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Seasonal Mesozooplankton Dynamics of Marine-dominated Estuaries of Indian Sundarbans

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ABSTRACT

Mesozooplankton dynamics of Indian Sundarbans was studied by conducting a seasonal sampling between October 2012 and October 2017 from Saptamukhi, Thakuran and Matla estuaries. It was hypothesised that seasonal change and physicochemical variability limit the mesozooplankton dynamics of those estuaries. Saptamukhi, Thakuran and Matla estuaries demonstrated polyhaline salinity profiles, except in monsoon season when their salinity profiles were mesohaline in nature. Water temperature varied narrowly among seasons, which is a typical characteristic of many tropical estuaries. During pre-monsoon and post-monsoon seasons, spatial variability of pH, chlorophyll-a, dissolved oxygen, dissolved organic carbon, partial pressure of carbon dioxide, dissolved inorganic nitrate and phosphate was not significant for all three estuaries. Spatial homogeneity of physicochemical gradients breaks down in monsoon season, which in consequence possibly reduces the mesozooplankton abundance significantly in monsoon compared to the abundances of mesozooplankton in pre- and post-monsoon seasons. Mesozooplankton community is primarily built around copepods *Pseudodiaptomus serricaudatus, Paracalanus parvus, Bestiolina similis, Acartia spinicauda* and *Chaetognath Zonosagitta bedoti*. Each estuary had its own sets of abundant populations of mesozooplankton that succeeded seasonally. Physicochemical gradients possibly have a lesser role in limiting the diversity and distribution of mesozooplankton in the marine-dominated estuaries of Indian Sundarbans. Instead, the monsoon largely influences the community, which indicates the need for freshwater in marine-dominated estuaries of Indian Sundarbans.

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1. Introduction

An estuarine complex is an agglomerate of many interconnected estuaries and sub-estuaries before it meets a sea (Chew and Chong, 2011; Miyashita *et al.,* 2012; Chatterjee *et al.,* 2013; Bhattacharya *et al.,* 2015). Physicochemical and ecological variability of estuarine complexes are much higher than in a single estuary; however, such is far less studied (Biswas *et al.,* 2010; Chew and Chong, 2011; Miyashita *et al.,* 2012; Banerjee *et al.,* 2017). Estuarine ecological research is typically single estuary based and mostly is biased towards a few economically serving large river estuaries of the world (Lotze *et al.*, 2006). Limited funding for sustained research, inadequate technology, equipment and scarcity of trained human resources compel estuarine scientists to focus on a single estuary at a time with relatively short-term (a few days to a few seasons) research objectives (Paul and Calliari, 2019; Paul *et al.,* 2019b; Paul *et al.,* 2020a,b).

Plankton ecology of tropical estuarine complexes is less understood (Biswas *et al.*., 2010; Chew and Chong, 2011; Miyashita *et al.,* 2012; Bhattacharya *et al.,* 2015). Sundarbans estuarine complex of India and Bangladesh and Matang mangrove forest of Malaysia hosts multiple inter-connected mangrove estuaries, which have distinguished high productivity, efficient nutrient recycling, diverse mesozooplankton communities (Biswas *et al.*2010; Chew and Chong, 2011; Bhattacharya *et al.,* 2015). Those are the critical recruitment areas for commercially exploited fishes and fin-fish that prey on mesozooplankton (Sarkar and Bhattacharya, 2003). Indian Sundarbans is a wide network of mangrove estuaries that receive semi-diurnal tides from the northern Bay of Bengal, which underlie all their basic physicochemical processes (Mukhopadhyay *et al.,* 2006; Biswas *et al.,* 2010; Bhattacharya *et al.,* 2015). A few studies have looked into the seasonal variability of the mesozooplankton community of Indian Sundarbans (Nandy *et al.,* 2018; Nandy and Mandal, 2020); however, those studies have focused on a single estuary at a time and are of a few months to a few seasons. The current seasonal study is medium-term (October 2012 to October 2017) in nature where mesozooplankton diversity and distribution were studied in multiple marine-dominated estuaries of Indian Sundarbans with a hypothesis that seasonal change and physicochemical variability limit mesozooplankton dynamics of Saptamukhi, Thakuran and Matla estuaries.

2. Materials and Methods

2.1. Study area

Sundarbans (21˚32’, 22˚40’N; 88˚05’, 89˚00’E), a UNESCO World Heritage site, is the largest deltaic mangrove forest in the world, dominated by estuaries on the land-ocean boundary of Ganges-Brahmaputra delta (Mukhopadhyay *et al.,* 2006). It covers an area of 10200 km^2 of reserved forest, of which 41% is in India (Mukhopadhyay *et al.,* 2006). Indian Sundarbans (Fig.1) has three distinct seasons

