Revisiting the copepod diversity of Indian Sundarbans through estimation of carcasses

Debarati Sengupta[1], Danilo Calliari[1,2,3*], Sourav Paul[1*]
[1]Estuarine and Coastal Studies Foundation, Howrah, West Bengal-711101, India
[2]Facultad de Ciencias, Universidad de la República, Uruguay
[3]Instituto de Ciencias Oceánicas, Universidad de la República, Uruguay
*Corresponding authors: dcalliar@fcien.edu.uy (D. Calliari) and souravpaul@ecsfindia.org, souravpaul4@gmail.com (S. Paul)

ABSTRACT

Diversity assessment of plankton traditionally considers species richness and abundance, overlooking the vital state of individuals (i.e., alive or dead). This study aimed to integrate the vital state of zooplankters into diversity indices, using the copepods of the Indian Sundarbans (IS) as an example community. It was hypothesized that when carcasses estimation (CE) is incorporated diversity estimates deviate from those derived from the traditional diversity assessment (TDA) method. Seasonal sampling was conducted between 2022 and 2024 from seven sampling stations of the IS. The monsoon had the highest variability in temperature, salinity and pH, followed by the pre- and post-monsoon periods, and the overall highest abundance of copepod carcasses (51%), followed by the post-monsoon (18%) and pre-monsoon (11%).Variations were also noted in the relative abundances of species calculated through the TDA and CE methods, which even affected the dominance hierarchy of the community, in particularly during the monsoon. Species richness deviated more than the Shannon index, which deviated more than the Simpson and Pielou's indices when the TDA and CE methods were compared. The maximum deviations of diversity indices were observed in the monsoon compared to pre- and post-monsoon. The CE corrected method for copepod diversity estimation indicates the need to revisit zooplankton diversity estimates, especially for volatile environments like estuaries, coastal areas. Current results together with novel approaches to characterize biological diversity (e.g., environmental DNA) suggest the need to discriminate '*living diversity*' and '*holistic diversity*' for a better understanding of the structure and functions of plankton, including microscopic life.

Keywords: Plankton, Vital status, Diversity indices, Seasonal change, Estuary

1. Introduction

Diversity of a biological system refers to the variety and variability of life at different levels, from genes to ecosystems (Purvis et al., 2000). A generally accepted definition of '*diversity*' has been elusive, due to multiple meanings and interpretations attached to the term, many of which involve considerable confusion of concepts, models, and measures (Peet, 1974). Diversity indices based on information theory (Margalef, 1973), such as the Species richness, Shannon and Simpson indices are still the most commonly used for characterizing aquatic communities, but their usefulness and accuracy are critiqued at various levels (Washington, 1984; Roswell et al., 2021). According to Kempton (1979), diversity measures mostly focus on species which hold medium abundance in a given habitat, and emphasize neither the very common nor the rare species, but they rather provide maximum discrimination between sampling sites. The quantification of species richness and population abundance are daunting tasks given the detailed taxonomic information for species' identity and the corresponding abundances that are required. '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 evenness informs on the uniformity of their abundances (Gotelli et al., 2001; Lakicevic et al., 2018). Other widely used indices of diversity are the Shannon-Wiener (H′) and Simpson's (D) dominance (DeJong, 1975; Heip, 1974).

As diversity is primarily concerned with variability of life, when calculating information theory-based diversity indices attention is generally placed on organisms that are alive, whereas dead individuals are hardly accounted for (Zetsche and Meysman, 2012). Zooplankton contributes to the interactions and energy transfers at the lower levels of the food web of diverse aquatic ecosystems, including the open ocean, coastal seas and estuaries (Tang et al., 2014; Steinberg and Landry, 2017). The traditional approach to diversity assessment (TDA) as applied to the zooplankton does not take into consideration the vital status (i.e., alive or dead) of individual zooplankters (Tang et al., 2014). In case of the TDA, scientists sampling zooplankton in the field assume that all collected individuals are alive, preserve samples, identify one or more life history stages, sex, then enumerate individuals to produce a data matrix which is then used for calculation of information theory-based indices (Margalef, 1973; Tang et al., 2006). However, it is now well established that zooplankton carcasses are widespread and sometimes present in high numbers in the pelagic realm of marine ecosystems (Tang et al., 2014). Lack of discrimination between live and dead individuals may lead to overestimation of zooplankton abundance, biomass, production, and food resources for their predators (Tang et al., 2006). The mechanisms leading to non-predatory mortality may arise from unique or multiple stressors, which may impact species as well as individuals differently (Tang et al., 2014; Jyothibabu et al., 2016); therefore, diversity indices may also be sensitive to the vital status of individual zooplankton within a given assemblage.

Copepods dominate the marine meso-zooplankton and may constitute the most abundant metazoan life form on Earth (Mauchline, 1998). They link primary producers and medium to large consumers such as macro-invertebrates and fishes, and are widely used as indicators of environmental variability of marine ecosystems (Dahms, 1995; Hooff et al., 2006). Accurate quantification of copepod species diversity and population abundance is, therefore, crucial for characterizing the structure and functions of the lower food web of any aquatic ecosystem, including estuaries (Paffenhöfer et al., 2024). Over the last few decades, coastal-marine ecosystems, including estuaries, are experiencing changes in biodiversity, and understanding those changes has now become integral to many biodiversity studies (Gamfeldt et al., 2014). Therefore, the methods, processes, and approaches for the estimations of diversity are under scrutiny, and some of them may require revisions based on the advancement of scientific arguments and evidences (Zetsche and Meysman, 2012; Iknayan et al., 2014). Considering those perspectives, recent studies have raised critical questions on the merit and accuracy of the TDA method for estimating copepod diversity of coastal-marine ecosystems including estuaries (Zetsche and Meysman, 2012; Tang et al., 2014). Diverse approaches exist to differentiate in preserved samples alive from dead individuals at the time of sampling, each with its own strengths and weaknesses specific to the taxonomic group and habitat (Tang et al., 2014). Over the past two decades the Neutral Red vital staining method was established as an efficient and practical option for copepods and other marine zooplankton taxa (Tang et al. 2014). Since then, it has been widely applied in estuaries and other marine habitats, from high latitudes to the tropics, in both hemispheres (Tang et al., 2006; Zetsche and Meysman, 2012; Martinez et al., 2013; Tang et al., 2014). Such a method of copepod carcass estimation (CE) may help in correcting the estimates of copepod diversity indices, as the indices assume the number recorded for each group is made up of copepods which were alive at the time of sampling (Tang et al., 2006; Elliot and Tang, 2009; Zetsche and Meysman, 2012; Tang et al., 2014).

