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Reassessing copepod diversity estimates in the Indian Sundarbans by incorporating the vital status of individual plankton

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ABSTRACT

Traditional estimates of abundance and diversity are based on the total number of individuals, both living and dead, without distinguishing between them. Traditional diversity assessment method (TDAM), when applied to microscopic organisms (e.g., copepods), overlooks the vital status of individuals, which may result in biased estimates of diversity. Copepods are widely studied as model organisms in estuaries. Hypothesis was, copepod diversity estimates calculated through the TDAM deviate from the results of a carcasses estimation approach method (CEAM) which considers vital status of individuals in the sample at the time of collection and focuses on live components only. Copepods were sampled three times between 2022 and 2023 from the six sampling stations spread across the Indian Sundarbans. The highest abundance of the carcasses (i.e. 48%) was found during the August-September 2022 sampling, followed by November 2022 to January 2023 (i.e. 18%) and March to May 2023 (i.e. 11%) periods. The TDAM and CEAM when compared, variations in the diversity metrics, relative abundances, and dominance hierarchy were found, particularly for the August-September 2022 samples. Species richness deviated more than the Shannon index, which in turn deviated more than the Simpson and Pielou's indices when the TDAM and CEAM were compared. These deviations were at their respective maximum in the August-September 2022 sampling period. Results provided the first ever evidence that the vital status of a plankton quantitatively affects the diversity metrics specially if the environment is volatile. The future use of the term '*living diversity*' is proposed for the estimates based only on living individuals. That is necessary for an unambiguous reference to report diversity metrics and to better understand the diversity of plankton and other microscopic organisms.

1. Introduction

The diversity of a biological system refers to the variety and variability of life at different levels, from genes to ecosystems (Purvis and Hector, 2000). Over decades, ecologists have provided various explanations of diversity but no 'one size fits all' accepted definition of diversity has emerged (Hurlbert, 1971; Peet, 1974; Hubel, 2001). Diversity indices based on information theory (Magalef, 1973), such as the species richness, Shannon and Simpson indices, are commonly used to characterise communities. 'Richness' and 'Evenness' are among the primary alpha-diversity indicators of a habitat, where richness describes the number of species present in a given space-time of an ecosystem, and the evenness informs the uniformity of their abundance (Gotelli and Colwell, 2001; Lakicevic and Srdjevic, 2018). Other widely used indices of diversity are the Shannon-Wiener (H′) and Simpson's (D) dominance (Heip, 1974; DeJong, 1975). As diversity is primarily concerned with the variability of life, when calculating information theory-based diversity indices, attention is generally placed on organisms that are alive or assumed to be alive (Zetsche and Meysman, 2012). This is true for most microscopic organisms including plankton, a highly diverse group of living beings that play critical roles in the trophic dynamics of all aquatic ecosystems including estuaries (Hansen and Van Boekel, 1991; Winder and Jassby, 2011).

Copepods are the most abundant metazoan life form on Earth (Mauchline, 1998). They link primary producers and medium-to-large consumers, such as macro-invertebrates and fish, and they are widely

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used as biological indicators of environmental variability in coastal-marine ecosystems such as estuaries (Dahms, 1995; Hooff and Peterson, 2006). Therefore, accurate quantification of copepod species diversity and population abundance is crucial for characterising the structure and functions of the lower food web of aquatic ecosystems including estuaries (Paffenhöfer & Köster, 2024). The traditional approach to quantify the abundance and diversity of plankton (including copepods) is based on the collection of samples using nets fitted with fine meshes, typically with pore sizes between 10 and 300 μm, depending on the target groups. Samples are typically fixed immediately, assuming that all individuals are alive at the time of collection. After collection, taxonomic processes, such as identification and quantification, are performed in the laboratory. Traditional estimates of abundance and diversity are based on the total number of individuals, both living and dead, without distinguishing between them. A traditional diversity approach method (TDAM) applied to plankton (including copepods) does not consider the vital status (i.e. alive or dead) of individuals found in the sample. However, it is now well established that carcasses of dead zooplankton including copepods are widespread and sometimes present in high numbers in marine environments including estuaries (Tang et al., 2014; Jyothibabu et al., 2016). The lack of discrimination between live and dead individuals may lead to the overestimation of copepod and in general plankton abundances, biomass, production, and food resources for their predators; therefore, it has serious consequences in delineating the structure and functions of the lower food web of aquatic ecosystems including estuaries (Tang et al., 2006, 2014).

Therefore, methods, processes, and approaches for the estimation of copepod diversity and, in a larger context, plankton diversity, should be subjected to scrutiny, and some of them may require revisions based on the advancement of scientific arguments and evidences (Zetsche and Meysman, 2012; Tang et al., 2014). Considering these perspectives, recent studies have raised critical questions on the merit and accuracy of the TDAM for estimating zooplankton (including copepod) diversity in the different types of coastal-marine ecosystems, including estuaries (Zetsche and Meysman, 2012; Tang et al., 2014). This study reports an evaluation of the sensitivity of the TDAM to the presence of varying proportions of live and dead copepods in the field samples of an important tropical estuarine system, the Sundarbans of India. This was achieved by estimating the abundances and several diversity metrics in parallel for copepod samples, one following the TDAM and a second for which abundances and diversity metrics were estimated after correcting for the fraction of the carcasses in a given sample, that is, the carcase estimation approach method (CEAM).

