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RESEARCH ARTICLE

Copepods (Zooplankton) of Muriganga Estuary, at West Bengal Coast, India

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Abstract Estuarine plankton are often influenced by seasonal change and abiotic variability. The copepod community of India's Muriganga estuary was hypothesized to be affected by seasonal and abiotic (e.g., salinity, water temperature and pH) changes; therefore, seasonal sampling of the copepod assemblages and those abiotic parameters was conducted between February 2019 and October 2020 from three sites of the estuary. It was found that the salinity of premonsoon was significantly different than monsoon and postmonsoon. Further, salinity showed a significant negative relationship with the diversity indices and the total abundance of the copepod community. Seasonal ordination of the copepod assemblages was significantly different. Dissimilarities observed in the abundances of species such as *Bestiolina similis*, *Acartiella tortaniformis*, *Acartia spinicauda* and *Paracalanus parvus* could be a possible reason of that. *Bestiolina similis* was the most abundant and dominant population of the copepod community. Species such as *Acartiella tortaniformis*, *Acartia spinicauda*, *Paracalanus parvus* were also highly abundant. Occasionally, along with *Bestiolina similis* those species co-dominated the copepod community of the Muriganga estuary. The results overall indicate the resilience of the copepod community to the abiotic and seasonal changes of the tropical estuarine environment.

Keyword Abiotic variability · Abundance · Diversity · Dominance · Seasonal change · Indian Sundarbans

Introduction

An estuary is generally considered as a transitional ecosystem between a freshwater river and a saltwater ocean (Whitfield 1992); however, a global definition of an estuary is still debatable because of the extreme variability of estuarine morphology, environment, biology, ecology and so on (Paul et al. 2019). River-estuaries are subjected to various seasonal and abiotic changes as well as stochastic disruptions such as cyclones and floods (Chen et al. 2013; Feebarani et al. 2016; Mitra et al. 2018; Mitra et al. 2019) and are often the examples of depleted and degraded ecosystems (Lotze et al. 2006; Harrison et al. 2008). In the tropical river-estuaries, seasonal changes of salinity, water temperature and pH may limit the diversity and distribution of the copepods (Costa et al. 2008; Duggan et al. 2008; Chew and Chong 2011; Bhattacharya et al. 2015). In the Ganges River estuary (GRE) of India, plankton communities are largely influenced by the semi-diurnal tides and the arrival and departure of the south-west monsoon which brings about 1800 mm of rain to the region (Mukhopadhyay et al. 2006; Choudhury et al. 2015; Bhattacharya et al. 2015). Previous research on the GRE's mesozooplankton community, including on the copepods, suggested the existence of two peaks of diversity and abundance occurring late premonsoon (between May and early June) and from the middle of postmonsoon (between December and January) (Sarker et al. 1986; Bhattacharya et al. 2015). Diversity of the GRE's mesozooplankton community, which

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is largely dominated by copepods, is significantly influenced by the salinity gradients of the estuary (Sinha et al. 1996; Bhattacharya et al. 2015). Further, annual storm surges and/or cyclones of varying intensities hit the region and disrupt the copepod community structure (e.g., species richness, abundance) for a few days to a few weeks (Paul et al. 2020a, b, 2023). Such changes of the copepod community structure may have short to medium-term consequences for the benthic and pelagic coupling of the estuary because copepods are the prey item for many macro-invertebrates and fish species (Paul et al. 2020a, b, 2023).

The Muriganga estuary (ME), is a bifurcation of the lower reach of the GRE before it meets the Bay of Bengal (Mukhopadhyay et al. 2006). Within each tidal cycle, hourly variations of water temperature and pH of the ME are not that significant and have only limited impacts on the copepod diversity and distribution of the ME (Paul et al.2019). The copepod community of the ME is often dominated by *Bestiolina similis* (Paul et al. 2019). *Paracalanus parvus* is also highly abundant in the ME and along with *B. similis* occasionally *P. parvus* co-dominates the estuary (Paul et al. 2019). In contrast, after cyclones 'Fani' and 'Bulbul, *Acartiella tortaniformis* and *Acartia spinicauda* became highly abundant in the ME for a few days to a few weeks and co-dominated the estuary with *B. similis* and *P. parvus* (Paul et al. 2020a). The ME copepod community also includes occasional marine intruders such as *Acrocalanus gibber* and *Eucalanus elongates* but their abundances remain generally are low (Sarkar et al. 1986; Paul et al. 2019). Even though short-term (a few hours to a few weeks) information on the copepod community exists for the ME (Sarkar et al. 1986; Paul et al. 2019; Paul et al. 2020a, b) but there is not any study which has ever focused on the seasonal variability of the copepod community of the ME. The aim of the study was to evaluate the effects of abiotic and seasonal changes on the diversity, abundance and dominance of the copepod community. That would provide more in-depth understanding of the resilience and vulnerabilities of the copepod community of a tropical river-estuary.

