Environmental Science and Pollution Research (2021) 28:42477–42495
https://doi.org/10.1007/s11356-021-13634-x

RESEARCH ARTICLE

Hydrodynamic variability and nutrient status structuring the mesozooplankton community of the estuaries along the west coast of India

Kusum Komal Karati[1] · Chettiparambil Raghavan Ashadevi[1] · Naroju Veera Harikrishnachari[1] · Sudheesh Valliyodan[1] · Munnooru Kumaraswami[2] · Sura Appala Naidu[2] · Mallavarapu Venkata Ramanamurthy[2]

Received: 30 November 2020 / Accepted: 22 March 2021 / Published online: 4 April 2021
© The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2021

Abstract

The influence of distinct tidal characteristics and nutrient status on mesozooplankton community was studied in six major estuaries along the west coast of India during the late-monsoon (MS) and post-monsoon (PM) periods. The macro-tidal estuaries in the north (Amba and Thane) exhibited higher nutrient concentration compared to the micro- and meso-tidal estuaries located in the south (Cochin and Nethravati) and central (Zuari and Mandovi) west coast of India. The markedly higher nitrate and phosphate levels in the macro-tidal estuaries during PM indicated anthropogenic contributions from domestic and industrial effluents, which significantly impacted the mesozooplankton community structure. Nutrient enrichments favored higher phytoplankton standing stock leading to low DO levels. In the micro- and meso-tidal estuaries, meso- and euryhaline copepods dominated whereas in the macro-tidal estuaries, the copepod community was dominated by euryhaline and coastal species. Furthermore, the high-saline eutrophic environment of macro-tidal estuaries formed congenial for the increased jellyfish preponderance during PM. The predation pressure exerted by the jellyfish population on the crustacean zooplankton and ichthyoplankton exerted an adverse impact on the potential fishery stock in the macro-tidal estuaries. Thus, the study reveals that the nutrient enrichment favoring a shift in the mesozooplankton community structure from nutritionally superior crustacean plankton to less desirable jellyfishes, which in turn, may lead to a threat on the estuarine pelagic energy transfer and ecosystem deliverables.

Keywords Estuary · Jellyfish · Eutrophication · Ichthyoplankton · Ecological impact

Introduction

Estuaries, the ecotone between the marine and freshwater ecosystems, are dynamic environments, where habitat modifications occur in association with the changing tides and fluctuations in the freshwater flow regimes (Wolanski and Elliott 2015). Although estuaries form one of the most productive ecosystems globally (McLusky and Elliott 2004), the increased human settlements and industrialization along its banks and the associated sewage and industrial outfalls turn them into a fragile ecosystem heavily impacted by the nutrient and pollutant enrichments (Lotze et al. 2006). The increased nutrient loads and the resultant variation in the estuarine water chemistry often disrupt its ecological balance through the promotion of undesirable algal blooms leading to low dissolved oxygen levels and hypoxia (Howarth et al. 2011). Furthermore, the nutrient enhancement can also cause a shift in its biotic composition from economically significant species to less desirable organisms reducing the ecosystem deliverables of these productive coastal habitats (Li et al. 2010).

Indian coastline is bordered by many ecologically diverse estuaries, though sharing the typical tropical nature, but is distinct in its tidal features, freshwater flow regimes and geomorphological characteristics (Qasim 2003). These productive coastal zones supporting a diverse community of economically harvestable fishery resources form a major source of livelihood for a vast number of coastal population (Jhingran

Responsible Editor: V. V.S.S. Sarma

✉ Kusum Komal Karati
kusum.kk1@gmail.com; karatikusum@cmlre.gov.in

[1] Centre for Marine Living Resources & Ecology, Kochi 682508, India

[2] National Centre for Coastal Research, Chennai 600100, India

and Gopalakrishnan 1973). Thus, considering their socio-economic importance and the vulnerability to the increased anthropogenic pressures, the regular monitoring of the health of these ecologically important estuarine systems gains highlight.

Zooplankton, the intermediary conduit between the primary producers and economically harvestable higher trophic levels, have a vital role in the trophic dynamics and productivity of the estuaries (David et al. 2016). However, the eutrophication associated with anthropogenic interferences in the estuarine system has been found to influence the zooplankton community structure thus altering the trophic gradients (Park and Marshall 2000). In the pretext of the increasing anthropogenic pressures on the Indian estuaries, we hypothesized that the variability in the nutrient distribution along different estuaries of the west coast of India will have a significant influence on their zooplankton distribution and community structure. Among the zooplankton community, the crustacean taxon characterized by superior proximate composition and nutritional quality is often taken as the good index of the secondary productivity and habitat quality compared to the gelatinous groups having more than 90% water as their body content (Spitz et al. 2010). Jellyfish are important constituents of the zooplankton community in both estuarine and marine ecosystems and here, the word "jellyfish" has been specifically used to represent gelatinous zooplankton comprising medusoid forms of the phylum Cnidaria (hydromedusae, scyphomedusae, and siphonophora) and members of the phylum Ctenophora (Richardson et al. 2009; Brotz et al. 2012). Being voracious carnivores, their massive outbreaks can elicit huge impacts on the tourism, fishery, and ecological health of estuaries (Purcell et al. 2007; Richardson et al. 2009). Although the jellyfish community of the Indian estuaries has received research attention, it was mostly carried out during the 1970s–1990s (Vannucci et al. 1970; Santhakumari 1992; Santhakumari et al. 1997) and provided knowledge mostly on their seasonal distribution patterns and community composition. However, the reports on the increasing frequency of occurrence and rising abundance of jellyfish in Indian estuaries and their possible impacts on the ecosystem health make it a major concern (www.thehindu.com/news/cities/Thiruvananthapuram/jellyfish-blooms-pose-threat-to-state/article7836016.ece).

Considering the socio-economic importance of the estuarine systems along the Indian coast, the study was aimed at understanding the influence of the variable hydrodynamics and nutrient status on the mesozooplankton community of the estuaries along the west coast of India. Among the zooplankton community, as the rising jellyfish population and their expected threat to the estuarine ecosystem functioning and economic yields has become a serious concern, additional focus was given to understand the factors favoring the preponderances of this gelatinous taxa in estuaries bordering the west coast of India and their possible impacts on the plankton community dynamics. The output of the study will be beneficial in validating the ecosystem health of these ecologically vital coastal zones and also for formulating management measures for improving the habitat quality in relation to its productivity and fishery potential.

Material and methods

Study area

Sampling was carried out in six major estuaries positioned south to north of the west coast of India (Fig. 1). The southernmost Cochin estuary is a micro-tidal estuary (~1m) located along the Kerala coast (Qasim 2003). It covers an area of 231 km^2 with a depth range of 2–7 m (Menon et al. 2000) and receives an annual freshwater influx of 22,000 × 10^6 m^3 (Revichandran et al. 2012). The next estuary, Netravati, located along the Karnataka coast is also a micro-tidal estuary experiencing mixed semi-diurnal tide (<2 m, John and Cheryan 1975) and an annual freshwater influx of 12,015 × 10^6 m^3 (Shankar and Manjunatha 1997). The depth of the estuary varies from 2 to 4 m near the inlet to about 0.5 m in the upstream region (Fernandes et al. 2019). The third and fourth estuaries, the Zuari and Mandovi, both located in the coastal belts of Goa, are positioned along the central part of the west coast of India (Fig. 1). The average depth of both Mandovi and Zuari is about 5 m (Shetye et al. 1995). Both these estuaries are characterized by mixed tides with semi-diurnal dominance and are meso-tidal in nature (Manoj and Unnikrishnan 2009). The fifth and the sixth estuaries, Thane and Amba, located along the northern part of the west coast of India lie in the state of Maharashtra (Fig. 1). The depth of the Thane estuary is 12 m in the inlet region with a gradual reduction in depth towards the upstream (Thomas et al. 2019). The Amba estuary is relatively shallower than Thane with a depth of 6 m in the barmouth (Velamala et al. 2016). The Amba estuary experiences a spring tidal range of >5 m (Dineshkumar et al. 1997), and in case of Thane, it is >4 m (Figs. 2, 3, 4, 5, and 6, Thomas et al. 2019), and thus can be categorized as macro-tidal estuaries.

Sampling strategy

In all estuaries, sampling was carried out at 4 locations along the salinity gradient from the inlets towards the upstream locations (Fig. 1). As monsoon plays a prominent role in governing the abiotic and biotic characteristics of Indian estuaries (Madhu et al. 2007; Pednekar et al. 2011), the study was carried out during the late summer monsoon (MS, September 2018) and post-monsoon (PM, December 2018) periods.

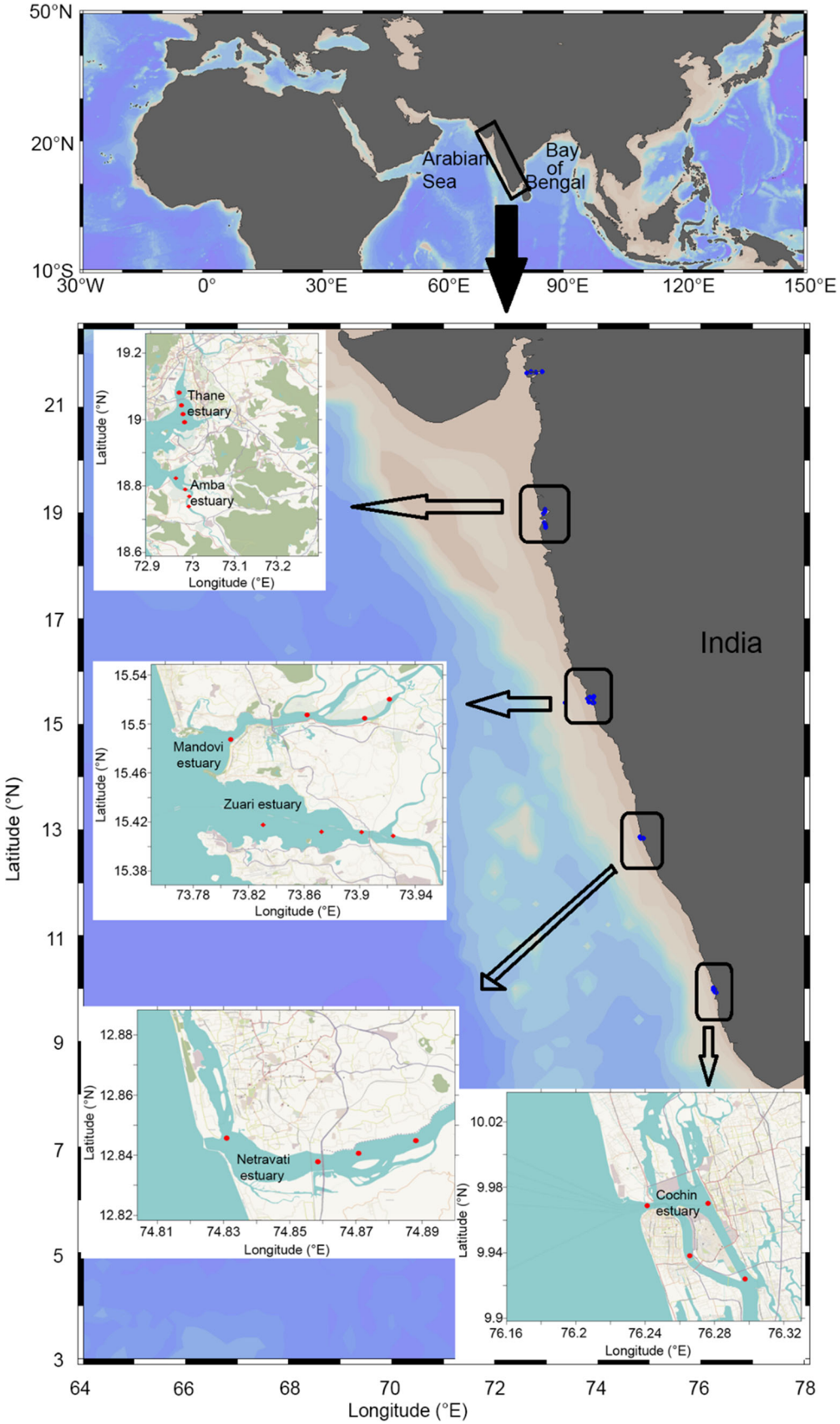

Fig. 1 Sampling locations in six major estuaries positioned south to north of the west coast of India (sampling locations in estuary are marked by red dots)

Hydrography

For estimating the surface water (0.5 m) temperature and salinity, a SBE Seabird 911 plus CTD was deployed at each station location. A quadrated, Secchi disk was used to measure the water transparency. The Secchi disc was vertically lowered into the water column with a calibrated rope and the depth at which the disk was no longer visible was considered as the Secchi depth.

