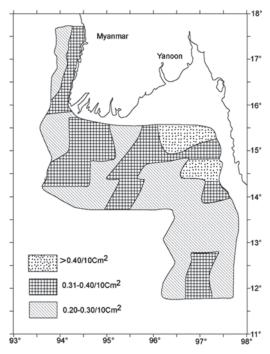


Fig. 3-Distribution of DW biomass

Oncholaimidae, Comesomatidae, Desmodoridea, Xyalidae and Linhomoidae, represented by several species of nematodes. Hey were more abundant in fine deposit of silt and clay. Dominant Harpacticoid families encountered were Longipediidae, Canuellida,

Table 2–Distribution of meiofauna (No/10 cm²) in relation to depth

Depth (m)	No of observation	Total density Range and mean with SD
20-50	13	419-590 (550±44.7)
51-100	19	44-531 (412±99)
101-200	6	301-425(399±57.7)
201-500	4	353-612(416±42.3)
501-1000	4	329-368(349±14)

Ectinosomatidae, Diosaccidae, ameiridae, Paramesochridae and Laophontidae. Many of the families were represented by few individual and were not confined to a particular habitat or sediment types. Copepods had dominant members of interstitial and soft bottom sediment.

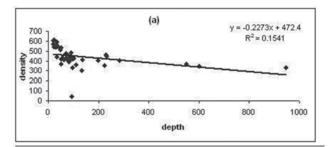
### Distribution in relation to depth

A depth-wise profile of the density distribution of major taxa (Table 2) and total density (Table 3) is given. Statistical analysis (T- test using 46 samples) revealed a significant difference in the average depthwise numerical abundance of meiofauna (P<0.05)

Table 3-Percentage composition of meiofaunal taxa in different depths.

Taxa	20-50 m	51-100 m	101-200 m	201-500 m	>500 m
Nematoda	75	78	82	77	83
Harpacticoida	5	6	5	8	5
Turbellaria	4	2	2	2	2
Foraminiferans	3	2	3	3	4
Polychaeta	3	2	2	1	-
Gastrotricha	-	2	-	1	-
Tardigrada	2	1	-	2	2
Kinorhyncha	1	2	-	-	2
Ostracoda	2	3	2	1	-
Nemertine	2	-	3	3	1
Crustacea nauplii	3	2	1	2	1

except at 201-500 m . Higher count in 201-500 m was due to the occurrence of large number of foraminiferans. Fauna declined with increasing depth. These changes were more pronounced in the shallower region than in the deeper water. Nematodes were more consistent in occurrence at all depths. Benthic copepods remained low in all depths (< 8%). However, among other groups the turbellarians were found to decrease with increasing depth. Foraminiferans, on the other hand, showed no effect of depth. Other groups of polychaeta, gastrotricha, tardigrada, ostracoda and crustacean nauplii were inconsistent in occurrence. Numerical abundance and biomass of meiofauna showed negative but insignificant correlation with depth (Fig. 4).



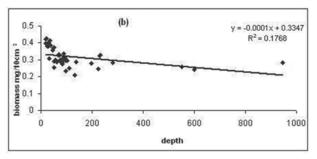


Fig. 4-Distribution of meiofaunal density (a) and Biomass (b) in relation to depth

Total meiofauna and dominant taxa nematode when plotted on a latitudinal scale, showed some variation in density distribution (Fig.5). Faunal density showed increasing trend towards north. A slight lowering in number was seen between Latitude 16° and 17° probably because there were fewer number of samples and smaller area covered in the sampling. Nematodes being numerically the dominant group, showed a trend similar to total density. Due to the sheer numerical dominance the nematodes become the main representative of meiobenthic organisms that is reflected in spatial and temporal distribution trend.

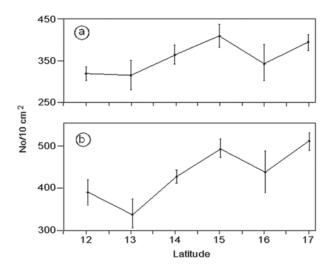


Fig. 5-Trends of average total density ( ±SD) with latitude.

(a) Nematoda (b) Total meiobenthos.

According to Sajan *et al.*<sup>15</sup> variables such as depth, latitude and organic matter are the most relevant parameters influencing the biomass and density of subtidal meiofauna.

