

Small copepods structuring mesozooplankton community dynamics in a tropical estuary-coastal system[☆]



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ABSTRACT

It is important to know the ultimate role of small copepods in structuring mesozooplankton community pattern and diversity on an estuary-coastal gradient. Here multivariate analyses were used to elucidate this in the Godavari estuary, on the east coast of India. During May 2002, corresponding to the spring intermonsoon, mesozooplankton were sampled from 4 GPS fixed stations in the estuarine reaches of River Godavari and 19 in the coastal waters where Godavari enters the Bay of Bengal. There were 91 mesozooplankton taxa represented by 23 divergent groups. Copepods were by far the most prominent in terms of species richness, numerical abundance, and widespread distribution followed by appendicularians. Small copepods of families Paracalanidae, Acartiidae, Oithonidae, Corycaidae, Oncaidae, and Euterpinae dominated. There were differing regional mesozooplankton/copepod communities, that segregated the estuary-coastal sites into different biotic assemblages: Group-I representing the estuary proper, Group-II estuary mouth and near shore, Group-III the intermediate coastal stations and Group-IV the coastal-offshore waters. Alpha (SRp, H' , J' , Δ^*) and beta diversity (MVDISP, β , β -dissimilarity) measures varied noticeably across these assemblages/areas. The significant correlation of small copepod abundance with total mesozooplankton abundance and biomass ($\text{mgDM}\cdot\text{m}^{-3}$) in the estuarine ($r: 0.40$) and coastal ($r: 0.46$ – 0.83) waters together with a regression analysis of diversity measures have revealed the importance of small copepods in the overall mesozooplankton/copepod community structure. There were 'characterizing' and 'discriminating' species, responsible for the observed assemblage patterns. Mesozooplankton/copepod community structure and the size-spectra observed during this study indicate an estuarine-coastal gradient in plankton tropho-dynamics that may shift between a microbial dominated system inside the estuary and mixotrophy in the coastal waters. The functional diversity of copepods revealed features of an effective niche sharing and efficient utilization of the coastal resources by the resident zooplankton some of which are brought out for the first time showing a tropical estuary under the influence of monsoons. The present study also illustrates the importance of, and advocates the need for, incorporating complementary or additional biodiversity measures while describing biotic communities vis-à-vis environmental gradients.

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1. Introduction

During the last three decades, estuaries and the adjacent coastal systems around the world have shown increasing signs of degradation, primarily as a result of human activities. This is of concern as,

apart from being necessary breeding grounds for a number of commercially relevant fish and invertebrates, these areas are of high ecological importance in terms of species diversity and biogeochemical processes. In addition, they are highly productive with respect to both phytoplankton and mesozooplankton. Mesozooplankton distribution in estuaries is spatially and temporally heterogeneous, more so than in any other aquatic ecosystem. In addition to changes caused by climatic alterations, the dynamic hydrographical conditions that prevail in estuaries influence zooplankton community structure both in time and space are of interest (Hansen et al., 1988; Schlacher and Wooldrige, 1995). While the mesozooplankton could be reliable indicators of ecosystem health, they also play an inevitable role in channelling

[☆] A tribute to D.V. Ramasarma for his pioneering research on Gautami Godavari.

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pelagic carbon flux in the water column or benthic communities. A systematic monitoring programme, therefore, requires a comprehensive baseline assessment of this component in an estuarine system (Soetaert and Rijswijk, 1993; Kibirige and Perissinotto, 2003).

Planktonic copepods are vital components of marine pelagic food webs, especially in the estuaries and coastal regions where they often provide over 80–90% of the total zooplankton abundance. Being notable consumers of microplankton, and prey for fish and other predators, these keystone trophic links in aquatic ecosystems transfer energy and carbon to higher trophic levels (e.g. Howlett, 1998) more efficiently than any other zooplankton taxa. The classical food chain suggests that large copepods (mainly calanoids) mediate energy available with primary producers (mainly diatoms) to the higher trophic components of economic importance (Cushing, 1989), whereas small-sized copepods are capable of efficiently exploiting the 'microbial' food chain (Turner, 2004). Despite their very high abundance and important role in marine food webs as principal grazers of microplankton, and thereby acting as direct linkages between the classical and the microbial food webs, there is less information on small copepods compared to their larger counterparts. In India, there are many previous studies on mesozooplankton that focused on the importance of copepods in estuarine and coastal waters, both from west (Madhupratap, 1978, 1979, 1987; Haridas, 1982; Goswami, 1983; Padmavati and Goswami, 1996) and east coasts (Pati, 1980; Sai Sastry and Chandramohan, 1995; Sreenivas, 1998; Chandramohan and Sreenivas, 1998; Chandramohan et al., 1999; Sterling et al., 2006; Rakesh et al., 2006, 2008). However, very few of them (e.g., Rakesh et al., 2008) have attempted a multivariate approach to delineate the zooplankton/copepod community structure and diversity in the estuary-coastal environment, and none focussing on the potential importance of small sized copepods on the zooplankton community composition.

At present, coastal species assemblages are under threat and until a better understanding of diversity for a wide range of marine habitats and what control it, is available, we have little hope of conserving biodiversity or determining the impact of human activities (Neumann-Leitao et al., 2008) or climate induced changes. Ecologists have long distinguished different components of species diversity. Proper use of these would certainly help us overcome the problems associated with biodiversity conservation and management. Based on different aspects or levels of diversity, Whittaker (1960) originally proposed partitioning the diversity into alpha, beta, and gamma components. Alpha diversity (α) or local diversity shows the total number of species in a sampling unit, while gamma diversity (γ) reveals the total number of species within a geographical area. Beta diversity (β), spatially defines species turnover between local and regional assemblages. The greater the beta diversity the higher is the difference between individual localities (Whittaker, 1960, 1972; Cody, 1975; Wilson and Shmida, 1984; Koleff et al., 2003). Further, diversity indices based on the phylogeny structure of a given assemblage would better describe the functional diversity or energy flow in an ecosystem. An assemblage comprising a group of closely related species (and therefore closely related functional habits) must be regarded as less 'biodiverse' compared to an assemblage of the same number of more distantly related species, all belonging to even different phyla (Clarke and Warwick, 2001). Hence, if we continue with conservative measures of diversity for monitoring biodiversity aspects, changes may go unnoticed until highly advanced stages of biodiversity loss reached (Clarke and Warwick, 1998).

Following previous studies from Indian waters, the present study aimed to demonstrate the efficacy of various univariate and multivariate biodiversity measures, not commonly used to date in plankton research, in defining the community characteristics of

mesozooplankton in an estuarine-marine gradient in the western Bay of Bengal. We hypothesised that under spring intermonsoon conditions, small copepods dominate the mesozooplankton community (similar to oceanic situations) while the local dynamics and system gradient supports different plankton assemblages. It is believed that a proper combination of various statistical measures, together with significant sample sizes will interrogate aspects of pelagic and/or benthic biodiversity issues not easily shown by traditional diversity measurements especially for tropical inshore areas.

2. Materials and methods

2.1. Study area, sampling and sample processing

The study sites (Fig. 1) comprise the lowermost estuarine section of Gautami Godavari of Godavari river system, which has an average width of about 1 km at the confluence, and the inshore waters of the western Bay of Bengal (16°39'–16°49'N, 82°13'–82°29'E). The estuary, a 'drowned river-mouth type', is the largest in the central, east coast of India. The average tidal range is about 1.4 m, and the bottom topography is uneven with depths varying between 1 m and 16 m (Rao, 2001). The dense mangrove vegetation (*Avicennia*, *Excoecaria*, *Sonneratia* and *Rhizophora*) fringes the shores of the lower estuary (Satyanarayana et al., 2002) and the bottom sediment consists mainly of sand, clay and silt. In general, 4 climate divisions could be identified in the study area: cool and dry season from December to February; hot and dry period from March to June; abundant rains during the hot summer monsoon (July to September) when freshwater conditions prevail in the area; cool transitional period during which estuarine and marine conditions re-establish (October to November) (Ramasarma, 1966). As well as being the second largest river in India with a mean annual discharge of $1.1 \times 10^{11} \text{ m}^3$, Godavari is also globally one of the largest particulate organic carbon (POC)-transporting rivers (Gupta et al., 1997). Thus, the Godavari delta constitutes one of the most important habitats showcasing how the plankton assemblages could be influenced by the unique ecological settings typical of the tropics.

Mesozooplankton samples were collected from 23 GPS (Garmin 45, USA) fixed locations using a Bongo net (mouth area: 0.13 m², mesh size: 120 μm) equipped with a digital flow meter (Hydrobios, Kiel, Germany). Of these, 4 stations represented a ~14 km stretch of the estuarine environment from the head of the estuary near Yanam (St.1) to the mouth at Bhairavapalem (St.4), and the remaining 19 stations (St.5–23) represent the coastal waters from the mouth up to ~16 km, covering ~148 km² of inshore waters (Fig. 1). Soon after sampling, on each occasion the two mesozooplankton samples from the Bongo net were mixed (to avoid differences between nets) and then subsampled using a Folsom plankton splitter (1–3 times depending on zooplankton volume). Prior to this, all large-sized forms were separated and their measurements noted. One half of the sample intended for dry mass measurement ($\text{mgDM}\cdot\text{m}^{-3}$) was deep-frozen until analysis at the shore laboratory; the other portion(s) fixed in 4% buffered formaldehyde for taxonomic identification and numerical enumeration ($\text{ind}\cdot\text{m}^{-3}$) (Wickstead, 1965; ICES, 2000). Usually, 5% of the total sample was counted with not less than 300 individuals for the most abundant species. The study was carried out during May 2002 coinciding with the spring intermonsoon.