Dissolved oxygen (DO), pH, and nutrients

A Hydrobios Niskin water sampler (5L) was used at every sampling location for collecting the surface water (0.5 m) samples for the dissolved oxygen (DO), pH, and nutrient analysis. Subsamples for dissolved oxygen were taken in 60 mL glass bottles and was fixed by adding 0.5 mL each of Winkler reagents, and titrated against 0.001N Hypo using a Dosimat (Metrohm, Switzerland) following standard procedures (Grasshoff et al. 1983). Samples for pH (125 mL each) were collected carefully without introducing air bubbles, poisoned with saturated mercuric chloride (0.3 mL/60 mL) to arrest microbial activity, and were analyzed using a potentiometric titrator (907 Titrando; Metrohm, Switzerland). The pH was calibrated on the NBS scale as described by Frankignoulle and Borges (2001) using NIST-certified buffers (Merck) at 25°C. The pH values on NBS scale were first converted to the pH in situ and then to the total scale. Analytical precision of pH was ± 0.005. Nutrients (nitrite, phosphate, and silicate) were estimated following the standard colourimetric techniques (Grasshoff et al. 1983) using a segmented flow autoanalyzer (SKALAR SAN++). Nitrate was also analyzed using an autoanalyzer but following the method of Garcia-Robledo et al. (2014). The analytical precision, expressed as standard deviation based on replicate analyses, was ± 0.005, 0.027, 0.009, and 0.037 μM for NO_2^-, NO_3^-, PO_4^{3-}, and

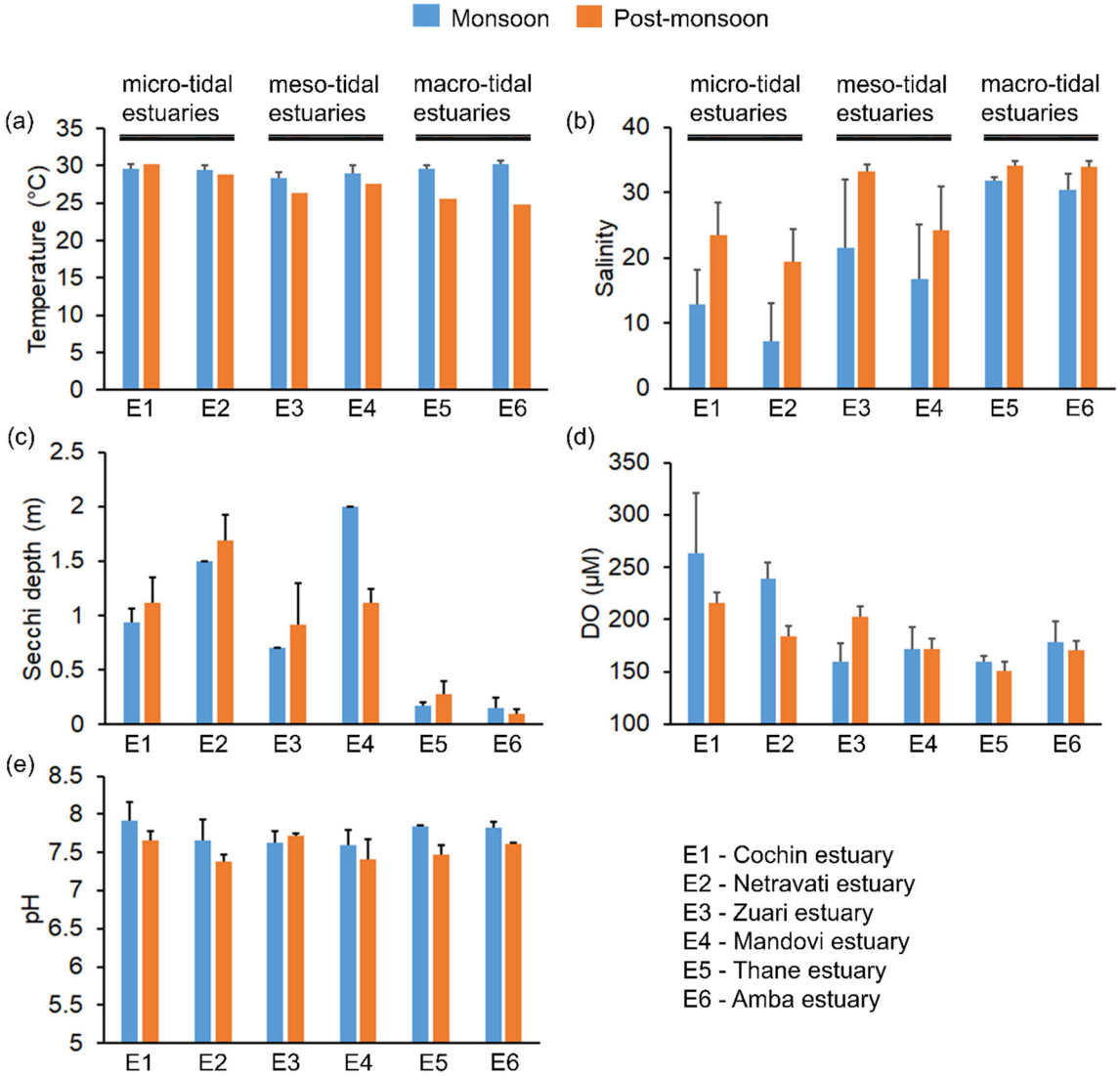

Fig. 2 Distribution of physico-chemical variables along the major estuaries in the west coast of India

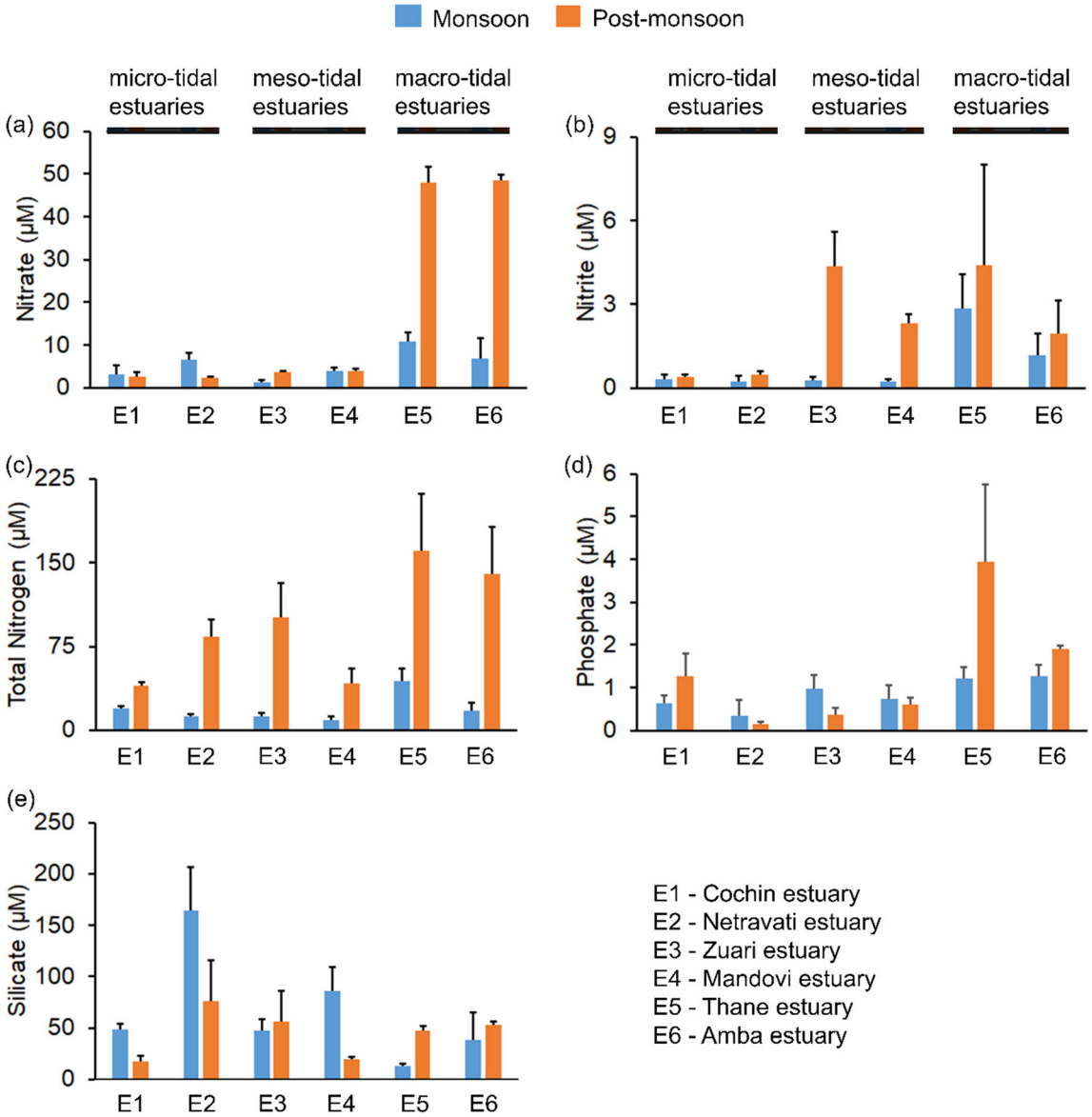

Fig. 3 Distribution of nutrients along the major estuaries in the west coast of India

SiO_4^{2-}, respectively. The total nitrogen (TN) was measured following the high-temperature combustion technique (at 720°C) following a chemiluminescence method using TN analyzer (Shimadzu, Japan). The accuracy of TN was checked using the Certified Reference Material supplied by Hansell Laboratory, University of Miami, USA (batch 6) and the internal standard prepared using potassium nitrate and found within ± 1%.