# Fauna-sediment relationship

The distribution and abundance of meiofauna is strongly related to sediment granulometry. Although the sediment was classified originally into five types, for convenience it was grouped into three types namely (1) clayey sand and sand silt clay, (2) siltyclay and clayey silt and (3) sandy. Average meiofauna density and biomass was calculated in each type and the result is presented in Fig. 6. Density and biomass were maximum in sediments of silty clay and clayey silt. In the other two types of sediment the density and biomass distribution was lower. Richness or paucity of fauna in different sediment types depends, to some extent, on the inter-particle space created by the particle size of the deposit. Nematode families showed preference to fine silty-clay and clayey-silt while the benthic copepods were more common in sandy substratum.

Dispersion pattern of meiofauna when compared between replicates showed clumped or contagious distribution. Of the 46 sets of Green's index value, only three indicated a uniform distribution and non-a random distribution. This corroborate the earlier report that meiofauna density was clumped<sup>2</sup>. Such negative distribution is attributed to patchy food dispersion in the sediment and oxygen availability.

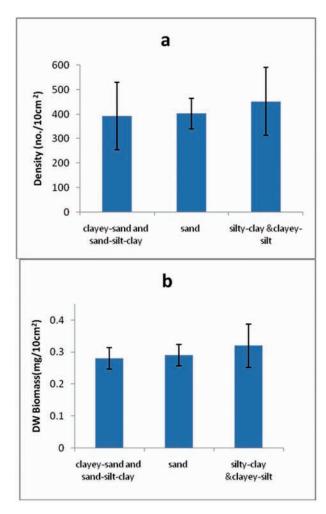


Fig. 6–Abundance of meiofauna (average±SD) in different sediment type. (a) density (b) biomass

The hierarchical grouping of stations resulting from cluster analysis using groups average linkage on meiobenthos taxa is shown in Fig. 7. Bray Curtis similarity was calculated on the root transformed data

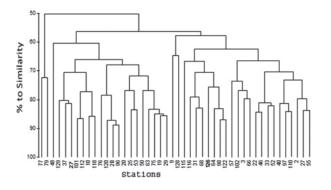


Fig. 7–Hierarchical classification of the stations with respect to percent similarity in abundance of major taxa

of meiofaunal density and from the resulting dendrogram it was possible to differentiate 3 main clusters. Fine sediment of silty-clay formed the largest cluster while stations having clayey sand and sandy sediment were grouped in the second cluster. The stations having sand, silt and clay formed the intermediate group were and placed under third cluster. The main clusters were determined at 56% similarity. Each sub cluster was further sub divided and the maximum similarity of 88% was observed between station 28 and 96. A similar picture emerged when the stations were put under MDS plot (Fig. 8). This suggest that the heterogeneity in the occurrence

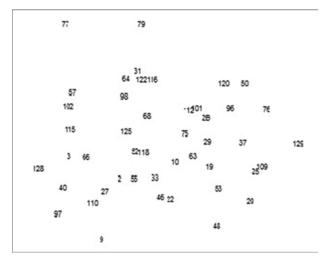


Fig. 8–MDS ordination of investigated stations for major meiobenthic taxa

of meiofaunal assemblages of the Gulf of Martaban is influenced significantly by sediment type and the organic input brought by. Large variation in the clustering suggests differences in the overall station wise abundance of dominant taxa. There was greater richness of same individuals at some station while others showed overlapping.

## **Discussion**

A general pattern relating benthic community to environmental factors across several spatial scales and their critical role have long been established<sup>16</sup>. The faunal abundance generally show a trend in number to decrease as water depth increases which is related to the amount of food reaching the seafloor. However, these general patterns are locally influenced by a number of abiotic factors such as hydrographic

regime and sediment biogeochemistry<sup>3</sup>. Diverse nature of meiobenthos appears to be the feature of Gulf of Martaban. Standing crop distribution does not strictly follow the well defined depth distribution and this could be explained by the major outlet of Ayeyarwady in the gulf. Sediment dispersal in the Ayeyawady shelf and Gulf of Martaban is strongly dependent on the reversing monsoon current<sup>13</sup>. Fine grained sediment coming through river discharge along with suspended material settled in the gulf and surrounding coastal area. It brings large amount of sediment and nutrient in the area.