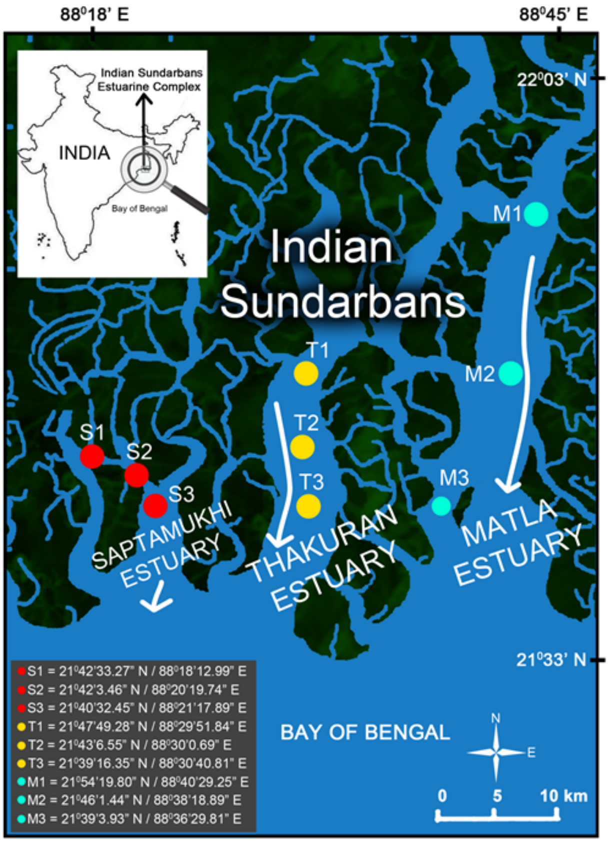

Fig. 1. Sampling stations on Saptamukhi, Thakuran and Matla estuaries of Indian Sundarbans

i) a hot and humid pre-monsoon (PRM) season from March to June (of late, it is extended by several weeks); ii) a warm and humid monsoon (MON) between July and October when most of the annual (>70% of annual average of 150 to 200 cm) rainfall occurs but the arrival of monsoon has often been delayed in recent years and iii) a mild winter (November to February) known as post-monsoon (POM) (Ganguly *et al.,* 2014; Bhattacharya *et al.,* 2015; Nandi *et al.,* 2018). Saptamukhi estuary receives intermittent freshwater flow from the Hooghly river; however, estuaries such as the Thakuran and Matla are long cut off from the Hooghly river (Rudra, 2014).

2.2. Analysis of physicochemical parameters

Samplings were conducted seasonally between October 2012 and October 2017 from the open waters of Saptamukhi, Thakuran and Matla estuaries of Indian Sundarbans. Water samples were collected in triplicate from each station out of three permanent stations on each estuary which were at least 5 K.M apart from each other in the north to south direction (see Fig.1). According to Dutta *et al.* (2019), those permanent sampling stations were representative (based on biogeochemical gradients) of the upper, middle and lower reaches of Saptamukhi, Thakuran and Matla estuaries. At each sampling station, a four-cylinder motorboat was used to collect water samples at high tide after sunset from 0.5 m water depth using a Niskin water sampler of 5 L capacity (Ocean Test Equipment, USA). The collected 5L water sample was divided into many aliquots for multiple analyses of physicochemical parameters, including nutrients. On the boat, the temperature of the collected water was measured using a thermometer (± 0.1°C), pH was measured by a portable pH meter (Orion Star A211) with a Ross type combination electrode on the NBS scale (reproducibility: ± 0.005 pH units), dissolved oxygen (DO) (mgL^{-1}) by Winkler titration method and salinity was measured by argentometric titration (Grasshoff *et al.*, 1983). For dissolved inorganic nitrogen (DIN) and dissolved inorganic phosphate (DIP), the water samples were filtered on the boat through GF/F filter paper and put inside falcon tubes which were brought back to the laboratory on ice. Within 48 hours of water collection, nutrient concentrations (µM) were measured in the laboratory following the standard spectrophotometric procedures (Grasshoff *et al.,* 1998). Similarly, for Dissolved Organic Carbon (DOC), the water sample was first filtered on the boat through pre-combusted GF/F filter papers for collecting in muffled glass vials. Later in the laboratory DOC concentration (ppm) was measured by high temperature combustion using a total organic carbon analyser (Model: TOC–L CPH, Shimadzu, Japan) calibrated using a potassium hydrogen phthalate solution containing 1, 2, 5, 10 and 20 mgL^{-1} of DOC (Ray *et al.,* 2018; Dutta *et al.,* 2019). For measuring Suspended Particulate Matter (SPM) in the laboratory, GF/F filter papers (pore size: 0.7 µm) were dried in a hot air oven at a constant temperature (60°C). Suspended Particulate Matter (mgL^{-1}) values were calculated based on differences between the final and initial weights of the filter paper divided by the volume of water filtered in each case. Chl-*a* ($\mu gm.L^{-1}$) was estimated in the laboratory by extracting the residue of filtered water in 90% acetone for 24 hours, followed by the standard spectrophotometric techniques (Systronics; Model: 108, UV–VIS Spectrophotometer) of Strickland and Parsons (1972). The partial pressure of Carbon-dioxide, i.e. pCO_2 (µatm) of the water sample, was measured in the laboratory-based on Frankignoulle and Borges (2001).

2.3. Mesozooplankton collection and laboratory processing

Mesozooplankton assemblages were sampled after sunset during high tide from 0.5m water depth. The plankton net (200 µm mesh size and 0.9 m diameter) was equipped with a horizontally placed flow meter (Ocean Test Equipment Inc., Model no. FF 325) and towed horizontally for 10 min from the motor boat. Mesozooplankton samples were collected in triplicate from each sampling station of Saptamukhi, Thakuran and Matla estuaries. Samples were preserved in 4% neutral buffered formalin. In the laboratory, mesozooplankton were identified to the lowest taxonomic level possible following the taxonomic literature of Kasturirangan (1963) and Al-Yamani *et al.* (2011). Samples were enumerated under a phase contrast microscope (Olympus (45x), Japan) fitted with a Sedgwick Rafter counting chamber. The abundance of each taxon was expressed as individuals per cubic metre ($ind.m^{-3}$).