Methods

Study Site

The ME (Fig. 1) adjoins moderately developed mangrove vegetation and an intensely cultivated hinterland. The Indian Sundarbans, including the ME, typically experience three seasons per year which are closely related to the arrival and departure of South-West monsoon rainfall in India

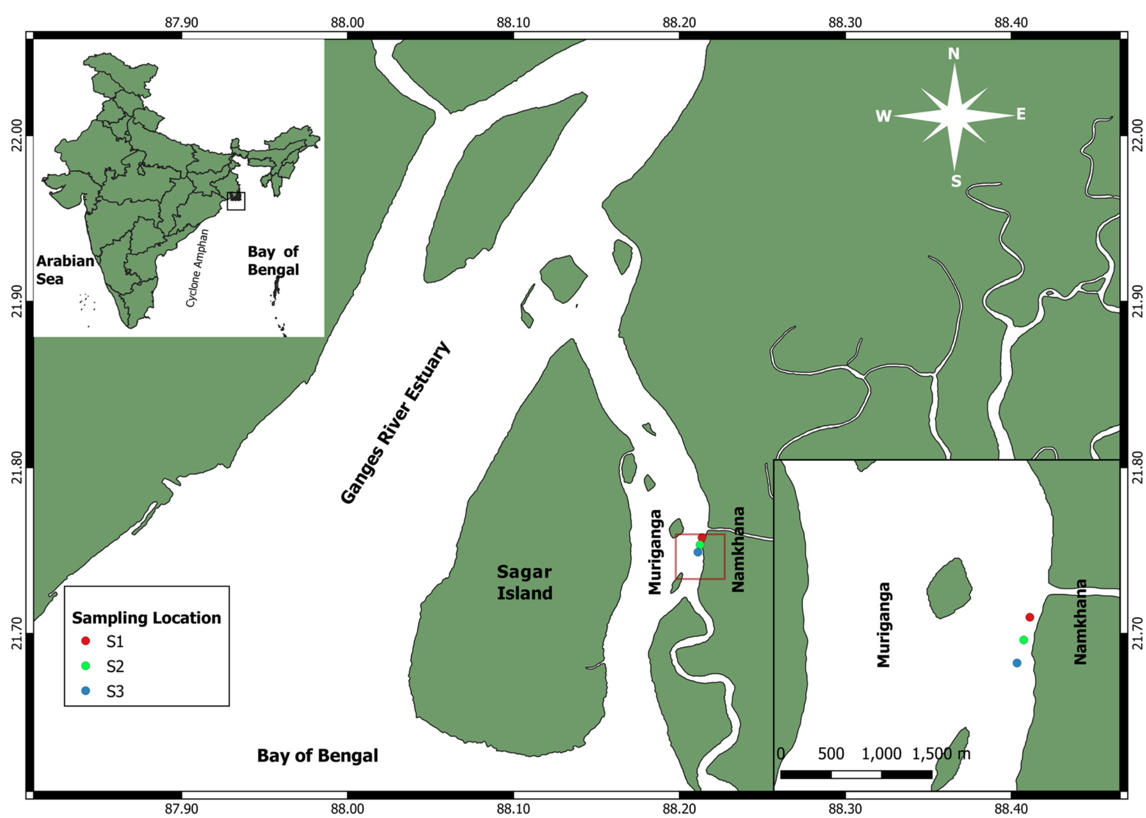

Fig. 1 Study sites on the Muriganga estuary of India

(Mukhopadhyay et al. 2006). Typical seasons in the Indian Sundarbans are pre-monsoon, which often occurs from late February until the middle of June, monsoon between middle of June to the end of September and post-monsoon from October to early February (Bhattacharya et al. 2015). The ME generally remains mesohaline and slightly basic (pH > 8) except during monsoon months when it receives excessive rainfall (Mukhopadhyay et al. 2006; Choudhury et al. 2015). Seasonal sampling of the copepods conducted between February 2019 and October 2020, was delayed on various occasions due to COVID-19 lockdown in India. Within a consecutive six month period during the study interval the ME was disrupted by three cyclones of varying intensity, 'Fani' (5 May 2019), 'Bulbul' (9 November 2019) and 'Amphan' (20 May 2020) (Paul et al. 2020a, 2023). On the Muriganga, the sampling site S1 is toward the upper end of the estuary (21°44′53.8″N, 88°12′46.2″E), S3 is towards the mouth of the estuary (21°44′55.4″N, 88°12′36.8″E) and S2 is at an equal distance between S1 and S2 (21°44′55.7″N, 88°12′40.0″E) (Fig. 1).