The Sundarbans of India – on the Northern Bay of Bengal (Fig. 1) – is part of a large-scale mangrove forest - deltaic system comprising a complex inter-twined network of estuaries (Chatterjee et al., 2013; Chakrabarty et al., 2022). The environment is subject to the strong climatic forcing of the seasonal monsoon cycle and also to stochastic events such as cyclonic disturbances (Bhattacharya et al., 2015; Nandy et al., 2018; Nandy and Mandal, 2020; Chakrabarty et al., 2022; Paul et al., 2024). Among copepods of the Indian Sundarbans (IS), Calanoida contributes the most to the total zooplankton abundance followed by Cyclopoida and Harpacticoida (Bhattacharya et al., 2015; Chakrabarty et al., 2022; Bhattacharjee et al., 2025). About 41 copepod species have been reported, among which *Bestiolina similis* and *Paracalanus parvus* most often dominate, while *Acartiella tortaniformis*, *Acartia spinicauda* are also highly abundant (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). The structure of the copepod community changes seasonally and each season (i.e., pre-monsoon, monsoon, and post-monsoon) has some species which are exclusive to a specific season (Nandy and Mandal, 2020; Basu et al., 2022; Chakrabarty et al., 2022). Those changes of the copepod community are linked to the physico-chemistry of the prevailing water masses (Nandy and Mandal, 2020; Basu et al., 2022; Chakrabarty et al., 2022; Paul et al., 2024). Copepod density in the IS generally peaks during the warm pre-monsoon and the lowest numbers occur in the late monsoon (Bhattacharya et al., 2015). The species diversity and abundance of the copepods have changed in the last decades (Bhattacharya et al., 2015; Basu et al., 2022; Paul et al., 2024; Bhattacharjee et al., 2025) with the addition of warm-water copepods such as the currently dominant *B. similis* and *P. parvus* linked to the rise of water temperature, while large sized copepods, which were common in 1980s, have been replaced by medium to small size copepods in the new millennium (Bhattacharya et al., 2015; Nandy et al., 2018; Nandy and Mandal, 2020; Chakrabarty et al., 2022; Bhattacharjee et al., 2025). All information on community structure, diversity, dominance and distribution patterns in the IS were derived by applying the TDA method, thus completely overlooking the incidence of copepod carcasses.

This study aims to estimate copepod diversity in the IS and to evaluate the extent to which different commonly used diversity metrics are sensitive to the incorporation of vital status information of the sampled individuals, as indicated by the Neutral Red live stain method of Tang et al. (2006) and Elliott and Tang (2009, 2011). In that regard, the copepod assemblages of the IS were used as case study to test the hypothesis that species richness, abundance and various other diversity indices provide biased estimates if the vital state of individual zooplankton is not taken into account. It is not intended to explore here the detailed mechanisms contributing to carcasses production (i.e., mortality). The study also sheds perspectives on how methods such as the TDA and CE may yield different results for the dominance hierarchy of a given habitat, and scenarios under which the alternative approach to copepod diversity estimation is most critically important.

2. Material and Methods

2.1. Study area

One of the UNESCO World Heritage Sites, the Sundarbans (21° 432´ - 21° 55´ N and 88° 42´ - 89° 04´ E), is the largest deltaic estuarine mangrove forest in the World, shared by India and Bangladesh (Mitra et al., 2012). Crisscrossed by a network of tributaries, the Indian part of the Sundarbans is dominated by semi-diurnal tides (Chatterjee et al., 2013; Rogers et al., 2014; Mitra et al., 2012).The three distinct seasons are pre-monsoon from March to early June and recently extended deep into the June; monsoon from late June to September, but sometimes extended to early October; and the post-monsoon usually between October and February, and sometimes shorter than expected (Mandal et al., 2019; Paul et al., 2024). The climatic condition in the pre-monsoon is hot and humid, the post-monsoon is mild, whereas the monsoon concentrates 52.7% to 89.4% of the total annual rainfall i.e., 1821 mm (± 341.8 mm) (Mandal et al., 2019) which infuses significant intra-monsoonal variability to the water quality (specifically salinity) of estuaries within the IS (Nandy et al., 2018). Salinity differs between three sectors of IS, namely a 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 were: 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), S6 (21°43´44.49´´N, 88°24´51.13´´E) and S7 (21°34´53.188´´N, 88° 14´9.898´´E), i.e., arranged in an approximately east to west orientation in the IS (see Fig.1).

2.2. Field sampling

From August 2022 to May 2023, a seasonal sampling approach (one sample per season) was taken to cover all stations (except for S6 in the pre-monsoon due to logistical issues). Copepod sample collections for both the TDA and the CE methods were conducted simultaneously, always from a slow-paced motor boat on high tide during day time with a 200 µm mesh sized plankton net (60 cm diameter and 150 cm in length) fitted with a mechanical flow meter (Hydro-Bios, Germany). The plankton net was towed for 3 minutes horizontally and slowly, to the extent possible, to minimize damage to zooplankton and handling errors. On each occasion of copepod sampling, a multi-parameter probe (YSI-1030, USA) was used to record salinity, water temperature (°C) and pH from near-surface waters (~0.5 m).