2.4. Statistical analysis

All the statistical analyses were performed using CRAN R.4.1.1. Statistically significant results (i.e. $\alpha < 0.05$)

were reported along with t, F, Kruskal-Wallis chi-square, q and P values and degrees of freedom (df). Dataset had a hierarchical design because there were three sampling stations within an estuary and three estuaries. On a given season, physiochemical variations among sampling stations of an estuary were not significant and such was observed for all three estuaries; therefore, they were not presented in the results and discussed further. Seasonal and spatial (i.e. among estuaries) variations of physicochemical parameters were assessed by conducting multiple ANOVA or Kruskal-Wallis tests (depending on the normality of the response variable) and if results of those tests were statistically significant, then either Tukey's or Nemenyi Post-hoc tests were performed by using the PMCMR Plus package version1.9.2.

For evaluating differences in abundances (i.e. count data) of mesozooplankton of each estuary in each season, multiple Kruskal-Wallis tests were conducted, followed by Nemenyi Post-hoc tests (if required) PMCMR Plus package version 1.9.2. The 'Vegan' package version 2.5.6 (Oksanen *et al.,* 2020) was used for calculating Shannon Index (H) (Shannon and Weaver, 1949) and Pielou's Evenness Index (J) (Pielou, 1966) of mesozooplankton assemblages. Spatial and temporal variations of those indices were analysed by conducting multiple ANOVA (because response variables were normally distributed) followed by post-hoc tests if required. Temporal associations of physicochemical parameters and H and J indices were analysed by building several generalised linear models (GLM) of the gaussian family, including interactive models up to three parameters. Temporal associations of a few abundant mesozooplankton and physicochemical parameters were analysed by conducting multiple GLM including interactive models up to three parameters of quasi-Poisson family because the response was over dispersed count data.

3. Results

3.1. Physicochemical variability

Spatial variations of the physicochemical parameters of Saptamukhi, Thakuran and Matla estuaries were not significant (Table 1). Water temperature significantly ($F = 41.2$, df = 2, $P < 0.0001$)varied among seasons but not necessarily between PRM and MON (Table 1). Salinity oscillated between 12 to 32 and varied significantly ($F = 68.4$, df = 2, $P < 0.0001$) among seasons, with the highest level observed in PRM and the lowest level in MON (Table 1).Suspended Particulate Matter values overall varied significantly among seasons (k-w chi-square = 18.86, df = 2, $P < 0.001$) but not particularly between PRM to MON (Table 1).Dissolve Oxygen varied within a narrow range but a distinct seasonal variation was evident ($F = 27.51$, df = 2, $P < 0.0001$) (Table 1). pH levels were significantly lower in the MON than the levels observed in PRM and POM (k-w chi-square = 14.99, df = 2, $P = 0.0005$) (Table 1).Levels of DIN varied significantly among seasons($F = 8.58$, df = 2, $P = 0.002$), but DIP levels did not vary significantly among seasons and were around 1µMin all seasons (Table 1). Chl-*a* concentration was at the minimum in MON, but then it increased and attained the maximum in POM and exhibited an overall distinct seasonal variation ($F = 7.96$, df = 2, $P = 0.0028$) but not necessarily between POM and PRM (Table 1). The highest and the lowest values of DOC and pCO_2levels were recorded during PRM and MON, respectively (Table 1). A significant (k-w chi-square = 11.439, df = 2, $P = 0.003$) seasonal variation of DOC level was observed; however, DOC levels of PRM

Table 1. Seasonal variability (mean ± standard deviation) of physicochemical parameters of Saptamukhi, Thakuran and Matla estuaries of Indian Sundarbans sampled between October 2012 to October 2017

Season	Estuary	T_W (°C)	Salinity (PSU)	SPM ($mg.L^{-1}$)	DO ($mg.L^{-1}$)	pH	DOC (ppm)	DIN (µM)	DIP (µM)	Chl-a ($\mu gm.L^{-1}$)	PCO_2 (µatm)
PRM	SAP	31.17±1.96	27.29 ± 2.62	153.7 ± 24.2	6.21 ± 0.6	8.19 ± 0.09	3.62 ± 0.09	19.26 ± 1.09	0.90 ± 0.06	3.24 ± 1.2	910 ± 581
	THA	30.88±1.81	26.96 ± 2.43	163.8 ± 29.5	6.15 ± 0.49	8.19 ± 0.10	4.11 ± 1.45	20.45 ± 1.13	0.86 ± 0.05	2.88 ± 1.15	875 ± 620
	MAT	30.75± 1.09	27.98 ± 1.78	157.41 ± 25.01	6.32 ± 0.77	8.21 ± 0.08	4.4 ± 1.32	20.10 ± 1.25	1.09 ± 0.01	2.90 ± 0.75	893 ± 604
MON	SAP	29.5 ± 0.14	15.75 ± 0.70	436.2 ± 30.9	6.16 ± 0.17	7.43 ± 0.12	3.05 ± 0.58	22.80 ± 2.70	0.88 ± 0.04	1.47± 0.41	840 ± 604
	THA	29.37 ± 0.12	13.65 ± 1.97	455.21 ± 33.84	6.06 ± 0.63	7.54 ± 0.09	2.38 ± 0.66	22.26 ± 2.68	0.86 ± 0.06	1.61± 0.31	1043 ± 493
	MAT	29.12 ± 1.46	14.1± 1.26	461.95 ± 34.8	6.12 ± 0.32	7.44 ± 0.10	2.84 ± 0.42	23.66 ± 2.68	0.84 ± 0.04	1.51± 0.45	597 ± 105
POM	SAP	25.15 ± 1.05	21 ± 4.01	80.36 ± 4.84	6.62 ± 0.74	7.99 ± 0.05	3.17± 0.89	21.07 ± 3.92	0.95 ± 0.07	4.8 ± 0.7	811 ± 658
	THA	25.45± 1.23	20.56 ± 3.85	69.63 ± 5.43	6.38 ± 0.42	8.01 ± 0.11	3.82± 1.09	17.92 ± 3.04	0.86 ± 0.04	4.18 ± 0.62	565 ± 197
	MAT	25.60± 0.93	20.17 ± 4.38	60.32 ± 6.42	6.97 ± 0.39	7.96 ± 0.04	3.72 ± 0.94	19.72 ± 1.57	1.13 ± 0.04	4.07 ± 0.36	671 ± 434