The Sundarbans of India is part of a large-scale mangrove forest deltaic system comprising a complex intertwined network of macro-tidal tropical river-estuaries (Chatterjee et al., 2013; Chakrabarty et al., 2022). Research on plankton, including copepods, in the Indian Sundarbans began in the early 1950s (Dutta et al., 1954). In the 20th century, most of the plankton (including copepods) work was limited to the freshwater-rich western Indian Sundarbans surrounding the Hooghly estuary (Sarkar et al., 1986; Sinha et al., 1996; Bhattacharya et al., 2024; Paul et al., 2024; Paul, 2026). Over the past two decades, researchers have investigated mesozooplankton populations within the central Indian Sundarbans, which encompass marine-dominated river-estuaries such as the Saptamukhi, Thakuran, and Matla (Nandy et al., 2018; Nandy and Mandal, 2020; Chakrabarty et al., 2022). Copepods dominate the mesozooplankton community in the estuaries of Indian Sundarbans, accounting for 70–80% of the community (Bhattacharya et al., 2015; Bhattacharjee et al., 2025). Calanoida contributes the most to the total copepod abundance, followed by Cyclopoida and Harpacticoida (Bhattacharya et al., 2015; Chakrabarty et al., 2022; Bhattacharjee et al., 2025). Approximately 41 copepod species have been reported in the region, among which species such as the *Bestiolina similis,Paracalanus parvus, Acartiella tortaniformis* and *Acartia spinicauda* are highly abundant; their abundances, however, vary based on seasonal cycles and different stretches of the local estuaries (Bhattacharya et al., 2015; Nandy et al., 2018; Nandy and Mandal, 2020; Basu et al., 2022; Chakrabarty et al., 2022; Paul et al., 2024; Bhattacharjee et al., 2025; Paul, 2026). Most of the mesozooplankton studies have employed monthly or seasonal sampling strategies to examine seasonal changes in the copepod communities of the Indian Sundarbans (Sarkar et al., 1986; Bhattacharya et al., 2015; Nandy et al., 2018; Nandy and Mandal, 2020; Basu et al., 2022; Chakrabarty et al., 2022; Paul et al., 2024; Paul, 2026). Among seasons, copepod diversity and abundances generally dip in the late monsoon months (e.g., August-September) and reach to peak between end of postmonsoon (e.g., February) and middle of premonsoon (e.g., April-May) (Sarkar et al., 1986; Nandy et al., 2018; Bhattacharjee et al., 2025). All those information on the copepods and to a larger extent on zooplankton of the Indian Sundarbans were derived from the previous studies, which followed the TDAM only so completely overlooked the incidence of carcasses in their samples.

This study estimated the current diversity of the copepods in the estuaries of the Indian Sundarbans by applying both the TDAM and CEAM. The aim was to evaluate the extent to which species richness, abundance, dominance hierarchy, and information theory-based alpha diversity indices (i.e. Shannon, Simpson, and Pielou's) are sensitive to the incorporation of vital status information of individuals in a sample population. The authors hypothesised that the abundances, dominance hierarchy, and alpha diversity indices provide biased estimates if the vital state of individuals is not considered. The hypothesis does not intend to explore the cause(s) of death of an individual plankton.

2. Material and methods

2.1. Study area

The Sundarbans (21° 432′–21° 55′ N and 88° 42′–89° 04′ E), one of the UNESCO World Heritage Sites, is the largest deltaic estuarine mangrove forest in the world, shared by India and Bangladesh (Mitra et al., 2012). Crisscrossed by a network of estuaries, the Indian part of the Sundarbans is dominated by mixed semi-diurnal tides because the local estuaries suffer from intense tide time-velocity assymetry (Mitra et al., 2012; Chatterjee et al., 2013). The Indian Sundarbans receives 70 to 80% of the total annual rainfall, that is, 1821 mm (±341.8 mm) between July and September of each year which infuses significant variability to the water quality (specifically salinity) of its estuaries (Nandy and Mandal, 2020). Throughout the year, the overall salinity differs between three sectors of the Indian Sundarbans, namely, the central sector with salinities of 25.43 ± 2.24, western 19.46 ± 3.46, and eastern: 13.85 ± 1.48 (Trivedi et al., 2016). Sampling stations for the current investigation did follow an east to west diagonal and they are S1 (22°07′4.192"N, 88° 55′20.463"E), S2 (22°06′40.896"N, 88°46′23.059"E), S3 (22°06′4.111"N, 88°48′0.176"E), S4 (22°05′18.02"N, 88°52′07.64"E), S5 (21°59′11.407"N, 88°44′15.561"E), and S6 (21°34′53.188"N, 88° 14′9.898"E) (see Fig. 1). In the Indian Sundarbans, both salinity and temperature are variable, not only based on the tide but also on a seasonal scale (Nandy and Mandal, 2020).

2.2. Field sampling

Three sampling trips were conducted at all sampling stations between 2022 and 2023. The first period was August to September 2022, the second was November 2022 to January 2023, and the final period was March to May 2023. Copepod samples for both the TDAM and CEAM were always collected from a slow-paced motorboat on high tide during the daytime with a 200 μm mesh-sized zooplankton net (60 cm diameter and 150 cm in length) fitted with a mechanical flow meter (Made: Hydro-Bios, Germany). The zooplankton net was towed horizontally and slowly for 3 min to the extent possible to minimise damage to mesozooplankton and handling errors. A single tow was performed to collect a standard quantitative mesozooplankton sample which was then