Biotic community

For estimating the phytoplankton biomass (chlorophyll *a*), 1 L surface water samples (0.5 m) were collected using a Niskin sampler and the chlorophyll *a* was estimated in different size classes following the standard procedures (for details see Madhu et al. 2010; Karati et al. 2017). The pigments were extracted with 90% acetone at 4 °C for 24 h in the dark and were subsequently estimated using a fluorometer (Turner Designs, 7200) (Strickland and Parsons 1972). The total chlorophyll *a* was estimated as the sum of the all the size-fractionated phytoplankton biomass. For collecting zooplankton, a Working Party net-2 of mouth area 0.28 m^2 and mesh size of 200 μm was used. In every sampling location, the net was hauled horizontally just below the surface for 10 min at a constant speed of ~ 1 knot and a digital flowmeter (Hydro-Bios, Model 438110) was used to estimate the amount of water filtered. The biomass of the zooplankton samples was estimated by the displacement volume method and was expressed as mL m^{-3} (Harris et al. 2000). After the biomass estimation, the samples were preserved in 4% formaldehyde solution for the detailed taxonomic analysis. The

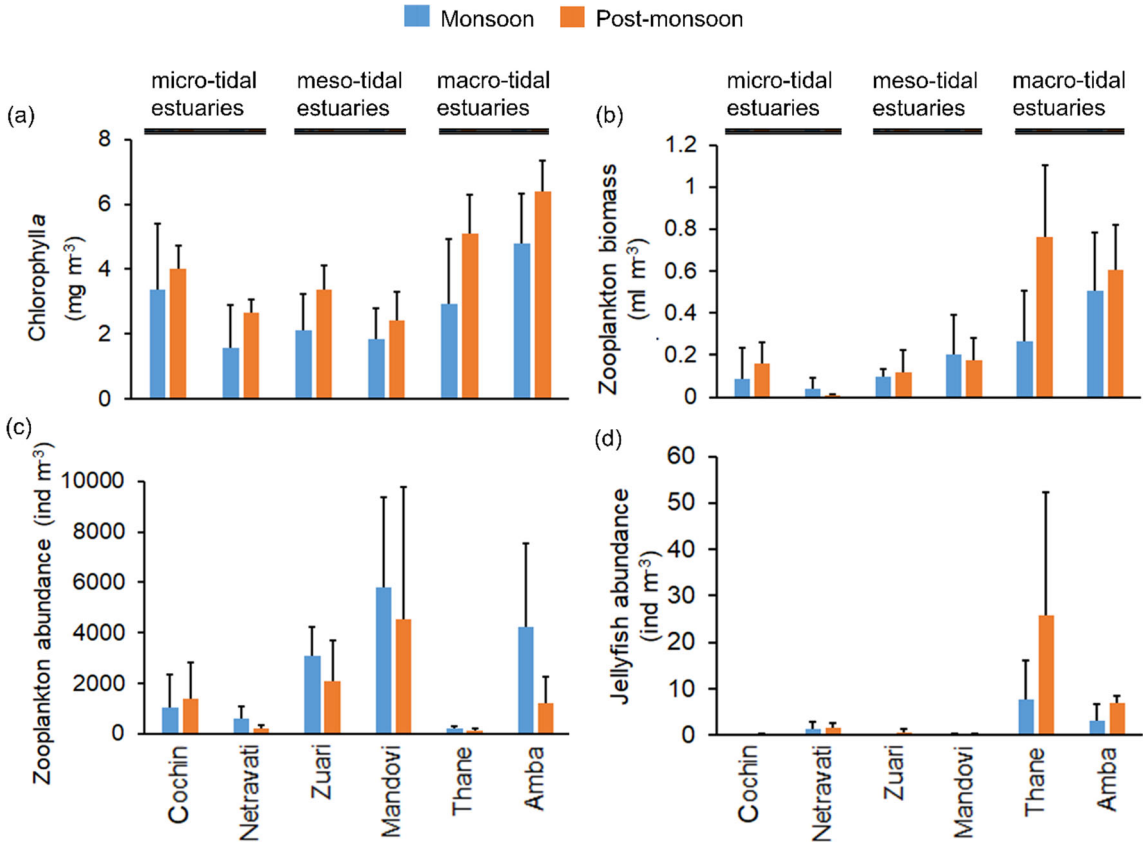

Fig. 4 Distribution of biotic variables along the major estuaries in the west coast of India

zooplankton was identified into different taxa, and their abundances were expressed as ind m^{-3}. After estimating the abundance of all individual taxa, the aggregated abundance of hydromedusae, scyphomedusae, siphonophore, and ctenophore was further expressed as the jellyfish abundance (Richardson et al. 2009). Similarly, the total abundance of both the fish eggs and fish larvae was taken as the ichthyoplankton abundance. The species-level identification of Copepoda, the dominant zooplankton taxon, was carried out following the standard identification protocols (Wellershaus 1969; Conway et al. 2003).

Statistical analysis

The hierarchical clustering was carried out based on the Bray-Curtis similarity matrix of the fourth-root transformed abundance data of zooplankton taxa along the sampling locations. The cluster was plotted based on the group average mode using PRIMER 7 (Clarke and Gorley 2015) to identify the similarity in the zooplankton distribution among the estuaries.

The constrained redundancy analysis (RDA) was used in multivariate space; it best explains the linear relationships between response and explanatory variables (Van den Wollenberg 1977). The RDA analysis was used to understand the interrelation between the abiotic and biotic community and thus helped in understanding the preferred environment of the Jellyfish community.

The constrained canonical analysis of principal coordinates (CAP) (Anderson and Willis 2003) was performed twice. First, it was used to understand the distinctness of the macro-tidal estuaries from the others during PM based on the nutrient distribution. The analysis was also carried out to understand the discrete nature of Amba and Thane estuaries between two seasons based on their nutrient distribution. This analysis was done based on the Bray-Curtis similarity index (Clifford and Stephensen 1975) and was applied to the fourth root-transformed data of the nutrient concentration using PRIMER (Clarke and Gorley 2015).

The Bio-Env analysis was carried out using PRIMER to identify the abiotic variables that best explain the preponderances of the jellyfish community. This analysis was based on the unconstrained choice of resemblance matrix appropriate to the data type and uses only the rank values of the among-sample resemblances (Clarke et al. 2008).

Results

Physical variables

The surface temperature did not show prominent inter-estuarine variation during both seasons. Temporally, the post-monsoonal temperature was slightly lower than the

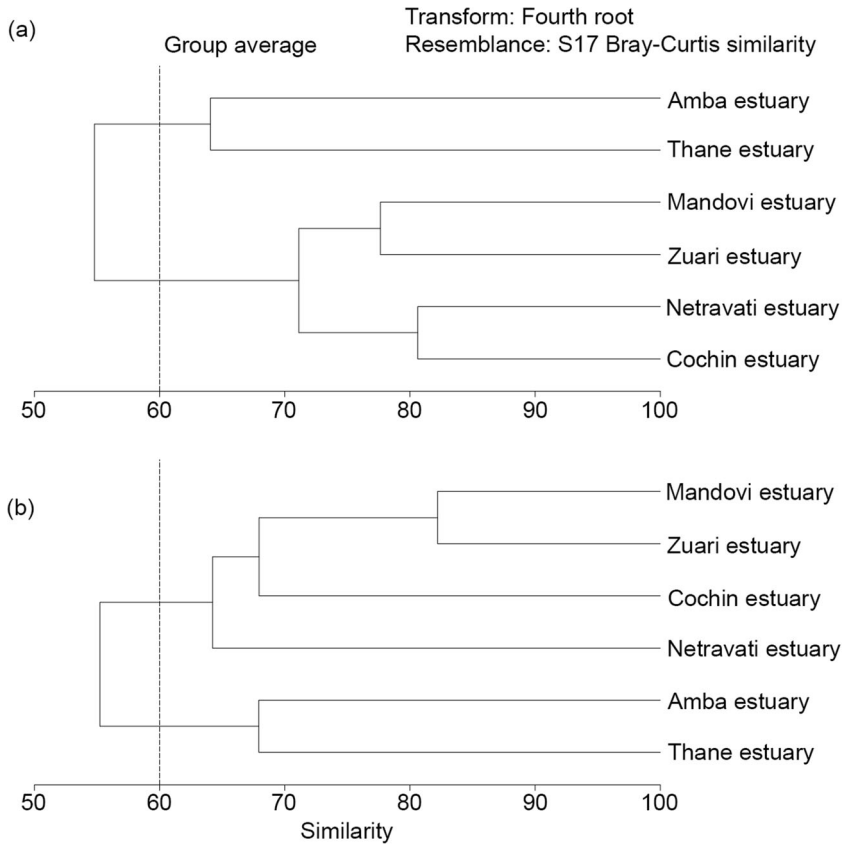

Fig. 5 Dendrogram of the Bray-Curtis similarity index based on hierarchical clustering of fourth-root transformed zooplankton abundance in the estuaries along the west coast of India during (a) monsoon and (b) post-monsoon period

monsoonal temperature in most of the estuaries (Fig. 2a). In general, the surface salinity exhibited a prominent spatial gradient with a gradual decrease from the inlets to the upstream locations. Among the estuaries, the salinity was relatively lower in the four micro- and meso-tidal estuaries in the south and central zone (12.9 ± 5.3, 7.3 ± 5.9, 21.6 ± 10.3, and 16.7 ± 8.4, Cochin, Netravati, Zuari, and Mandovi, respectively, ave. ± 1 S.D. values here and henceforth) compared to the macro-tidal estuaries in the north (31.8 ± 0.6 and 30.4 ± 2.4, Thane and Amba, respectively) during the MS (Fig. 2b). With post-monsoon, a gradual increase in salinity was noticed in all the estuaries, and similar to the MS, the average salinity was relatively high in the two estuaries along the north (34.1 ± 0.7 and 34 ± 0.8, Thane and Amba, respectively) compared to the others (23.5 ± 5, 19.3 ± 5.1, 33.2 ± 1, and 24.3 ± 6.7, Cochin, Netravati, Zuari, and Mandovi, respectively, Fig. 2b). During MS, the average Secchi depth in the four micro- and meso-tidal estuaries varied between 0.7 ± 0.1 m (Zuari) and 1.5 m (Netravati) whereas, in the macro-tidal estuaries, it was comparatively less (0.18 ± 0.03 and 0.15 ± 0.1 m, Thane and Amba, respectively, Fig. 2c). With PM, although the Secchi depth showed a gradual increase in most of the estuaries, the trend in the Secchi depth distribution of the estuaries was similar to the MS characterized by relatively less depths in the macro-tidal estuaries of the north (Fig. 2c).

Chemical variables

The DO distribution exhibited both spatial and temporal variations along the estuaries (Fig. 2d). During MS, the Cochin and Netravati estuaries had relatively high surface DO (Fig.

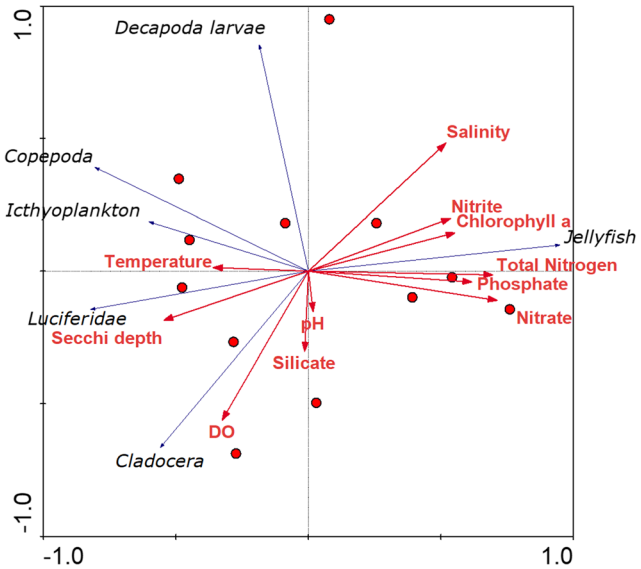

Fig. 6 The RDA triplot of interrelationships of the abiotic and biotic variables

2d). The DO levels dropped in most of the estuaries during PM compared to the MS. Although the inter-estuarine pH values did not differ much, along a temporal scale, it was relatively low during the PM in all the estuaries except Zuari (Fig. 2e).