Tw = Water temperature, SPM = Suspended particulate matter, DO = Dissolved oxygen, DOC = Dissolved organic matter, DIN = Dissolved inorganic nitrogen, DIP = Dissolved inorganic phosphate, Chl-*a* = Chlorophyll-*a*, PCO2 = Partial pressure of carbon dioxide; SAP = Saptamukhi, THA= Thakuran, MAT = Matla; PRM= Pre-monsoon, MON= Monsoon, POM= Post-monsoon.

and POM were not significantly different from each other (Table 1). An overall weak seasonal variation of pCO_2 was observed (k-w chi-square = 4.43, df = 2, P = 0.047) but seasonal variation between pCO_2 levels of PRM and POM was not significant (Table 1).

3.2. Mesozooplankton community

Mesozooplankton abundances showed only marginal seasonal variability in Saptamukhi estuary (K-w chi-square = 5.86, df = 2, P = 0.05) specially between PRM and MON (q value = 5.36, P = 0.0004), POM and MON (q value = 5.83, P = 0.0002) but not between PRM and POM (q value = 0.23, P = 0.98) (Fig.2).Mesozooplankton abundances of Thakuran estuary varied significantly among seasons (K-w chi-square = 16.51, df = 2, p-value = 0.0002) in particular between PRM and MON (q value = 6.02, P < 0.0001), POM and MON (q value = 5.25, P = 0.0005) but not between PRM and POM (q value = 0.81, P = 0.83) (Fig.2). Mesozooplankton abundances of Matla estuary varied significantly among seasons (K-w chi-square = 22.09, df = 2, P < 0.0001) estuaries (Fig.2) specially between PRM and MON (q value = 5.56, P = 0.0002), POM and MON (q value = 5.39, P = 0.0004) but not between PRM and POM (q value = 0.18, P = 0.99) (Fig.2). Copepods dominated the mesozooplankton community of all three estuaries (Table 2). In total, 27 species of copepods were identified, of which 4 were cyclopoids, 3 were harpacticoids and the rest were calanoids (Table 2). Copepods *Acartia spinicuada, Acartia plumosa, Acartiella tortaniformis*, *Corycaeus danae, Paracalanus parvus, Pseudodiaptomus serricaudatus, Eucalanus elongatus, Eucalanus subcrassus, Bestiolina similis, Labidocera euchaeta, Canthocalanus pauper, Oithona brevicornis* and *Euterpina acutifrons* were caught frequently (cumulative abundance ($ind.m^{-3}$) of each species >50000 $ind.m^{-3}$) (Table 2). Chaetognath *Zonosagitta bedoti* was highly abundant (Table 2). In the mesozooplankton community, many copepodite stages, Veliger and Bivalve larvae of molluscs, Nauplius, Megalopa and Zoea larvae of crustaceans, crab larvae, starfish larvae, mysid (*Mesopodopsis orientalis*), prawn (*Lucifer hanseni*), ctenophores, ichthyoplankton were also common in the Saptamukhi, Thakuran and Matla estuaries (Table 2).

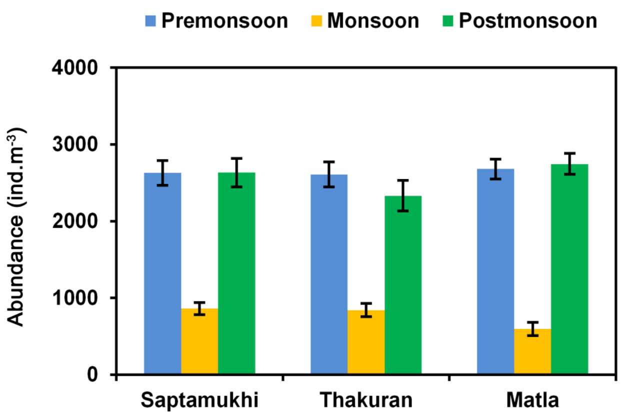

Fig. 2. Seasonal variation (median ± standard error) of total abundance (ind.m-3) of the mesozooplankton community of Saptamukhi, Thakuran and Matla estuaries of Indian Sundarbans sampled seasonally between October 2012 and October 2017