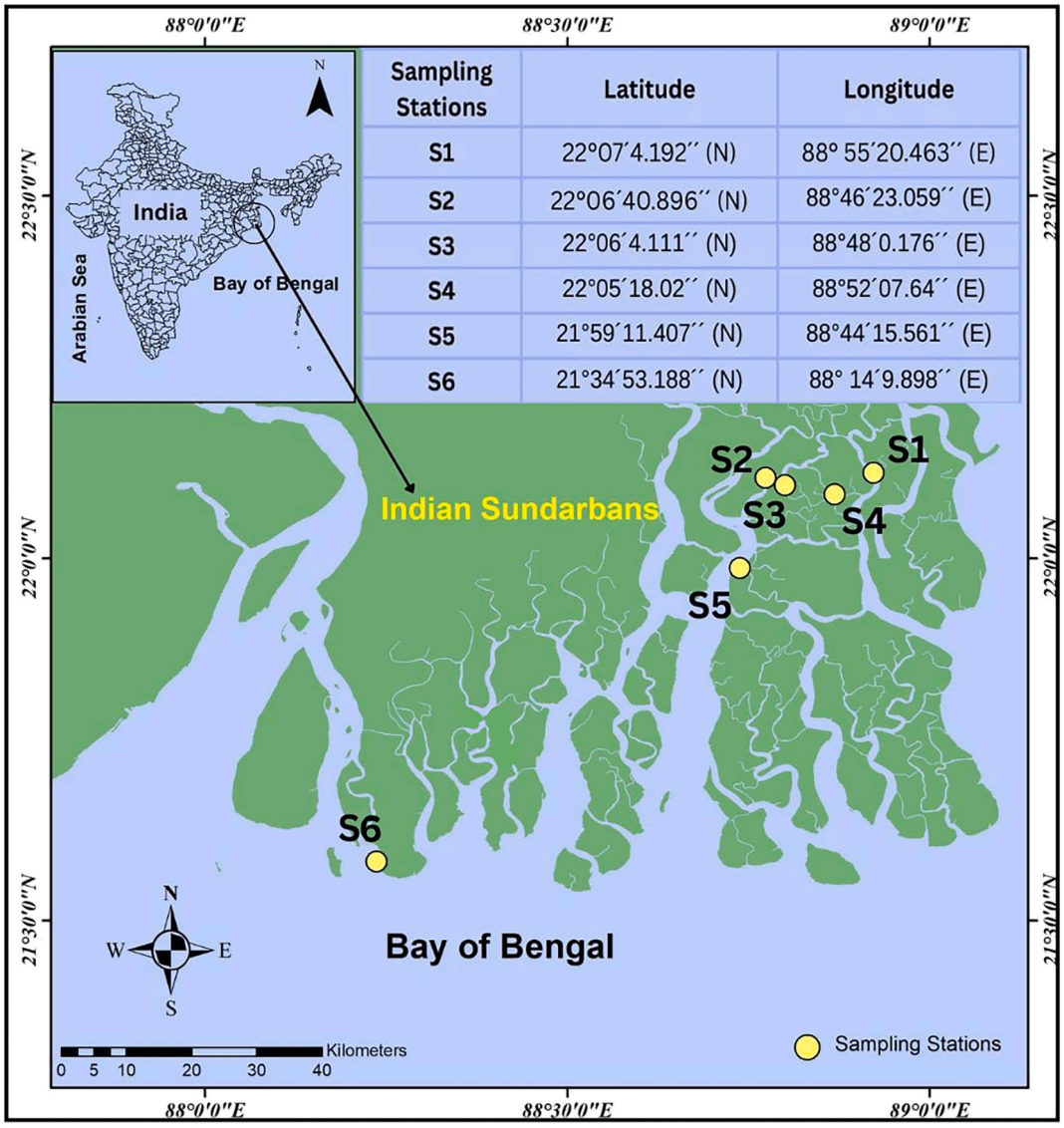


Fig. 1. Study area map along with the sampling stations on the Indian Sundarbans.

divided into two equal portions based on volume then the i. first portion was preserved in a 4% seawater/formaldehyde solution until laboratory analysis; ii. second portion was first gently transferred to a 1 L container (Made: Tarsons, India) with in situ GF/F (0.47 μm) filtered seawater (FSW) immediately after collection, to which Neutral Red stain was added to a 1:67000 final concentration, and kept in a thermally insulated bucket in the dark. After 20 min, the water was filtered through 200 μm mesh discs, the filtrate was rinsed with FSW, and transferred to 50 ml falcon tubes which were preserved immediately in ice, transported to the laboratory, and kept frozen (−20 °C) until analyses. On each occasion of copepod sampling, a multiparameter probe (Model: Pro-1030; Made: YSI, USA) was used to record in situ salinity (in Practical Salinity Unit) and water temperature (°C) of the sampling station with the purposes of checking if the Neutral Red Stain method (described below in detail) applied for the CEAM would serve the purpose, and also in order to provide information of the sampling stations from where the copepods were collected for future references.

2.3. Laboratory analysis

2.3.1. Use of Neutral Red for differentiating live vs. dead

Diverse approaches exist to differentiate copepod samples from live and dead individuals at the time of sampling, each with its own strengths and weaknesses (Tang et al., 2006, 2014). Over the past two decades, the Neutral Red vital staining method has been established as an efficient and practical option for copepods (for details, see Tang et al., 2006; Zetsche and Meysman, 2012; Martínez et al., 2014; Tang et al., 2014). The Neutral Red vital stain is the most robust and broadly applicable to marine and brackish plankton larger than 50 μm (Zetsche and Meysman, 2012). Further, the Neutral Red vital stain is most effective for estuaries where salinity ranges between mesohaline and polyhaline regimes (Jyothibabu et al., 2016). In the current study, salinity of the sampling stations in the Indian Sundarbans were mesohaline to polyhaline (see Fig. 2); therefore, the authors adopted the laboratory process described in detail by Tang et al. (2006) and Elliot and Tang (2009). In the current study, while conducting the CEAM, the methods of Jyothibabu et al. (2016), who worked with many similar copepod species in the Cochin backwater of India, were closely followed.

2.3.2. Laboratory procedures

Copepod samples collected for the TDAM were analysed according to routine procedures for zooplankton quantitative analysis. Samples were first split into multiple 1 ml aliquots, counted on a Sedgewick Rafter cell, and examined under a compound microscope (Model: B1; Motic, Hong