Sediment granulometary is closely related to the distribution and abundance of benthos. This was clearly demonstrated in the present case. High meiofaunal abundance in silty clay and impoverishment in sand silt clay type sediment was reported from Andaman Sea<sup>8</sup> also. The fine sediment particles adsorb high organics and attract microbial flora on which many meiofauna feeds<sup>17</sup>. Sediment pore waters are important as they allow for the mobility of nutrient ions (phosphate, nitrate, ammonium, silicate) across the sediment interface and in the sediment itself. There are number of sediment dwelling functional group among meiobenthos that are considered to enhance the porosity of the sediment via their activity<sup>18</sup>. Nematodes are known as the conveyor belt and help in the oxygenation and re-mineralization of the sediment<sup>2</sup>. This allows other functional groups to co-exist in the same niche.

The degree of heterogeneity and taxonomic distinctness is the result of interaction of physicochemical properties in the sediment distribution and prevailing environmental conditions. A comparison

of present data of meiofaunal density with data from other areas is given in Table 4. Although the density distribution in the Bay of Bengal was higher at all depth, the meiofaunal abundance in the Andaman sea was similar to the present area with similarity in faunal composition. Comparison of meiofauna data from depth transects of different geographical region imply that deviation in trend distribution of standing stock can be explained by variation in local productivity and prevailing hydrographical conditions<sup>3</sup>. The decreasing meiobenthic standing crop with increasing depth has also been reported by others and is attributed to the paucity of food in the deeper waters<sup>19</sup>. Subtidal meiobenthic abundance and community composition is governed by the sedimentary features and productivity of overlying water. Ayeyarwady river discharges large amount of sediment loaded with nutrient in the Martaban gulf which may provide the additional source of food for high population of metazoan meiofauna of the area. A number of meiofauna are reported to feed on microphytobenthos and adsorbed organic particles particularly in shallow areas<sup>17</sup>.

Abundance of benthic fauna support the food chain in marine ecosystem. High macrofaunal standing crop has been reported from the same area<sup>20</sup>. Recently it has been reported that meiofauna constitute very active component of the benthic ecosystem and is more efficient in transferring the energy to higher trophic levels in comparison to its larger counterpart<sup>21,22</sup>. This along with macrofauna appears to be key factor associated in benthic productivity of an area<sup>23</sup>. The data of present study has given a first hand information on meiofaunal densities, of Gulf of

Locality	Depth (m)	Total density Range and mean with SD	Reference
Bay of Bengal	15-50	358-987(505±112)	Ansari et al , 1977 <sup>9</sup>
Bay of Bengal	100-150	260-1630(638±276.5)	Ansari et al, 1977 <sup>9</sup>
Andaman Sea	30-2150	68-438(247±106.4)	Ansari & Parulekar, 1981 <sup>8</sup>
Malacca Strait	80-13500	50-250(149±54.6)	Parulekar and Ansari 1981 <sup>10</sup>
Present Study	50-1000	44-612(460+79.2)	

Table 4-Comparison of meiofaunal density from different areas

Martaban, Myanmar coast. It is possible that the meiobenthic population of Myanmar coast is influenced independently by a complex suit of environmental parameters such as sediment characteristics, depth, latitude and biological parameters. However, due to non-availability of data on environmental variables a significant correlation could not be drawn. It is suggested that more studies in the present area are required for a better understanding of the spatial and temporal distribution of meiobenthos and their critical role in the benthic system and local environmental policy.

# Acknowledgements

It is a part of the collaborative project "India-Myanmar joint Oceanographic studies in the Andaman Sea". Authors thank the Director, National Institute of Oceanography (NIO) (CSIR), for encouragement. This is NIO contribution number 5441.