2.2. Data analysis

Agglomerative hierarchical cluster analysis (AHCA), and non-metric multidimensional scaling (NMDS) on the fourth-root transformed mesozooplankton data matrix through Bray–Curtis similarity, and group-average linking classified the assemblages/

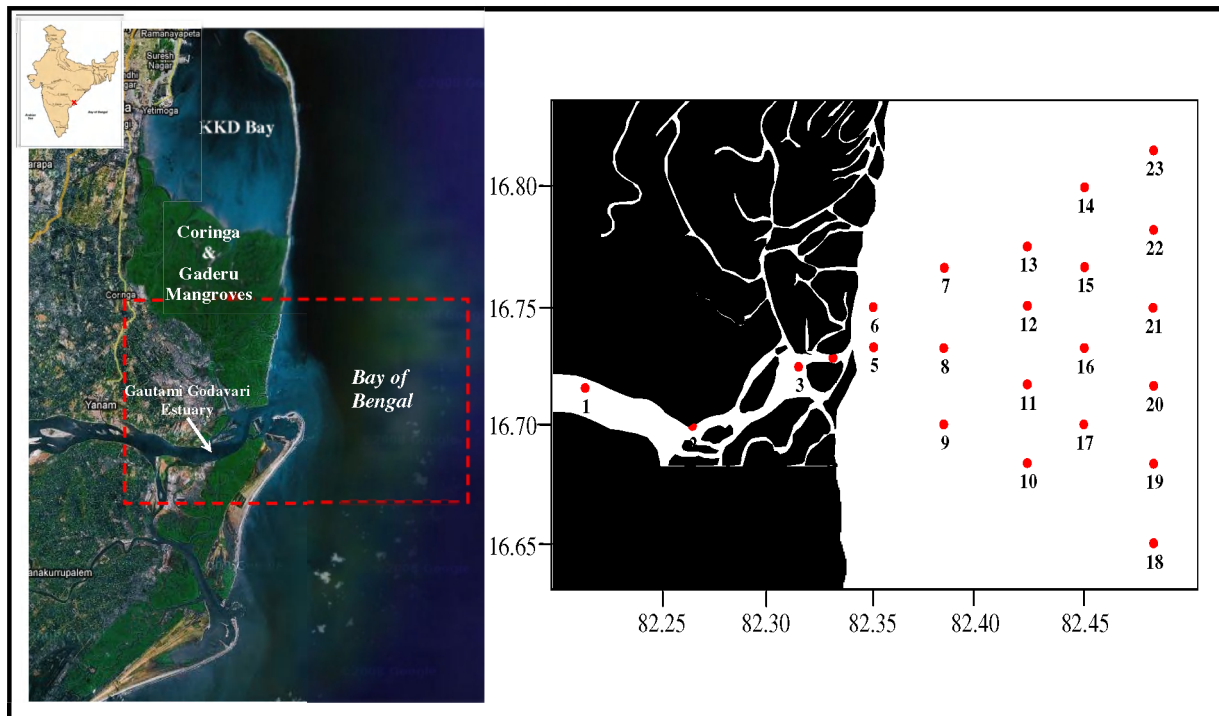


Fig. 1. Location of River Godavari on the east coast of India and mesozooplankton sampling stations in the estuarine-coastal gradient (May 2002).

clusters (Kruskal and Wish, 1978; Clarke and Green, 1988; Clarke and Warwick, 1994, 2001). A permutation-based hypothesis testing (ANOSIM, one way) probed the differences between assemblages, as detailed earlier (Rakesh et al., 2008).

Mesozooplankton diversity was measured using a range of univariate and multivariate diversity measures such as alpha diversity (α) based on species richness per sample (SRp), Shannon diversity index (H'), and Pielou's evenness index (J') (Pielou, 1977). To remove the dominating effect of the species abundance distribution on diversity (alpha diversity measure reflecting taxonomic hierarchy), average taxonomic distinctness (Δ^*) was also calculated (of copepods only, for reasons of taxonomic resolution). A classification from the literature (Russel, 1953; Kasturirangan, 1963; Zheng Zhong et al., 1989; Yamani and Prusova, 2003; Conway et al., 2003) was used to calculate average taxonomic distinctness (Δ^*). A high Δ^* (maximum 100) reflects high taxonomic diversity in the assemblage (Clarke and Warwick, 2001; Primo et al., 2009).

Most of the traditional diversity indices are measures of alpha diversity and are insensitive to the underlying biological differences between habitats. In order to emphasize the effectiveness of a multivariate approach in illustrating the inter-habitat differences, Beta diversity, originally proposed by Whittaker (1960, 1972) was calculated. Beta diversity index (β , Wilson and Shmida, 1984), index of multivariate dispersion (MVDISP, Warwick and Clarke, 1993), and β -dissimilarity index (Bray and Curtis, 1957) all proved valuable in interpreting the data (e.g. Magurran, 2004; Kappes et al., 2009).

Recognition of individual species contributing to the separation of two groups of samples, or the 'closeness' of samples within a group was carried out through the similarity percentages routine (SIMPER) implemented in PRIMER (Clarke and Gorley, 2006). For identifying 'characterizing species' in a particular assemblage, SIMPER calculates the average similarity (S) between all pairs of samples within a group. Because S is the algebraic sum of contribution from each species, within-group similarity can be expressed in terms of the average contribution from each variable. A good 'characterizing species' contributes heavily to intra-group similarity

and has a small standard deviation. To identify 'discriminating species' between different groups of samples, SIMPER calculates the average dissimilarity (δ) for all pairs of inter-group samples. Again since δ is the algebraic sum of contributions from each species, the mean intergroup δ could be expressed in terms of average contribution from each variable. A good discriminating species thus contributes largely to inter-group dissimilarity (see Clarke and Warwick, 1994). The analysis allowed us to determine the taxa responsible for patterns (resulting from AHCA and NMDS) and any differences between groups of sites. Similarity profile analysis (SIMPROF) was used as a confirmatory measure on copepods structuring mesozooplankton assemblages, in the study area. Considering the nature of data distribution (D'Agostino & Pearson omnibus normality test, $P > 0.05$; Skewness, 0.44; Kurtosis, -1.19; Coefficient of variation, 72.34%), differences in total zooplankton and copepod abundance, biomass, and diversity measures between faunistic areas (defined by the cluster analysis and NMDS) were tested with One-way ANOVA, followed by Bonferroni post-hoc multiple comparison tests taking into account unequal sample sizes within each group.

3. Results

3.1. Mesozooplankton abundance and distribution

Altogether 91 mesozooplankton taxa represented by 23 diverse groups were encountered during this study. Copepods were by far dominating in terms of species richness and numerical abundance exhibiting widest distribution (e.g. *Acrocalanus* spp., *Paracalanus* spp., *Acartia* spp., and *Oithona* sp.1) together with appendicularians (e.g., *Oikopleura* sp.). Copepods were represented by 50 species belonging to 28 genera and 22 families (Table 1). Of these, 4 species were unique to the estuary and 30 species to coastal waters, while the rest were common to the estuary and the sea. Three families, Paracalanidae (60%), Acartiidae (32%), and Pseudodiaptomidae (5%), comprised 97% of total copepods in the estuary. Coastal waters

Table 1

Numerical abundance (ind.m⁻³) of copepod and non-copepod taxa in the estuarine and coastal waters off Godavari. Shaded portion denotes small-sized copepods considered for community analysis.

Taxa	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23
Copepod taxa																							
<i>Acrocalanus</i> spp.	2144	909	4205	749	795	2036	608	516	733	1970	420	1200	4458	2121	319	695	874	692	792	525	284	317	617
<i>Paracalanus</i> spp.	339	61	1341	–	–	113	341	563	654	76	70	–	301	37	22	28	14	5	13	7	6	2	26
<i>Calocalanus pavo</i>	–	–	–	–	–	–	–	–	–	76	–	–	–	–	4	–	–	5	–	–	–	–	7
<i>Nannocalanus minor</i>	–	–	259	24	–	170	–	–	–	227	70	1333	542	37	11	–	22	16	13	–	4	7	85
<i>Eucalanus</i> sp.1	–	–	–	–	–	57	–	–	–	76	–	–	60	–	11	–	7	16	–	–	8	5	92
<i>Pareucalanus attenuatus</i>	–	–	–	–	84	–	–	–	–	985	350	–	60	–	–	–	7	–	13	–	–	–	53
<i>Subeucalanus crassus</i>	–	–	–	–	–	–	–	–	–	152	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>S. subcrassus</i>	–	–	–	24	–	113	324	390	407	909	699	–	60	–	–	–	–	–	–	–	2	–	7
<i>Canthocalanus pauper</i>	–	–	15	–	–	–	–	–	–	909	490	1867	181	–	7	28	7	–	26	15	6	10	39
<i>Undinula vulgaris</i>	–	–	–	–	–	–	–	–	–	303	70	133	120	–	–	–	–	–	6	–	–	–	46
<i>Longipedia</i> sp.	4	–	15	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Macrosetella gracilis</i>	–	–	–	–	–	–	–	–	–	76	–	–	–	18	4	28	51	27	26	–	15	27	59
<i>Euterpina acutifrons</i>	–	–	–	–	209	226	324	438	511	379	420	400	723	55	45	85	51	38	13	44	8	10	7
<i>Acartia</i> sp.1	134	577	213	169	42	113	–	–	–	–	–	133	60	37	7	28	7	5	19	–	–	5	26
<i>A. southwelli</i>	22	–	–	–	–	–	–	–	–	–	–	133	60	–	–	–	–	–	19	–	–	–	–
<i>A. chilkaensis</i>	49	25	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>A. centrura</i>	420	25	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7
<i>A. erythraea</i>	9	12	–	–	–	–	–	–	–	–	–	133	–	–	–	–	7	–	–	–	–	–	20
<i>A. spinicauda</i>	648	1892	701	24	–	113	–	–	–	–	70	133	60	–	–	–	–	–	–	–	2	5	–
<i>Pseudodiaptomus</i> sp.1	67	12	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>P. aurivilli</i>	125	295	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>P. serricaudatus</i>	121	111	61	–	209	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Temora turbinata</i>	–	–	–	362	1339	509	1257	1375	1214	303	140	–	–	–	–	–	65	–	–	–	9	2	–
<i>T. discaudata</i>	–	–	–	–	–	–	257	391	422	–	140	133	–	–	–	–	–	–	–	–	–	–	–
<i>Centropages</i> sp.1	–	–	–	–	84	–	81	57	80	–	70	–	–	18	–	14	7	11	–	–	–	5	–
<i>C. tenuiremis?</i>	–	–	–	–	42	113	–	–	–	–	–	133	60	–	4	14	43	11	6	7	6	7	79
<i>C. furcatus</i>	–	–	–	–	84	57	–	–	–	152	–	133	181	–	11	–	–	5	–	7	–	–	–
<i>C. dorsispinatus</i>	–	–	–	–	–	113	41	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>C. orsinii</i>	–	–	–	–	–	–	–	–	–	–	70	267	–	–	–	–	7	5	–	–	6	–	7
<i>Oithona</i> sp.1	36	–	30	145	628	2036	203	331	489	152	70	–	241	55	19	14	51	70	38	37	15	12	7
<i>O. plumifera</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	14	–	–	–	–	–	–
<i>Calanopia elliptica</i>	–	–	–	–	–	–	–	–	–	76	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Labidocera</i> sp.1	–	12	30	24	126	–	–	–	–	–	–	–	–	–	–	14	7	16	–	–	–	2	39
<i>Labidocera</i> sp.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	46
<i>L. pectinata</i>	–	–	30	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Lacuta</i>	–	–	–	–	–	–	–	–	–	–	140	133	60	–	4	–	–	5	13	–	–	–	–
<i>L. minuta</i>	–	–	15	–	–	57	–	–	–	76	–	–	60	–	4	–	–	5	13	–	–	–	7
<i>Tortanus gracilis</i>	9	–	15	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	6	–	–
<i>T. barbatus</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	18	–	–	–	–	–	–	–	–	–
<i>Pontella danae</i>	–	–	–	2	–	–	–	–	–	–	–	–	–	18	4	–	–	–	–	–	–	–	–
<i>Candacia bradyi</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	7
<i>Pontellopsis</i> sp.	–	–	–	–	–	–	–	–	–	76	–	–	60	–	–	–	–	–	6	7	–	–	–
<i>Oncaea venusta</i>	–	–	–	–	42	57	81	66	98	227	280	533	181	–	41	71	43	32	58	7	2	5	66
<i>O. conifera</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	37	–	–	7	11	19	7	–	12	7
<i>Corycaeus danae</i>	4	–	–	290	795	792	243	344	556	303	140	533	422	184	45	85	94	76	83	74	32	34	138
<i>C. speciosus</i>	–	–	–	–	–	–	–	–	–	76	70	267	60	74	19	57	43	135	64	59	92	85	79
<i>Onychocorycaeus catus</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	14	–	5	19	15	–	–	7
<i>Farranula gibbula</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	4	28	43	5	26	15	–	2	–
<i>Copilia mirabilis</i>	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	14	–	–	–	–	–	–
Copepod nauplii	–	–	–	72	–	–	423	391	556	–	–	133	120	–	7	14	7	–	–	–	–	–	–
Non-copepod taxa																							
Medusae	9	–	–	–	–	–	–	–	–	–	–	–	–	–	4	–	–	–	–	–	–	–	–
<i>Sartia</i> sp.	–	–	–	–	–	–	–	–	–	76	–	–	–	–	–	–	–	–	–	13	–	–	–
<i>Diphyes</i> sp.	–	–	–	–	–	–	–	–	–	–	–	133	–	–	–	–	–	5	–	–	–	–	–
<i>Lensia</i> sp.	–	–	–	–	–	–	–	–	–	–	–	133	–	–	–	14	–	–	6	–	–	–	–