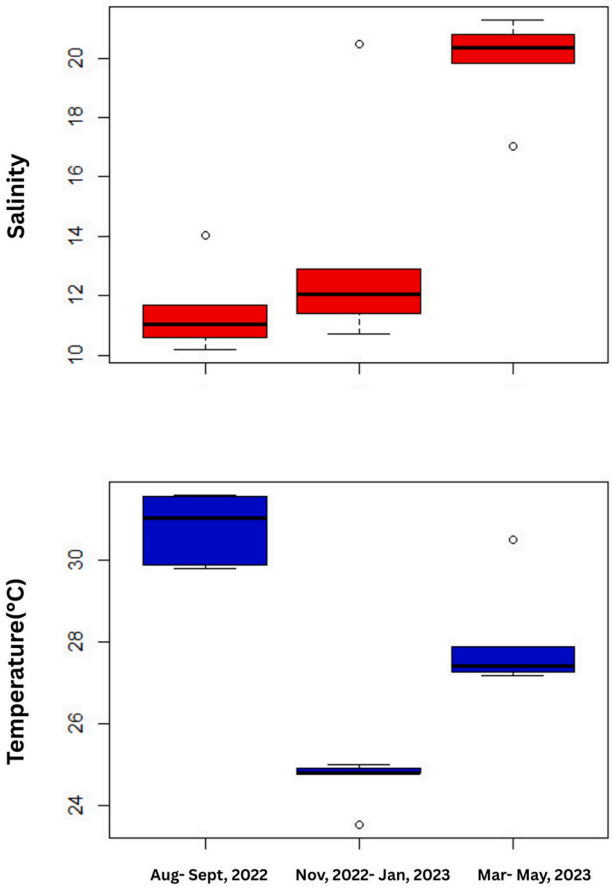


Fig. 2. Temporal variations of salinity and water temperature (°C) of Indian Sundarbans.

Kong). At least 10% of the entire sample (and minimin of 50 organisms) was analysed. The copepods (i.e. only adults) were taxonomically identified to the species level following Kasturirangan (1963), and their abundances were expressed as individuals per cubic metre (i.e. ind. m^{-3}).

For the CEAM, frozen copepod samples were first thawed. Then HCl was added to a 1:10 final concentration to facilitate the development of the colour of the Neutral Red stain. Multiple aliquots (each 1 ml, and at least 10% of each sample) were taken on Sedgewick Rafter counting cells and examined under a compound microscope (Model: B1, Made: Motic, Hong Kong). The taxonomic identification of copepods (i.e. only adults) was conducted at the species level following standard literature (Kasturirangan, 1963). The copepods showed three different patterns of staining: fully stained (considered 'alive' at the time of sample collection), partially stained (also considered 'alive' at the time of sample collection), and not stained (considered 'dead' at the time of sample collection) (Eliott and Tang, 2009). While conducting those taxonomic procedures copepod moults were identified too but they were not included in the estimates of alive/dead. Carcasses of the unstained dead individuals and live copepods (stained) were counted separately. Those counts were expressed in individuals per cubic meter (i.e. ind.m^{-3}).

2.4. Calculation of diversity indices and their deviations

The study resulted in two datasets: one for the TDAM and the other for the CEMA CEAM. For both the datasets the diversity indices such as Species Richness (S), Shannon-Wiener Diversity Index (H′), Simpson Diversity Index (D) and Pielou's Evenness Index (E) were estimated using the 'Vegan' Package (Version 2.6-10) of CRAN-R4.6.0 (R Core Team, 2026). The percentage deviation (Dev) between the corrected and non-corrected estimates of the diversity indices for a given sampling station and sampling period were taken as the sensitivity of the respective indices under the observed community structure and incidence of carcasses, which was calculated as

$$Dev_I = \frac{100^*|TDAM_I - CEAM_I|}{max(TDAM_I, CEAM_I)}$$

where $_I$ refers to a diversity index, and $TDAM_I$ and $CEAM_I$ stand for the value of the corresponding index according to the TDAM and CEAM, respectively.

3. Results

3.1. Abiotic conditions, copepod diversity and relative abundances

The salinity and water temperature varied both in terms of the sampling period and stations (Fig. 2). The temperature from August to September 2022 ranged from 29.80 to 31.60 °C, and the salinity ranged from 10.20 to 14.03. During the March to May 2023 sampling, salinity ranged from 17.03 to 21.27 and temperature ranged from 27.19 to 30.50 °C. From November 2022 to January 2023, salinity ranged from 10.70 to 20.47 and temperature ranged from 23.54 to 25 °C.

The relative abundances of each species following the TDAM and CEAM are listed in Table 1. A total of 22 copepod species belonging to 12 genera and 7 families were recorded (8 species from Paracalanidae, 5 species from Acartiidae, 2 species from Pseudodiaptomidae, 1 species from Eucalanidae, 2 species from Pontellidae, 3 species from Oithonidae, and 1 species from Corycaeidae (Table 1). Among the 22 species, 18 belonged to the Calanoida and the remaining 4 species to the Cyclopoida. *Acrocalanus monachus*, *Acartiella sewelli*, *Pseudodiaptomus binghami*, and *Pontella andersoni* were exclusively present in the samples collected during the August to September 2022 period (Table 1).

3.2. Abundant copepods

Table 2 presents the most abundant copepod species in each sampling period and their vital status that is alive and dead percentages. According to the TDAM, *Bestiolina similis*, *Acartiella tortaniformis*, and *Acartia spinicauda* were abundant during the August-September 2022 sampling period, but the CEAM found that the abundance was in the sequence of *B. similis*, *A. spinicauda*, and *Paracalanus aculeatus* (Table 2). When the TDAM and CEAM were compared for the sampling period November 2022 – January 2023, the former and the latter both found *A. tortaniformis*, *B. similis* and *Paracalanus parvus* to be highly abundant (Table 2). During the March to May 2023 sampling period, *P. parvus*, *A. tortaniformis*, and *B. similis* were abundant in both the TDAM and CEAM (Table 2).

3.3. Variations of carcasses and diversity metrics

Table 3 shows that the variability of alive and dead copepods at each sampling station during the different periods of 2022-2023. The highest percentage of the carcasses was found during the August-September 2022 sampling period. That was 45 ± 2.22 (median $\pm$ SE) and it had a range from 40% to 55%, followed by the November 2022 to January 2023 sampling period, when it was 16 ± 2.44, range 7% to 24%. During the March - May 2023 sampling period, the carcasses were 12 ± 1.86% and the range was 1% to 15% (Table 3). After pooling the station-wise datasets, the dead percentages were 48% in the August–September 2022 samples, followed by 18% in the November 2022 to January 2023, and 11% in the March to May 2023 sampling periods (Fig. 3).

Table 1
Relative abundances (%) of the copepod species of the Indian Sundarbans measured through both the traditional diversity assessment method (TDAM) and carcasses estimation approach method (CEAM).