Sample Collections

Copepod assemblages (size class > 200 µm) were collected during premonsoon (on the occasions 25.02.19, 14.05.19 and 05.06.2020), monsoon (on the occasions 24.08.19, 12.06.20 and 09.09.20) and postmonsoon (on the occasions 18.11.19, 28.12.19 and 03.10.20) from three sampling sites (i.e., S1, S2, and S3). At each sampling site, copepods were sampled in triplicate by towing a horizontal plankton net (200 µm mesh, 60 cm diameter and 1 m length) fitted with a mechanical flowmeter (Hydrobios, Germany) for 2 min from the sub-surface water. All the samples were collected after sunset on high tide from a dinghy boat. Copepod samples were preserved in 5 ml of 4% buffered formalin and then transported to the laboratory within 24 h of collection. On each sampling occasion, salinity, water temperature (°C) and pH levels were measured with a hand-held multi-parameter probe (YSI-1030, USA) from the sub-surface water. In the laboratory, multiple aliquot samples (1 ml each, at least 3 from each replicate of the triplicate) of the copepod assemblages were taken from the filtrate and each aliquot was placed on a Sedgwick Rafter counting cell and examined under a stereo-microscope (Bestscope-BS30T, China). Copepods (adults only) were identified to species level following the taxonomic literature of Kasturirangan (1963) and their abundances were expressed as individuals per cubic metre (ind.m^{-3}).

Statistical Analysis

All of the analyses were performed using CRAN-R version 4.1.1 (R Core Team 2021). Results of statistical tests were presented with corresponding W, F, K-W chi-square, Psuedo-F, R^2, p values and degrees of freedom (df). Alpha (α) was set at 0.05 level and only those results which are significant are presented and discussed. Abiotic parameters such as salinity (Shapiro test: $W = 0.9$, $p = 0.015$), water temperature (Shapiro test: $W = 0.85$, $p = 0.001$) and pH (Shapiro test: $W = 0.76$, $p < 0.001$) data showed non-parametric distributions. Spatial variations (between S1, S2 and S3) and temporal variations (seasonal) of abiotic data were assessed by conducting multiple Kruskal–Wallis tests. Shannon-index (H) (Shannon and Weaver 1963) and Pielou's index (J) (Pielou 1966) were calculated by using the 'Vegan' package version 2.5.7 (Oksanen et al. 2020). Values of H and J indices were normally distributed but species richness and total abundance data were count in nature. Spatial (among S1, S2 and S3) and temporal (seasonal) variations of the H and J indices were evaluated by conducting one-way analysis of variance (ANOVAs) and species richness and total abundance were assessed by conducting Kruskal–Wallis tests. The Ggeneralised linear models (GLMs) including interactive models of multiple parameters were built for studying the associations between diversity indices, copepod abundances, and abiotic data. If the response variable was count (i.e. species richness and total copepod abundance) then GLM of quasi-Poisson family was used. Where the response variable was normally distributed (i.e. H and J indices) GLM of Gaussian family was used. Non-metric Multidimensional Scaling (NMDS) was conducted on copepod assemblage data using the Bray–Curtis measure of dissimilarity ('Vegan' package version 2.5.7) (Oksanen et al. 2020). Copepod abundance database was square-root transformed for reducing the data dispersion (ranged 0–11.58). Inference of dimensionality of the NMDS (i.e. K = 2) was taken after examining the stress-scores (i.e., 0.174), Shepard diagram (Fig. A1), and non-metric and linear fit R^2 scores (0.97 and 0.85, respectively). For drawing NMDS biplots based on sampling site and season (see Fig. 2a and b), 'ggplot2' package version 3.3.5 (Wickham et al. 2021) was used. Copepod assemblages from different sampling sites and seasons were compared (i.e. centroids) using permutational multivariate analysis of variance (PERMANOVAs) (Adonis test, permutations = 999, method = Bray–Curtis, package: 'Vegan' version: 2.5.7) and the assumption of homogeneity of multivariate dispersion was tested by conducting ANOVAs. A similarity percentage analysis (SIMPER) (package: 'Vegan' version: 2.5.7) was performed on the copepod community data to evaluate the major component species that were causing the dissimilarity based on season. The analysis shows the contribution of each species to overall dissimilarities, mainly caused by variation in species abundances, and only partly by differences among groups (Oksanen et al. 2020). A Canonical Correspondence Analysis (CCA) (see Fig. 3) was conducted to evaluate the relationships of species