The dissolved inorganic nutrient distribution exhibited both spatial and temporal variations (Fig. 3). The nutrient concentration was relatively high during PM than the MS in all the estuaries. Except for silicate, all other nutrient concentrations in these estuaries were markedly lower compared to Thane and Amba estuaries (Fig. 3). In the macro-tidal Thane and Amba, marked temporal variation was evident in the nutrient concentration with significantly higher values during PM (Fig. 3). In the Thane estuary, with the seasonal progression from MS to PM, the nitrate (MS: 10.9 ± 1.9, PM: 47.9 ± 3.9 μM,), nitrite (MS: 2.9 ± 1.2, PM: 4.4 ± 1.2 μM), total nitrogen (MS: 44.3 ± 11.1, PM: 160.7 ± 51.5 μM), phosphate (MS: 1.2 ± 0.3, PM: 3.9 ± 1.8 μM), and silicate (MS: 12.7 ± 2.2, PM: 47.9 ± 3.9 μM) concentration experienced 4.4, 1.5, 3.6, 3.3, and 3.8 times increase in the surface water (Fig. 3). In the Amba estuary, also the concentration of major nutrients exhibited a significant increase from MS to PM (nitrate 6.8 ± 4.8 and 48.5 ± 1.3 μM, nitrite 1.1 ± 0.8 and 1.9 ± 1.2 μM, total nitrogen 17 ± 7.8 and 140 ± 42.2 μM, phosphate 1.3 ± 0.2 and 1.9 ± 0.1 μM, and silicate 39 ± 26 and 53 ± 4 μM, during MS and PM, respectively, Fig. 3).

Phytoplankton biomass

Phytoplankton biomass, represented as chlorophyll *a*, exhibited pronounced spatio-temporal variations in the study region. Among the micro- and meso-tidal estuaries, chlorophyll *a* varied between 1.6 ± 1.3 mg m^{-3} (Netravati) and 3.4 ± 2 mg m^{-3} (Cochin) during MS (Fig. 4a). During this period, the chlorophyll *a* in the macro-tidal estuaries, Thane and Amba, was 2.9 ± 2 and 4.8 ± 1.5 mg m^{-3}, respectively. With PM, the chlorophyll *a* increased in all the estuaries but it was relatively higher in Thane (5.1 ± 1.2 mg m^{-3}) and Amba (6.4 ± 0.9 mg m^{-3}) compared to other estuaries (Cochin 4 ± 0.7, Netravati 2.7 ± 1.3, Zuari 3.4 ± 0.7, and Mandovi 2.4 ± 0.9 mg m^{-3}).

Zooplankton biomass and abundance

Prominent spatio-temporal variation was evident in the zooplankton biomass and abundance distribution of the estuaries (Fig. 4 b–c). During MS, the biomass varied between 0.043 ± 0.051 and 0.202 ± 0.191 mL m^{-3} among the micro- and meso-tidal estuaries whereas in the macro-tidal estuaries, Thane (0.268 ± 0.241 mL m^{-3}) and Amba (0.507 ± 0.277 mL m^{-3}), it was relatively high (Fig. 4b). During PM, the biomass did not show much temporal variation in Zuari and Mondovi but slightly increased in Cochin while a drop was noticed in the Netravati (Fig. 4b). The biomass increased markedly in both Thane (0.762 ± 0.0.34 mL m^{-3}) and Amba (0.61 ± 0.21 mL m^{-3}, Fig. 4b). Although zooplankton biomass during MS was the highest in Thane, the abundance was highest in Mandovi (Fig. 4c). During PM, except Cochin, the zooplankton abundance was lower than MS in all the estuaries and this decrease in abundance was most prominent in Thane and Amba (Fig. 4c).

Zooplankton community structure

A total of 23 zooplankton taxa were observed during the study and among the estuaries, the number of zooplankton taxa varied between 9 (Cochin) and 15 (Thane) during MS whereas it was between 11 (Thane) and 15 (Netravati and Zuari) during PM (Tables 1 and 2). An evident change in the community composition, abundance, and relative contribution of different taxa to the total zooplankton population was observed among the estuaries and between the seasons (Tables 1 and 2). Irrespective of seasonal and hydrographic variability, Copepoda formed the dominant zooplankton taxon in all the estuaries. However, spatio-temporal variations were evident in their abundance and percentage contribution to the total zooplankton population along the estuaries. During PM, the Copepoda abundance got lower than MS in all the estuaries (except Cochin) and this decrease was most prominent in the Netravati, Thane, and Amba (Tables 1 and 2). Cladocera were observed only in the four micro- and meso-tidal estuaries during both the periods and had an important contribution to the zooplankton population especially in Cochin and Netravati during MS (Tables 1 and 2). Jellyfish population during the study was contributed by cnidarian hydromedusae, scyphomedusae, siphonophore, and pelagic ctenophore. During MS, the jellyfish population was observed mostly in Amba and Thane estuaries (Tables 1 and 2). During PM, although the jellyfishes were observed in all the four micro- and meso-tidal estuaries with minor abundances, a markedly higher abundance of these groups was observed in Amba and Thane (Fig. 4d). During PM, large-sized (bell diameter > 20 cm) cnidarian medusa was found along with mesozooplankton samples (one individual in two sampling locations) in Netravati estuary. Although their abundance was incorporated, their displacement volume was not considered for the biomass estimation due to their marked higher biovolume compared to the remaining zooplankton. During both the sampling periods, the carnivorous zooplankton taxa, Chaetognatha, was observed in all the estuaries but had relatively higher abundance in the Amba and Thane estuaries. The meroplanktonic decapoda larvae were observed in all the estuaries, during both seasons (Tables 1 and 2). Compared to MS, the decapoda larvae abundance increased in most of the micro- and meso-tidal estuaries during PM. However, in macro-tidal Amba and Thane, the trend was opposite with a marked decrease in abundance during PM (Table 2). The

Table 1 Abundance of zooplankton taxa (ind m^{-3}) in Cochin, Netravati, and Zuari estuaries along the west coast of India during the monsoon (MS) and post-monsoon (PM) periods. (Along with the individual taxon, the abundance of total crustacea, jellyfish, and ichthyoplankton have been included to understand the seasonal variation in abundance of these groups

	Cochin	Cochin	Netravati	Netravati	Zuari	Zuari
	MS	PM	MS	PM	MS	PM
Copepoda	745.0	1297.6	491.7	167.1	2914.7	2055.7
Ostracoda	0.7	0	0.051	0.13	0.07	0.07
Amphipoda	0.03	0.19	0.003	0	0	0.06
Decapoda larvae	2.96	4.4	4.95	48.84	38.19	16.7
Mysida	0	3.8	0	0.12	0	0.05
Luciferidae	13.4	7.4	1.8	0.18	20.88	7.74
Cladocera	293.1	23.04	97.4	1.09	99.18	0.3
Isopoda	0	0.02	0	0.022	0	0
Phylllosoma larvae	0	0	0	0	0	0
Stomatopoda	0	0.01	0	0	0	0
Total crustacea	*1055.1*	*1336.4*	*595.9*	*217.5*	*3073.1*	*2080.6*
Ctenophora	0	0.14	0	0	0	0.3
Siphonophora	0	0	1.3	1.13	0	0
Medusae	0	0	0	0.56	0	0.29
Jellyfish	*0*	*0.143*	*1.3*	*1.69*	*0*	*0.59*
Chaetognatha	1.36	0.06	0.11	0.15	0.48	0.91
Polychaeta larvae	0	0	0	0.18	0.04	0.31
Gastropoda larvae	0	45.1	0	0.37	0	0
Bivalve larvae	0	0.08	0	2.1	0.07	0.1
Pteropoda	0	0	0	0	0	0
Salpa	0	0	0	0	0	0
Doliolida	0	0	0.03	0	0	0
Copelata	0	0	0	0	0	0.17
Fish eggs	0.52	2.5	0.45	0.88	1.43	0.42
Fish larvae	0.15	0.12	0.06	0.28	0.17	0.24
Icthyoplankton	*0.67*	*2.61*	*0.51*	*1.16*	*1.60*	*0.65*
Unidentified nauplii	0	0	0.93	0	4.36	0

economically significant ichthyoplankton (fish egg and larvae) had relatively high abundance in the micro- and meso-tidal estuaries during both the sampling periods whereas in the macro-tidal estuaries, Thane and Amba, their abundance further decreased in PM from the MS with the subsequent increase in the jellyfish abundances (Tables 1 and2).

Copepoda community

Of the total 38 Copepoda species observed during the study, 24 species were common to both seasons and the number of species observed during each season was 30 (MS) and 31 (PM) (Tables 3 and 4). Euryhaline, *Bestiolina similis*, and mesohaline *Acartia (Acanthacaria) plumosa* formed the abundant species in most of the estuaries during both the sampling periods (Tables 3 and 4). However, *Acartia (Acartia) danae* formed the dominant species in the Amba and Thane estuaries. The mesohaline acartiid, *Acartia (Acanthacartia) plumosa*, were absent in these two estuaries. During PM, coastal copepods *Paracalanus parvus parvus*, *Labidocera minuta*, *Labidocera* spp., and *Tortanus (Tortanus) forcipatus* were observed exclusively in these two macro-tidal estuaries.

Data analyses

The dendrogram of the hierarchical clustering based on the abundance of zooplankton taxa in the estuaries exhibited similarities among the estuaries during both periods. Despite the inter-seasonal variation in the zooplankton abundance, two clusters were formed based on 60% similarity during both the seasons (Fig. 5). The micro- and meso-tidal estuaries (Cochin, Netravati, Mandovi, and Zuari) were found in one cluster whereas the macro-tidal Amba and Thane formed the other (Fig. 5).

The RDA triplot displayed the interrelation between the abiotic and biotic variables and helped in understanding the preferred environment of the jellyfish community. The jellyfish abundance was positively correlated with all the nutrients, phytoplankton biomass (chlorophyll *a*), and salinity, whereas it was negatively correlated with abiotic variable temperature,

Table 2 Abundance of zooplankton taxa (ind m^{-3}) in Mandovi, Thane, and Amba estuaries along the west coast of India during the monsoon (MS) and post-monsoon (PM) periods. (Along with the individual taxon, the abundance of total crustacea, jellyfish, and ichthyoplankton have been included to understand the seasonal variation in abundance of these groups

	Mandovi	Mandovi	Thane	Thane	Amba	Amba
	MS	PM	MS	PM	MS	PM
Copepoda	5514.5	4488.6	163.7	106.7	3394.8	1177.9
Ostracoda	0.14	0.1	0.81	0	1.97	0
Amphipoda	0.02	0.29	0.08	0	0.009	0
Decapoda larave	20.99	22.1	9.22	4.35	779.3	1.32
Mysida	0	0	0	0.06	0	0.93
Luciferidae	232.55	7.08	0.02	0.01	0.22	0.005
Cladocera	1.81	2.96	0	0	0	0
Isopoda	0	0	0	0	0.06	0
Phylllosoma larvae	0	0	0	0	0	0.014
Stomatopoda	0	0	0.12	0.04	2.01	0.1
Total crustacea	*5770.1*	*4521.2*	*174*	*111.2*	*4178.4*	*1180.3*
Ctenophora	0.009	0	2.22	23.76	1.5	2.61
Siphonophora	0	0	0.14	0.08	0.53	1.69
Medusae	0.10	0.16	5.46	5.67	1.23	2.78
Jellyfish	*0.11*	*0.16*	*7.82*	*29.5*	*3.26*	*7.09*
Chaetognatha	2.29	7.56	10.11	0.4	58.74	22.37
Polychaeta larvae	0	0.49	1.03	0	0.16	0.14
Gastropoda larvae	0	0	4.11	0.06	0	0
Bivalve larvae	0	0.96	0	0	0	0
Pteropoda	0	0.02	0	0	0	0
Salpa	0	0	0	0	0	0.07
Doliolida	0.009	0	0.02	0	0	0
Copelata	0	3.14	0	0	0	0
Fish eggs	0.32	9.59	0.16	0	0	0.09
Fish larvae	0.03	0.03	0.02	0.13	0.61	0.19
Icthyoplankton	*0.35*	*9.62*	*0.17*	*0.13*	*0.61*	*0.27*
Unidentified nauplii	21.97	0	13.25	0	0.15	0

DO, and Secchi depth (Fig. 6). Jellyfish abundance was also negatively correlated with the dominant zooplankton taxon, Copepoda, Lucifer, Cladocera, and the ichthyoplankton community (Fig. 6).