As salinity at all sampling stations ranged between mesohaline and polyhaline, conditions under which the Neutral Red Stain works best (Jyothibabu et al., 2016), the vital staining method of Eliott and Tang (2009) – for copepod CE in the Chesapeake Bay, U.S.A. – was used. Among several methods to discriminate live from dead individuals, the Neutral red vital stain is the most robust and broadly applicable to marine and brackish zooplankton and phytoplankton larger than 50 µm (Zetsche and Meysman, 2012). It is also the most widely used since its re-introduction by Tang et al. (2006). In the current study, a first tow was performed in order to collect a standard quantitative mesozooplankton sample which was subsequently preserved in a 4% seawater/ formaldehyde solution until laboratory analysis. For carcass estimation a second tow was performed under identical conditions after the net was thoroughly rinsed. In this case the sample was first gently transferred to a 1 L container with in situ GF/F filtered seawater (FSW) immediately after collection to which the Neutral Red stain was added to a 1:67000 final concentration, and kept in a thermally insulated bucket and in the dark. After 20 minutes the water was filtered through 200 µm mesh discs, the filtrate rinsed with FSW, and transferred to 50 ml falcon tubes which were preserved immediately in dry ice (-20ºC), transported to the laboratory and kept frozen (-20ºC) until analyses.

2.3. Laboratory analysis

Copepod samples collected for the TDS method were analyzed according to routine procedures for zooplankton quantitative analysis in the IS (e.g., Bhattacharya et al., 2015): samples were first split into 1 ml aliquots, counted on a Sedgewick Rafter cell, and examined under a compound-microscope (Model: B1 of Motic, Hong Kong). At least 1% of the whole sample was analyzed. The taxonomic identification of the copepods (i.e., only adults not sexed) was conducted to species level following Kasturirangan (1963) and the abundance was expressed as individuals per cubic metre (i.e., ind.m^{-3}).

For the CE method, frozen copepod samples were first thawed. Then ml HCl 1:10 final concentration was added to facilitate the Neutral Red Stain to further develop the color. Then multiple aliquots (each 1 ml, and at least 1% of all the samples) were taken on Sedgewick Rafter counting cells and examined under a compound-microscope (B1, Motic, Hong Kong). The taxonomic identification of the copepods (i.e., only adults not sexed) was conducted to species level following standard literature (Kasturirangan, 1963; Sewell, 1999; Conway et al., 2003). The copepods showed three different patterns of staining i.e., fully stained (considered as ‘alive’ at the time of sample collection), partially stained (also considered as ‘alive’ at the time of sample collection) and without stain (considered as 'dead' at the time of sample collection) (Eliott and Tang, 2009). While conducting the CE method in the current study, methods of Jyothibabu et al. (2016) who worked with many similar copepod species in the Cochin backwater of India were closely followed. Abundances of alive and dead copepods were expressed as individuals per cubic metre (i.e., ind.m^{-3}). All the samples were analyzed within a month after the sample collection date.

2.4. Calculation of diversity indices and their deviations

The study resulted in two datasets, one for the TDA method and the other for the CE method. For both datasets the diversity indices 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-R4.4.3 (R Core Team, 2025). The percentage deviation (Dev) between corrected and non-corrected estimates of diversity index for a given station and sampling time was taken as the sensitivity of the respective index under observed community structure and incidence of carcasses, and was calculated as:

$$Dev_I = \frac{100 * |TDA_I - CE_I|}{max(TDA_I, CE_I)}$$

where I refers to the diversity index (Richness, Shannon, Simpson, Pielou), and TDAI and CEI stand for the value of the corresponding index according to the TDA and CE approaches, respectively.

3. Results

3.1. Abiotic variability

The water temperature was the highest during the monsoon: 30.90°C ± 0.28 (median ± SE) with a range of 29.8°C to 31.6°C, followed by the pre-monsoon: 27.50°C ± 0.76 with a range of 27.1°C to 32.3°C, and the post-monsoon: 24.8°C ± 0.20, with a range 23.5°C to 25.2°C (Fig.2). Salinity was the highest in the pre-monsoon: 20.58 ± 1.33, range 17.03 to 28.5, followed by post-monsoon: 12.20 ± 1.26, range 10.7 to 20.4, and monsoon: 11.15 ± 0.47, range 10.2 to 14.03 (Fig.2). The pH was the highest in the pre-monsoon: 7.93 ± 0.04, range 7.76 – 8.07, followed by the monsoon: 7.90 ± 0.37, range 6–8.10, and the post-monsoon: 7.49 ± 0.11, range 6.86–7.77 (Fig.2).

3.2. Copepod diversity and relative abundances

The relative abundances of each species before and after incorporating the CE method are given in Table 1. A total of 23 copepod species belonging to 13 genera and 8 families (8 species from Paracalanidae, 5 species from Acartiidae, 2 species from Pseudodiaptomidae, 1 species from Eucalanidae, 2 species from Pontellidae, 3 species from Oithonidae, 1 species from Oncaeidae and 1 species from Corycaeidae) were recorded (Table 1). Among the 23 species, 18 belonged to Calanoida and the remaining 5 species to Cyclopoida. *Acrocalanus monachus*, *Acartiella sewelli*, *Pseudodiaptomus binghami*, *Pontella andersoni* and *Oncaea venusta* were exclusively present in the monsoon (Table 1).