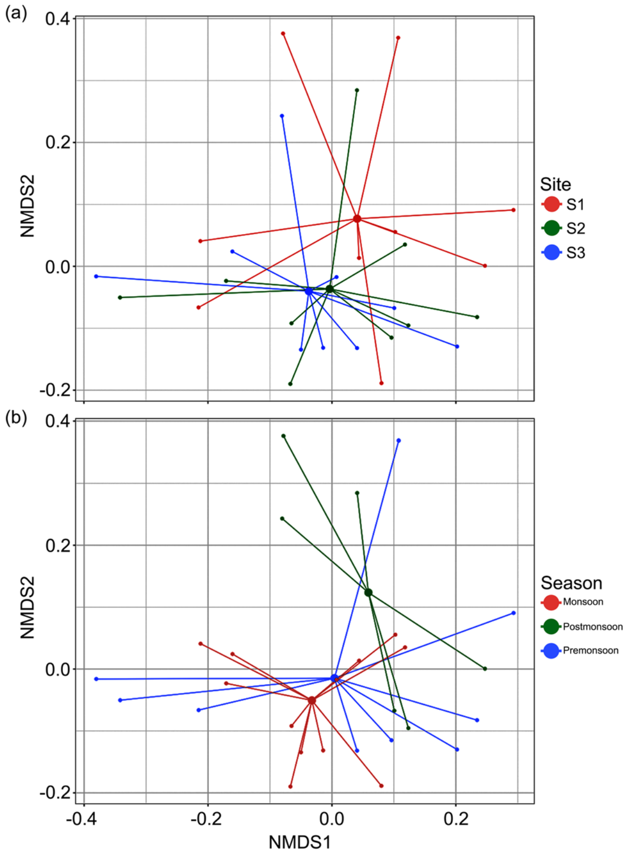

Fig.2 Non-metric Multidimensional Scaling (NMDS) plots using the Bray–Curtis measure of dissimilarity exhibiting ordination of the copepod community of the Muriganga estuary of India. **a** = spatial and **b** = seasonal

populations in the copepod community with salinity, water temperature and pH gradients in the ME.

Results

Abiotic Variability

Seasonal variations of the salinity, water-temperature and pH levels of the Muriganga are summarized in Table 1. Kruskal Wallis tests conducted on salinity (K–W chi-squared = 0.05, df = 2, $p = 0.97$), water temperature (K–W chi-squared = 0.04, df = 2, $p = 0.97$) and pH (K–W chi-squared = 0.09, df = 2, $p = 0.95$) data showed no significant spatial variations among the sampling sites. Seasonal variability of salinity (K-W chi-squared = 13.947, df = 2, $p = 0.0009$) was significant but the seasonal variability of water temperature (K–W chi-squared = 3.42, df = 2, $p = 0.18$) and pH (K–W chi-squared = 3.48, df = 2, $p = 0.17$) was not significant.

Variability of Community Indices and Their Relations with Abiotic Changes

Spatial variability of species richness (K–W chi-squared = 1.66, df = 2, $p = 0.43$), total copepod abundance (K–W chi-squared = 3.88, df = 2, $p = 0.14$), H index (F = 0.49, df = 2, $p = 0.35$) and J index (F = 0.41, df = 2, $p = 0.66$) were not significant. Significant seasonal variability of species richness (K-W chi-square = 3.88, df = 2, $p = 0.14$), total copepod abundance (K–W chi-square = 0.45, df = 2, $p = 0.79$), H index (F = 2.37, df = 2, $p = 0.11$) and J index (F = 1.17, df = 2, $p = 0.32$) was absent. Temporal variability of salinity showed significant negative associations with species richness (t = − 3.05, df = 26, $p = 0.005$), total copepod abundance (t = − 2.90, df = 26, $p = 0.007$) and H index (t = − 2.44, df = 26, $p = 0.02$); however, it was not significantly associated with J index (t = − 0.02, df = 26,