Variations of species diversity index (H) and species evenness index (J) among estuaries and seasons were not significant. Overall (data pooled together), species diversity index (H) and species evenness index (J) were 1.96 ± 0.36 and 0.57 ± 0.06 during PRM, 1.65 ± 0.71 and 0.54 ± 0.13 in MON and 1.79 ± 0.28 and 0.48 ± 0.07 in POM, respectively. Index H and index J values were 1.81 ± 0.59 and 0.51 ± 0.07 for Matla estuary, 1.80 ± 0.34 and 0.51± 0.1 for Thakuran estuary, and 1.78 ± 0.43 and 0.53 ± 0.11 for Saptamukhi estuary. pCO_2 had a significant negative temporal association with H index (t = -2.43, df = 22, P = 0.024). Interaction of pCO_2 and salinity had significant positive (t = 2.4, df = 22, P = 0.024) temporal association with H index. pCO_2 and Chl-a interaction (t = 2.93, df = 22, P

Table 2. Cumulative abundance ($ind.m^{-3}$) of mesozooplankton of Saptamukhi, Thakuran and Matla estuaries of Indian Sundarban sampled between October 2012 to October 2017.

Species /Group	Group	Cumulative abundance
Pseudodiaptomus serricaudatus	Copepoda (Calanoida)	3129981
Paracalanus parvus	Copepoda (Calanoida)	1898857
Bestiolina similis	Copepoda (Calanoida)	806960
Acartia spinicauda	Copepoda (Calanoida)	803721
Oithona brevicornis	Copepoda (Cyclopoida)	517705
Acartia plumose	Copepoda (Calanoida)	389030
Canthocalanus pauper	Copepoda (Calanoida)	374943
Acartia tortaniformis	Copepoda (Calanoida)	343724
Clytemnestra scutellate	Copepoda (Harpacticoida)	189445
Euterpina acutifrons	Copepoda (Harpacticoida)	95616
Oithona similis	Copepoda (Cyclopoida)	86425
Undinula sp.	Copepoda (Calanoida)	85277
Labidocera euchaeta	Copepoda (Calanoida)	76225
Oncaea venusta	Copepoda (Cyclopoida)	72403
Eucalanus subcrassus	Copepoda (Calanoida)	68450
Acartia erythraea	Copepoda (Calanoida)	26400
Corycaeus danae	Copepoda (Cyclopoida)	6083
Acrocalanus gibber	Copepoda (Calanoida)	5453
Eucalanus elongatus	Copepoda (Calanoida)	4500
Microsetella rosea	Copepoda (Harpacticoida)	2155
Paracalanus indicus	Copepoda (Calanoida)	1506
Labidocera minuta	Copepoda (Calanoida)	833
Acartia sp.	Copepoda (Calanoida)	206
Eucalanus sp.	Copepoda (Calanoida)	182
Paracalanus sp.	Copepoda (Calanoida)	153
Labidocera sp.	Copepoda (Calanoida)	94
Oithona sp.	Copepoda (Cyclopoida)	82
Nauplius	Copepoda	244866
Copepodites	Copepoda	113491
Megalopa	Decapoda	55641
Zoea	Decapoda	71291
Lucifer hanseni	Decapoda	32591
Crab larvae	Decapoda	567
Zonosagitta bedotti	Chaetognatha	248548
Bivalve larvae	Mollusc larva	74909
Veliger larvae	Mollusc larva	3750
Mesopodopsis orientalis	Mysida	5241
Ichthyoplankton	Fish larvae	782
Starfish larvae	Echinoderm	115
Ctenophora		355
Unidentified mesozooplankton		64

= 0.0008),and pCO_2 and DOC interaction (t = 2.78, df = 22, P = 0.012) had significant positive impacts; however, pCO_2 and SPM interaction had significant negative impact (t = -2.4, df = 22, P = 0.027) on the H index. Dissolve Oxygen level had a significant negative temporal association (t = -2.34, df = 22, P = 0.029) with index J. All other parameters and their two- or three-way interactions had no significant temporal associations with index H or index J.

3.3. Abundant mesozooplankton populations and their relations with habitat

Copepods dominated the mesozooplankton community of marine-dominated estuaries of Indian Sundarbans (Table 2). Each estuary had its own set of copepod populations that were highly abundant than many other copepod populations (Table 3); however, *P. serricaudatus, P. parvus, B. similis* and *A. spinicauda* were the four most frequently sampled mesozooplankton of Saptamukhi, Thakuran and Matla estuaries (Table2). Variation of *P. serricaudatus* abundance was not significant among the estuaries; however, its abundance was significantly low in MON (df = 22, t_{PRM} = 2.57, P_{PRM} = 0.18, t_{POM}= 2.94, P_{POM} = 0.007) than PRM and POM. Chlorophyll-*a* (t = 2.28, df = 22, P = 0.03) showed significant positive association with *P. serricaudatus* abundance. A significant positive association (t = 2.44, df = 22, P = 0.02) was observed between DO and *P. serricaudatus* abundance. Abundance of *P. serricaudatus* was significantly negatively associated with SPM (t = -2.97, df = 22, p = 0.007) and DIP (t = -2.56, df = 22, p = 0.01), respectively. *Paracalanus parvus* abundance showed no significant variation among the estuaries but varied significantly among the seasons (df = 22, t_{PRM} = 2.28 , P_{PRM} = 0.02 , t_{POM}= 2.65, P_{POM} = 0.015). Levels of Chl-*a* (t = 3.61, df = 22, P = 0.001), DO (t = 2.85, df = 22, P = 0.008) and DIP (t = 2.74, df = 22, P = 0.01) showed significant positive and SPM level showed significant negative (t = -2.24, df = 22, P = 0.038) associations with *P. parvus* abundance. *Bestiolina similis* abundance neither varied significantly among the estuaries nor among the seasons. *Bestiolina similis* abundance was negatively associated with SPM (t = -2.15, df = 22, P = 0.04) and SPM*Chl-*a* interactions (t = -3.02, df = 22, P = 0.007). *Acartia spinicauda* population abundance neither varied significantly among the estuaries, seasons and showed no significant temporal associations with any of the physicochemical parameter and their interactions considered in this study.