3.3. Dominant copepods

Table 2 shows a few abundant species of copepods in each season and their vital status (i.e., alive and dead (%)). According to the TDA method, in the monsoon, *B. similis*, *A. tortaniformis* and *Pseudodiaptomus serricaudatus* were abundant (Table 2) with *B. similis* as the most abundant species (Table 1). The TDA method further showed that in the post-monsoon, *A. tortaniformis*, *B. similis* and *P. parvus* were abundant (Table 2), with *A. tortaniformis* the most abundant species (Table 1). In the pre-monsoon, *P. parvus*, *A. tortaniformis* and *B. similis* were abundant (Table 2) and *P. parvus* was the most abundant species (Table 1). After the CE method was incorporated into the estimates, in the monsoon

B. similis was the most abundant species followed by *A. spinicauda* and *Paracalanus aculeatus* (Table 1 and 2).

3.4. Spatial-temporal variations of the copepod carcasses

Table 3 shows the seasonal variability of the alive and dead copepods at each sampling station. The highest percentage of carcasses was found in the monsoon (45 ± 2.22 (median ± SE) and range 40% to 56%) followed by post-monsoon (16 ± 2.44, range 7% to 24%) and pre-monsoon (12 ± 1.86, range 1% to 15%) (Table 3). After pooling the station-wise data sets the dead percentages were 51% during the monsoon, followed by 18% in the post-monsoon and 11% in the pre-monsoon (Fig.3).

3.5. Diversity indices estimated through the TDA and the CE methods

3.5.1. Species richness

Following the TDA method, the pre-monsoon had the highest species richness (16 and range 15 to 18), followed by the post-monsoon (16 and range 7 to 18) and the monsoon (9 and range 7 to 11) (Table 4). According to the CE method, the species richness in the pre-monsoon was 16 (range 15 to 18), followed by the post-monsoon (16, and range 7 to 18), and the monsoon (7, range 5 to 8) (Table 4). In the monsoon, the deviation of species richness between the TDA and the CE estimates was up to 33.33% (median 27.27%) and in the post-monsoon up to 6.25%, while in the pre-monsoon no deviation was found (Table 4).

3.5.2. Shannon-diversity index

The Shannon index when assessed through the TDA method, was the highest in the pre-monsoon (2.6 ± 0.37 (median ± SE) and range 2.45 to 2.74) followed by the post-monsoon (2.58 ± 0.14 and range 1.57 to 2.72) and the monsoon (1.83 ± 0.08 and range 1.58 to 2.27) (Table 4). Following the CE method, the Shannon index was 1.71 ± 0.05, range 1.49 to 1.91 in the monsoon and 2.53 ± 0.14, range 1.59 to 2.71 in the post-monsoon, while in the pre-monsoon it was 2.6 ± 0.37, range 2.45 to 2.74 (Table 4). The highest deviation of the Shannon index between the TDA and the CE methods was found during the monsoon, which was up to 18.75% followed by post-monsoon up to 5.8% and in the pre-monsoon no deviation was found (Table 4).

3.5.3. Simpson-dominance index

When the TDA method was followed, the Simpson index showed the highest value in the pre-monsoon (0.91 ± 0.13 (median ± SE), range 0.89 to 0.92) followed by the post-monsoon (0.91± 0.022, range 0.75 to 0.92) and the monsoon (0.81 ± 0.016, range 0.75 to 0.88) (Table 4). According to the CE method the Simpson index of the pre-monsoon was 0.91 ± 0.13 and range 0.89 to 0.92, in the post-monsoon 0.90 ± 0.022 and range 0.75 to 0.92, and in the monsoon 0.80 ± 0.010 and range 0.74 to 0.83 (Table 4). The deviation between the TDA and the CE methods was highest in the monsoon, up to 6.97 %, followed by the post-monsoon, up to 2.2%, and the pre-monsoon when no deviation was found (Table 4).

3.5.4. Pielou's-evenness index

According to the TDA method, the Pielou's index was the highest in the pre-monsoon (0.93 ± 0.13 (median ± SE) and range 0.90 to 0.96) followed by the post-monsoon (0.91 ± 0.017 (SE) and range 0.81 to 0.96) and monsoon (0.92 ± 0.02 and range 0.79 to 0.95) (Table 4). Following the CE method, the Pielou's index in the monsoon ranged from 0.87 to 0.97 (0.92 ± 0.01), in the post-monsoon 0.91 ± 0.015, range 0.82 to 0.96, and in the pre-monsoon 0.92 ± 0.13 and range 0.90 to 0.96 (Table 4). Deviations between the TDA and the CE methods during the monsoon, post-monsoon and pre-monsoon were up to 11.95%, 3.2% and 1%, respectively (Table 4).

4. Discussion

4.1. Habitat conditions and existing copepod diversity of the IS

Currently the IS receives (except the western part) less freshwater than in the past because the tributaries are cut off from the main flow of the Ganges river of India, which is the primary source of freshwater of the region (Rudra, 2018). Consequently, sampling stations S1 to S6 are now marine-dominated, whereas S7 receives freshwater of the Ganges River but remains meso- to poly-haline due to its proximity to the estuary mouth (Nandy et al., 2018; Nandy and Mandal, 2020; Chakrabarty et al., 2022; Paul et al., 2024). Abiotic variability at sub-annual scale is largely driven by the monsoon as it brings heavy rainfall in the region every year resulting in lowered salinity during such periods (Bhattacharya et al., 2015; Nandy et al., 2018; Chakrabarty et al., 2022; Paul et al., 2024). The local estuaries are generally alkaline unless prolonged rains reduce the salinity and lower the pH during the monsoon (Mukhopadhyay et al., 2006; Nandy et al., 2018; Paul et al., 2024). Present results on environmental characteristics are consistent with previous studies that focused on abiotic variability and its impact on plankton community, from both the freshwater- and marine-dominated sections of the IS: the dilution of salinity constitutes a first-order factor for the modulation of zooplankton diversity and distribution (Bhattachraya 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).