<i>Beroe</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-
<i>Pleurobrachia</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	18	-	-	-	-	-	-	-	-	-	-
<i>Sagitta</i> sp. ?	-	-	-	-	-	-	-	-	152	-	-	60	-	4	14	36	11	-	-	-	6	22	39
<i>Aidanosagitta neglecta</i>	-	-	-	-	-	-	-	-	455	-	267	120	6	-	14	29	-	-	-	-	-	-	7
<i>Flaccisagitta enflata</i>	-	-	11	-	42	17	12	39	-	76	-	60	-	-	-	-	-	-	-	-	-	-	-
<i>Zonosagitta bedoti</i>	49	9	215	5	42	-	62	78	68	76	210	400	-	100	11	57	7	11	13	7	13	2	66
Polychaete larvae	4	-	-	24	-	57	41	-	111	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Cirripede nauplii	103	12	-	24	126	-	41	-	-	-	-	-	-	-	-	14	-	-	-	-	4	2	-
Copepod nauplii	-	-	-	72	-	-	423	391	556	-	-	133	120	-	7	14	7	-	-	-	-	-	-
Crustacean nauplii	-	-	-	-	-	-	122	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Crustacean protozoa	40	-	-	-	-	-	62	53	56	227	-	-	-	-	-	14	-	-	-	-	-	-	7
Crustacean zoea	-	-	-	290	502	509	81	-	-	-	-	-	-	37	-	-	-	-	-	-	2	2	13
Crustacean mysis stage	40	25	15	48	-	57	81	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Brachyuran zoea	45	-	-	48	-	-	-	-	-	-	-	133	60	37	-	14	36	32	13	7	9	19	26
Megalopa	-	14	15	24	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Porcellanid zoea	4	-	-	-	42	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Stomatopod juveniles	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-
Lucifer juveniles	-	-	-	-	209	113	81	75	111	-	-	-	-	-	4	-	-	-	-	-	6	10	13
<i>Lucifer hansenii</i>	9	-	-	5	42	1035	138	156	117	-	-	-	-	42	-	7	-	-	-	-	15	12	20
Ostracod	-	12	15	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-
<i>Conchoecia</i> sp.	-	-	-	-	-	-	81	-	-	-	-	-	-	18	-	14	-	-	-	-	-	2	-
<i>Evadne</i> sp.	-	-	-	-	126	-	-	-	-	-	-	-	-	37	-	-	-	-	-	-	9	2	-
<i>Pseudevadne tergestina</i>	-	-	-	-	167	-	128	391	333	152	70	133	904	-	182	284	903	513	307	399	77	455	151
<i>Penilia avirostris</i>	-	-	-	1788	7741	6505	933	953	1142	76	70	-	-	74	4	43	116	11	-	-	6	17	33
<i>Diamysis</i> sp.	18	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Erythrospidinium</i> sp.	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
<i>Siriella</i> sp.	13	57	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Gastropod veliger	299	221	2514	97	84	57	-	-	-	-	-	-	-	7	14	14	-	-	-	-	9	5	-
Bivalve veliger	27	37	899	121	167	57	-	-	-	-	70	-	-	18	-	14	29	-	6	-	6	-	-
<i>Creseis</i> sp.	-	-	-	-	42	-	-	-	-	-	140	-	-	-	-	-	-	-	-	-	2	-	-
<i>C. acicula</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	2	7
<i>C. virgula</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-
<i>Desmopterus papilio</i>	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7
<i>Doliolum</i> sp.	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	6	-	-	-	-	-
<i>Oikopleurasp.</i>	27	12	-	169	167	170	288	250	111	1818	1538	2133	1145	44	30	85	58	59	83	96	19	5	98
Fish eggs	4	-	-	121	42	57	203	-	-	-	-	-	60	-	4	-	-	11	-	-	-	-	-
Fish larvae	-	-	-	53	-	11	53	-	-	76	-	-	-	2	4	-	-	-	-	-	-	-	13

exhibited higher taxonomic breadth compared to the estuary, with nine families, Paracalanidae (35.6%), Temoridae (12.2%), Calanidae (10.6%), Corycaeiidae (10.2%), Oithonidae (7.2%), Eucalanidae (6.9%), Euterpinidae (6.5%), Centropagidae (3.2%), and Oncaeiidae (3.1%), together contributing 95.5% of total copepod population.

The estuarine copepod community comprised mainly of 17 calanoid taxa that formed 99.4% of the total population. Cyclopoids, poecilostomatoids, and harpacticoids were represented by one taxon each. In contrast, coastal waters had more diverse copepod fauna, still dominated by calanoids (34 taxa, 65–78%), followed by poecilostomatoids (7 taxa, 1–5%), cyclopoids (1 taxon, 8–23%), and harpacticoids (2 taxa, 6–8%). The relative importance of non-copepod taxa varied throughout with larval forms contributing up to 32.4% of total zooplankton in the estuary and 18% in coastal waters (Table 1). The meroplanktonic forms were represented mainly by gastropod and bivalve veligers in the lower reaches of the estuary, while the crustacean larvae (copepod nauplii and decapod larvae) typified the coastal waters. In contrast, holoplankton numbers increased seawards comprising up to 88–98% in coastal waters and dominated by cladocerans (3.7%–36.6%), chaetognaths (1.4%–4.9%), and appendicularians (2.1%–17.4%).

Within the estuary, species with high frequency of occurrence (>80%) were *Zonosagitta bedoti*, *Siriella* sp., *Acrocalanus* sp., *Paracalanus* sp., *Acartia* sp., *Acartia spinicauda*, *Pseudodiaptomus serricaudatus*, among holoplankton and mysis stage of crustacea, gastropod and bivalve veligers among meroplankton. In coastal waters, *Zonosagitta bedoti*, *Pseudevadne tergestina*, *Penilia avirostris*, *Acrocalanus* sp., *Paracalanus* sp., *Euterpina acutifrons*, *Oithona* spp., *Oncaea venusta*, *Corycaeus danae*, and *Oikopleura* sp., were the dominant forms.

3.2. Mesozooplankton community structure

Multivariate analysis of data based on relative abundance of species yielded discrete zooplankton/copepod communities, distinguished through the first two cut-off levels of the dendrogram (Fig. 2A–C,G). The first cut-off level (at 41.5%) separated the estuarine stations (Group I) from coastal waters. The next hierarchical level at 52.6% similarity divide the coastal waters into three clusters: (1) the estuary mouth and near shore stations (Group II), (2) intermediate coastal stations (Group III), and (3) coastal-offshore stations (Group IV). The two-dimensional ordination of the samples by NMDS (stress: 0.12) prevented any overlapping of the same groups. Group I consisted of three strongly related stations (St.1–3) representing the middle and lower reaches of Gautami Godavari estuary, subjected to riverine influx, outwelled water from the mangroves, and neritic incursion from the sea. Group II corresponded to St.4 at the estuarine mouth and St.5–9 in the inshore waters at the immediate vicinity of the mouth. Ten stations (St.14–23) away from the coast, in relatively deep waters, formed group IV and finally four stations (St.10–13) in the transition zone between groups II and IV, formed group III. The One-way ANOSIM test revealed the significant differences between the four assemblages (Global R: 0.957; p : 0.1% for total zooplankton and Global R: 0.952; p : 0.1% for copepods). Among these assemblages, Group III stations showed the highest ($9560 \pm 2467 \text{ ind.m}^{-3}$) and Group IV the lowest ($1735 \pm 791 \text{ ind.m}^{-3}$) average zooplankton abundance in the study area. Copepods also showed a similar distribution pattern with highest numerical abundance in Group III ($6804 \pm 2032 \text{ ind.m}^{-3}$) and lowest in Group IV ($1196 \pm 661 \text{ ind.m}^{-3}$). However, their relative contribution to total zooplankton abundance was maximal in the estuary (Group I, 80.6%) followed by Group III (70.4%), Group IV (67.7%) and Group II (53.9%) in the coastal waters. Group-II also had high mesozooplankton biomass (15.1 mgDM.m^{-3}), compared either to Group-I (8.4 mgDM.m^{-3}) or Group-IV (5.8 mgDM.m^{-3}) stations

(Table 2 gives numerical abundance, with more details in Fig. 3 covering abundance and biomass). One-way ANOVA followed by Bonferroni multiple comparison test assigned various significant levels for their difference in prevalence across the assemblages (Fig. 3).