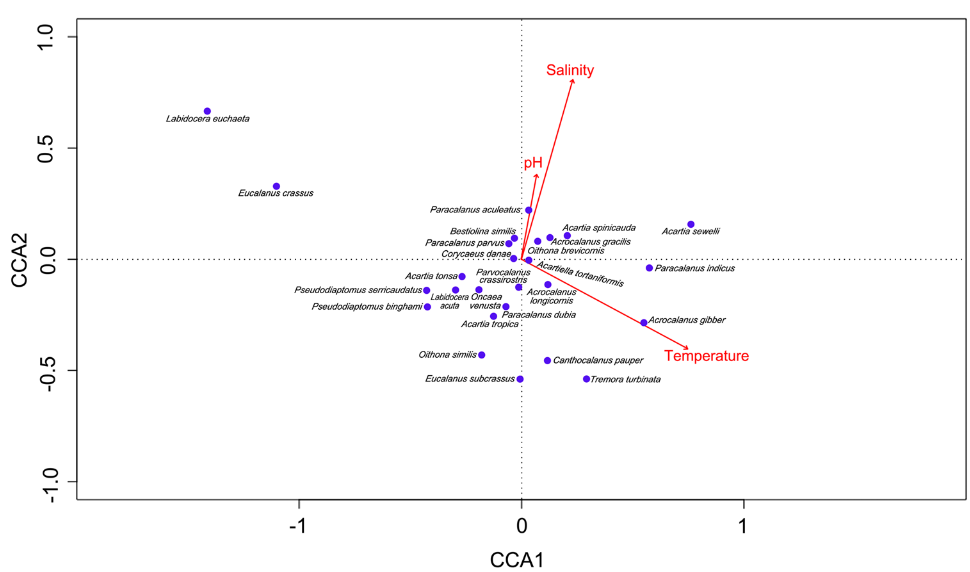

Fig.3 Canonical Correspondence plot demonstrating the correlations among the species populations of the copepod community and salinity, water temperature (°C) and pH gradients of the Muriganga estuary of India

Table 1 Seasonal variability of salinity, water temperature (°C) and pH of the Muriganga estuary of India

Season	Salinity			Water temperature (°C)			pH		
	Median	Range	SE	Median	Range	SE	Median	Range	SE
Pre-monsoon	18.30	13.27–19.30	0.87	29.90	23.00–31.30	1.22	7.80	6.10–8.56	0.34
Monsoon	8.85	5.10–16.30	1.63	28.30	27.10–29.70	0.35	8.11	7.76–8.51	0.09
Post-monsoon	10.00	4.80–10.90	0.89	23.20	20.4–30.2	1.43	8.42	6.00–8.64	0.28

$p = 0.987$). Neither water temperature nor pH showed any significant temporal associations with species richness, total copepod abundance and H and J indices of the copepod community. Two-way and three-way interactions of salinity, water temperature and pH also showed no significant temporal relationships with species richness, total copepod abundance and H and J indices.

Variability of Species Assemblages

Spatial variability of the copepod assemblage was not significant (PERMANOVA: df = 2, Sum of Square site = 0.12, Pseudo-F = 0.74, $R^2 = 0.05$, $p = 0.69$) and in that regard the assumption of homogeneity of multivariate dispersion was not violated (ANOVA: df = 2, F = 0.12, $p = 0.88$) (Fig. 2a). Seasonal variability of the copepod assemblage was found to be significant (PERMANOVA: df = 2, Sum of Square site = 0.30, Pseudo-F = 2.07, $R^2 = 0.14$, $p = 0.03$) and in that regard the assumption of homogeneity of multivariate dispersion was not violated (ANOVA: df = 2, F = 1.3, $p = 0.27$) (Fig. 2b). The SIMPER analysis showed that the uneven abundances of *B. similis*, *Acartiella tortaniformis*, *Acartia spinicauda* chiefly caused the dissimilarities between pre-monsoon, monsoon and post-monsoon species assemblages within the copepod community. Along with those species, *Oithona brevicornis*, *Paracalanus parvus, Acartia tropica*, and *Pseudodiaptomus serricaudatus* contributed considerably to the observed dissimilarities of the copepod assemblages sampled between pre-monsoon and monsoon, and between monsoon and post-monsoon. Comparison between pre-monsoon and post-monsoon species assemblages showed abundance of *A. tropica* was less responsible for the dissimilarity of the copepod community but abundances of *Oithona brevicornis*, *Paracalanus parvus* and *Pseudodiaptomus serricaudatus* continued their significant contributions to the dissimilarity matrix. The eigen values of constrained axes such as CCA1, CCA2 and CCA3 were 0.059, 0.028 and 0.020 respectively, which were considerably lower than the eigen values of the 23 unconstrained axes; therefore, the constrained proportion of the three CCA axes amounted for only 16% compared to the unconstrained proportion of 84%. So, correlations between species assemblage with salinity, water temperature and pH gradients of the estuary remained mostly unexplained (Fig. 3). Abundances of a few species such as *Paracalanus aculeatus* and *Acartia spinicauda* were positively correlated with salinity and pH and the abundance of *Acrocalanus gibber* was positively correlated with water temperature (Fig. 3).

Dominance in the Copepod Community

Bestiolina similis was the most abundant copepod (Table 2) and maintained its dominant status throughout the study (Table 3). Also highly abundant were *Acartiella tortaniformis*, *Acartia spinicauda* and *Paracalanus parvus* (Table 2). According to the index of dominance, species such as *A. tortaniformis*, *A. spinicauda*, *P. parvus* co-dominated the estuary on different occasions (Table 3).