Historically, all the investigations focused on zooplankton taxonomy and ecology of the IS considered only the TDA method for estimating diversity and abundances. Those studies suggested that the copepods constitute 70% to 80% of the total abundance of the zooplankton community of the IS (Bhattacharya et al., 2015) with 41 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). Among copepods, *B. similis* is currently the most abundant; however, species such as *P. parvus*, *A. tortaniformis*, *A. spinicauda* and *O. brevicornis* were also highly abundant in different seasons (Bhattacharya et al., 2015; Nandy et al., 2018; Chakrabarty et al., 2022; Paul et al., 2024; Bhattacharjee et al., 2025). In the marine-dominated section of the IS the highest abundance of zooplankton (including copepods) was found in the late winter followed by the rainy season, summer and spring (Nandy and Mandal, 2020). In the freshwater-dominated section of the IS the copepod diversity and abundance peaked during the warm pre-monsoon and the lowest Of both diversity and abundance occurred in the late monsoon (Paul et al., 2024). From the existing plankton literature on the IS, it is obvious that late monsoon is the season when the copepod diversity and abundance plummets (Bhattacharya et al., 2015; Nandy et al., 2018; Nandy and Mandal, 2020; Chakrabarty et al., 2022; Paul et al., 2024; Bhattacharjee et al., 2025). Present results of copepod diversity obtained through the TDA method are thus aligned with earlier studies on the IS.

4.2. Spatial-temporal variability of copepod carcasses

Non-predatory copepod mortality has on many occasions been linked to environmental variability (Tang et al., 2014). The temporal variation of carcass incidence in the Cochin backwaters of India have been linked with the advent and departure of the South-West monsoon (Jyothibabu et al., 2016): at the starting phase of the monsoon over 80 % of estuarine and neritic copepods such as *P. parvus*, *Acrocalanus gracilis* and *Acartia danae* were found dead, possibly due to the sudden salinity change. The monsoon brings the strongest gradients of salinity, pH and temperature in the IS (Bhattachraya et al., 2015; Nandy et al., 2018); therefore, plankton may experience substantial environmental stress leading to higher non-predatory mortality; for example, species such as *P. parvus* and *A. gracilis* suffered substantial mortality during the monsoon season. Salinity changes have been often associated with mortality of copepods, e.g., in the Norwegian fjords (Kaartvedt and Aksnes, 1992), in the Westerschelde estuary of the Netherlands (Soetaert and Herman, 1994), as well as in the estuaries of Brazil, Chile and Uruguay (Martínez et al., 2013; Giesecke et al., 2017; da Silva et al., 2020; da Cruz et al., 2024). Even euryhaline copepods that tolerate broad salinity ranges suffer high mortality when exposed to sudden changes in salinity

(Calliari et al., 2006, 2008). In the IS, carcasses of a few of the most abundant species never reached beyond 11.30% during the pre-monsoon and 23.28% in the post-monsoon, but jumped to 40.19% in the monsoon. Consequences of such high incidence of carcasses in the monsoon impacted species richness and relative abundances of copepods, and deviations between estimates gained from the TDA and the CE methods were at the highest. The non-predatory mortality may also arise from wakes created by numerous boats and ferries that operate in the IS, senescence, injury, diseases, parasitism, harmful algal blooms and so on (Cervetto et al., 1999; Kimmerer and McKinnon, 1990; Kirillin et al., 2012; Tang et al., 2024). While in the IS environmental variability during the monsoon seems to have been a primary source of mortality, future eco-physiological and molecular approaches could address the species-specificity of such mortality and provide better understanding of the mechanisms behind the variable carcass generation in the different seasons and the sampling stations.

4.3. Revisiting the copepod diversity estimates

Results demonstrate that when the CE method is applied, the existing estimates of the copepod diversity, total abundance as well as the relative abundances for the IS may change. Not only that, the dominance hierarchy of the community may also change particularly at times when the incidence of carcasses is the highest, i.e., in the monsoon as *A. spinicauda* and *P. aculeatus* emerged as co-dominants, which otherwise were *A. tortaniformis* and *P. serricaudatus*. Those changes may have consequences for inferences regarding intra- and inter-specific competition for the spatial niche occupancy, as found in both the freshwater- and marine-dominated sections of the IS by Paul et al. (2019) and Chakrabarty et al. (2022). The overestimation of the copepod abundances due to overlooking the vital states of individuals has been previously reported from the Cochin backwaters of India (Jyothibabu et al., 2016), tropical estuaries of Brazil (da Cruz et al., 2024), Chesapeake Bay of U.S.A. (Elliot and Tang, 2011), the Rijpfjorden-Svalbard of Norway (Dasse et al., 2013; Dasse and Søreide, 2021). During the pre-monsoon, incidence of carcasses was up to 15% but there were no deviations between the corrected and non-corrected indices; in the post-monsoon the maximum deviation was 6.25%, for incidence of carcasses between 7% and 24%; and the deviation climbed to 33% during the monsoon when the incidence of the carcasses reached 40% to 55%. Further, among those indices explored here, species richness and Shannon-diversity were most sensitive (in that order) to the vital status of the individuals, compared to Simpson's and Pielou's indices. The reason for that is mathematical, as the latter two are derived forms of the former (Boyle et al., 1990; Izsák, 1996). While any improvement of the diversity estimates of an ecosystem is appreciated, one may ponder the relevance of the additional (or at least supplementary) ecological information yielded by the CE method compared to the TDA, given the higher cost of the former in terms of the extra time and effort involved. That argument may suffice if a habitat does not face a volatile environment due to an absence of substantial gradients in either time or space. However, for most coastal-marine ecosystems subjected to tidal and pronounced seasonal cycles, human interventions in flow regimes, freshwater discharge, pollution loads, the CE method is possibly a wiser alternative over the TDA method. The incidence of carcasses in the coastal-marine environments ranges between 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 of India is included (Jyothibabu et al., 2016). Therefore, quantitative results without the exclusion of carcasses carry a certain percentage of error which may induce biased conclusions on the structure and functions of coastal-marine plankton communities (Hansen and Van Boekel, 1991; Tang et al., 2009; Elliott and Tang, 2011a, b; Frangoulis et al., 2011; Jyothibabu et al., 2016). The CE literature on plankton and the current results suggest that most often there will be scope for improvement of the diversity estimates through the incorporation of vital state information of individual zooplankters, and that current diversity estimates of the zooplankton (including copepods) of coastal-marine ecosystems across the world may need to be revisited.