4. Discussion

4.1. Seasonal variability of habitat

Some degrees of spatial variability of physicochemical parameters were present in the marine-dominated Saptamukhi, Thakuran and Matla estuaries; however, those were not statistically significant. Physicochemical variability was essentially related to the arrival and departure of MON, possibly because rainfall during MON brings variability of freshwater availability to estuaries of Indian Sundarbans, which otherwise remain considerably freshwater starved in PRM and MON. The humid tropical climate of Indian Sundarbans is predominantly influenced by the South-West monsoon, with an annual average rainfall of 150-200 cm (Mukhopadhyay *et al.,* 2006; Ganguly *et al.,* 2014). Such a climatic pattern is assumed to be imprinted in the variability of the physicochemical parameters of the Indian Sundarbans (Dutta *et al.*, 2013, 2015, 2019). Water temperature followed the typical tropical coastal climate pattern with a maximum in PRM and varying with the changes in insolation received over the year (Mukhopadhyay *et al.,* 2006; Biswas *et al.,* 2010). Monsoon rainfall to the marine-dominated estuaries of Indian Sundarbans and their catchments cause oligohaline to mesohaline conditions which otherwise remain polyhaline in PRM and POM (Mukhopadhyay *et al.,* 2006; Dutta *et al.,* 2013; Nandy *et al.,* 2018). Whilst the marine-dominated mangrove estuaries of Indian Sundarbans are part of the Ganges delta, their upstream connectivity with the Ganges River is long lost (Rudra, 2014). Those estuaries have limited length and catchment area, and their riverine freshwater input (combining agricultural, sewage and industrial) is minimal, so salinity variation is marginal during non-MON periods (Chatterjee *et al.,* 2013; Dutta *et al.,* 2015). Saptamukhi, Thakuran and Matla estuaries are

Table 3. Seasonal variation of median (± SE) and maximum abundances of a few frequently caught copepods of Saptamukhi, Thakuran and Matla estuaries of Indian Sundarbans between October 2012 to October 2017.

Estuary	Season	Species	Median abundance ± SE(ind.m^{-3})	Maximum abundance (ind.m^{-3})
Saptamukhi	Pre-monsoon	*Pseudodiaptomus serricaudatus*	459 ± 136	2936
	Monsoon	*Bestiolina similis*	129 ± 56	1332
	Post-monsoon	*Eucalanus subcrassus*	662 ± 234	2835
Thakuran	Pre-monsoon	*Acartia spinicauda*	742 ± 103	1956
	Monsoon	*Bestiolina similis*	204 ± 65	1849
	Post-monsoon	*Paracalanus parvus*	414 ±109	3125
Matla	Pre-monsoon	*Pseudodiaptomus serricaudatus*	882 ± 207	3812
	Monsoon	*Oithona brevicornis*	189 ± 35	1770
	Post-monsoon	*Pseudodiaptomus serricaudatus*	552 ± 287	4162

better to be designated as freshwater-starved (except during MON) mangrove estuaries with polyhaline salinity. Strong tidal influence in those estuaries causes high turbulence and a well-mixed water column without any salinity gradient, resulting in further re-suspension of river bed sediment (Banerjee *et al.,* 2012). During MON, the reversal of wind direction further intensifies turbulence in the water column. Along with extensive surface runoff, the water column is highly turbid with a very high suspended sediment concentration (Mukhopadhyay *et al.,* 2006; Biswas *et al.,* 2010). Solubility of Oxygen depends on water temperature, and salinity is further influenced by different degrees of biological processes (Weiss, 1971). Seasonal variation of DO levels in the water column has been previously observed in the estuaries of Indian Sundarbans (Mukhopadhyay *et al*., 2006; Biswas *et al.,* 2010). pH showed a marginal seasonal variation with the minimum values during MON, indicating the effects of dilution through runoff which washed the products of organic matter mineralisation in the catchment area (Mukhopadhyay *et al.,* 2006; Biswas *et al.,* 2010; Dutta *et al.,* 2019; Nandy and Mandal, 2020). The supply of suspended materials and dissolved nutrients (DIN, DIP) reached their maximum during MON and were primarily contributed by catchment runoff (Mukhopadhyay *et al.,* 2006). A low SPM level favours more penetration of light energy and the availability of moderate nutrients in the water column cause the maximum Chl-*a* production during POM in the mangrove estuaries of Indian Sundarbans (Biswas *et al.,* 2010; Nandy and Mandal, 2020). In contrast, high water temperature during PRM favours the breakdown of organic matter, evidenced by the maximum values of DOC and pCO_2 during the summer months (Ray *et al.,* 2015). Overall, Saptamukhi, Thakuran and Matla estuaries responded mainly to MON associated changes that might have influenced their biological communities (Biswas *et al.,* 2010; Nandy *et al.,* 2018; Nandy and Mandal, 2020).