### References

- Hyrenbach K D, Forney K A, & P K Dayton, P K, Marine protected areas and ocean basin management. Aquat. Conserv. Mar Fresh Ecosyst 10 (2004) 437-458.
- 2. Coull B C and Bell S S, Perspective of marine meiofauna ecology. In Livingston R.J. (ed), *Ecological processes in coastal and marine system* (Plenum Publishing Corporation) (1979) 189-216.
- 3. Soltwedel T, Metazoan meiobenthos along continental margin: A review. Prog Oceanogr, 46 (2000) 59-84.
- Sajan S, & Damodaran R, Fauanal composition of meiobenthos from the shelf region of the west coast of India. J. Mar. Biol. Asso. India, 49 (2007)19-26.
- 5. Coull B C, Are members of the meiofauna food for higher trophic levels? *Transactions of the American Microscopical Society*, 109 (1990) 233-246.
- Michaeta M, On the relevance of meiobenthic research for policy makers. 14<sup>th</sup> International meiofauna conference, Ghent Belgium, 11-16 July 2010, Book of Abstract, Veliz Special publication 44.
- 7. Ansari Z A and Abidi S A H, Andaman Sea its physical, chemical and biological characteristics. *Management of Aquatic Ecosystem*, (Agrawal, V.P. & S. A. H. Abidi eds), (1989) pp. 21-32.
- Ansari Z A and Parulekar A H, Meiofauna of the Andaman Sea. *Indian J. Mar. Sci.* 10(1982) 285-288.
- Ansari Z A, Harkantra S N, Nair S A, & Parulekar A H, Benthos of the Bay of Bengal: A preliminary account. Mahasagar- Bull. National Inst. Oceanogr., 10(1977) 55-60.

- Parulekar, A H & Ansari Z A, Bottom fauna of the Malacca strait. Mahasagar: Bull. Natn. Inst. Oceanogr. 14(1981)155-158.
- Elliot J M, Some methods for the statistical analysis of samples of benthic invertebrate. Freshwater Biological association Scientific Publication No., 25(1971) 159.
- Shepard F P, Nomenclature based on sand, silt, clay ratios.
   J Sedimen Petrolog, 24(1954)151-158.
- 13. Rao P S, Ramaswamy V and Thwin Swe, Sediment texture, distribution and transport on the Ayeyarwady continental 19. Giere O, Meiobenthology The microscopic fauna in aquatic sediment. (Springer Verlag, New York) 1993 pp.328.
- Ramaswamy V, Rao P.S, Rao K. H, Thwin S, Srinivas Rao V, Raiker V, Tital influence on suspended sediment distribution and dispersal in the northern Andaman Sea and Gulf of Martaban. Mar, Goel, 208 (2004) 33-42.
- Sajan S, Joyadas T V, Damodaran R, Meiofauna of the western continental shelf of India, Arabian Sea, Est Coastl shel Sci, 86 (2010) 665-674.
- 16. Weslawski J.M, Snelgrove R U R, Levin L.A. Austen M C, Kneib R T, Iliffe T M, Carey J R, Hawkins S J, & Whitlatch R B, Marine sedimentary biota as providers of ecosystem goods and services. In: D H Wall, Editor, Sustaining biodiversity and ecosystem services in soil and sediment, Island Press Washington (2004) pp. 73-98.
- 17. Ansari ZA, Inter-relationship between marine meiobenthos and microbes, *Marine Biotechnology: Facets & opportunities*. (In: Ramaiah N eds., National Institute of Oceanography, Dona Paula, Goa, India) 2004 251-257.
- Blackford J C, An analysis of benthic biological dynamics in a North Sea ecosystem model. *J Sea Research*. 38 (1997) 213-230.
- Giere O, Meiobenthology The microscopic fauna in aquatic sediment. (Springer Verlag, New York) 1993 pp 328.
- Ansari Z A, Furtado R, Badesab S, Mehta P, and Thwin S, Benthic macroinvertebrate community structure and distribution in the Ayeyarwady continental shelf, Andaman Sea. *Indian J Ma Sc.*, 41 (2012) 272-278.
- Coull B C, Greenwood J G and Donald R F, Subtropical Australian juvenile fish eat meiofauna: Experiment with winterwhiting, Sillago mculata and observation on other species. *Marine Ecology Progress Series*, 125 (1995) 13-19.
- Leguerrier D, Nathalie N, Nicolas B, Jadwiga R, Pierre

   Guy S, Le Moine Olivier and Cedric B, Numerical analysis of food web of an intertidal mud flat ecosystem Atlantic coast France. *Marine Ecological Progress Series* 246 (2003) 17-37.
- Kunitzer A, Basford D, Craeymeetsch J A, Dewarumez J M, Dorjes J, Duineveld. G C A, Eleftheriou A, Heip C, Herman P, Kingston P, Niermann U, Rachor E, Rumohr H & P A J de Wilde, The benthic infauna of the north sea. *ICES J Mar Sci*, 49 (1992) 127-144.