4.5. Living vs. holistic diversity

Over decades ecologists have provided various explanations of diversity patterns in ecological systems, but no 'one size fits all' accepted definition of diversity has emerged (Hurlbert, 1971; Peet, 1974; Hubbell, 2001). In fact, Hurlbert (1971) recommended not to use the term '*diversity*' because of the many unresolved and confounding concepts attached to it. Diversity indices discussed here are routine and widely used as the key indicators of alpha diversity of aquatic ecosystems worldwide (Washington, 1984; Roswell et al., 2021); therefore, it is desirable that their estimates remain globally consistent, unbiased and comparable (Peet, 1974; Iknayan et al., 2014). That is currently not the case for zooplankton, in contrast to most other marine taxa for which only alive individuals are taken into consideration since the live/ dead discrimination is obvious at the time of collection, or for which dead individuals are simply not targeted by recording protocols, or sampling gear (i.e., fish, mammals, reptiles, birds) (Hammond et al., 2021). In those cases, there seems to be little scope for further refinement of diversity estimates by including vital status corrections. Regarding copepods and more generally the zooplankton and maybe other microscopic organisms whose vital status determination is challenging at the time of sample collection, current findings potentially have far-reaching implications. First, from now on the co-existence of diversity datasets in the literature arising from the corrected and the non–corrected estimates (the latter being all, or most of currently existing datasets) may require to address the former as the '*Living diversity*' of the corresponding community. That is for consistency and to avoid confusion. In the long run, it is foreseen that most of the new plankton datasets will refer strictly to the '*Living diversity*', since that provides a better approximation to the underlying diversity concept, as generally understood, either explicit or implicit (i.e., abundance, variety and variability of life in space and time (Purvis et al., 2000; Hubbell, 2001)). Second, the very concept of diversity in a broader sense may need to be revisited to include not only the actual living diversity as considered *ut supra*, but also those life-forms *sensu latto* found in a non-living or in a non-determinate live status, as indicated by recovered carcasses, body parts, exuviae, genetic material, without positive evidence of live representatives *sensu stricto* at the site and time of observation. That would imply a broader perspective of our conceptual approach to diversity, i.e., one that encompasses both the actual and potential extant '*holistic diversity*', which shall also accommodate datasets and knowledge arising from new perspectives linked to microbial communities and molecular ecological approaches, such as metagenomics and environmental DNA. While such '*holistic diversity*' may be of little practical interest for ecological research strictly concerned with the activity of macroscopic living organisms (e.g., population dynamics), it seems highly relevant to those focused on numerous microscopic organisms, on energy and matter fluxes mediated through biological *sensu stricto*, physical and chemical processes, like carbon cycling, export production and coastal-marine biogeochemistry, generally speaking.

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Declaration of competing interest

All authors declare that they have no competing interest on connection with this study.

Ethical approval

No ethical standards were required to execute the study. No permits for sampling and observational field studies were required from authorities.

Data availability

Data would be provided with a reasonable request for non-commercial purpose.

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CRediT authorship contribution statement

Debarati Sengupta: Methodology; Formal analysis and investigation, Writing - review and editing. Danilo Calliari: Conceptualization, Methodology; Writing - review and editing, Supervision. Sourav Paul: Conceptualization, Funding acquisition, Resources, Writing original draft, Writing - review and editing; Supervision.

Table and figure captions:

Table 1. Relative abundances (%) of the copepod species of Indian Sundarbans measured through both the traditional diversity assessment (TDA) and the carcasses estimation (CE) methods.

Table 2. Seasonal variations of a few abundant copepods of Indian Sundarbans following both the traditional diversity assessment (TDA) and the carcasses estimation (CE) methods.

Table 3. Spatial and temporal variations of total abundances (ind.m-3) and percentages of the alive and dead copepods sampled from Indian Sundarbans

Table 4. Deviations (%) in the diversity indices of the copepod community of Indian Sundarbans estimated through the traditional diversity assessment (TDA) and the carcasses estimation (CE) methods.

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

Fig. 2. Seasonal variations of water temperature (ºC), salinity and pH of Indian Sundarbans.

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

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Table 1

Order	Family	Species	Monsoon		Post-monsoon		Pre-monsoon	
			TDA	CE	TDA	CE	TDA	CE
Calanoida	Paracalanidae	*Paracalanus parvus*	7.74	3.26	11.71	11.45	11.28	11.24
		Paracalanus aculeatus	10.04	12.66	3.50	3.16	5.42	5.43
		Paracalanus indicus	1.56	1.22	2.29	2.67	3.85	3.87
		Acrocalanus gracilis	7.29	2.11	4.54	4.44	2.81	2.84
		Acrocalanus monachus	0.13	0.26	0.00	0.00	0.00	0.00
		Bestiolina similis	16.58	20.40	15.04	16.05	10.24	10.21
		Parvocalanus dubia	0.00	0.00	0.55	0.66	0.93	0.96
		Parvocalanus crassirostris	0.00	0.00	2.51	2.65	2.88	2.86
	Acartiidae	*Acartia spinicauda*	10.22	13.74	4.80	5.05	6.17	6.20
		Acartia tonsa	2.00	2.52	3.21	3.12	4.36	4.41
		Acartia tropica	0.00	0.00	1.97	2.16	2.93	2.92
		Acartiella sewelli	0.17	0.35	0.00	0.00	0.00	0.00
		Acartiella tortaniformis	14.75	12.30	20.43	19.08	10.42	10.43
	Pseudodiaptomidae	*Pseudodiaptomus serricaudatus*	11.65	12.49	5.74	5.79	7.87	7.84
		Pseudodiaptomus binghami	3.01	1.99	0.00	0.00	0.00	0.00
	Eucalanidae	*Subeucalanus subcrassus*	0.77	1.11	3.45	3.49	4.26	4.25
	Pontellidae	*Labidocera euchaeta*	0.00	0.00	2.30	2.07	2.91	2.88
		Pontella andersoni	1.08	0.00	0.00	0.00	0.00	0.00
Cyclopoida	Oithonidae	*Oithona simlis*	4.97	5.58	2.69	2.39	3.77	3.75
		Oithona brevicornis	5.73	6.57	6.99	6.96	7.91	7.97
		Oithona nana	0.00	0.00	4.05	4.40	5.76	5.74
	Oncaeidae	*Oncaea venusta*	1.13	2.32	0.00	0.00	0.00	0.00
	Corycaeidae	*Corycaeus crassiusculus*	1.18	1.11	4.23	4.42	6.23	6.20