4.2. Mesozooplankton dynamics of Indian Sundarbans

Spatial variation of the mesozooplankton community of the Saptamukhi, Thakuran and Matla estuaries was not significant, which possibly indicates a well-distributed resident pool of mesozooplankton in the Indian Sundarbans. Such was also observed by Nandy *et al.* (2018) and Nandy and Mandal (2020) in the Saptamukhi and Matla estuaries of the Indian Sundarbans. Such spatial homogeneity of the mesozooplankton community is not usual as often the distribution of mesozooplankton is patchy, being restricted to micro-habitats that offer favourable gradients of salinity, nutrients, Chl-*a* and low riverine advection rate which prevents mesozooplankton being washed seawards (Madhupratap, 1979; Costa *et al.,* 2008; Chew and Chong, 2011; Bhattacharya *et al.,* 2015). Mesozooplankton assemblages of the Indian Sundarbans consisted mostly of specialist estuarine species and a few neritic species that reside within the maximum turbidity zones of the mangrove estuaries of the Indian Sundarbans (Bhattacharya *et al.,* 2015). Seasonal variability of the mesozooplankton community of the Indian Sundarbans has similarities to the marine-dominated Cochin backwaters, Godavari mangrove estuary of India, Matang mangrove forest of Malaysia and Alligator Creek of Australia (Robertson *et al.,* 1988; Jyothibabu *et al.,* 2006; Chew and Chong, 2011; Bhattacharya *et al.,* 2015; Venkataramana *et al.,* 2017). Mesozooplankton abundance was significantly higher in PRM and POM compared to MON, which supports the previous works conducted in the mangrove estuaries of Indian Sundarbans (Bhattacharya *et al.,* 2015; Nandy and Mandal, 2020).Variable physicochemical conditions of MON are stressful for the recruitment stages of many mesozooplankton, so many of them do perish, which negatively impacts the overall abundance, diversity and distribution of the mesozooplankton community (Wellershaus, 1974; Bhattacharya *et al.,* 2015; Nandy *et al*., 2018). Further, MON increases river flow in the estuaries of the Indian Sundarbans, which in consequence increases their advection rates, so mesozooplankton are flushed out towards the Bay of Bengal, resulting in a depressed species richness and abundance, especially in the upper reaches of estuaries. After MON, the estuaries of Indian Sundarbans accumulate large volumes of DIN and DIP, which trigger the primary production (Chl-*a*) to peak in POM (Biswas *et al.,* 2010). Previous authors observed a distinct peak of mesozooplankton species richness and density in late POM (Bhattacharya *et al.,* 2015), supporting the present results. In POM, positive associations of Chl-*a* and mesozooplankton density and diversity were previously observed in the Matla and Godavari mangrove estuaries of India and in the Matang mangrove forest of Malaysia (Sarma *et al*., 2009; Chew and Chong, 2011; Venkataramana *et al.,* 2017; Nandy and Mandal, 2020). Phytoplankton blooms do not always immediately respond to MON nutrient input but happen after a lag period during which the nutrients gradually build up (Biswas *et al.,* 2010). Copepod recruitment peaks before phytoplankton bloom which is a part of the copepod's reproductive strategy in the Matang mangrove forest of Malaysia where recruits exploit the larger biomass of phytoplankton in POM (Chew and Chong, 2011). The SPM load increases with the progress of MON further reducing euphotic zones of already highly turbid mangrove estuaries of the Indian Sundarbans (Mukhopadhyay *et al.,* 2006; Bhattacharya *et al.,* 2015). That negatively affects production, diversity and distribution of phytoplankton, which are essential for sustaining a healthy mesozooplankton community (Biswas *et al.,* 2010; Bhattacharya *et al.,* 2015). The DO level showed a significant negative temporal association with the species evenness index of the mesozooplankton community. A depressed DO level of the Indian Sundarbans is often a characteristic of MON and it generally reduces species richness (Sarkar *et al.,* 1986; Mukhopadhyay *et al.,* 2006). Many estuarine mesozooplankton fail to withstand the higher physicochemical variability of MON so few specialist populations flourish under such conditions (Nandy *et al.,* 2018). Populations of *P. serricaudatus*, *P. parvus, B. similis,* and *A. spinicauda* abundances were relatively less affected by MON; however, many other species of mesozooplankton were caught in very low numbers during MON. That might have resulted in a community structure which has considerably less species richness but a few specialized species that had built significantly large populations. Such was also observed in the marine-dominated Kromme estuary of South Africa (Paul *et al.,* 2016). Results showed a significant temporal association of mesozooplankton diversity with pCO_2 and its interaction with other physicochemical parameters. The effects of elevated CO_2 levels on mesozooplankton diversity and abundance are poorly understood. It; however, is suggested that mesozooplankton of tropical estuaries may remain less impacted because mesozooplankton reproduce throughout the year (Biswas *et al.,* 2011; Sommer and Lewandowska, 2011). Eco-physiological studies of life-histories of mesozooplankton may, in future, elucidate to what extent a warm acidic estuarine environment of Indian Sundarbans may benefit or cause stress to mesozooplankton.