Order	Family	Species	Aug-Sept, 2022		Nov, 2022 –Jan, 2023		Mar-May, 2023	
			TDAM	CEAM	TDAM	CEAM	TDAM	CEAM
Calanoida	**Paracalanidae**	*Paracalanus parvus*	7.86	5.53	11.93	11.59	11.28	11.24
		Paracalanus aculeatus	4.26	4.89	3.63	3.25	5.42	5.43
		Paracalanus indicus	2.83	2.07	2.25	2.69	3.85	3.87
		Acrocalanus gracilis	5.42	3.58	4.71	4.65	2.81	2.84
		Acrocalanus monachus	0.23	0.44	0.00	0.00	0.00	0.00
		Bestiolina similis	20.19	25.87	15.00	16.17	10.24	10.21
		Parvocalanus dubia	0.00	0.00	0.55	0.68	0.93	0.96
		Parvocalanus crassirostris	0.00	0.00	2.00	2.02	2.88	2.86
	Acartiidae	*Acartia spinicauda*	12.37	11.45	5.03	5.34	6.17	6.20
		Acartia tonsa	3.62	4.26	3.21	3.16	4.36	4.41
		Acartia tropica	0.00	0.00	2.13	2.34	2.93	2.92
		Acartiella sewelli	0.31	0.60	0.00	0.00	0.00	0.00
		Acartiella tortaniformis	17.70	20.82	21.43	19.97	10.42	10.43
	Pseudodiaptomidae	*Pseudodiaptomus serricaudatus*	3.90	2.25	5.76	5.79	7.87	7.84
		Pseudodiaptomus binghami	5.46	3.37	0.00	0.00	0.00	0.00
	Eucalanidae	*Subeucalanus subcrassus*	1.39	1.87	2.62	2.56	4.26	4.25
	Pontellidae	*Labidocera euchaeta*	0.00	0.00	2.03	1.74	2.91	2.88
		Pontella andersoni	1.95	0.00	0.00	0.00	0.00	0.00
		Oithona simlis	0.00	0.00	2.86	2.54	3.77	3.75
	Oithonidae	*Oithona brevicornis*	10.38	11.12	7.04	7.11	7.91	7.97
Cyclopoida		*Oithona nana*	0.00	0.00	3.78	4.12	5.76	5.74
	Corycaeidae	*Corycaeus crassiusculus*	2.14	1.88	4.03	4.26	6.23	6.20

Table 2
Temporal variations of a few abundant copepods of the Indian Sundarbans following both the traditional diversity assessment method (TDAM) and carcasses estimation approach method (CEAM).

Traditional diversity assessment method								
August - September, 2022			November, 2022 - January, 2023			March – May, 2023		
Species	Alive (%)	Dead (%)	Species	Alive (%)	Dead (%)	Species	Alive (%)	Dead (%)
Bestiolina similis	100	0.00	*A. tortaniformis*	100	0.00	*P. parvus*	100	0.00
Acartiella tortaniformis	100	0.00	*B. similis*	100	0.00	*A. tortaniformis*	100	0.00
Acartia spinicauda	100	0.00	*Paracalanus parvus*	100	0.00	*B. similis*	100	0.00
Carcasses estimation method								
B. similis	66.61	33.39	*A. tortaniformis*	76.05	23.95	*P. parvus*	88.70	11.30
Acartia spinicauda	61.18	38.82	*B. similis*	87.94	12.06	*A. tortaniformis*	89.05	10.95
Paracalanus aculeatus	48.11	51.89	*P. parvus*	79.26	20.74	*B. similis*	88.76	11.24

Table 3
Temporal variations of the total abundances (ind.m^{-3}) and percentages of alive and dead copepods sampled from the different sampling stations across the Indian Sundarbans.

Sampling stations	Sampling period	Total abundance (Ind.m^{-3})	Alive (Ind. m^{-3})	Dead (Ind. m^{-3})	Alive (%)	Dead (%)
S1	**August-**	17743	9770	7973	55	45
S2	**September,**	7612	4174	3438	55	45
S3	**2022**	832	459	373	55	45
S4		5502	2751	2751	50	50
S5		18652	8432	10220	45	55
S6		7301	4381	2920	60	40
S1	**November,**	35281	29782	5499	84	16
S2	**2022 –**	37953	31650	6303	83	17
S3	**January,**	22840	20195	2645	88	12
S4	**2023**	39317	30000	9317	76	24
S5		35154	32577	2577	93	7
S6		91999	69982	22017	76	24
S1	**March –**	39427	34288	5139	87	13
S2	**May, 2023**	38537	33810	4727	88	12
S3		24798	24467	331	99	1
S4		36270	31005	5265	85	15
S5		39368	34539	4829	88	12
S6		50532	45531	5001	90	10

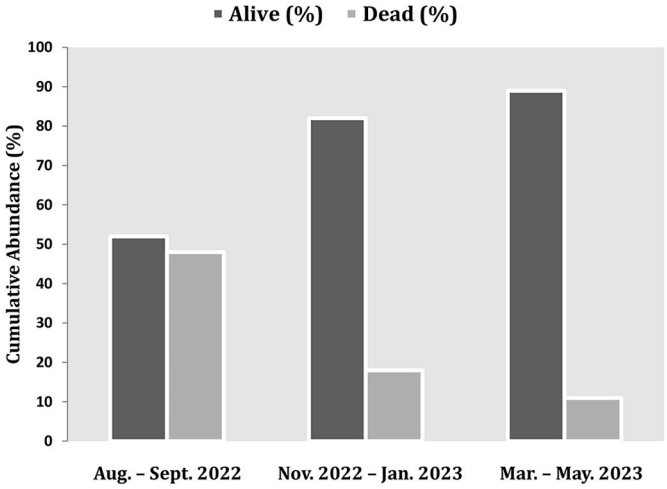


Fig. 3. Temporal variations of the cumulative abundances (ind.m^{-3}) of the copepod community of the Indian Sundarbans before and after incorporating the carcasses.