Table 2

Traditional diversity assessment (TDA) method								
Monsoon			**Post-monsoon**			**Pre-monsoon**		
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
Pseudodiaptomus serricaudatus	100	0.00	*Paracalanus parvus*	100	0.00	*B. similis*	100	0.00
Carcasses estimation (CE) method								
B. similis	59.81	40.19	*A. tortaniformis*	76.72	23.28	*P. parvus*	88.70	11.30
Acartia spinicauda	65.31	34.69	*B. similis*	87.70	12.30	*A. tortaniformis*	89.05	10.95
Paracalanus aculeatus	61.29	38.71	*P. parvus*	80.34	19.66	*B. similis*	88.76	11.24

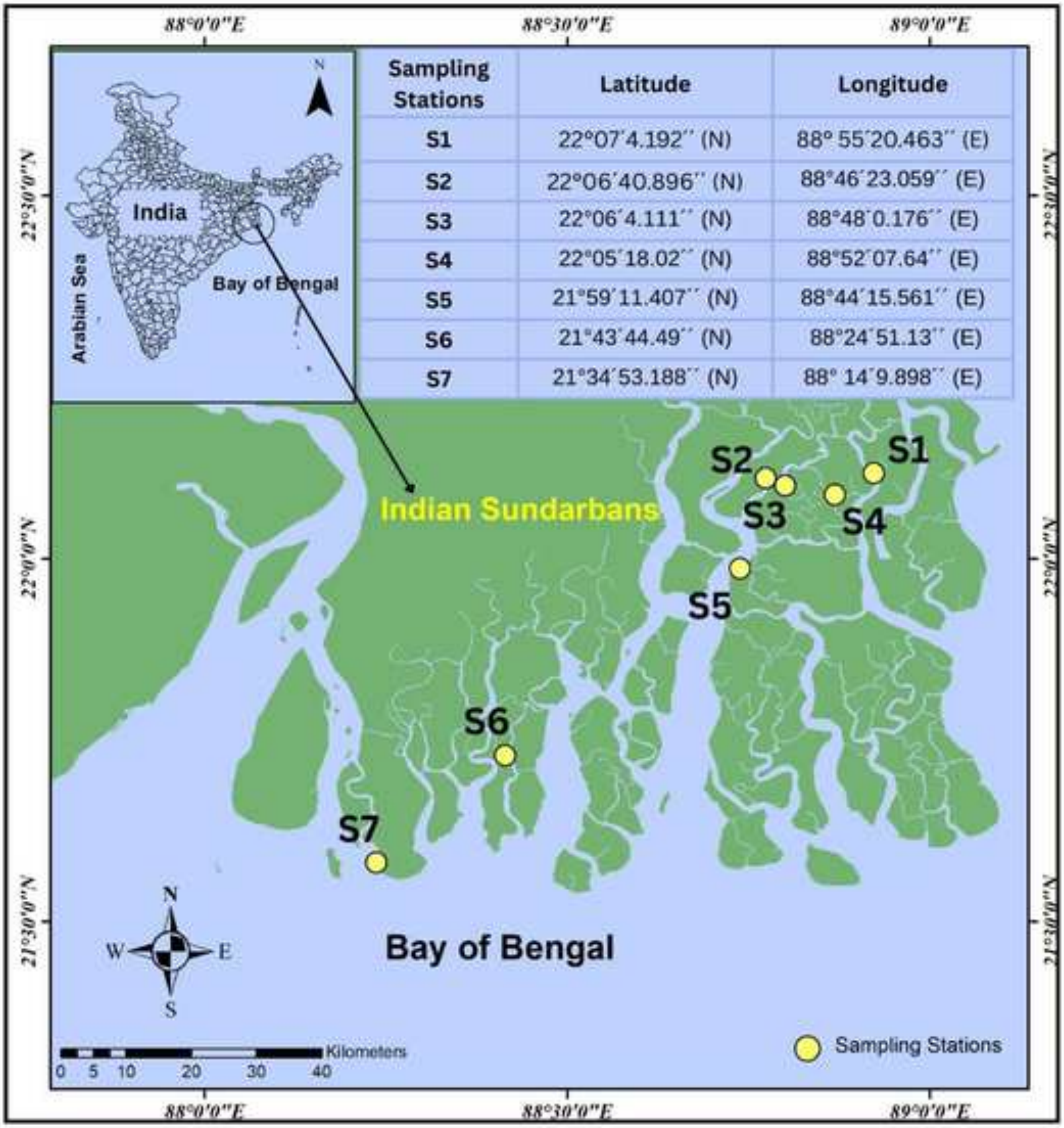
Table 3

Sampling stations	Season	Total abundance (Ind.m^{-3})	Alive (Ind.m^{-3})	Dead (Ind.m^{-3})	Alive (%)	Dead (%)
S1	**Monsoon**	17743	9770	7973	55	45
S2		7612	4174	3438	55	45
S3		832	459	373	55	45
S4		5502	2751	2751	50	50
S5		18652	8432	10220	45	55
S6		46701	20755	25946	44	56
S7		7301	4381	2920	60	40
S1	**Post-monsoon**	35281	29782	5499	84	16
S2		37953	31650	6303	83	17
S3		22840	20195	2645	88	12
S4		39317	30000	9317	76	24
S5		35154	32577	2577	93	7
S6		22693	20220	2473	89	11
S7		91999	69982	22017	76	24
S1	**Pre-monsoon**	39427	34288	5139	87	13
S2		38537	33810	4727	88	12
S3		24798	24467	331	99	1
S4		36270	31005	5265	85	15
S5		39368	34539	4829	88	12
S6		Sampling not conducted	Sampling not conducted	Sampling not conducted	Sampling not conducted	Sampling not conducted
S7		50532	45531	5001	90	10