4.3. Abundant mesozooplankton populations of Indian Sundarbans

Holoplankton dominated the mesozooplankton community of Saptamukhi, Thakuran and Matla estuaries. Such results have similarities with Cochin backwaters of India, Matang mangrove forest of Malaysia, mangrove swamps (Alligator Creek) of tropical Australia and Taperaçu estuary of the Amazon region (Brazil); there, too, mesozooplankton assemblages vary seasonally based on arrival and departure of MON (i.e. wet season) and are numerically dominated by holoplankton especially by calanoid copepods (Robertson *et al*., 1988; Costa *et al*., 2008; Chew and Chong, 2011; Venkataraman *et al.,* 2017; Nandy *et al.,* 2018; Nandy and Mandal, 2020). Seasonal variability of total mesozooplankton abundance in the Indian Sundarbans often arises from the variability of a few copepod populations such as *P. serricaudatus, P. parvus, B. similis, A. spinicauda, Oithona brevicornis* and *E. subcrassus* (Nandy *et al.,* 2018; Nandy and Mandal, 2020). Often the most abundant copepod populations responded less to the physicochemical (including) variability, as observed in the sub-tropical Rio de la Plata estuary of South-West Atlantic (Paul *et al.,* 2017; Paul and Calliari, 2019). *Paracalanus parvus* and *B. similis* tolerate highly variable physicochemical gradients of freshwater dominated Ganges estuary, which runs through Western Indian Sundarbans (Paul *et al.,* 2019b). Bhattacharya *et al.* (2014) and Paul *et al.* (2020a,b) observed a significant presence of *P. serricaudatus, P. parvus, B. similis, A. spinicauda* and *O. brevicornis* even after Indian Sundarbans is disrupted by cyclone Aila, Fani and Bulbul, which demonstrate the flexibility of those copepod populations adapting extreme and abrupt changes of physicochemical gradients of the estuaries of Indian Sundarbans. Nandy *et al.* (2018) observed incessant rains in the Himalayas (triggered by a massive cloud burst) had affected the water quality of the Ganges estuary. Those changes; however, had a limited impact on mesozooplankton diversity and distribution of the Saptamukhi estuary, which is connected to the Ganges estuary (Nandy *et al.*2018). The seasonal transitions, i.e. arrival and departure of MON, had driven mesozooplankton diversity in the Saptamukhi estuary of the Indian Sundarbans (Nandy *et al.*2018). In the mangrove estuaries of Malaysia, *B. similis* and *A. spinicauda* abundances do not vary with seasonal change (Chew and Chong, 2011). *Pseudodiaptomus serricaudatus* and *P. parvus* were herbivore copepods, so their abundances were possibly sensitive to Chl-*a* and SPM levels of the marine-dominated estuaries of Indian Sundarbans. Chlorophyll-*a* and SPM levels had hardly affected the abundances of *omnivorous B. similis* and *A. spinicauda* (Paul *et al.,* 2019b).

4.4. Mesozooplankton of Indian Sundarbans in future

Monitoring multiple marine-dominated river estuaries is globally rare and has never taken place in Indian Sundarbans (Aguilera *et al.,* 2013). Bhattacharya *et al.* (2015) observed less species richness within the copepod community of Indian Sundarbans, particularly the cyclopoid and harpacticoid groups, which declined from their 1980s levels. Bhattacharya *et al.* (2015) further observed that many large-bodied copepod species were replaced by many small to medium-bodied copepod species, and many herbivore species were replaced by omnivores. The increasing dominance of warm water calanoid copepod species was observed in Matla estuary of the Indian Sundarbans by Nandy and Mandal (2020), which possibly indicate local estuaries are becoming warmer than ever. In some patches of the Indian Sundarbans, salinity has increased significantly in recent years from 1980s levels, which has consequences for the eco-physiology of mangroves, small pelagic fish and shrimps (Banerjee *et al.,* 2017; Brown *et al.,* 2018; Paul *et al.*, 2019a; Karan *et al.,* 2020). According to the Ministry of Environment and Forest and Climate Change of the Government of India, the Bay of Bengal adjacent to the Indian Sundarbans has experienced a 6.1 mm / year sea-level rise between 2003 and 2013. In the Indian Sundarbans, PRM is prolonging its presence. In contrast, POM is becoming shorter, MON is arriving later and it is often rain-deficient, except 2013 when it rained heavily (Mandal *et al.,* 2016). Cyclones in PRM and POM are periodically disrupting the mesozooplankton community by temporarily bringing marine intrusions (Paul *et al.,* 2020a,b). In future, the mesozooplankton community of the Indian Sundarbans may have more marine species than the present community; therefore, consequences for benthic-pelagic linkages of the marine-dominated estuaries could not be ruled out. Re-introducing freshwater in the marine-dominated estuaries of the Indian Sundarbans may limit that possibility. That, however, would require channelizing freshwater of Hooghly river to the central Indian Sundarbans and / or transboundary freshwater management of the Sundarbans by India and Bangladesh. If such is achieved, than long-term studies of mesozooplankton from multiple estuaries having gradients of freshwater are recommended to delineate the importance of regular freshwater input in the Indian estuaries.

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Compliance with ethical standards

Mesozooplankton samples were collected in accordance with the ethical standards of University of Calcutta, India, and with the permission of Sundarbans Biosphere Reserve authority. Divisional Forest Officer (DFO) South 24 Parganas Government of West Bengal granted the permission to work in Reserve Forest areas.

Conflict of interest

Authors declare no conflict of interest.

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