In the CAP, performed based on the distribution of nutrients during both seasons, the position of the Amba and Thane estuaries differed from the micro- and meso-tidal estuaries (Cochin, Netravati, Zuari, and Mandovi) along the axis of the CAP, and the squared canonical correlation of the axis was 0.7471 and 0.8247 during MS and PM, respectively (Fig. 7 a–b). The plot based on the distribution of the nutrients of the Amba and Thane estuaries during both periods exhibited distance between the two seasons along the CAP axis, with the squared canonical correlation of the axis 0.979 (Fig. 7c).

The result of the Bio-Env analysis indicated that total nitrogen was the most important factor that best explained the variability in the abundance and distribution of the jellyfish (Table 5). Interestingly, among the 10 controlling variables, the combination of different dissolved nutrients formed the major determining factor that best explained the variability in the abundance and distribution of the jellyfish community (Table 5).

Discussion

Responses of the biota to fluctuating environmental conditions and hydrographic instabilities form prime determinants governing their spatio-temporal distribution and community structure in the aquatic ecosystems (Madhu et al. 2007; Vezi et al. 2019). The present study has given prime focus to elucidate the changes in the zooplankton community composition concurrent to the variability in the hydrodynamics and nutrient distribution of the six major estuaries along west coast of India. The study also helped to understand the varied jellyfish distribution, factors favoring their preponderances, and their impact on the estuarine ecology. We first discuss the variation in the abiotic variables, its effect on the biotic components (phytoplankton biomass and zooplankton community), the influence of both the abiotic and biotic components on

Table 3 Abundance of Copepoda species (ind m^{-3}) in Cochin, Netravati, and Zuari estuaries along the west coast of India during the monsoon (MS) and post-monsoon (PM) periods

Species	Cochin	Cochin	Netravati	Netravati	Zuari	Zuari
	MS	PM	MS	PM	MS	PM
Acartia (Acartia) danae Giesbrecht, 1889	0	0	0	4.7	616.99	53.53
Acartia (Odontacartia) erythraea Giesbrecht, 1889	48.77	104.3	7.25	2.1	309.39	41.98
Acartia (Acanthacartia) plumosa Scott T, 1894	32.08	107.43	145.20	43.01	87.49	51.78
Acartia (Odontacartia) centrura Giesbrecht, 1889	0	31.89	0	0	0	0
Acartia (Odontacartia) spinicauda Giesbrecht, 1889	0.56	4.27	0	0	109.86	0
Acartia Copepodid	0	0	0	0	0	8.96
Acartiella gravelyi Sewell, 1919	1.78	0	0	0.34	0	0
Acartiella keralensis (Wellershaus, 1969)	0	0	6.21	0	62.69	0
Undinula vulgaris (Dana, 1849)	3.75	11.22	0	0	10.68	22.33
Bestiolina similis (Sewell, 1914)	463.09	513.37	116.07	56.36	941.08	881.53
Paracalanus parvus parvus (Claus, 1863)	0	0	0	0	24.03	0
Acrocalanus gracilis Giesbrecht, 1888	7.5	11.71	0	0	41.84	9.41
Subeucalanus crassus (Giesbrecht, 1888)	0	0	0	0	0	0
Subeucalanus subcrassus (Giesbrecht, 1888)	0	0.5	0	0	21.26	1.38
Pseudodiaptomus aurivillii Cleve, 1901	0.56	26.25	22.54	8	234.64	377.76
Pseudodiaptomus annandalei Sewell, 1919	15.01	192.72	0	0	0	0
Pseudodiaptomus serricaudatus (Scott T, 1894)	3.75	1.96	0.43	12.52	2.67	68.52
Pseudodiaptomus malayalus Wellershaus, 1969	0	0	0	0	0	0
Pseudodiaptomus copepodid	0	0	0	0.21	0	0
Centropages furcatus (Dana, 1849)	0	1.29	0	4.16	0	60.63
Centropages alcocki Sewell, 1912	3.75	1.16	0	0	0	0
Centropages dorsispinatus Thompson IC & Scott A, 1903	0	0	0	0	0	0
Centropages tenuiremis Thompson IC & Scott A 1903	32.7	0	1.29	3.13	50.73	0
Labidocera pectinate Thompson IC & Scott A 1903	0	111.56	0	2.73	0	214.63
Labidocera kroyeri kroyeri (Brady, 1883)	0	1.16	0	0	0	34.58
Labidocera minuta Giesbrecht, 1889	0	0	0	0	10.24	0
Labidocera spp.	0	0	0	0	0	0
Euchaeta concinna Dana, 1849	0	0	0	0	0	0
Euchaeta marina (Prestandrea, 1833)	0	0	0	0	0	0
Temora discaudata Giesbrecht, 1889	0	0	0	0	0	0
Tortanus (Tortanus) barbatus (Brady, 1883)	0	0	0	0	0	0
Tortanus (Tortanus) forcipatus (Giesbrecht, 1889)	0	0	0	0	0	7.67
Oithona brevicornis brevicornis Giesbrecht, 1891	111.01	120.95	92.66	10.26	296.32	156.27
Dioithona rigida (Giesbrecht, 1896)	0	0	0	0	0	24.79
Oithona similis Claus, 1866	0	0	94.23	0	0	0
Corycaeus crassiusculus Dana, 1849	4.11	5.95	0	4.33	68.12	11.03
Oncaea venusta Philippi, 1843	0	0	0	0	10.68	0
Sapphirina sp.	0	0	0.43	0	2.67	0
Euterpina acutifrons (Dana, 1847)	15.95	3.47	5.39	10.74	13.35	28.91
Longipedia sp.	0.56	0.64	0	0	0	0

Table 4 Abundance of Copepoda species (ind m^{-3}) in Mandovi, Thane, and Amba estuaries along the west coast of India during the monsoon (MS) and post-monsoon (PM) periods

Species	Mandovi	Mandovi	Thane	Thane	Amba	Amba
	MS	PM	MS	PM	MS	PM
Acartia (Acartia) danae Giesbrecht, 1889	27.3	46.0	45.1	37.5	863.7	154.6
Acartia (Odontacartia) erythraea Giesbrecht, 1889	208.8	38.9	23.1	5.7	518.3	60.2
Acartia (Acanthacartia) plumosa Scott T, 1894	723.9	999.8	0	0	0	0
Acartia (Odontacartia) centrura Giesbrecht, 1889	0	22.137	0	0	0	0
Acartia (Odontacartia) spinicauda Giesbrecht, 1889	133.1	45.5	3.8	7.0	192.9	14.8
Acartia Copepodid	0	272.6	0	10.47	0	0
Acartiella gravelyi Sewell, 1919	0	0	0.59	0	0	0
Acartiella keralensis (Wellershaus, 1969)	227.7	416.9	0	0	0	0
Undinula vulgaris (Dana, 1849)	8.4	47.1	3.0	2.56	0	45.8
Bestiolina similis (Sewell, 1914)	981.4	1385.1	17.5	22.0	509.5	321.8
Paracalanus parvus parvus (Claus, 1863)	12.6	28.2	8.4	5.2	0	19.5
Acrocalanus gracilis Giesbrecht, 1888	0	8.5	2.2	0	84.8	16.5
Subeucalanus crassus (Giesbrecht, 1888)	0	0	0	0	30.5	0
Subeucalanus subcrassus (Giesbrecht, 1888)	71.0	25.3	5.6	0.7	189.2	314.4
Pseudodiaptomus aurivillii Cleve, 1901	1822.2	578.8	33.4	3.3	0	73.8
Pseudodiaptomus annandalei Sewell, 1919	0	60.6	0	0	0	0
Pseudodiaptomus serricaudatus (Scott T, 1894)	4.2	67.3	0.6	0.05	0	1.1
Pseudodiaptomus malayalus Wellershaus, 1969	17.8	0	0	0	0	0
Pseudodiaptomus copepodid	0	0	0	0	0	16.0
Centropages furcatus (Dana, 1849)	0	21.3	0	4.7	0	6.5
Centropages alcocki Sewell, 1912	0	0	0	0	0	0
Centropages dorsispinatus Thompson IC & Scott A, 1903	0	0	0	0	807.2	4.0
Centropages tenuiremis Thompson IC & Scott A 1903	52.4	0	12.2	0	0	0
Labidocera pectinata Thompson IC & Scott A 1903	396.7	220.5	1.0	1.6	0	29.9
Labidocera kroyeri kroyeri (Brady, 1883)	0	3.4	0	0	0	0
Labidocera minuta Giesbrecht, 1889	0	3.2	0.9	0	0	0
Labidocera spp.	0	10.1	0	0.05	0	5.46
Euchaeta concinna Dana, 1849	0	0	0.88	0	0	0
Euchaeta marina (Prestandrea, 1833)	0	0	0	0	0	10.91
Temora discaudata Giesbrecht, 1889	0	0	0	0	15.3	0
Tortanus (Tortanus) barbatus (Brady, 1883)	0	0	5.6	0	45.8	0
Tortanus (Tortanus) forcipatus (Giesbrecht, 1889)	0	0	0	1.97	0	9.7
Oithona brevicornis brevicornis Giesbrecht, 1891	776.5	119.5	0	3.2	0	70.9
Dioithona rigida (Giesbrecht, 1896)	0	0	0	0	0	0
Oithona similis Claus, 1866	0	0	0	0	0	0
Corycaeus crassiusculus Dana, 1849	20.3	34.1	0	0.7	137.5	0
Oncaea venusta Philippi, 1843	0	8.5	0	0	0	1.8
Sapphirina sp.	0	0	0	0	0	0
Euterpina acutifrons (Dana, 1847)	30.2	25.3	0	0	0	0
Longipedia sp.	0	0	0	0	0	0

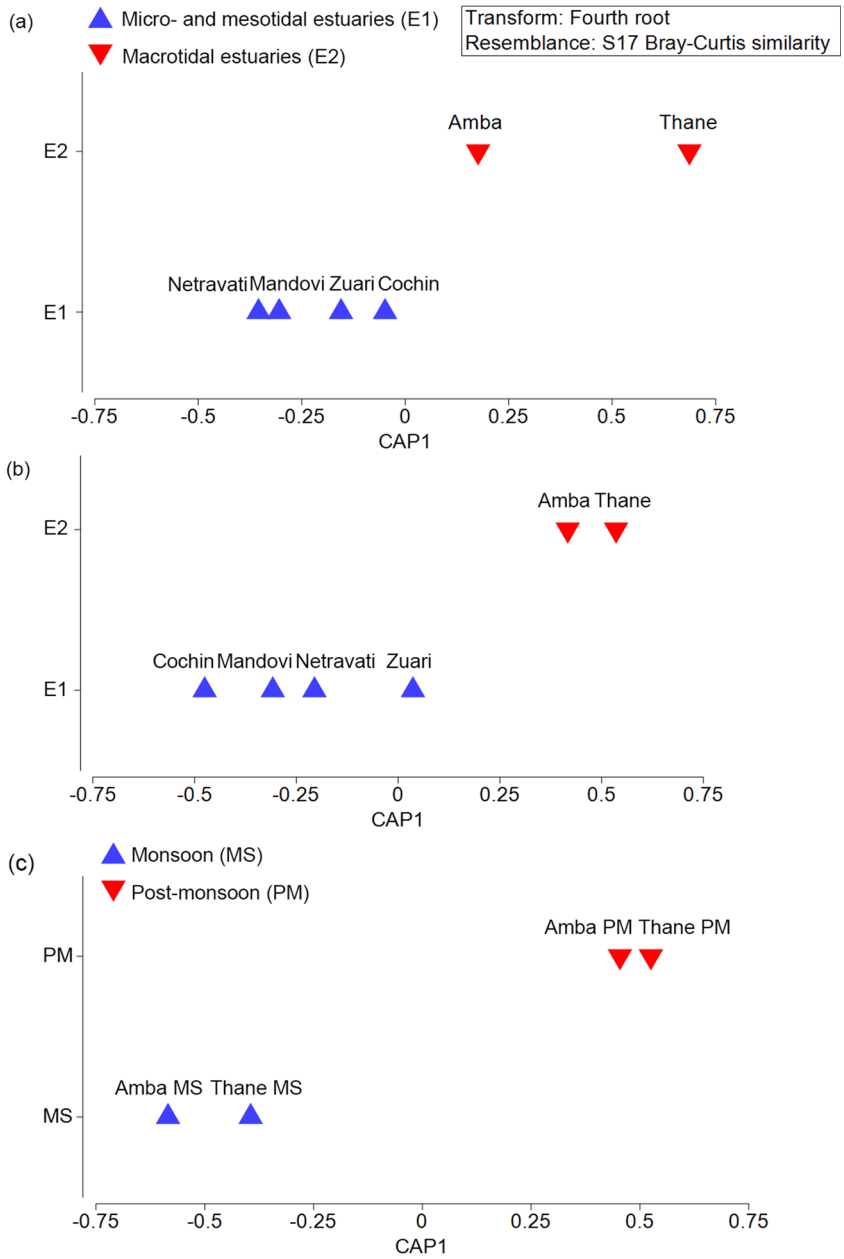

Fig. 7 Canonical analysis of principal coordinates (CAP) based on the distribution of nutrients along the estuaries during (a) monsoon, (b) post-monsoon, and (c) the CAP based on the distribution of the nutrients of the Amba and Thane estuaries during both periods