3.3. The importance of small-sized copepods

The study demonstrated the overwhelming dominance and diversity of copepods that shaped the zooplankton community structure across the study area. The differences in copepod size spectra and trophic preferences were evident across the assemblages. Small copepods numerically dominated the copepod taxa (see Table 1), reducing the importance of large-sized forms to 8.4% in the estuary and 12.3–47.1% in coastal waters. Multivariate analysis revealed a slightly different assemblage structure (only 3 groupings i.e., estuary, coastal-near shore and coastal-offshore, Fig. 2D) for small copepods compared to total zooplankton/copepods. Small copepods represented by Paracalanidae, Acartiidae, Oithonidae, Corycaeiidae, Oncaeiidae, and Euterpinidae dominated the spectra with 92% (10 taxa) of total copepods in estuarine waters declining to 55–87% (17 taxa) in the neritic waters. The numerical abundance of small copepods was about 12 times that of large-sized forms in the estuary, and up to a maximum of 7 times in the coastal waters (Fig. 4).

As with large copepods, calanoids constituted the principal taxa. Their relative contribution within the small size fraction varied from 99.5% in the estuary to 53% (Group II) –70.1% (Group IV) in coastal waters. Conversely, members of the second principal taxon, Poecilostomatoida that favour high saline waters exhibited an opposite trend with a maximum contribution in coastal waters (29.9%–47%), and a mere 0.5% in the estuary. The correlation of small copepod abundance with total zooplankton abundance (Group-I, r : 1.00; Groups II–IV, r : 0.74–0.92) and biomass in the estuarine (r : 0.40) and coastal (r : 0.46–0.83) waters, and also the results of regression analysis with different zooplankton diversity indices (H' , J' , SRp) showed the significant role of small copepods in zooplankton/copepod community, in the study area (Fig. 5). Although herbivorous forms made similar proportions in the estuary (56%) and coastal waters (38–73%), the omnivorous forms were higher in the estuary (maximum up to 75% of total copepods in the estuary with an average of 43%) and the carnivorous taxa in the coastal waters (13.2–21.8%) (Table 2).

3.4. Mesozooplankton diversity measures

Irrespective of the underlying data matrix, alpha diversity (SRp , H' , J'), the powerful taxonomic phylogeny based average taxonomic distinctness (Δ^* for copepods only) as well as the species turnover measure, beta diversity (MVDISP, β , β -dissimilarity) varied markedly among the assemblages in the estuary and coastal waters.

3.4.1. Alpha diversity

Mesozooplankton species occurrence varied considerably between the assemblages (39 species in the estuary and 72 in the coastal-offshore waters). Eight species were found only in Group I stations, 15 species in Group IV, and 2 species each in Groups II and III, while 14 species were common in all assemblages (Fig. 6A). Average species richness (SRp) of total zooplankton varied between 24 ± 6 species in the estuary (Group I) to 31 ± 6 species in the coastal-offshore waters (Group IV). Within the estuary, St.1 in the upstream showed maximum species richness (31 species), samples collected from middle and lower reaches did not indicate any significant difference (20–21 species). Within coastal waters, Group IV recorded maximal number of species and variations in species occurrence.

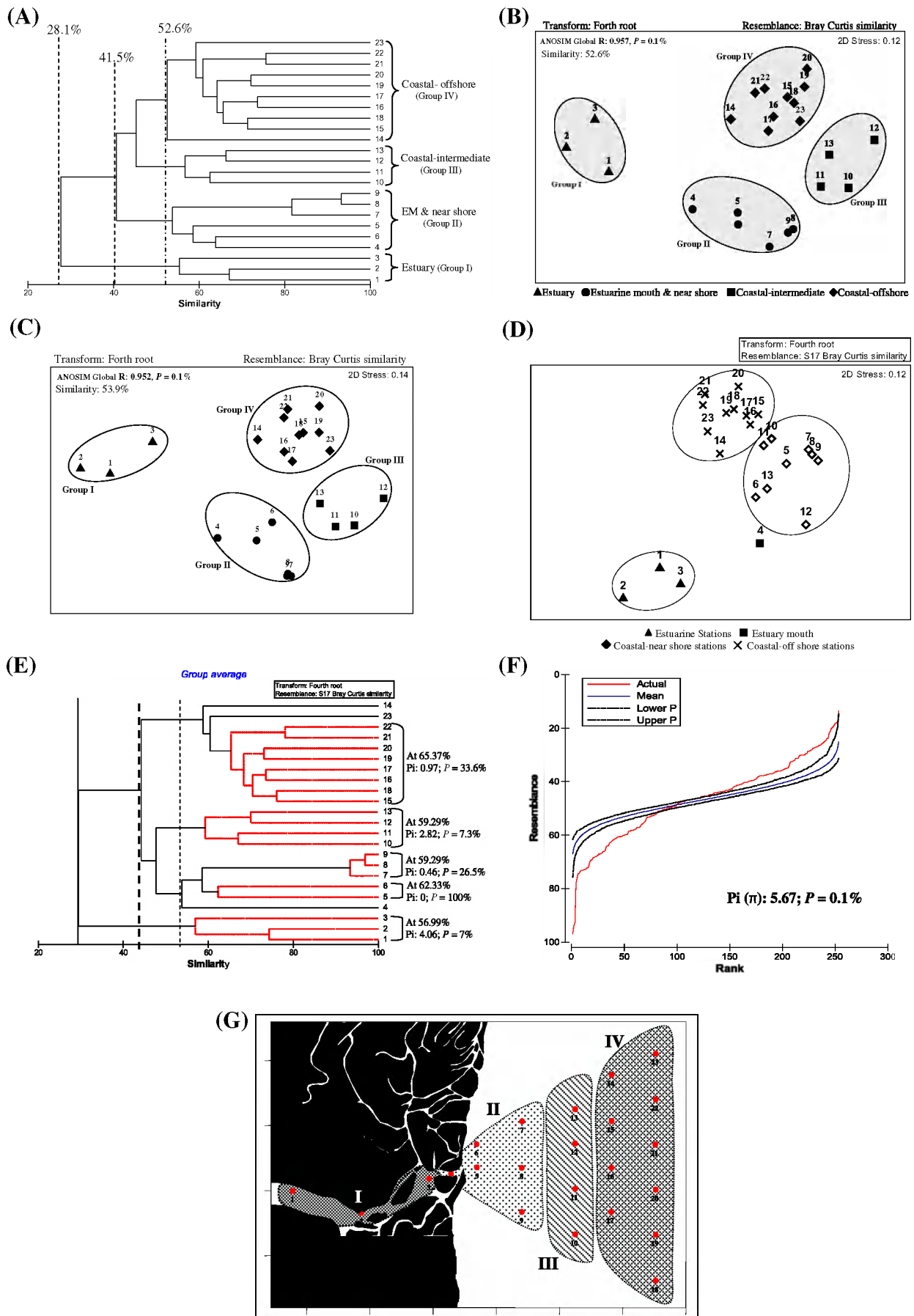


Fig. 2. Bray–Curtis similarity based hierarchical clustering of stations manifested through dendrogram and NMDS for total zooplankton (A & B), total copepods (C) and small copepods (D); E. Similarity profile (SIMPROF) analysis showing significant internal structure in the copepod community organization (Samples connected by red dotted lines can not be significantly differentiated); F. Diagram showing the absolute distance (π) between the real similarity profile (in red) and the 99% limit of the simulated mean profile; G. Zooplankton assemblages superimposed on geographical locations. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Table 2
Copepod characteristics in the study area.

Characteristics	Assemblages			
	I	II	III	IV
Number of samples	3	6	4	10
Min–max, mean±1SD				
Numerical abundance (Ind.m ⁻³)	3932–6932	1887–6674	3776–8133	501–2712
	4998 ± 1677	4633 ± 1623	6804 ± 2032	1196 ± 661
% Contribution to total zooplankton	65.27–90.81	31.94–73.61	64.29–77.14	49.67–86.17
	80.55 ± 13.49	53.94 ± 17.60	70.43 ± 5.26	67.73 ± 10.73
Within copepods				
% Small copepods	89.06–93.63	53.15–82.20	40.74–82.22	63.75–95.92
	91.60 ± 2.32	64.27 ± 12.39	52.88 ± 19.72	87.68 ± 9.12
% Large copepods	6.37–10.94	17.80–46.85	17.78–59.26	4.08–36.25
	8.40 ± 2.32	35.73 ± 12.39	47.12 ± 19.72	12.32 ± 9.12
% Herbivorous copepods	24.69–84.18	24.30–42.25	63.79–81.00	65.83–83.67
	56.36 ± 29.93	37.49 ± 6.61	73.33 ± 8.51	70.37 ± 5.16
% Carnivorous copepods	0.31–1.32	7.75–21.50	10.37–18.97	12.24–26.36
	0.65 ± 0.58	13.24 ± 5.24	14.25 ± 4.23	21.81 ± 4.36
% Omnivorous copepods	14.51–75.00	37.13–54.21	8.00–15.52	4.08–13.53
	42.99 ± 30.40	43.98 ± 6.07	11.62 ± 4.11	7.53 ± 2.58
% Calanoids	98.92–100.00	53.39–73.11	74.07–84.00	66.38–84.35
	99.42 ± 0.54	64.62 ± 7.02	78.11 ± 4.33	71.18 ± 5.69
% Cyclopoids	0.00–0.97	10.66–42.37	7.00–10.34	11.56–27.86
	0.47 ± 0.49	23.33 ± 11.91	8.41 ± 1.52	19.25 ± 5.42
%Poecilostomatoids	0.00–0.00	0.00–1.94	2.22–7.41	0.38–6.92
	0.00 ± 0.00	1.13 ± 0.70	4.88 ± 2.65	3.69 ± 2.15
%Harpacticoids	0.00–0.22	0.00–9.01	5.17–11.11	2.72–9.30
	0.11 ± 0.11	5.63 ± 3.59	7.79 ± 2.73	5.59 ± 2.14
α – diversity				
Number of species (SRp)	11.00–15.00	11.00–16.00	18.00–22.00	13.00–27.00
	13.00 ± 2.00	12.33 ± 1.97	20.25 ± 2.06	19.30 ± 4.42
Shannon–Weiner diversity (H')	1.25–1.62	1.64–2.12	1.83–2.62	1.00–2.40
	1.44 ± 0.18	1.96 ± 0.17	2.34 ± 0.36	1.68 ± 0.35
Pielou's evenness (J')	0.49–0.60	0.71–0.93	0.61–0.89	0.39–0.73
	0.56 ± 0.07	0.82 ± 0.09	0.79 ± 0.12	0.57 ± 0.08
Taxonomic distinctness (Δ^*)	46.49–66.85	71.75–83.17	70.69–74.27	75.38–85.35
	59.60 ± 11.37	78.49 ± 4.79	72.82 ± 1.69	81.16 ± 2.75