3.4. Diversity indices estimated through the TDAM and CEAM

3.4.1. Species richness

According to the TDAM, samples collected between March and May 2023 had the highest species richness (median 17 and range 15–18), followed by samples collected from November 2022 to January 2023 (median 16, range 7–18) and August–September 2022 (median 8, range 7–11) (Table 4). According to the CEAM, species richness was the highest in the March to May 2023 sampling period (median 17, range 15–18), followed by the November 2022 to January 2023 period (median 16, range 7–18), and the August to September 2022 period (median 7, range 5–8) (Table 4). In the August to September 2022 sampling period, the deviation of the species richness between the TDAM and CEAM estimates was up to 28.57%, in the November 2022 to January 2023 sampling period that deviation was up to 6.25%, whereas in the March to May 2023 sampling period, no such deviation was found (Table 4).

3.4.2. Shannon index

The Shannon index, when assessed using the TDAM, was the highest in the March to May 2023 period (that is 2.64 and ranged from 2.45 to 2.74), followed by the November 2022 to January 2023 period (that is 2.54 and ranged from 1.57 to 2.72) and the August to September 2022 period (that is 1.82 and ranged from 1.58 to 2.27) (Table 4). Following the CEAM, the median of the Shannon index value was 1.74, and it ranged from 1.49 to 1.91 in the August to September 2022 sampling period. During the November 2022 to January 2023 sampling period, the median of the Shannon index value was 2.5, and it ranged from 1.59 to 2.71. In the March to May 2023 sampling period, the median of the Shannon index value was 2.64 and ranged from 2.45 to 2.74 (Table 4). The highest deviation in the Shannon index value calculated following the TDAM and CEAM was found during the August to September 2022 sampling period, which was up to 15.85%, followed by the November 2022 to January 2023 period, when it was up to 5.80%. However, from March to May 2023, no deviation was found in the Shannon index calculated either following the TDAM or the CEAM (Table 4).

3.4.3. Simpson index

Regarding the Simpson index, according to the TDAM from March to May 2023, the median was 0.91, and it ranged from 0.89 to 0.92. From November 2022 to January 2023 period, the median of the Simpson index value was 0.91, ranging from 0.75 to 0.92. During the August to September 2022, the median was 0.81, and it had a range of 0.75 to 0.88 (Table 4). According to the CEAM, during the March to May 2023 sampling period, the median of the Simpson index value was 0.91 and it ranged from 0.89 to 0.92, during November 2022 to January 2023, the median was 0.90 and it ranged from 0.75 to 0.92. On the August to September 2022 sampling occasion, the median value of the Simpson index was 0.80, and it ranged from 0.74 to 0.83 (Table 4). The deviation between of the Simpson index value calculated by following the TDAM and CEAM was the highest in the August to September 2022 sampling period, up to 5.68%, followed by the November 2022 to January 2023 period, up to 2.20%, while in the March to May 2023 period, no such deviation was found (Table 4).

3.4.4. Pielou's index

The Pielou's index estimated according to the TDAM for the March to May 2023 sampling period had a median of 0.93 and it ranged from 0.90 to 0.96. During the November 2022 to January 2023 sampling period, the median value of the Pielou's index was 0.92, ranging from 0.81 to 0.96, and the lowest value of the Pielou's index was found in the samples collected from August to September 2022 (i.e. median 0.90, ranging from 0.79 to 0.95) (Table 4). Following the CEAM, during the August to September 2022 period, the median value of the Pielou's index was 0.92, ranging from 0.87 to 0.97. For November 2022 to January 2023 sampling period, the median was 0.91, ranging from 0.82 to 0.96. For March to May 2023 period, the median value of the Pielou's index was 0.92, ranging from 0.90 to 0.96 (Table 4). The deviations of the Pielou's index values calculated y following the TDAM and CEAM for August to September 2022, November 2022 to January 2023, and March to May 2023 sampling periods were up to 11.95%, 3.2%, and 1%, respectively (Table 4).

4. Discussion

Current results showed that when analysing preserved copepod samples, discriminating the vital state at the time of collection quantitatively affects several alpha diversity metrics estimated from such

Table 4
Deviations (%) in the diversity indices of the copepod community of the Indian Sundarbans estimated through the traditional diversity assessment method (TDAM) and carcasses estimation approach method (CEAM).

Sampling stations	Species Richness			Shannon Index			Simpson's Index			Pielou's Index		
	TDAM	CEAM	Dev (%)	TDAM	CEAM	Dev (%)	TDAM	CEAM	Dev (%)	TDAM	CEAM	Dev (%)
August-September, 2022												
S1	11	8	27.27	2.27	1.91	15.85	0.88	0.83	5.68	0.95	0.92	3.15
S2	9	7	22.22	1.94	1.71	11.85	0.84	0.80	4.76	0.88	0.88	0.00
S3	7	5	28.57	1.81	1.55	14.36	0.81	0.78	3.70	0.93	0.97	4.12
S4	10	8	20.00	1.83	1.81	1.09	0.79	0.79	0.00	0.79	0.87	9.19
S5	7	7	00.00	1.78	1.78	0.00	0.81	0.81	0.00	0.92	0.91	1.08
S6	7	5	28.57	1.58	1.49	5.69	0.75	0.74	1.33	0.81	0.92	11.95
November, 2022 – January, 2023												
S1	15	15	0.00	2.50	2.47	1.20	0.90	0.90	0.00	0.92	0.91	1.00
S2	17	17	0.00	2.72	2.71	0.30	0.92	0.92	0.00	0.96	0.96	0.00
S3	16	16	0.00	2.47	2.53	2.40	0.90	0.90	0.00	0.89	0.91	2.20
S4	16	15	6.25	2.58	2.43	5.80	0.91	0.89	2.20	0.93	0.90	3.20
S5	18	18	0.00	2.63	2.65	0.70	0.91	0.91	0.00	0.91	0.92	1.00
S6	7	7	0.00	1.57	1.59	1.20	0.75	0.75	0.00	0.81	0.82	1.20
March – May, 2023												
S1	16	16	0.00	2.57	2.57	0.00	0.91	0.91	0.00	0.93	0.92	1.00
S2	18	18	0.00	2.74	2.74	0.00	0.92	0.92	0.00	0.94	0.94	0.00
S3	16	16	0.00	2.60	2.60	0.00	0.91	0.91	0.00	0.93	0.94	1.00
S4	15	15	0.00	2.45	2.45	0.00	0.89	0.89	0.00	0.90	0.90	0.00
S5	18	18	0.00	2.68	2.68	0.00	0.91	0.91	0.00	0.92	0.92	0.00
S6	17	17	0.00	2.73	2.73	0.00	0.92	0.92	0.00	0.96	0.96	0.00

samples. The metrics explored here presented different sensitivities to the presence of dead individuals in the samples, and the overall effect seemed to be dependent on the relative incidence of carcasses.