Table 5 Results of the Bio-Env analysis indicating the factors that best explained the variability in the abundance and distribution of the jellyfish community in estuaries along the west coast of India. The environmental variables used for the study were Secchi depth (cm), temperature (°C), salinity, dissolved oxygen (μM), pH, nitrate (μM), nitrite (μM), total nitrogen (μM), phosphate (μM), and silicate (μM)

No. variables	Correlation	Factors
1	0.817	total nitrogen (μM)
2	0.874	silicate (μM), total nitrogen (μM)
3	0.903	nitrate (μM), silicate (μM), total nitrogen (μM)
4	0.903	nitrite (μM), nitrate (μM), silicate (μM), total nitrogen (μM)
5	0.904	phosphate (μM), nitrite (μM), nitrate (μM), silicate (μM), total nitrogen (μM)

jellyfish community, and the impact of jellyfish community on the estuarine ecology.

Among physical variables, the spatial gradient evident in the salinity distribution from the upstream to inlet locations in all the estuaries during both the sampling periods can be linked to their proximity to the river mouths and coastal waters and their subsequent effects on the salinity distribution (Menon et al. 2000). The observed seasonal variation in the salinity distribution especially in the micro- and meso-tidal estuaries can be attributed to the changes associated with monsoonal precipitation and associated fluvial influxes (Vijith et al. 2009; Janardanan et al. 2015). However, a mesohaline (5-18) dominance was noticed in the salinity distribution of the four micro- and meso-tidal estuaries compared to the euhaline prevalence in the macro-tidal, Thane and Amba estuaries. The discrete tidal and hydrodynamic characteristics of these estuaries might have contributed for this variability in the salinity pattern as the increased seawater intrusion and subsequent changes in the salinity distribution in estuaries often occur corresponding to the increase in the tidal range and their progression (Haddout et al. 2019). The limited inter-estuarine variation in the surface temperature distribution indicated the tropical nature of the Indian estuaries characterized by the relatively less spatial variability in their temperature distribution (Nair et al. 1983; Vineetha et al. 2015). The relatively lower surface water temperature of PM can be attributable to the low atmospheric temperature and the resultant surface water cooling associated with the north-east monsoon period.

As increasing anthropogenic interventions and the resultant variability in the nutrient dynamics are known to influence zooplankton community (Park and Marshall 2000), the nutrient status of all the estuaries were well examined during the present study. It was observed that the dissolved nutrient concentration was relatively high in Thane and Amba compared to all other estuaries during both periods and most evidently during the PM (Fig. 3). These two estuaries receive enormous domestic and industrial effluent discharges from Mumbai, the most populous city of India, and in turn have serious impact on their water quality (Zingde and Govindan 2000; Vijay et al. 2014; NIO 2018). The markedly high nutrient concentration during PM supports their categorization as eutrophic estuaries and the post-monsoonal relatively less river discharges might have augmented the nutrient concentrations in these estuaries. The observation gets supported by the distinct position of the Thane and Amba estuaries from the micro- and meso-tidal estuaries along the axis of the CAP based on the nutrient concentration and their discrete location along the CAP axis in MS and PM based on their nutrient concentration (Fig. 7). Prior reports on the eutrophic status of these estuaries as a consequence of the increased human settlements and industrialization along its watersheds (Quadros et al. 2001; Ponkshe 2012; Hardikar et al. 2021) corroborates the view of the varied nutrient dynamics of these estuaries. The earlier observation of relatively lower nutrient concentration during monsoon compared to other seasons in these estuaries (Table 1 in Quadros et al. 2001) supports our observation of post-monsoonal increase in nutrient concentration. The high precipitation associated with monsoon is known to generate heavy fluvial runoff leading to effective flushing of these estuaries (Vijith et al. 2009). Though all the estuaries had a similar trend in the temporal distribution of nutrients with markedly high dissolved inorganic nutrients during the PM, the relatively high nutrient levels in both Thane and Amba estuaries irrespective of seasons indicate their distinct nutrient status (Fig. 3).

The distinctness in the nutrient status of the estuaries was reflected in their phytoplankton biomass. Compared to the micro- and meso-tidal estuaries, the significantly higher chlorophyll *a* in Thane and Amba during PM indicates the role of higher nutrient concentration in supporting the higher phytoplankton biomass (Figs. 3, 4a). Although a multitude of environmental factors, inclusive of nutrients, have a crucial role in governing the phytoplankton biomass and distribution in estuaries, the dissolved inorganic nutrient distribution often forms prime determinants in phytoplankton preponderances in diverse habitats ranging from freshwater to marine ecosystems (Bledsoe et al. 2004) which was found to be true in the present study also.

An apparent paradox was observed in the zooplankton biomass and abundance distribution characterized by relatively high biomass in the macro-tidal estuaries and higher abundance in the micro- and meso-tidal estuaries (Fig. 4 b–c). The conspicuous variability observed in the zooplankton community structure in the estuaries contributed to the observed paradox in their biomass and abundance distribution. The relatively high density of the small-sized crustacean zooplankton contributed towards the higher abundance in the micro- and meso-tidal estuaries, whereas the higher abundance of the gelatinous zooplankton (hydromedusae, ctenophore, and siphonophore) was responsible for higher biomass in the macro-tidal estuaries. Community structure has a crucial role in the pelagic ecology, the key determinant of trophic structure and energy flow (Naman et al. 2016; Giering et al. 2019) and hence the two clusters (first: all meso- and micro-tidal estuaries together; second: macro-tidal estuaries) formed based on the abundance of different zooplankton taxa indicates a discrete trophic pathway and energy transfer among these estuaries defined by their discrete nutrient status. Although Copepoda formed the dominant taxon in all the estuaries irrespective of seasons, an evident variation in community structure was observed in the macro-tidal estuaries from others. The dominance of copepod species, *Bestiolina similis*, *Acartia (Acanthacartia) plumosa*, and *Oithona (brevicornis) brevicornis* among the copepod community was observed in

the tropical micro- and meso-tidal estuaries is consistent with earlier reports (Goswami 1982; Vineetha et al. 2015, 2020). The mesohaline dominance in the salinity distribution of these estuaries might have provided an amiable salinity for the proliferation of these species thus increasing their abundances. Compared to the Acartiid population of other estuaries, the species, *Acartia (Acartia) danae*, formed the dominant representative in the macro-tidal estuaries. Being a representative of the coastal copepod community with preferences for high-saline waters (Bradford-Grieve 1994, 1999; Kang 2011), the higher salinity of the Thane and Amba estuaries might have favored their preponderances. The exclusive occurrence of coastal species like *Tortanus (Tortanus) forcipatus*, in the macro-tidal estuaries, can also be linked to their inhabitance concurrent to their specific salinity preferences (Chew et al. 2015).

The exclusive occurrence of the neritic zooplankton taxon, Cladocera, in the micro- and meso-tidal estuaries irrespective of seasons contributed to the discrete zooplankton community structure from the macro-tidal estuaries. Cladocera is one among the major zooplankton taxa along the south-west coast of India. Being primarily filter feeder notable for their parthenogenetic reproduction upon favorable environmental conditions, their peak abundance often coincides with the south-west monsoon period characterized by high primary production following the coastal upwelling and the concomitant nutrient enrichments (Selvakumar 1970; Haridas et al. 1980). Hence, their occurrence in the micro- and meso-tidal estuaries with relatively high abundance during MS points towards an estuarine extension of their coastal population (Madhupratap 1981). Contrarily, the carnivorous zooplankton taxon, Chaetognatha, though observed in all the estuaries, had higher abundance in the macro-tidal Amba and Thane irrespective of seasons. Chaetognatha are primarily marine and hence their relative higher abundances in the macro-tidal estuaries can be linked to their specific preferences for a high-saline environment (Nair 1971; Júnior et al. 2019).

During MS, jellyfish community was mostly observed in the two macro-tidal estuaries, Thane and Amba, and both of these estuaries experienced a sharp increase in their abundance during PM. Recently, there has been an upsurge in studies depicting the factors behind the occurrence, abundance, and outbreaks of jellyfishes and the responsible factors may vary depending on the community composition and the characteristics of ecological systems (Richardson et al. 2009; Naman et al. 2016). Temperature is an important controlling variable in temperate seas as the warming of sea surface temperature is considered to have a beneficial role in higher jellyfish occurrence in those environments (Lynam et al. 2011; Purcell et al. 2012). In the present study, the seasonal variation in the surface water temperature was less and was found to be slightly lower during PM, when the jellyfish abundance was higher. Considering the tropical nature of these estuaries characterized by generally warmer surface temperature and insignificant seasonal variations, the temperature is expected to exert less influence on the jellyfish community of these ecosystems. The works of Santhakumari et al. (1997) refuting the influence of the surface water temperature on the hydromedusae community of the Thane-Bassein creek further substantiates our observation.

Salinity is often considered as the prime factor governing the estuarine zooplankton community dynamics as it often undergoes wide spatio-temporal variability concurrent to the seasonal fluvial and tidal influxes and also by the position of sampling locations from the inlet to upstream locations (Padmavati and Goswami 1996; Menon et al. 2000). In the micro- and meso-tidal estuaries, jellyfish community was almost absent during MS, and their concomitant increase in abundance with the prominent increase in salinity during PM indicates a possible role of salinity in their prevalence. In the macro-tidal estuaries, Thane and Amba, although jellyfishes were observed during both the sampling periods, they had relatively higher abundance during PM. However, salinity in both these estuaries was relatively high during both the periods with less variability from MS to PM, thus implying the fact that although the meso- to high-saline environment might have favored their occurrence, some other factors also determined the increase in the jellyfish community in these estuaries.