Although one-way ANOVA revealed no significant overall difference in SRp between the assemblages (F : 1.98, $P > 0.05$), the Bonferroni multiple comparison test showed a significant difference between the estuary and coastal offshore waters ($P < 0.05$). Shannon–Wiener diversity and Pielou's evenness recorded lower values in the estuary ($H' = 1.87 \pm 0.19$ and $J' = 0.59 \pm 0.01$) and higher values ($H' = 2.62 \pm 0.25$ and $J' = 0.79 \pm 0.08$ bits.ind⁻¹) in coastal intermediate waters (Fig. 7A). Differences observed across assemblages were statistically significant (H' - F : 3.63, $P < 0.05$; J' - F : 4.46, $P < 0.05$). Copepod species richness, H' , and J' exhibited a similar pattern with low values in the estuary. Average taxonomic distinctness (Δ^*) based on taxonomic phylogeny of copepods revealed a lower taxonomic breadth within the estuary compared to Group IV stations in the coastal offshore waters (Table 2). As with total zooplankton, one-way ANOVA followed by Bonferroni multiple comparison test revealed significant differences in copepod SRp (F : 8.00, $P < 0.001$), H' (F : 6.87, $P < 0.01$), J' (F : 12.50, $P < 0.001$), and Δ^* (F : 16.21, $P < 0.001$) between the assemblages (Fig. 7B).

3.4.2. Beta diversity

A difference in mesozooplankton species composition between the assemblages yielded species turnover rate (β -diversity) in the estuary-marine gradient of Godavari River. The concept of beta diversity was explored using three different univariate and multivariate approaches, namely, beta similarity index (β , based on SRp turnover), beta dissimilarity index (based on the Bray–Curtis dissimilarity) and index of multivariate dispersion (MVDISP, i.e. intra-group beta diversity/within area heterogeneity).

The β -diversity index calculated for all pairs of contiguous and non-contiguous zooplankton assemblages showed values higher

than zero, revealing that all the four assemblages identified in the estuarine and coastal waters during spring inter-monsoon differ in terms of their species composition. In general, assemblages III & IV ($\beta = 0.27$) which otherwise had 58% of species in common, exhibited the lowest β -diversity index. Conversely, groups I & III and I & IV exhibited highest β -diversity values ($\beta = 0.58$, sharing 28% of species in common). Absolute species turnover was not registered even among the farthest assemblages, as none of the values reached $\beta = 1$. Among contiguous assemblages, Group I and Group II showed the highest species turnover ($\beta = 0.44$) with a gradual decrease towards the coastal-offshore segment (Groups II & III, $\beta = 0.36$; Groups III & IV, $\beta = 0.27$). Similarly, β -dissimilarity index calculated using the Bray–Curtis dissimilarity revealed significant intergroup differences in species distribution patterns in the study area. The estuary (Group I) and coastal-intermediate (Group III) stations exhibited the maximum β -dissimilarity (75.3%); Group III and coastal-offshore stations (Group IV) the minimum (54.6%). As with β -diversity index, β -dissimilarity also showed a gradual decrease towards coastal-offshore segment. ANOSIM further substantiated the observed significant differences between these assemblages (Fig. 6B).

The relative variability within each zooplankton assemblage (i.e. Intragroup β -dissimilarity) calculated using the multivariate dispersion index (MVDISP) showed higher values in the estuary, estuarine mouth and near shore as well as coastal intermediate waters indicating high β -diversity and a low predictability of the zooplankton species composition in these waters compared to the homogenous interspecific associations in coastal-offshore segment (Fig. 6C).

SIMPER analysis based on abundance estimates of total zooplankton revealed the percent contribution of species to within-

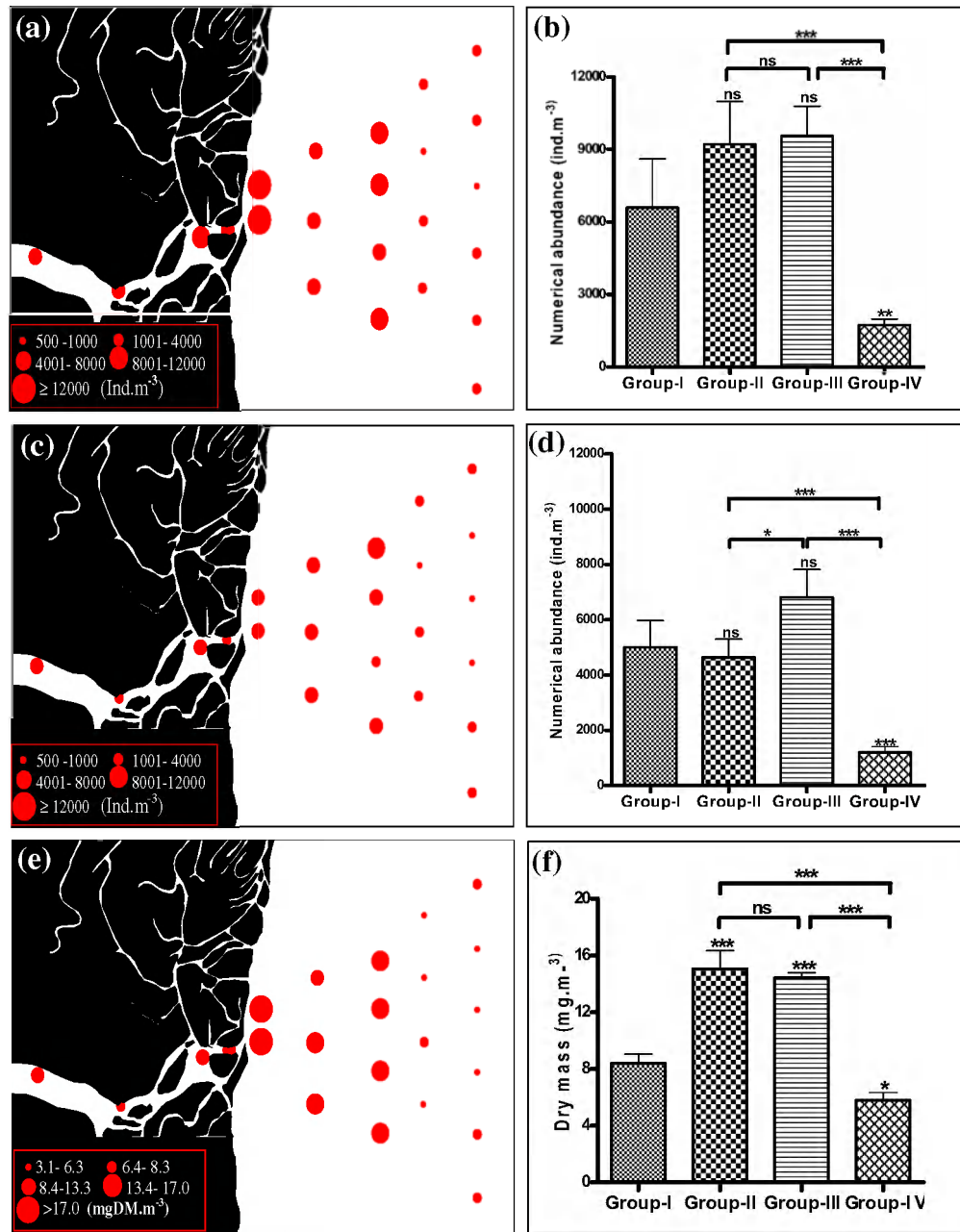


Fig. 3. Density plots and histograms of the results of one-way ANOVA with Tukey's multiple comparison test: total zooplankton (a & b), copepods (ind.m⁻³) (c & d), and total zooplankton dry mass (mgDM.m⁻³) (e & f). Whiskers indicate standard deviation; ns-not significant; and asterisks-significant levels (** – $P < 0.01$, *** – $P < 0.001$).

group similarity ('characterizing species') as well as between group dissimilarity ('discriminating species'). Table 3 summarizes information on (characterizing) species that contribute foremost to the average similarity together with their percent contribution to the total zooplankton abundance, within each group. There was little variation in the intragroup similarities (59.3%–62.2%). Unlike in other groups, Cladocera (36.6% of total abundance) were the most prominent group with the species *Penilia avirostris* alone contributing to 34.5% of total zooplankton abundance, and 10.7% of average similarity between the stations within Group II. Similarly, when small sized copepods such as *Acrocalanus* sp. (14.2%) and *Acartia spinicauda* (12.3%) accounted for >10% of within group similarity in Group I (estuary), *Oikopleura* sp. (9.8%) and *Acrocalanus* sp. (11.5%) were the main contributors among others in Group III and Group IV.

SIMPER analysis based on the Bray–Curtis dissimilarity between groups revealed species that differentiate between the assemblages or responsible for observed β -dissimilarity between the assemblages. Table 4 shows the key zooplankton species that differentiate between the assemblages as well as the significance in community structure differences (between assemblages) as revealed by the ANOSIM Global R test. While estuarine waters sustained a population of *Acartia spinicauda*, *Pseudodiaptomus serricaudatus*, gastropod veligers, crustacean mysis, and the mysid *Siriella* sp., the coastal waters at the estuarine mouth and farther offshore showed characteristic distribution of the appendicularian *Oikopleura* sp., the cladocerans *Penilia avirostris* and *Pseudeudadne tergestina*, and the copepods *Temora turbinata*, *Canthocalanus pauper*, *Undinula vulgaris*, *Euterpina acutifrons*, *Corycaeus danae*, *Corycaeus speciosus*, and *Oncaea venusta*. Their variability in distribution within the

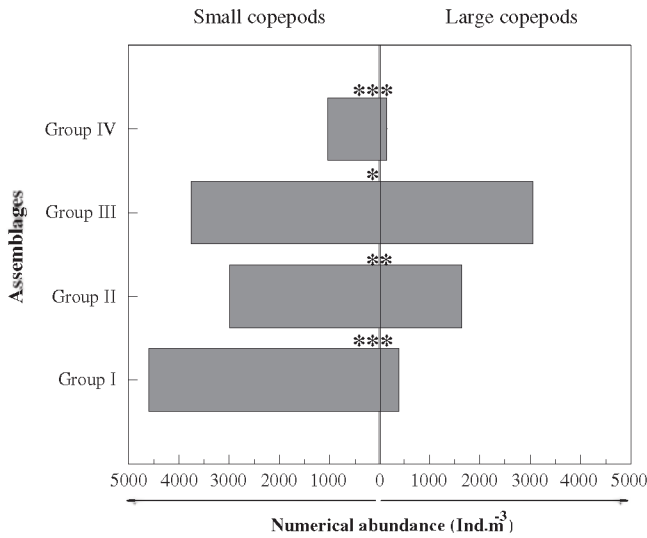


Fig. 4. Numerical abundance of small and large sized copepods in zooplankton assemblages. ANOVA, $P < 0.001^{***}$; $P < 0.05^{**}$; $P < 0.1^*$.

estuary and coastal waters made them ‘discriminating species’ for various zooplankton assemblages identified during this study.