Table 4

Monsoon												
Sampling stations	**Species Richness**			**Shannon Index**			**Simpson's Index**			**Pielou's Index**		
	TDA	**CE**	**Dev (%)**	**TDA**	**CE**	**Dev (%)**	**TDA**	**CE**	**Dev (%)**	**TDA**	**CE**	**Dev (%)**
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	9	6	33.33	2.08	1.69	18.75	0.86	0.80	6.97	0.95	0.94	1.05
S7	7	5	28.57	1.58	1.49	5.69	0.75	0.74	1.33	0.81	0.92	11.95
Post-Monsoon												
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	18	18	0.00	2.59	2.58	0.30	0.91	0.91	0.00	0.89	0.89	0.00
S7	7	7	0.00	1.57	1.59	1.20	0.75	0.75	0.00	0.81	0.82	1.20
Pre-Monsoon												
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*	---	---	---	---	---	---	---	---	---	---	---	---
S7	17	17	0.00	2.73	2.73	0.00	0.92	0.92	0.00	0.96	0.96	0.00

*****Sampling not conducted



Sampling Stations	Latitude	Longitude
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)
S6	21°43′44.49′′ (N)	88°24′51.13′′ (E)
S7	21°34′53.188′′ (N)	88° 14′9.898′′ (E)

Fig.2

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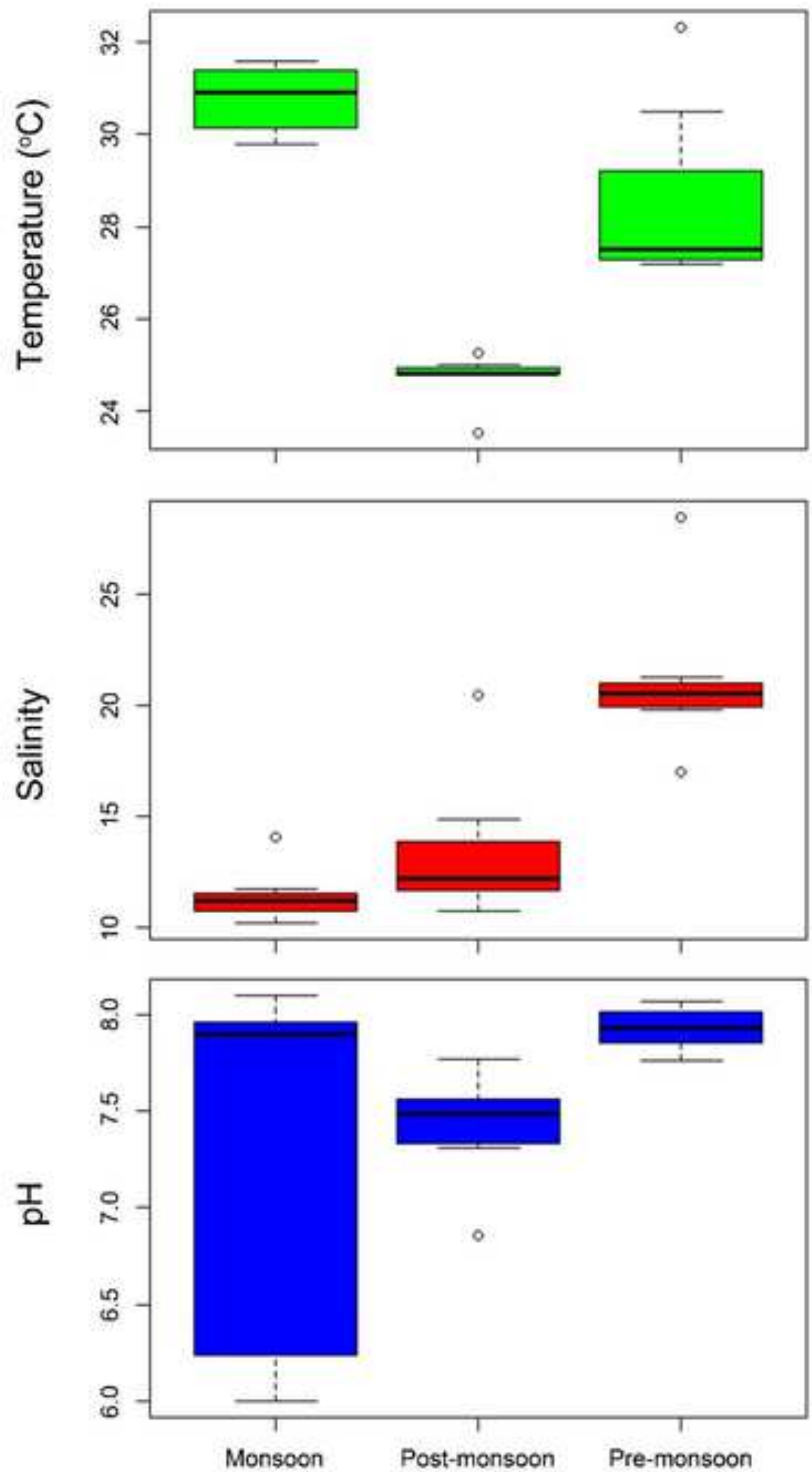

Fig.3

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