With increased urbanization and industrialization along their watersheds, the estuarine ecosystems are often on the verge of nutrient enrichments eliciting potential influence on the water quality and on its biota ranging from phytoplankton to higher trophic levels including the jellyfishes (Lotze et al. 2006, Li et al. 2010; Howarth et al. 2011). Though in general, the nutrient concentration in Thane and Amba was relatively high during both periods, it attained the eutrophic status during PM compared to MS (Fig. 3). The nutrient-rich waters often promote higher phytoplankton biomass resulting in greater preponderances of primary consumers like Copepoda, in turn, forming an amiable food-rich environment for the congregation and proliferation of secondary consumers such as jellyfishes (Purcell 2012). Although higher phytoplankton biomass was observed during PM in these two eutrophic estuaries, a sharp decrease was noticed in the zooplankton abundance (especially Copepoda) from MS to PM. Jellyfishes are potential predators of the crustacean zooplankton in pelagic ecosystems and are capable for consuming their major prey copepod within short periods (Olesen 1995; Hansson et al. 2005) and hence their rise in population and the resultant predation pressure on the crustacean plankton might have led to the marked decline in the zooplankton abundance of these two estuaries during PM. The relatively minor variations in the crustacean plankton abundance from MS to PM in meso-tidal Mandovi and Zuari estuaries, where the observed jellyfish population was relatively less compared to

Thane and Amba, further substantiate the increased predatory impact exerted by the jellyfish community. In case of the Netravati estuary, although the jellyfish abundance in PM was much lower compared to the macro-tidal estuaries, the presence of the large-sized medusa (bell diameter > 20 mm) and their grazing pressure on the crustacean plankton might has resulted in the low zooplankton abundance.

The strong positive relation of jellyfish with the total nitrogen, nitrate, nitrite, and phosphate in the RDA plot (Fig. 6) indicates the role of nutrient enrichment favoring their population in these estuaries. Interestingly, the output of the Bio-Env analysis also exhibited the combination of different nutrients as the most important factors that best explained the variability in the jellyfish abundance and distribution. This result further substantiates the role of nutrient enrichment in Thane and Amba during PM favoring the jellyfish occurrences.

Nutrient enrichment by itself and their subsidiary effects on the water quality such as low DO levels, high turbidity, and increased algal growth may elicit potential impacts on the healthy sustenance and survival of its inherent biota. The present study also witnessed relatively low DO in Thane and Amba compared to all other estuaries with a drop during the PM when nutrient levels were markedly high further raising it to a eutrophic status. Many jellyfish species are known to survive well in a low DO concentration of 2–3 mg l^{-1} (Shoji et al. 2010), and can even tolerate up to low DO levels of 1 mg l^{-1} through actively trapping oxygen in their watery body (Purcell et al. 2007). Although Thane and Amba were characterized by high nutrient levels, the DO concentration in these estuaries did not go down below their tolerance limits during the post-monsoonal highly eutrophic condition (150.4 ± 10.6 and 170.1 ± 9.7 μM, (~ 4.8 ± 0.3 and 5.4 ± 0.3 mg l^{-1}) respectively, and hence might have not limited their distribution in these estuaries. Turbidity is another ancillary factor associated with eutrophic waters that may impede with the survival of the primary and secondary consumers especially the predators which rely on the visual stimulus as a cue for foraging (Utne-Palm 2002). In the present study, the turbidity was relatively higher in Thane and Amba than all other estuaries. Jellyfishes being a non-visual predator relying on tactile rather than the visual stimulus (Ohata et al. 2011), the comparatively higher turbidity of the macro-tidal estuaries exerting an impact on their foraging can be ruled out. Thus, their distinct adaptation strategies aiding them to inhabit even highly turbid waters compared to other organisms might have helped them in their effective survival and proliferation leading to their expansion of population in these eutrophic macro-tidal estuaries.

Jellyfishes are often considered as a negative indicator of fishery in aquatic ecosystems (Purcell et al. 1999; Riisgård et al. 2012). This view was observed to be true in the present study as the ichthyoplankton abundance in the Amba and Thane estuaries declined conspicuously with the increasing jellyfish population. The negative relation observed between these zooplankton communities in the RDA plot further justifies the adverse effect of the jellyfishes on the ichthyoplankton community. Jellyfish community can affect the fishery of these estuaries in two ways. Being indiscriminate feeders, jellyfishes preying upon the eggs and larvae of fishes can lead to a substantial reduction in the future standing stock and fishery yield from the estuaries (Purcell et al. 1999). Furthermore, jellyfishes often compete with the zooplanktivorous adult fishes for their common prey, mostly copepods and other crustacean plankton, and outcompete them through their ability of continuous feeding and prey intake of larger populations of prey of varying sizes within short periods (Purcell 1992). The jellyfish impact on the estuarine fishery potential was further augmented by the negative influence they exerted on the economically relevant decapod larval population. The higher jellyfish abundance and the concurrent grazing pressure resulted in a marked decline in the decapod larval abundance from MS (9.2 ± 4.7, 779 ± 1457 ind m^{-3}, Thane and Amba, respectively) to PM (4.3 ± 3.3, 1.3 ± 0.7 ind m^{-3}, Thane and Amba, respectively). Hence, in the present study, the macro-tidal estuaries, characterized by turbid, high-saline, and nutrient-enriched waters, might have turned out to be an amiable environment for the higher jellyfish abundances.

Jellyfishes are capable of thriving in environments with low DO and at the same time, their occurrence can also lead to a decline in the DO concentration. The markedly higher predation of jellyfish on the zooplankton community will subsequently reduce the grazing pressure of the crustacean plankton on the phytoplankton community leading to their blooming and resultant increased settling of the dead and decayed phytoplankton community in the estuarine bottom. The microbial decomposition of this settled phytoplankton may further lower the DO level (Møller and Riisgård 2007) thus affecting the habitat quality of the ecosystem. Furthermore, the decomposition of jellyfishes at times of their peak abundances also leads to a further drop in the oxygen levels. Hence, the low DO environment in Thane and Amba might be the resultant effect of their nutrient-enriched status and the influence exerted by the rising jellyfish population.

Anthropogenic inputs have been reported to alter the basal trophic pathways in the coastal and estuarine ecosystems (Naman et al. 2016). Compared to the micro- and meso-tidal estuaries, the higher jelly abundances and the subsequent steeper decline in the crustacean plankton abundances from MS to PM in Thane and Amba indicate a structural and functional modification in the pelagic food web and energy transfer. Jellyfishes having less natural predator might lead to an inefficient energy transfer in the estuarine food web and carbon cycling. As these tropical estuarine ecosystems evidenced conspicuous changes in their water chemistry corresponding to the changes in the tidal dynamics and anthropogenic interventions at short periods, elaborate studies focusing on the

alterations in their hydrographical attributes and consequent ecological changes are inevitable for the effective sustenance of the ecosystem functioning and productivity of these sensitive coastal zones.

Acknowledgements We thank the Secretary, Ministry of Earth Sciences (MoES), Government of India for the support of this study. We are grateful to Dr. Gupta GVM, Director, Centre for Marine Living Resources and Ecology (CMLRE), for his guidance towards the completion of the work. We are thankful to Dr. Vineetha G, CMFRI, Kochi, for her kind help in the identification of Copepoda. We extend our gratitude to Thasneem N, KUFOS, Kochi, for her help in the analysis of samples. This work is an output of the MEDAS project of CMLRE and funded by Ministry of Earth Sciences, Government of India. This is CMLRE contribution no 136.

Author contribution All authors contributed to the study conception and design. Material preparation, data collection, and analysis were performed by Kusum Komal Karati, Naroju Veera Harikrishnachari, Sudheesh Valliyodan, Munnooru Kumaraswami, and Sura Appala Naidu. The first draft of the manuscript was written by Kusum Komal Karati and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Funding This work funded by Ministry of Earth Sciences, Government of India.

Data availability The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate Not applicable

Consent for publication Not applicable

Competing interests The authors declare that they have no competing interests

References

Anderson MJ, Willis TJ (2003) Canonical analysis of principal coordinates: a useful method of constrained ordination for ecology. Ecology 84:511–525

Bledsoe EL, Phlips EJ, Jett CE, Donnelly KA (2004) The relationships among phytoplankton biomass, nutrient loading and hydrodynamics in an inner-shelf estuary. Ophelia 58:29–47

Bradford-Grieve JM (1994) The marine fauna of New Zealand: pelagic calanoid Copepoda: Megacalanidae, Calanidae, Paracalanidae, Mecynoceridae, Eucalanidae, Spinocalanidae, Clausocalanidae. New Zealand Oceanogr Inst Mem 102:5–156

Bradford-Grieve JM (1999) The marine fauna of New Zealand: pelagic calanoid copepoda: bathypontiidae, arietellidae, augaptilidae, heterorhabdidae, lucicutiidae, metridinidae, phyllopodidae, centropagidae, pseudodiaptomidae, temoridae, candaciidae, pontellidae, sulcanidae, acartiidae, tortanidae. NIWA Biodivers Mem 111:1–268

Brotz L, Cheung WW, Kleisner K, Pakhomov E, Pauly D (2012) Increasing jellyfish populations: trends in large marine ecosystems. Hydrobiologia 690:3–20

Chew LL, Chong VC, Ooi AL, Sasekumar A (2015) Vertical migration and positioning behavior of copepods in a mangrove estuary: interactions between tidal, diel light and lunar cycles. Estuar Coast Shelf Sci 152:142–152

Clarke KR, Gorley RN (2015) PRIMER v7: user manual/tutorial. PRIMER-E Ltd, Plymouth.

Clarke KR, Somerfield PJ, Gorley RN (2008) Testing of null hypotheses in exploratory community analyses: similarity profiles and biota-environment linkage. J Exp Mar Biol Ecol 366:56–69

Clifford HT, Stephensen W (1975) An introduction to numerical classification. Academic Press, New York, USA

Conway DVP, White RG, Hugues-Dit-Ciles J, Gallienne CP, Robins DB (2003) Guide to the Coastal and Surface Zooplankton of the South-Western Indian Ocean. Marine Biological Association of the United Kingdom, Plymouth

David V, Selleslagh J, Nowaczyk A, Dubois S, Bachelet G, Blanchet H, Gouillieux B, Lavesque N, Leconte M, Savoye N, Sautour B (2016) Estuarine habitats structure zooplankton communities: Implications for the pelagic trophic pathways. Estuar Coast Shelf Sci 179:99–111

Dineshkumar PK, Josanto V, Sarma RV, Zingde MD (1997) Physical aspects of estuarine pollution- a case study in Amba river. J Hum Ecol 8:175–178

Fernandes D, Wu Y, Shirodkar PV, Pradhan UK, Zhu ZY, Zhang J, Limbu SM (2019) Spatial and temporal variations in source, diagenesis, and fate of organic matter in sediments of the Netravati River, India. Hydrol Process 33:2642–2657

Frankignoulle M, Borges AV (2001) European continental shelf as a significant sink for atmospheric carbon dioxide. Global Biogeochem Cy 15:569–576

García-Robledo E, Corzo A, Papaspyrou S (2014) A fast and direct spectrophotometric method for the sequential determination of nitrate and nitrite at low concentrations in small volumes. Mar Chem 162:30–36

Giering SL, Wells SR, Mayers KM, Schuster H, Cornwell L, Fileman ES, Atkinson A, Cook KB, Preece C, Mayor DJ (2019) Seasonal variation of zooplankton community structure and trophic position in the Celtic Sea: a stable isotope and biovolume spectrum approach. Prog Oceanogr 177:101943

Goswami SC (1982) Distribution and diversity of copepods in the Mandovi-Zuari estuarine system, Goa. Indian J Mar Sci 11:292–295

Grasshoff K, Ehrhardt M, Kremling K (1983) Methods of sea water analysis. Verlag Chemie, Weinheim

Haddout S, Baimik I, Maslouhi A, Igouzal M, Magrane B, Marah H (2019) The influence of spring and neap tide on salt intrusion and stratification in Sebou estuary (Morocco). Int J River Basin Manag 17:131–142

Hansson LJ, Moeslund O, Kiørboe T, Riisgård HU (2005) Clearance rates of jellyfish and their potential predation impact on zooplankton and fish larvae in a neritic ecosystem (Limfjorden, Denmark). Mar Ecol Prog Ser 304:117–131

Hardikar R, Haridevi CK, Ram A, Parthipan V (2021) Distribution of size-fractionated phytoplankton biomass from the anthropogenically stressed tropical creek (Thane creek, India). Reg Stud Mar Sci 41: 101577