4. Discussion

As with temperate regions, copepods usually comprise the principal zooplankton component in tropical estuaries (Madhupratap,

1987; Duggan et al., 2008). The importance of copepods in the estuarine zooplankton community has already been reported from several estuaries worldwide. For example, in the Cochin backwaters (CBW), west coast of India, they constituted 74.5% of total zooplankton annually (Madhupratap, 1979, 1987) with a 70.6% contribution during intermonsoon (Madhu et al., 2007). In the Mandovi-Zuari estuarine system (W coast of India), copepods formed up to 84.4% (Zuari) and 86.1% (Mandovi) (Padmavati and Goswami, 1996) of total zooplankton with 71% contribution during premonsoon (Achuthankutty et al., 1981; IOC workshop report no.142). A similar picture was observed in different estuaries along the east coast of India (e.g. Sarkar et al., 1986; Sai Sastry and Chandramohan, 1995; Ramaiah et al., 1996). Earlier studies (1958–1961) from the Gautami-Godavari estuary also showed copepods contributing about 30% to >60% during the intermonsoon periods (Chandramohan, 1977). Four decades later, current observations were similar for the bay (Kakinada Bay, ~60%, Rakesh et al., 2008) and estuarine waters (80.6%, present study) of the River Godavari during this season. The numerical abundance (99% of total copepods), diversity and contribution to the total zooplankton stock of small-sized calanoid copepods within Godavari estuary illustrated their central role in channelling energy under non-flood high saline conditions. Earlier reports (Sai Sastry and Chandramohan, 1995) and current observations were remarkably similar to the findings made from Cochin backwaters revealing that calanoids dominate the copepods followed by cyclopoids and harpacticoids during the premonsoon season with herbivorous and omnivorous copepods being the principal trophic components (Madhupratap, 1979; Madhu et al., 2007). Thus, considering the geomorphology of CBW (Arabian Sea) and Godavari estuary (BoB), and also the high incidence of neritic

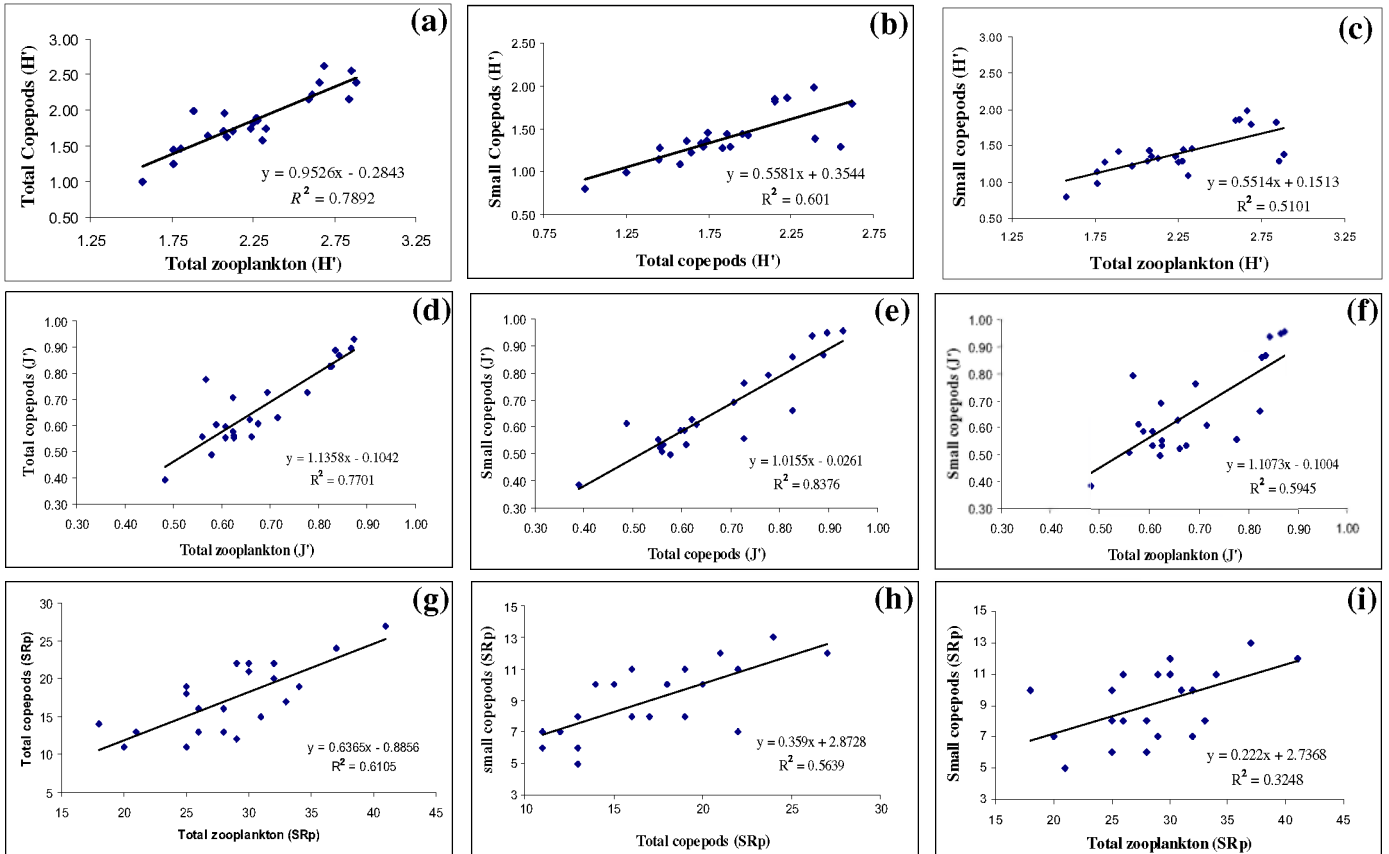


Fig. 5. Regression analysis of different diversity indices of total zooplankton, copepods and small copepods. a–c: Shannon–Weiner index (H'); d–f: Pielou’s evenness (J') and g–i: Species richness (S).

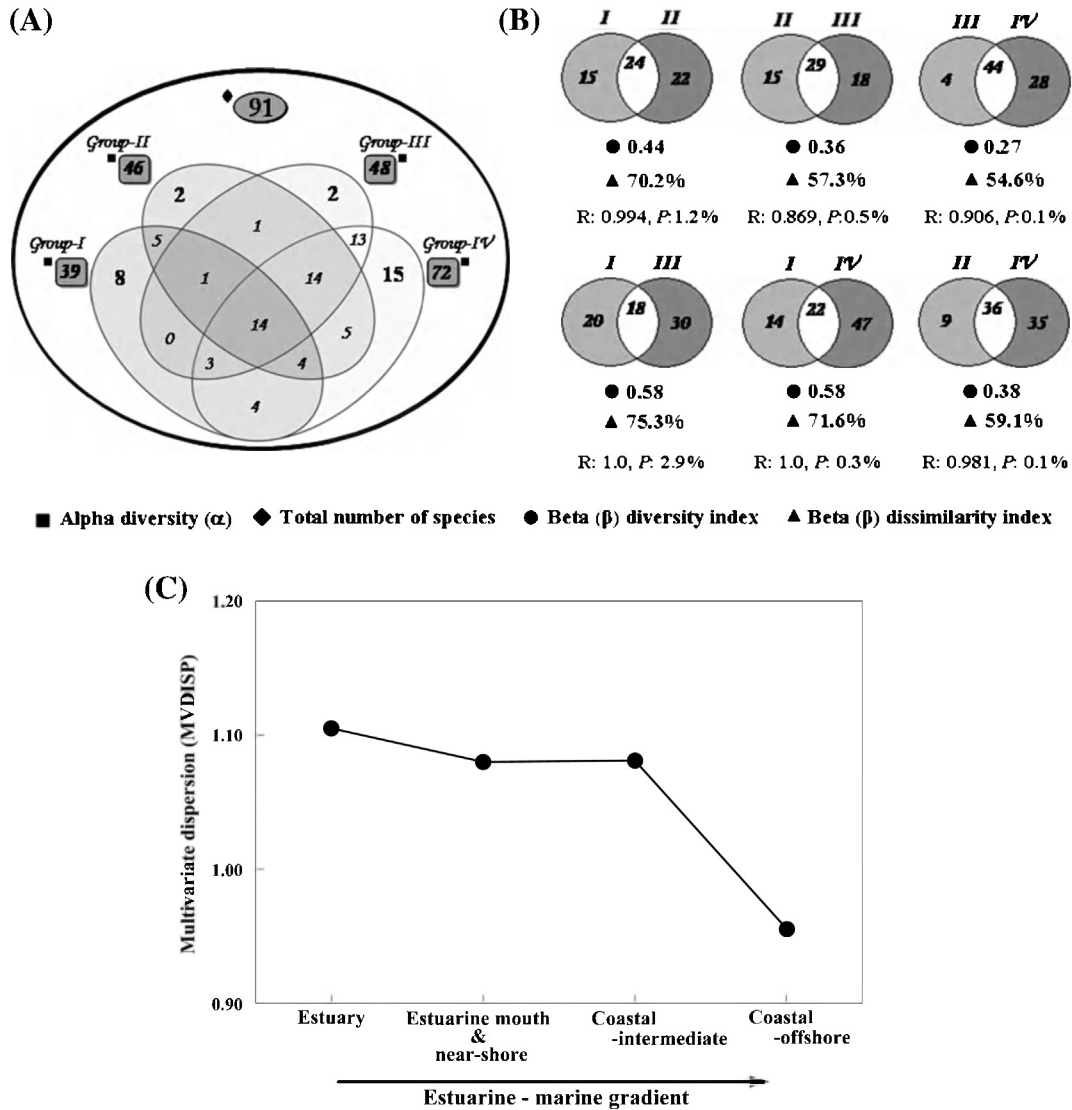


Fig. 6. Venn diagram showing alpha (A) and beta (B) diversity measures, and within group variability (C) for zooplankton assemblages.

species during the premonsoon season (Chandramohan, 1977; Madhupratap, 1979), it was expected that both ecosystems exhibited similar copepod functional diversity during this season.