4.1. Existing copepod diversity of Indian Sundarbans

The Indian Sundarbans, except its western part, currently receives less freshwater because the tributaries are cut off from the main flow of the Ganges River of India, which is the primary source of freshwater in the region (Rudra, 2018). Consequently, sampling stations S1 to S5 are now marine-dominated (Nandy and Mandal, 2020; Chakrabarty et al., 2022), whereas S6 receives freshwater from the locally known Hooghly River(which is the lower course of the Ganges River of India) (Rudra, 2018). The S6 remains mesohaline to polyhaline because of its proximity to the estuary mouth. In the Indian Sundarbans, heavy rainfall from late June to September and recently extended till early October (considered as south-west monsoon rain) results in lowered salinity for local estuaries (Bhattacharya et al., 2015; Nandy et al., 2018; Chakrabarty et al., 2022; Paul et al., 2024). This configuration, combined with the spatial and temporal sampling design, and allowed the authors to evaluate the performance of the TDAM and CEAM under a wide range of salinity and temperature conditions.

Historically, all investigations focusing on the mesozooplankton and copepod taxonomy and ecology of the Indian Sundarbans have followed the TDAM for estimating the diversity and abundances. Overall, these results suggested that the copepods constitute 70–80% of the total abundance of the mesozooplankton community (Bhattacharya et al., 2015), with approximately 41 recorded species (Bhattacharya et al., 2015; Nandy et al., 2018; Basu et al., 2022; Chakrabarty et al., 2022; Paul et al., 2024; Bhattacharjee et al., 2025; Paul, 2026). During the current investigation, *B. similis* was the most abundant species among the copepods, and *P. parvus*, *A. tortaniformis*, *A. spinicauda*, *Pseudodiaptomus serricaudatus* and *O. brevicornis* were also highly abundant in the different months of a typical year, which is consistent with the previous studies conducted in the estuaries of the Indian Sundarbans (Bhattacharya et al., 2015; Nandy et al., 2018; Chakrabarty et al., 2022; Paul et al., 2024; Bhattacharjee et al., 2025; Paul, 2026). In the Indian Sundarbans, the abundances of mesozooplankton (including copepods) generally varies between months, as suggested by the work of the Nandy and Mandal (2020). The Copepod diversity and abundance in the Indian Sundarbans generally peak from the middle of February and last till May, and the lowest values are generally observed in the months of August and September (Bhattacharya et al., 2015; Nandy et al., 2018; Nandy and Mandal, 2020; Basu et al., 2022). It is also observed that many neritic species (*Acrocalanus gracilis* and *Paracalanus aculeatus*) associate themselves with the resident copepod assemblages based on the seasonal variability (Sarkar et al., 1986; Basu et al., 2022; Paul, 2026). Further the contribution of the Cyclopoida group of copepods does vary in the community and generally picks up in the monsoon season specially of in the marine-dominated mangrove estuaries of the Indian Sunbarbans (Nandy et al., 2018; Chakrabarty et al., 2022). Overall, it could be concluded that the present results of the copepod diversity obtained through the TDAM are, therefore, aligned with the earlier studies on conducted on the copepods as well as mesozooplankton in estuaries of the Indian Sundarbans.

4.2. Copepod carcasses affecting diversity estimates

A novel finding in line with the main goal of this investigation was that diversity metrics were sensitive to the vital status of individual copepods. Such finding supports the working hypothesis irrespective of the causal factor(s) of copepod mortality (except the handling stress which in every study causes death of some individuals during the sample procurement), a matter that was beyond the scope of the current study. Disentangling the actual mechanism of an individual copepod mortality based on field observations is highly challenging, due to multiple potential factors and processes acting simultaneously in any natural environment. Non-predatory copepod mortality has been linked to abiotic variability (Tang et al., 2014), for instance, to changes in salinity in estuaries in Norway (Kaartvedt and Aksnes, 1992), the Netherlands (Soetaert and Herman, 1994), Brazil, Chile, and Uruguay (Martínez et al., 2014; Giesecke et al., 2017; da Silva et al., 2020, da Cruz et al., 2023). Even euryhaline copepods that tolerate broad salinity ranges suffer high mortality when exposed to wide or sudden changes in salinity (Calliari et al., 2006, 2008). In India, temporal variation in copepod carcasses in the Cochin backwaters has been linked to the advent and departure of the South-West monsoon which modulates the salinity and temperature regimes of the ecosystem so at the start of the monsoon, over 80% of estuarine and neritic copepods, such as *Pseudodiaptomus parvus*, *Acrocalanus gracilis*, and *Acartia danae*, were found dead, possibly due to the sudden salinity change (Jyothibabu et al., 2016). The monsoon brings the strongest gradients of salinity and temperature to the Indian Sundarbans (Bhattacharya et al., 2015; Nandy et al., 2018); therefore, many copepods may experience substantial stress, leading to higher non-predatory mortality Jyothibabu et al. (2016). For example, species such as *P. parvus* and *A. gracilis* suffered substantial mortality during the August-September 2022 sampling period which is typically considered monsoon months in the Indian Sundarbans. More generally, copepod carcasses of the most abundant species never exceeded 11.30% in the March to May 2023 sampling period and 23.28% in the November 2022 to January 2023 sampling period, but jumped to 40.19% during the August-September 2022 sampling period.