Discussion

Variability of Habitat Characteristics

The ME is a wide but relatively shallow river-estuary that receives freshwater from the mainstream of the Ganges River in India (Mukhopadhyay et al. 2006). At times of ecosystem stability, hourly variability of the abiotic parameters of the ME is not particularly significant (Paul et al. 2019). Results showed that the spatial variations of salinity, water temperature and pH levels of the ME were not significant. The ME receives freshwater flow from the Ganges River while tidal movements and offshore winds churn the water mass of the ME, causing surface water layers to be well mixed so that abiotic gradients are often not pronounced (Mukhopadhyay et al. 2006). The highest salinity recorded was in May 2019, possibly due to the reduced freshwater flow of the ME in the middle of pre-monsoon (Mukhopadhyay et al. 2006). The ME is a macrotidal estuary situated close to the mouth of the Ganges River and receives saltwater intrusion on a regular basis from the Bay of Bengal, resulting in significant temporal variation of its salinity (Mukhopadhyay et al. 2006; Choudhury et al. 2015). Water temperature did not vary significantly on a temporal scale, a result consistent with Bhattacharya et al. (2015) who observed that seasonal temperature of the Indian Sundarbans estuaries varies only within a narrow range and such a variability is often not significant. The overall pH level of the ME was alkaline. Choudhury et al. (2015) observed an alkaline pH profile of

Table 2 List of the copepod species sampled and their abundances (ind.m^{-3}) in different seasons in the Muriganga estuary of India

Species	Pre-monsoon	Monsoon	Post-monsoon	Total catch
Bestiolina similis	59,500	118,800	97,033	275,333
Acartiella tortaniformis	37,900	90,900	65,500	194,300
Acartia spinicauda	32,510	73,383	57,167	163,060
Paracalanus parvus	30,800	64,967	41,733	137,500
Pseudodiaptomus serricaudatus	17,510	24,234	21,533	63,277
Paracalanus aculeatus	13,270	21,683	21,567	56,520
Acartia tropica	12,900	27,283	13,767	53,950
Oithona brevicornis	0	40,433	11,233	51,667
Paracalanus dubia	8510	28,300	4767	41,577
Parvocalanus crassirostris	7900	23,850	6667	38,417
Acrocalanus gracilis	6510	18,900	12,433	37,843
Paracalanus indicus	2000	27,950	6400	36,350
Acrocalanus longicornis	1900	17,633	4267	23,800
Canthocalanus pauper	5000	12,167	5600	22,766
Eucalanus subcrassus	6000	11,317	3933	21,250
Acartia sewelli	0	15,083	3200	18,283
Acartia tonsa	4629	10,467	533	15,629
Pseudodiaptomus binghami	8510	5817	0	14,327
Corycaeus danae	0	7800	4767	12,567
Temora turbinata	0	9734	0	9734
Eucalanus crassus	6510	1800	867	9177
Labidocera acuta	0	6350	1333	7683
Labidocera euchaeta	6510	833	0	7343
Oncea venusta	0	7334	0	7334
Acrocalanus gibber	0	2983	2667	5650
Oithona similis	0	1533	0	1533

Table 3 Index of dominance of a few frequently sampled copepod species of the Muriganga estuary of India

Season	Sampling date	*Bestiolina similis*	*Acartiella tortaniformis*	*Acartia spinicauda*	*Paracalanus parvus*
Pre-monsoon	25/02/2019	0.12	0.01	0.06	0.08
Pre-monsoon	14/05/2019	0.23	0.18	0.13	0.11
Monsoon	24/08/2019	0.13	0.06	0.04	0.11
Post-monsoon	18/11/2019	0.22	0.15	0.09	0.11
Post-monsoon	28/12/2019	0.29	0.28	0.11	0.07
Pre-monsoon	05/06/2020	0.22	0.14	0.21	0.07
Monsoon	12/06/2020	0.19	0.14	0.12	0.11
Monsoon	09/09/2020	0.17	0.14	0.10	0.08
Post-monsoon	03/10/2020	0.16	0.13	0.11	0.07

the ME throughout the year with the exception of periods of excess rainfall in the estuary during monsoon which temporarily depresses the pH profile. Paul et al. (2019) and Paul et al. (2020a, b, 2023) also observed persistent alkaline pH of the ME during periods of ecosystem stability as well as under extreme (i.e. cyclone) conditions; therefore, results mostly agree with recent works conducted in the ME.