The permanently open Godavari estuary system has discrete zooplankton assemblages characteristic of an estuarine-coastal gradient. The four different zooplankton assemblages identified through multivariate analysis correlated well with the copepod assemblage structure. Chew and Chong (2011) also found distinct copepod assemblages along a salinity gradient in the estuary, near shore and offshore waters in the Sagga estuary, Malaysia. This indicates the significance of copepods on zooplankton community structure in the estuarine coastal environment under tropical settings. SIMPROF analysis revealed significant internal organization in zooplankton/copepod community association, in the study area (Fig. 2E and F). Small-sized copepods followed a similar pattern, except for their distinct distribution at estuarine mouth and extended penetration into the coastal waters, with little difference between near shore and coastal intermediate group of stations.

According to Elliott and McLusky (2002) and McLusky and Elliott (2007), estuaries are now regarded as being 'transitional waters', and their internal population dynamics may be more

dependent on external population sources from the adjoining ecosystems (Elliott and Whitfield, 2011). Thus, in our study the increased abundance of small coastal marine copepods (size: <1 mm) in the middle and lower reaches of the estuary and mesozooplankton assemblage pattern in the estuarine mouth and coastal waters show the neritic supply of estuarine mesozooplankton under spring intermonsoon conditions.

The influence of copepods, especially the small-sized fraction, on estuarine zooplankton has also been reported from other tropical (Darwin Harbour, northern Australia, Duggan et al., 2008; Sangga estuary, Malaysia, Chew and Chong, 2011), and temperate (Waquoit Bay, MA, Lawrence et al., 2004; Galway Bay, west coast of Ireland, McGinty et al., 2012; Gironde estuary, south-west Europe, Chaalali et al., 2013) systems.

Although small copepods of size <200 μm easily outnumber larger copepods, especially in the upper levels of the water column (Falk-Peterson et al., 1999; Porri et al., 2007), they have historically been under-sampled because of the large mesh sizes (>200–333 μm) commonly used in mesozooplankton sampling programmes (Turner, 2004; Hopcroft et al., 2005; Rakhesh et al., 2006). Even after a large amount of study, this viewpoint still persists in

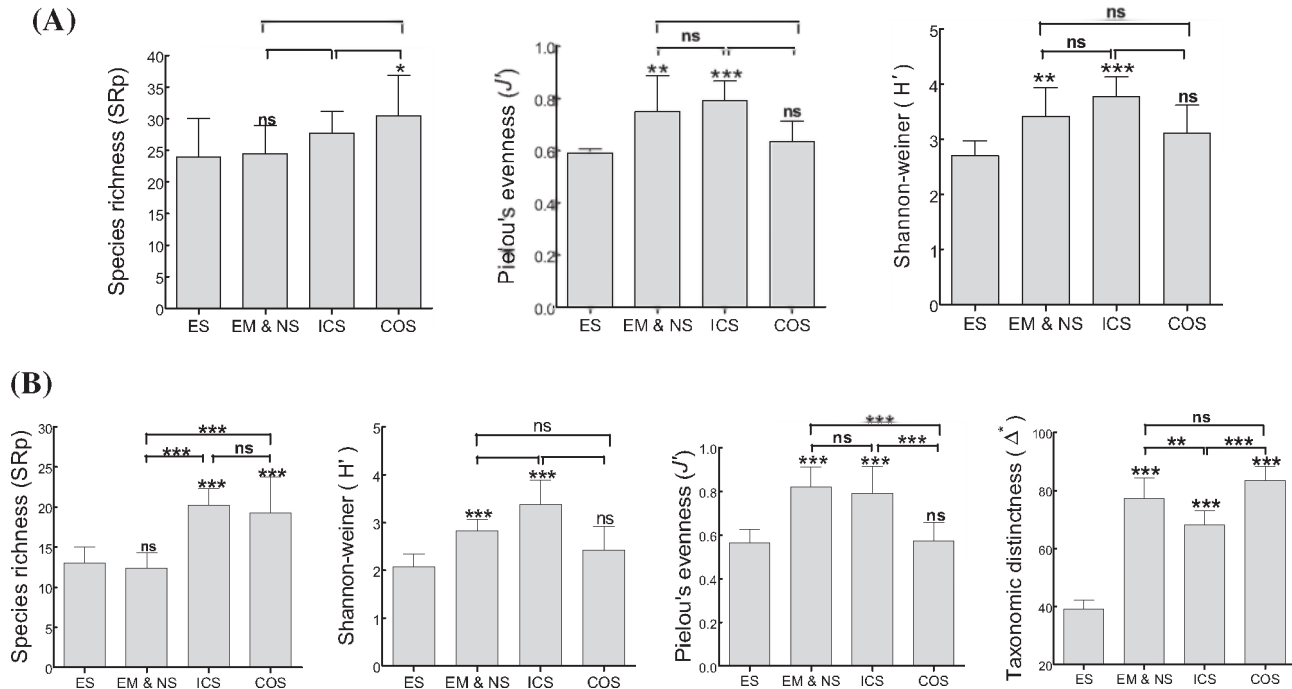


Fig. 7. Spatial variations in the diversity pattern of (A) total zooplankton and (B) copepod assemblages. Whiskers indicate standard deviation; ns- not significant; and asterisks-significant levels ($P < 0.001^{***}$, $P < 0.01^{**}$, $P < 0.05^*$, ANOVA, the Bonferroni post-hoc multiple comparison test).

the recently concluded JGOFS and GLOBEC, for which larger copepods such as *Calanus* remain key target species. In support of this view, evidence is accumulating that when appropriate nets of $\leq 100 \mu\text{m}$ are used, the abundance and sometimes even the biomass of small copepods could greatly exceed that of larger ones, as reported for example from the Long Island estuaries (Turner, 1982), the Sargasso Sea (Roman et al., 1993), the continental shelf off the south-eastern United States (Paffenhöfer et al.,

1995), coastal and oceanic waters of Jamaica (Chisholm and Roff, 1990a,b; Hopcroft and Roff, 1998), the North Sea (Nielsen and Sabatini, 1996), the Mediterranean (Calbet et al., 2001), the Red Sea (Böttger-Schnack, 1988), the North and South Atlantic (Gallienne and Robins, 2001), the equatorial Pacific (Roman and Gauzens, 1997), coastal waters of Japan (Uye and Sano, 1998; Uye et al., 2002), and the shallow near shore waters off the south coast of South Africa (Porri et al., 2007). These studies have

Table 3
Major zooplankton taxa and *characterizing species* that contribute to the average similarity within each assemblage, percentage contribution to average similarity in bold, and percentage contribution within the assemblage in parenthesis.

Assemblages	Main groups	Major contributors to similarity within each assemblage ('characterising species')
I Sim: 59.3%	Calanoida (75.4%) Gastropod veligers (15.3%) Bivalve veligers (4.9%) Chaetognatha (1.4%)	<i>Acrocalanus</i> sp., 14.2% (36.7%); <i>Acartia spinicauda</i> , 12.3% (16.4%) Gastropod veligers, 9.5% (15.3%); <i>Acartia</i> sp., 8.6% (4.7%); <i>Paracalanus</i> sp., 7.9% (8.8%); <i>Pseudodiaptomus serricaudatus</i> , 7.1% (1.5%); bivalve veligers, 5.7% (4.9%); Crustacean mysis, 5.0% (0.4%); <i>Zonosagitta bedoti</i> , 4.8% (1.4%); <i>Siriella</i> sp., 3.9% (0.4%)
II Sim: 62.2%	Cladocera (36.6%) Calanoida (31.6%) Cyclopoida (12.4%) Sergestidae (3.8%) Harpacticoida (3.1%) Crustacean larvae (3.0%) Copepod nauplii (2.6%) Appendicularia (2.1%)	<i>Penilia avirostris</i> , 10.7% (34.5%); <i>Temora turbinata</i> , 9.2% (11.0%); <i>Acrocalanus</i> sp., 9.0% (9.8%); <i>Corycaeus danae</i> , 7.7% (5.5%); <i>Oithona</i> sp.1, 7.2% (6.9%); <i>Oikopleura</i> sp., 6.3% (2.1%); <i>Lucifer hanseni</i> , 4.5% (2.7%)
III Sim: 59.3%	Calanoida (56.0%) Appendicularia (17.4%) Cyclopoida (6.1%) Harpacticoida (5.2%) Chaetognatha (4.9%) Cladocera (3.7%) Poecilostomatoida (3.2%)	<i>Oikopleura</i> sp., 9.8% (17.3%); <i>Acrocalanus</i> sp., 8.5% (21.0%); <i>Euterpina acutifrons</i> , 7.2% (5.0%); <i>Canthocalanus pauper</i> , 6.9% (9.0%); <i>Corycaeus danae</i> , 6.2% (3.7%); <i>Oncaea venusta</i> , 6.1% (3.2%); <i>Nannocalanus minor</i> , 5.7% (5.7%); <i>Pseudevadne tergestina</i> , 5.1% (3.3%); <i>Undinula vulgaris</i> , 5.0% (1.6%); <i>Corycaeus speciosus</i> , 4.6% (1.2%)
IV Sim: 61.3%	Calanoida (50.8%) Cladocera (20.9%) Cyclopoida (12.0%) Harpacticoida (3.5%) Appendicularia (3.3%) Chaetognatha (2.7%) Poecilostomatoida (2.5%) Decapod larvae (1.1%)	<i>Acrocalanus</i> sp., 11.5% (41.7%); <i>Pseudevadne tergestina</i> , 7.6% (18.9%); <i>Corycaeus danae</i> , 6.8% (4.9%); <i>Corycaeus speciosus</i> , 6.7% (4.1%); <i>Oikopleura</i> sp., 5.9% (3.3%); <i>Oithona</i> sp.1, 5.1% (1.8%); <i>Euterpina acutifrons</i> , 5.1% (2.0%); <i>Zonosagitta bedoti</i> , 4.3% (1.7%); <i>Paracalanus</i> sp., 4.2% (0.9%); <i>Macrosetella gracilis</i> , 3.8% (1.5%); Brachyuran zoea, 3.8% (1.1%); <i>Oncaea venusta</i> , 3.7% (1.9%)

Table 4

Discriminating zooplankton species and Global R and P values along with mean abundances of species that contribute to the maximum dissimilarity between the assemblages (in bold italic).