Within that context, present results based on hard data demonstrated that the estimates of the relative abundances and diversity of the copepods of the Indian Sundarbans may change when the CEAM is applied but the extent of change may depend on the season or specific month (s) of an year. In addition, the dominance hierarchy of the copepod community may also change, particularly at times when the incidence of the carcasses is the highest (i.e. in the August-September 2022 sampling, *P. aculeatus* emerged as dominant, which otherwise it was *A. tortaniformis*). The overestimation of the copepod abundances due to overlooking the vital state of copepod individuals had been previously reported from the Cochin backwaters of India (Jyothibabu et al., 2016), tropical estuaries of Brazil (da Cruz et al., 2023), Chesapeake Bay of the U.S.A. (Elliott and Tang, 2011b), and the Rijpfjorden-Svalbard of Norway (Daase et al., 2013; Daase and Søreide, 2021), but the effect on the copepod diversity estimates has not been specifically addressed so far.

All the diversity metrics considered here were sensitive to the incorporation of the vital state of individuals in the samples, with deviations between corrected and uncorrected metrics when the incidence of carcasses was high. From March to May 2023, the incidence of carcasses was at its lowest (i.e. up to 11%), and no deviations were observed for most metrics between the corrected and non-corrected indices. During the November 2022 to January 2023 period, the incidence of the carcasses was between 7% and 24% - the maximum deviation was 6.25%, but the deviation between the metrics climbed to 28.57% during the August-September 2022 period when the incidence of the carcasses reached 40% to 55%. Furthermore, among the alpha diversity indices explored here, species richness and Shannon diversity were the most sensitive (in that order) to the vital status of the individuals, compared to Simpson's and Pielou's indices. This is because the latter two are derived forms of the former (Boyle et al., 1990; Izsák, 1996).

The TDAM implicitly assumes all organisms are alive at the time of capture or, alternatively, that the discrimination between live and dead status is irrelevant in this context. Results of the current as well as the previous sudies indicated that in the estuaries, coastal and marine waters ,the '*all alive*' assumption for the copepod assemblages is not tenable under most conditions (Tang et al., 2014; Jyothibabu et al., 2016). The relevance of the vital status of individual copepod or any other plankton for describing and understanding the diversity of plankton communities arises from the fact that the ecological roles of live and dead plankton

differ in aquatic ecosystem (Tang & Elliott, 2014). For instance, vital activities of live copepods such as feeding and production contribute mostly to the herbivory food chain (Hansen and Van Boekel, 1991; Tang & Elliott, 2014), while the carcases of copepods promote the microbial web (Steinberg and Landry, 2017). Thus, the TDAM and CEAM serve as different, complementary descriptions of the biological diversity. Joint consideration of both sets of results may enrich the interpretation of patterns of diversity in time or space or both, and help in advances behind the understanding of underlying processes ecosystem structure and functions.

While any improvement in the diversity estimates of an ecosystem should be appreciated, one may ponder the relevance of the additional (or at least supplementary) ecological information yielded by the CEAM compared to the TDAM, given the higher cost of the former in terms of the extra time and effort involved. This argument may suffice if a habitat does not face a volatile environment owing to the absence of substantial gradients in either time or space. The incidence of copepod carcasses in the coastal-marine environments ranges from 11.6% to 59.8%, according to data reviewed by Tang et al. (2014), and the upper end of the range extends to 80% when more recent data from an estuarine environment in India are included (Jyothibabu et al., 2016). Therefore, quantitative estimates without the exclusion of carcasses may carry a substantial error and induce biased conclusions regarding the structure and functions of coastal-marine plankton communities if underlying assumptions are not met, or properly incorporated into the interpretation framework (Hansen and Van Boekel, 1991; Tang et al., 2009; Elliott and Tang, 2011a, 2011b; Frangoulis et al., 2011; Jyothibabu et al., 2016). The growing literature on copepods and their vital state in natural samples and the current results also suggested that there is often scope for improvement in the diversity estimates through the incorporation of vital state information of an individual copepod (Tang & Elliott, 2014), and that the current diversity estimates of copepods (and to larger extent plankton) in coastal-marine ecosystems worldwide may need to be revisited.

4.3. *Proposing 'living diversity' for plankton literature*

Diversity indices discussed here are routine and widely used as key indicators of alpha diversity of all kinds of aquatic ecosystems worldwide (Washington, 1984; Roswell et al., 2021); therefore, it is desirable that their estimates remain globally consistent, unbiased, and comparable across ecosystems and studies (Peet, 1974; Iknayan et al., 2014). Diversity surveys usually target only live individuals, particularly in biological groups for which live/dead discrimination is obvious at the time of sample collection, or for which dead individuals are simply not targeted by recording protocols or sampling gear, for example, fish, mammals, reptiles, birds, and many benthic taxa (Hammond et al., 2021). In these cases, there seems to be little scope for further refinement of diversity estimates by including vital status corrections. Regarding copepods, more generally plankton, and perhaps most other microscopic organisms whose vital status determination is challenging at the time of sample collection, the current findings have potentially far-reaching implications. The co-existence of diversity datasets arising from the corrected (i.e. only live individuals) and the non–corrected (i.e. live + dead individuals) estimates, where the latter being all or most of the currently existing datasets of many microscopic organisms including plankton, may require addressing the former as the '*living diversity*' of the corresponding community/assemblage for achieving consistency and to avoid confusion in the biological diversity literature. In the long run, it is foreseen that most diversity datasets dealing with microscopic organisms will refer strictly to '*living diversity*', as, considered in tandem with the traditional diversity (i.e. live + dead), for a better approximation to the root of the diversity concept, as generally understood either explicit or implicit, i.e., abundance, variety, and variability of life in space and time (Purvis and Hector, 2000; Hubel, 2001), and to underlying processes in nature.

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CRediT authorship contribution statement

Debarati Sengupta: Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Danilo Calliari:** Conceptualization, Investigation, Methodology, Validation, Writing – original draft, Writing – review & editing. **Sourav Paul:** Conceptualization, Formal analysis, Funding acquisition, Investigation, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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