Copepod Community Composition

The ME copepod community consisted mainly of calanoids, with Paracalanidae and Acartiidae accounting for most of the total abundance, results that are consistent with previous studies on the ME (Sarkar et al. 1986; Paul et al. 2019). In India's coastal waters, which include the mangrove estuaries of the Indian Sundarbans, Paracalanidae play an significant and crucial role for the overall structure of the estuarine copepod community since many species of that family build dense populations (Padmavati and Goswami 1996; Fernandes and Ramaiah 2014; Paul et al. 2019; Nandy and Modal 2020). There was no evidence of significant spatial ordination in the copepod community. Diversity of copepod species (i.e. Shannon index and Pielou's index) did not vary between sampling sites, which is consistent with Paul et al. (2019) who observed no significant spatial change of copepod diversity in the ME. Copepods such as *B. similis*, *A. tortaniformis*, *A. spinicauda*, *A. tropica*, *P. parvus*, *P. aculeatus* and *P. serricaudatus* were ubiquitous as previously observed by Paul et al. (2019) and Paul et al. (2020b). During monsoon, the relative abundances of *P. indicus*, *Acrocalanus gibber*, *A. gracilis*, *A. spinicauda* and *A. sewelli* were considerably higher than in pre-monsoon and post-monsoon. Many of those species are stenohaline and during monsoon their abundance increases in the resident copepod community, which is otherwise largely comprised of euryhaline species populations (Paul et al. 2019, 2020a). Throughout this study *Bestiolina similis* was the most abundant and dominant copepod of the community, results are consistent with the studies conducted the by Bhattacharya et al. (2015) and Paul et al. (2020a) in the region. *Bestiolina similis* tolerates extreme and abrupt changes of salinity, water temperature and pH levels of the mangrove estuaries of the Indian Sundarbans, including the Muriganga (Bhattacharya et al. 2014) and it dominates the copepod community irrespective of a stable or perturbed condition of the ME (Paul et al. 2019, 2020a). The dominance index of *B. similis*, *A. tortaniformis* and *A. spinicauda* shows those species were the dominant in the ME and their dominances remained during the course of the study. Those copepod species may coexist by changing their feeding habit according to the variable conditions of an estuary (Klippel 1993). *Bestiolina similis* continued to hold a dominant position in the community whereas *A. spinicauda* was occasionally replaced by *A. tortaniformis*. *Acartiella tortaniformis* is found exclusively in India's coastal waters and tolerates a wide range of salinity, water temperature and organic loads, which may be one reason for its higher abundance in the ME where abiotic gradients fluctuate with every incoming and outgoing tide (Gajbhiye et al. 1991; Bhattacharya et al. 2014). *Paracalanus parvus*, which is generally found in coastal, neritic and brackish waters, is a warm-water herbivorous copepod that generally feeds on diatoms (Checkley 1980; Paul and Calliari 2019). The niche of *P. parvus* overlaps with *B. similis* when the estuary is not disrupted by any cyclone for a few months according to a study of hourly changes in the ME copepod community; however, after cyclonic disruptions *P. parvus* is replaced by *A. tortaniformis* (Paul et al. 2019, 2020b). The presence of cyclopoid copepods *Oithona brevicornis* and *Oithona similis* were recorded throughout the study. The relative abundance of *O. brevicornis* was considerably higher during the monsoon of 2020, which may indicate an increase of carnivorous individuals in the copepod community during that time, which may trigger a change in the predator–prey relationships within the copepod community of the region (Bhattacharya et al. 2015; Paul et al. 2020a).

Seasonal Change of the Copepod Community

Seasonal variability of the plankton community in Indian estuaries, including in the Sundarbans, has been studied previously (Padmavati and Goswami 1996; Biswas et al. 2010; Nandy et al. 2018; Gogoi et al. 2020; Nandy and Mandal 2020). Copepod species richness and abundance in the ME generally has two distinct peaks. The first peak occurs in late post-monsoon (December to middle of February) and the second in late pre-monsoon (April to early June), while species richness tends to be relatively low in late monsoon (August to September) (Sarkar et al. 1985, 1986). That observation by Sarkar et al. (1986) was supported by Bhattacharya et al. (2015) while studying the dominance of copepods in the mesozooplankton of the Indian Sundarbans. The ME receives high nutrient inputs from its catchment during the monsoon (Mitra et al. 2018, 2019) which contributes to the proliferation of the ME phytoplankton community in early post-monsoon. Consequently, the ME supports a higher diversity and density of mesozooplankton in the late post-monsoon (Biswas et al. 2010; Bhattacharya et al. 2015; Choudhury et al. 2015; Gogoi et al. 2020). Results contradict previous studies on the copepods of the ME and other mangrove estuaries of the Indian Sundarbans (Sarkar et al. 1985, 1986; Bhattacharya et al. 2015; Nandy et al. 2018; Nandy and Mandal 2020). Three successive cyclones, i.e. Fani (May 2019), Bulbul (November 2019) and Amphan (May 2020), severely disrupted the ME in recent years (Paul et al. 2020a,b), which may have also disrupted the copepod community for a few weeks at a time during six consecutive months. Due to such disruptive events it may be possible that the copepod community of the ME has less time to build up its usual seasonal peaks of species richness and abundance. Significant ordinations within the ME copepod community were observed when comparisons were drawn based on seasons. Large populations of copepods *B. similis*, *A. tortaniformis*, *A. spinicauda*, *O. brevicornis*, *P. parvus*, *A. tropica* and *P. serricaudatus* were built possibly because they are estuarine specialists and tolerate a wide variability of abiotic conditions (Bhattacharya et al. 2015; Nandy et al. 2018; Nandy and Mandal 2020).