Haridas P, Menon PG, Madhupratap M (1980) Annual variations in zooplankton from a polluted coastal environment. Mahasagar 13:239–248

Harris R, Wiebe P, Lenz J, Skjoldal HR, Huntley ME (Eds.) (2000) ICES zooplankton methodology manual. Academic, London

Howarth R, Chan F, Conley DJ, Garnier J, Doney SC, Marino R, Billen G (2011) Coupled biogeochemical cycles: eutrophication and hypoxia in temperate estuaries and coastal marine ecosystems. Front Ecol Environ 9:18–26

Janardanan V, Amaravayal S, Revichandran C, Manoj NT, Muraleedharan KR, Jacob B (2015) Salinity response to seasonal runoff in a complex estuarine system (Cochin estuary, west coast of India). J Coast Res 31:869–878

Jhingran VG, Gopalakrishnan V (1973) Estuarine fisheries resources of India in relation to adjacent seas. J Mar Biol Assoc India 15:323–334

John EJ, Cheryan KP (1975) Geomorphological Studies of the Estuary of River Netravati Near Mangalore. P Coast Eng Conf ASCE 2:1304–1318

Júnior MN, da Costa BS, Martinez TA, Brandini FP, Miyashita LK (2019) Diversity of gelatinous zooplankton (Cnidaria, Ctenophora, Chaetognatha and Tunicata) from a subtropical estuarine system, southeast Brazil. Mar Biodivers 49:1283–1298

Kang JH (2011) The occurrence of Acartia species and their environmental characteristics at three ports in Korea. Ocean Sci J 46:219–237

Karati KK, Vineetha G, Madhu NV, Anil P, Dayana M, Shihab BK, Muhsin AI, Riyas C, Raveendran TV (2017) Variability in the phytoplankton community of Kavaratti reef ecosystem (northern Indian Ocean) during peak and waning periods of El Niño 2016. Environ Monit Assess 189:653

Li Y, Li D, Tang J, Wang Y, Liu Z, He S (2010) Long-term changes in the Changjiang Estuary plankton community related to anthropogenic eutrophication. Aquat Ecosyst Health Manag 13:66–72

Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH, Cooke RG, Kay MC, Kidwell SM, Kirby MX, Peterson CH, Jackson JB (2006) Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312:1806–1809

Lynam CP, Lilley MKS, Bastian T, Doyle TK, Beggs SE, Hays GC (2011) Have jellyfish in the Irish Sea benefited from climate change and overfishing? Glob Chang Biol 17:767–782

Madhu NV, Jyothibabu R, Balachandran KK (2010) Monsoon-induced changes in the size-fractionated phytoplankton biomass and production rate in the estuarine and coastal waters of southwest coast of India. Environ Monit Assess 166:521–528

Madhu NV, Jyothibabu R, Balachandran KK, Honey UK, Martin GD, Vijay JG, Shiyas CA, Gupta GVM, Achuthankutty CT (2007) Monsoonal impact on planktonic standing stock and abundance in a tropical estuary (Cochin backwaters–India). Estuar Coast Shelf Sci 73:54–64

Madhupratap M (1981) Cladocera in the estuarine and coastal waters of south-west coast of India. Mahasagar 14:215–219

Manoj NT, Unnikrishnan AS (2009) Tidal circulation and salinity distribution in the Mandovi and Zuari estuaries: case study. J Waterw Port Coast Ocean Eng 135:278–287

McLusky DS, Elliott M (2004) The estuarine ecosystem: ecology, threats and management. Oxford University Press, Oxford

Menon NN, Balchand AN, Menon NR (2000) Hydrobiology of the Cochin backwater system- a review. Hydrobiologia 430:149–183

Møller LF, Riisgård HU (2007) Impact of jellyfish and mussels on algal blooms caused by seasonal oxygen depletion and nutrient release from the sediment in a Danish fjord. J Exp Mar Biol Ecol 351:92–105

Nair VR (1971) Seasonal fluctuations of chaetognaths in the Cochin backwater. I Mar Biol Assc India 13:226–233

Nair NB, Dharmaraj K, Azis PKA (1983) Nature of primary production in a tropical backwater. Proc Indian Natn Sci Acad B49:581–597

Naman SM, Greene CM, Rice CA, Chamberlin J, Conway-Cranos L, Cordell JR, Hall JE, Rhodes LD (2016) Stable isotope-based trophic structure of pelagic fish and jellyfish across natural and anthropogenic landscape gradients in a fjord estuary. Ecol Evol 6:8159–8173

National Institute of Oceanography NIO (2018) Assessment of impact of release of effluents on ecology of inshore and coastal areas of Maharashtra and their management. Part A: Main report.

Ohata R, Masuda R, Ueno M, Fukunishi Y, Yamashita Y (2011) Effects of turbidity on survival of larval ayu and red sea bream exposed to predation by jack mackerel and moon jellyfish. Fish Sci 77:207–215

Olesen NJ (1995) Clearance potential of jellyfish *Aurelia aurita*, and predation impact on zooplankton in a shallow cove. Mar Ecol Prog Ser 124:63–72

Padmavati G, Goswami SC (1996) Zooplankton ecology in the Mandovi-Zuari estuarine system of Goa, west coast of India. Indian J Mar Sci 25:268–273

Park GS, Marshall HG (2000) Estuarine relationships between zooplankton community structure and trophic gradients. J Plankton Res 22:121–136

Pednekar SM, Matondkar SP, Gomes HDR, Goes JI, Parab S, Kerkar V (2011) Fine-scale responses of phytoplankton to freshwater influx in a tropical monsoonal estuary following the onset of southwest monsoon. J Earth Sys Sci 120:545–556

Ponkshe C (2012) A comparative study of some chemical and biological characteristics of coastal and estuarine waters of three regions along coastal Maharashtra. Nat Environ Pollut Technol 11:125–128

Purcell JE (1992) Effects of predation by the scyphomedusan *Chrysaora quinquecirrha* on zooplankton populations in Chesapeake Bay, USA. Mar Ecol Prog Ser 87:65–76

Purcell JE (2012) Jellyfish and Ctenophore blooms coincide with human proliferations and environmental perturbations. Annu Rev Mar Sci 4:209–235

Purcell JE, Atienza D, Fuentes V, Olariaga A, Tilves U, Colahan C, Gili JM (2012) Temperature effects on asexual reproduction rates of scyphozoan species from the northwest Mediterranean Sea. Hydrobiologia 690:169–180

Purcell JE, Malej A, Benović A (1999) Potential links of jellyfish to eutrophication and fisheries. In: Malone TC, Malej A, Harding LW, Smodlana N, Turner RE (eds) Ecosystems at the Land-Sea Margin: Drainage Basin to Coastal Sea. Coastal Estuar, Stud, pp 241–263

Purcell JE, Uye SI, Lo WT (2007) Anthropogenic causes of jellyfish blooms and direct consequences for humans: a review. Mar Ecol Prog Ser 350:153–174

Qasim SZ (2003) Indian estuaries. Allied publishers, New Delhi

Quadros G, Mishra V, Ullal V, Gokhale KS, Athalye RP (2001) Status of water quality of Thane creek (India). Ecol Env Cons 7:235–240

Revichandran C, Srinivas K, Muraleedharan KR, Rafeeq M, Shivaprasad A, Vijayakumar K, Jayalakshmy KV (2012) Environmental set-up and tidal propagation in a tropical estuary with dual connection to the sea (SW coast of India). Environ Earth Sci 66:1031–1042

Richardson AJ, Bakun A, Hays GC, Gibbons MJ (2009) The jellyfish joyride: causes, consequences and management responses to a more gelatinous future. Trends Ecol Evol 24:312–322

Riisgård HU, Andersen P, Hoffmann E (2012) From fish to jellyfish in the eutrophicated Limfjorden (Denmark). Estuar Coasts 35:701–713

Santhakumari V (1992) Ecology and distribution of hydromedusae from Beypore and Korapuzha, tropical estuaries of southwest coast of India. P Kerala Sci Congress 4:280–281

Santhakumari V, Ramaiah N, Nair VR (1997) Ecology of hydromedusae from Bombay Harbour-Thana and Bassein Creek estuarine complex. Indian J Mar Sci 27:162–168

Selvakumar RA (1970) Cladoceran swarm in relation to mackerel fishery along the west coast of India. Curr Sci 39:481–482

Shankar R, Manjunatha BR (1997) Onshore transport of shelf sediments into the Netravati-Gurpur estuary, west coast of India: geochemical evidence and implications. J Coast Res 13:331–340

Shetye SR, Gouveia AD, Singbal SY, Naik CG, Sundar D, Michael GS, Nampoothiri G (1995) Propagation of tides in the Mandovi-Zuari estuarine network. P Indian Acad Sci-Earth Planet Sci 104:667–682

Shoji A, Kudoh T, Takatsuji H, Kawaguchi O, Kasai A (2010) Distribution of moon jellyfish *Aurelia aurita* in relation to summer

hypoxia in Hiroshima Bay, Seto Inland Sea. Estuar Coast Shelf Sci 86:485–490

Spitz J, Mourocq E, Schoen V, Ridoux V (2010) Proximate composition and energy content of forage species from Bay of Biscay: high-or low-quality food? ICES J Mar Sci 67:909–915

Strickland JDH, Parsons TR (1972) A Practical Handbook of Seawater Analysis. Bulletin of Fisheries Research Board, Canada

Thomas J, Velamala SN, Prasad KVSR (2019) Numerical simulation of tidal constituents in Thane creek and the Ulhas estuary, west coast of India. J Coast Res 35:376–388

Utne-Palm AC (2002) Visual feeding of fish in a turbid environment: physical and behavioural aspects. Mar Freshw Behav Physiol 35: 111–128

Van den Wollenberg AL (1977) Redundancy analysis. An alternative for canonical correlation analysis. Psychometrika 42:207–219

Vannucci M, Santhakumari V, Dos-Santos EP (1970) The ecology of hydromedusae from the Cochin area. Mar Biol 7:49–58

Velamala SN, Thomas J, Bari S, Kachave S (2016) The impact of dredging on residence time in the Amba estuary, west coast of India. Environ Earth Sci 75:108. https://doi.org/10.1007/s12665-015-4851-3

Vezi M, Downs CT, Wepener V, O'Brien G (2019) Response of zooplankton communities to altered water quality and seasonal flow changes in selected river dominated estuaries in KwaZulu-Natal, South Africa. Ecohydrol Hydrobiol 19:393–406

Vijay R, Khobragade PJ, Sohony RA, Kumar R, Wate SR (2014) Hydrodynamic and water quality simulation of Thane creek, Mumbai: an impact of sewage discharges. Indian J Geo Mar Sci 43:1891–1898

Vijith V, Sundar D, Shetye SR (2009) Time-dependence of salinity in monsoonal estuaries. Estu Coastal Shelf Sci 85:601–608

Vineetha G, Kripa V, Karati KK, Rehitha TV, Vishal CR, Vineetha V, Manu M (2020) Impact of a catastrophic flood on the heavy metal pollution status and the concurrent responses of the bentho-pelagic community in a tropical monsoonal estuary. Mar Poll Bull 155: 111191

Vineetha G, Madhu NV, Kusum KK, Sooria PM (2015) Seasonal dynamics of the copepod community in a tropical monsoonal estuary and the role of sex ratio in their abundance pattern. Zool Stud 54:54. https://doi.org/10.1186/s40555-015-0131-x

Wellershaus S (1969) On the taxonomy of planktonic copepod in the Cochin backwater (a south Indian estuary). Veröff Inst Meeresforsch Bremerh 11:245–286

Wolanski E, Elliott M (2015) Estuarine ecohydrology: an introduction. Elsevier, New York

Zingde MD, Govindan K (2000) Health status of the coastal waters of Mumbai and regions around. In: Sharma VK (ed) Environmental problems of coastal areas in India. Bookwell publications, New Delhi, pp 119–132

Publisher's note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.