Average dissimilarity: 70.15% (Global R: 0.99, P:1.2%)	Group I	Group II	Av. Diss	SD	Diss/SD	Contrib.%
	Av. Abund	Av. Abund				
<i>Penilia avirostris</i>	0	6.96	4.34	0.83	5.22	6.19
<i>Temora turbinata</i>	0	5.52	3.48	0.57	6.11	4.96
<i>Acartia spinicauda</i>	5.6	0.91	2.99	1.12	2.66	4.27
<i>Corycaeus danae</i>	0.48	4.64	2.63	0.65	4.03	3.76
<i>Euterpina acutifrons</i>	0	3.54	2.21	1.11	2	3.15
<i>Pseudodiaptomus serricaudatus</i>	3.12	0.63	1.73	0.66	2.63	2.47
Average dissimilarity: 75.33% (Global R: 1, P:2.9%)	Group I	Group III				
Gastropod veliger	5.03	0	2.89	0.89	3.24	3.83
<i>Oikopleura</i> sp.	1.38	6.35	2.86	0.68	4.21	3.79
<i>Euterpina acutifrons</i>	0	4.65	2.67	0.32	8.4	3.55
<i>Canthocalanus pauper</i>	0.66	5.11	2.55	0.86	2.95	3.39
<i>Oncaea venusta</i>	0	4.11	2.37	0.36	6.54	3.14
<i>Pseudekadna tergestina</i>	0	3.82	2.19	0.60	3.68	2.9
<i>Corycaeus danae</i>	0.48	4.24	2.17	0.59	3.7	2.88
<i>Undinula vulgaris</i>	0	3.44	1.96	0.18	10.87	2.61
<i>Acartia spinicauda</i>	5.6	2.27	1.89	0.84	2.24	2.51
<i>Corycaeus speciosus</i>	0	3.17	1.82	0.35	5.24	2.42
<i>Pseudodiaptomus serricaudatus</i>	3.12	0	1.79	0.21	8.38	2.38
Crustacean mysis	2.24	0	1.28	0.14	8.84	1.7
Average dissimilarity: 71.58% (Global R: 1, P:0.3%)	Group I	Group IV				
<i>Acartia spinicauda</i>	5.6	0.27	4.01	1.02	3.94	5.6
Gastropod veliger	5.03	0.88	3.09	1.34	2.31	4.32
<i>Pseudekadna tergestina</i>	0	3.78	2.81	1.12	2.5	3.93
<i>Pseudodiaptomus serricaudatus</i>	3.12	0	2.32	0.34	6.74	3.25
<i>Corycaeus speciosus</i>	0	2.84	2.12	0.36	5.84	2.96
<i>Corycaeus danae</i>	0.48	2.95	1.86	0.68	2.73	2.6
<i>Euterpina acutifrons</i>	0	2.3	1.72	0.46	3.78	2.41
Crustacean mysis	2.24	0	1.66	0.23	7.29	2.33
<i>Siriella</i> sp.	2.04	0	1.54	0.54	2.85	2.15
Average dissimilarity: 57.27% (Global R: 0.87, P:0.5%)	Group II	Group III				
<i>Penilia avirostris</i>	6.9	1.46	2.81	1.05	2.68	4.9
<i>Canthocalanus pauper</i>	0	5.11	2.64	0.58	4.54	4.6
<i>Undinula vulgaris</i>	0	3.44	1.77	0.18	9.95	3.09
<i>Lucifer hanseni</i>	3.32	0	1.7	0.61	2.78	2.96
<i>Corycaeus speciosus</i>	0	3.17	1.64	0.31	5.33	2.86
<i>Oikopleura</i> sp.	3.69	6.35	1.37	0.27	5.07	2.4
Average dissimilarity: 59.06% (Global R: 0.98, P: 0.1%)	Group II	Group IV				
<i>Penilia avirostris</i>	6.96	1.79	3.35	1.25	2.69	5.67
<i>Temora turbinata</i>	5.52	0.58	3.23	0.90	3.58	5.47
<i>Corycaeus speciosus</i>	0	2.84	1.85	0.31	5.97	3.14
Average dissimilarity: 54.59% (Global R: 0.91, P:0.3%)	Group III	Group IV				
<i>Oikopleura</i> sp.	6.35	2.64	2.2	0.45	4.93	4.03
<i>Canthocalanus pauper</i>	5.11	1.56	2.09	0.82	2.55	3.83
<i>Undinula vulgaris</i>	3.44	0.42	1.79	0.58	3.06	3.29
<i>Euterpina acutifrons</i>	4.65	2.3	1.39	0.36	3.84	2.54

corroborated the importance of small copepod species and/or early developmental stages ignored in most zooplankton studies (see Hopcroft et al., 1998; and references therein). This bias is aggravated when we consider their ecological roles and rates of processes within the zooplankton community, for most physiological rates are size dependent. Their small size also implies that as they feed on particles smaller than those utilized by larger copepods, nauplii-copepodites-smaller copepods move microbial food web energy normally un-utilised by the larger metazoans, into the classical food chain (Kiorboe and Nielsen, 1994; Roff et al., 1995; Turner, 2004). Also, an insight into the distribution pattern of small copepods in inshore waters is critical to the understanding of benthic-pelagic coupling (Davenport et al., 2000; Porri et al., 2007). These observations have indicated the central role of small-sized copepods in energy transfer, especially in the dynamic coastal ecosystems. The predominance of smaller copepods observed in the estuary-coastal waters during this study, and also their prevalence in the shelf and oceanic waters (Rakesh and Raman,

unpublished work), indicate homogeneous sea conditions within the very large Bay of Bengal during this season.

Bouillon et al. (2000) identified mangrove litter as a significant source of high DOC in the upper reaches of Gautami-Godavari estuary (corresponding to St. 1 & 2 in the present study), and its effective conversion into microbial biomass (Benner et al., 1986; Bouillon et al., 2003) during the spring intermonsoon. Their theory of mangrove outwelling in coastal enrichment, if proved true, would significantly increase the importance of microbial production (and hence that of the microbial loop) and thereby alter the mesozooplankton community structure in the coastal waters off the Godavari estuarine system. During the present study, it was noticed that with progression from the estuary to offshore, larger species added to community, some largely predatory (Group-IV) and others mostly suspension feeders. Their role as 'discriminating species' between the assemblages during this study also emphasized the importance of these fast growing secondary producers in tropical near shore systems (Mullin and

Onbé, 1992; Hopcroft and Roff, 1995). Such an increase in taxonomic diversity, in turn, would increase the average number of coastal planktonic trophic links.

In support of this view, the various measures of alpha diversity revealed low diversity of total zooplankton in the estuary compared to the maximum diversity in coastal-offshore waters. H' and J' for various mesozooplankton/copepod assemblages showed values and patterns similar to that from different tropical (Sagga estuary, Malaysia, Chew and Chong, 2011) and temperate estuarine systems (Mondego estuary, Portugal, Primo et al., 2009). Average taxonomic distinctness (Δ^*) based on taxonomic hierarchy of copepods also revealed a pattern similar with minimum taxonomic breadth within the estuary. In the coastal waters, Δ^* exhibited a trend contrasting to the Shannon diversity. We observed a similar trend in the oceanic waters of the Bay of Bengal during the same season (unpubl. work). Such differences between copepod diversity measures were earlier reported from the southwestern Atlantic Ocean by Berasategui et al. (2006). Environmental heterogeneity and species adaptability to the habitat could be the deciding factors. Similarly, different beta diversity measures used in the study revealed zooplankton species turnover, intergroup differences and intragroup variability in species association patterns among the assemblages. Many physical and local factors could influence such discrete zooplankton assemblages. In tropical waters, where seasonality is not so pronounced with temperature shows little variations, salinity is regarded as the most important variable that determines the spatial distribution of species within an estuary (Elliott and Hemingway, 2002). In the present study, the reduced mesozooplankton diversity and the distribution pattern of estuarine copepods such as *Acartia* spp. (especially *Acartia spinicauda*), and *Pseudodiaptomus* spp within the estuary was in agreement with species tolerance to salinity gradients as recorded from several other tropical systems (example, Darwin Harbour estuary, Australia, Duggan et al., 2008; Sagga estuary, Malaysia, Chew and Chong, 2011). Changes in salinity affect the resident copepod population through regulation of respiration and feeding activity (Lawrence et al., 2004) resulting in a reduction in inter-specific competition and survival rate (Vilas et al., 2009). This partly explains why mesozooplankton/copepods with high salinity tolerance only could survive in the estuarine waters.

Studies from other tropical areas have indicated several other factors responsible for dominance of small copepods in estuarine systems. The key factors are the predominance of picoflagellates within the estuary (Uye, 1994), efficient feeding at low food concentration (Lampitt and Gamble, 1982), lower predation by visual predators compared to larger copepods (Kimmerer, 1991), high egg production rate and rapid per-stage growth rate (Turner, 2004), low metabolic rates (Boto and Bunt, 1981), eutrophication and a balance between food concentration and predation pressure (Ueda, 1991).

The present study, has implications for the Convention of Biological Diversity and many other biodiversity conservation programmes (Gray, 1997), and shows that environments identified as more diverse using one measure can be less diverse (and *vice versa*) when evaluated by another. This emphasizes the need for a greater use of complementary diversity indices, in any environmental sampling programme to identify hidden biological information.

Given the main objectives of this study, small copepods on mesozooplankton community dynamics, little effort was made to correlate the observed zooplankton/copepod assemblage patterns with physical, chemical and biological changes associated with upwelling observed along this coast between 13°N and 16°N latitudes, during the same period. However, the proximity of the study areas and seasonality indicates the role of regenerated/recycled nutrients in shaping the zooplankton community through the

phytoplankton-microzooplankton organization (Rakesh et al., 2008) in the coastal waters.

5. Conclusions

The zooplankton/copepod community structure and copepod size-spectra studied here revealed the importance of small copepods in the pelagic food web structure, in the estuary-coastal waters in the Bay of Bengal during summer. This showed the existence of an estuarine-coastal gradient in plankton trophodynamics which was reflected by the overall dominance of smaller copepods, and increased dominance of carnivores in the coastal-offshore segment. Evidence suggests that the estuarine-coastal waters of the Bay of Bengal could become an extension of shelf and oceanic waters during the spring intermonsoon, when pelagic energy flow is mainly channelled through the microbial food chain. The present study illustrates the importance of, and advocates the need for incorporating complementary or additional biodiversity measures while describing biotic communities with regard to environmental gradients. Such approaches should help to resolve biodiversity related issues especially in the highly dynamic, heterogeneous and species-rich tropical systems.

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