Effects of Abiotic Variability on the Copepod Community

Abiotic variability affects copepod diversity and distribution in India's tropical river-estuaries (including the Sundarbans region), Brazil, Malaysia and Australia (Duggan et al. 2008; Magalhães et al. 2009; Chew and Chong 2011; Rakhesh et al. 2013; Nandy and Mandal 2020). Temporal variability of water temperature and pH, and their interactions, showed no significant impact on diversity indices and total abundance of the ME copepods. That is possibly because the water temperature varies only within a narrow range in the estuaries of Indian Sundarbans so the resident copepods reproduce throughout the year, for which the total abundance and diversity are less affected by the temperature variability (Bhattacharya et al. 2015). A decline of pH levels in an estuary may be stressful for many of its copepod populations because that would reduce their reproductive output (egg production and brood release), and would likely negatively impact their diversity and total abundance (Aguilera et al. 2013; Paul et al. 2020b). However, that is unlikely for the copepods of the ME since the habitat mostly maintains its alkaline characteristics (Choudhury et al. 2015; Paul et al. 2019). In the ME, relationships between salinity, species richness, abundance and Shannon index were inversely related to each other. However, the abundances of *Paracalanus aculeatus* and *Acartia spinicauda* were higher with the increasing levels of salinity and pH, and the abundance of *Acrocalanus gibber* was found to be high in higher temperatures. The extended monsoon of recent years and successive cyclones during the study interval have possibly kept the overall salinity profile of the ME between oligohaline and mesohaline range (Paul et al. 2020a,b, 2023). Subjected to such salinity, *B. similis*, *A. tortaniformis*, *A. spinicauda*, *A. tropica*, *P. parvus*, *P. aculeatus* and *P. serricaudatus* built large populations, possibly because they are typically estuarine residents that can withstand wide fluctuations of salinity, which many other marine origin species fail to tolerate (Paul et al. 2020a). Cyclone induced changes of the ME are temporary, lasting for a few days to a few weeks and the intensity of those changes depends on the landfall site of a cyclone (Paul et al. 2020a, b, 2023). Changes in the copepod community following cyclone 'Bulbul' and 'Amphan' which made their landfall in the Indian Sundarbans; therefore, are likely to be more intense and last longer than those after cyclone 'Fani'.

Copepods as Indicators of Changes of Estuarine Environment

To draw inferences about the natural variability in an estuarine environment, traditional estuarine ecological studies focused on the presence and or absence of certain plankton species, diversity indices, distribution, and relationships with abiotic gradients of an estuary (Lawrence et al. 2004; Rice et al. 2015; Paul et al. 2016; Paul and Calliari 2019). Changes in the diversity indices, abundance and distribution of plankton (including copepods) are often considered to be indicators of abiotic and seasonal variability of river-estuaries (Sinha et al. 1996; Sullivan et al. 2007; Lin et al. 2011; Paul et al. 2016; Araujo et al. 2017). Detailed studies of different coastal-marine ecosystems focusing on seasonal and inter-annual changes of the copepod assemblages aim to predict the impacts of long-term abiotic changes on the estuarine food web and its implications for commercial fisheries that exploit copepods as food (Beau grand and Ibanez 2004; Sullivan et al. 2007; Rice et al. 2015). Previous studies on the ME and other mangrove estuaries of the Indian Sundarbans conducted at tidal, daily, monthly, seasonal, inter-seasonal and inter-annual scales focused on variability of diversity, abundance and dominance of mesozooplankton (including copepods) and have indicated an ongoing decadal change (a switch from a herbivore-dominated to an omnivore dominated community) and climate change (e.g. warming) of estuaries in the region (Sarkar et al. 1986; Sinha et al. 1996; Bhattacharya et al. 2015; Nandy et al. 2018; Paul et al. 2019; Nandy and Mandal 2020). The current results, however, suggested that the copepod community of the ME was not that affected by the abiotic and seasonal changes even after successive cyclonic disruptions that occurred during the study interval. That is plausible when an ecological community has high flexibility; therefore, short to medium-term seasonal studies of the copepods may be less suitable to indicate many ecological changes of a tropical river-estuary such as the Ganges River estuary.

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Data Availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Declarations

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