



Delineating the food web structure in an Indian estuary during tropical winter employing stable isotope signatures and mixing model

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Abstract

The food and feeding links and sources in an impacted tropical estuary situated along India's western coast, the Ulhas River Estuary (URE) was analyzed employing the stable carbon and nitrogen isotopic signatures ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$). Three basal carbon sources, such as mangrove leaves, particulate organic matter (phytoplankton), and detritus, were analyzed together with eight consumer groups from various trophic guilds. The $\delta^{13}\text{C}$ varied from -19.67 to -24.61‰ , whereas $\delta^{15}\text{N}$ ranged from 6.31 to 15.39‰ from the primary consumer to the top predator species. The stable isotope mixing model developed for URE revealed a phytoplankton based pelagic food chain and detritus based benthic food chain in URE. The fairly larger value of SEA (Standard Ellipse Area) in the URE suggest a much broader food web structure and high trophic diversity in the ecosystem. Higher influence of detritus on the assimilated diet of majority of consumers and evidences of nitrogen enrichment in the basal sources such as detritus and particulate organic matter by anthropogenic activities in URE point towards nitrogen pollution and subsequent trophic disturbance in this tropical estuarine ecosystem.

Keywords Stable isotopes · Trophic guild · Food web · Mixing model · Trophic level · Estuary

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Introduction

Estuaries are considered one of the most productive ecosystems, compared to rivers and the marine ecosystems that influence them from either side (Pritchard 1967). They are important transition zones, where matter and energy from terrestrial origin intermix with that from aquatic origin. Estuarine food webs generally rely on a high level of primary production and detritus pathways in association with adjacent ecosystems like salt marshes, mangroves, and mud flats (Duarte and Cebrián 1996). They are characterized by a high degree of complexity that suffers well marked spatio-temporal variability in ecological conditions as well as biodiversity (Simenstad and Wissmar 1985; Pasquaud et al. 2008). Therefore, these ecosystems primarily support populations of aquatic species with specific ecological functions such as residence and shelter, migration channels, and feeding and breeding grounds for juvenile fish species (Cardoso et al. 2004; Elliott et al. 2007). Food webs are recognized as key components in ecology and have been structured by complex species interactions, which govern the flow of organic matter in natural systems (Summerhayes and Elton 1923). Many research works have underlined the uniqueness

of the estuarine food web structure, which is more complex and dynamic than other aquatic ecosystems. Firstly, due to the high degree of intra annual fluctuations in fish diversity as a result of seasonal marine and freshwater emigrants and the subsequent community changes (Amara et al. 2000; Maes et al. 2004; Selleslagh et al. 2009; Sreekanth et al. 2019) and secondly, the monsoon mediated inflow of allochthonous inputs and the raise in primary productivity in particular seasons (Simenstad and Wissmar 1985; Pasquaud et al. 2008). These events will be more pronounced in the case of tropical estuaries, which are under the influence of monsoon (Sreekanth et al. 2019).

Characterization of food web functioning is still challenging due to the complexity in precisely measuring species interactions within a food web. Novel tracing methods that estimate species diet uptake and trophic positions are therefore required to determine food web dynamics. The application of stable isotope analysis to characterize the food webs has improved the understanding of sources and niche properties along with the quality of trophic level (TL) estimations, especially for the aquatic ecosystems, which are less amenable to the traditional tracking methods (Boecklen et al. 2011). Despite the direct methods like, visual or molecular measures of analyzing fecal or gut content analyses (Pompanon et al. 2012) that provide the snapshot of the prey ingested at a particular time, this technique provides direct estimates of the prey assimilated and a longer-term integration of the feeding habits of the consumer species (e.g. Kwak and Zedler 1997; Riera et al. 1999; Vinagre et al. 2008, 2011). The data on stable carbon isotopic ratio ($\delta^{13}\text{C}$) can provide important clues on the sources of primary production that forms the basis of the food web. The basal sources often differ in their $\delta^{13}\text{C}$ values based on the photosynthetic pathway followed and also, enrichment in $\delta^{13}\text{C}$ is much smaller between diet and consumer. Thus, $\delta^{13}\text{C}$ can be used to trace prey–consumer connections in the food chains (Fry and Sherr 1989; Post 2002). The nitrogen isotopic ratio ($\delta^{15}\text{N}$) enriches more or less by 3.4‰ ($\pm 1\%$) from prey to the predator (Peterson and Fry 1987; Post 2002). Therefore, $\delta^{15}\text{N}$ has been increasingly used as a marker of trophic position and have been used for the estimation of the TL of many species and the establishment of food web structure for various ecosystems (e.g. Kwak and Zedler 1997; Le Loc'h et al. 2008; Pasquaud et al. 2010; Vinagre et al. 2011, 2012; Potapov et al. 2019). Since the last two decades, several researchers employed stable isotopic ratios for the estimation of TL and niche attributes in the estuarine and coastal ecosystems (Akin and Winemiller 2008; Lavoie et al. 2010; Le Loc'h et al. 2008; Vinagre et al. 2012; Filgueira and Castro 2011; Kwak and Zedler 1997; Pasquaud et al. 2010; Bird et al. 2018; Golikov et al. 2019; Barton et al. 2019).

The ecological or trophic structure studies from India that used stable isotopic signatures are meager and mainly

focused on large oceanic predators, viz., yellowfin tuna and swordfish in the western Indian Ocean (Ménard et al. 2007), on elasmobranchs caught off Gujarat (Borrell et al. 2011), sharks from the south-western Indian Ocean (Kiszka et al. 2015), on mesopelagic communities over shallow seamounts of the south-western Indian Ocean (Annasawmy et al. 2020) etc. The stable isotopic studies in the estuarine ecosystems in India are also limited to a few, including a study on the benthic invertebrates in an estuarine mangrove ecosystem in Andhra Pradesh (Bouillon et al. 2002), and a study to characterize the sources and fate of organic matter in the Pichavaram estuarine-mangrove ecosystem, east coast of India (Prasad and Ramanatha 2009).

Stable isotope mixing models (SIMMs) have increasingly been used to determine the relative contributions of several sources to a mixture in ecological and geochemical research over the last several decades (Schwarcz 1991; Phillips and Gregg 2001). As a consumer's tissues are ultimately derived from the dietary sources they consume, it is possible to use SIMMs to derive the assimilated diet of an individual, or a group of individuals, given the isotopic ratios of the consumers' tissues and food sources (Phillips 2012). The earliest attempts in applying a mixing model framework were restricted to systems involving a single consumer, later Phillips and Gregg (2001) through their IsoError model, provided propagation of error calculations to establish confidence intervals around the estimates based on variances of the consumer and source isotopic measurements. Subsequently, the method was expanded in the IsoSource (Phillips and Gregg 2003) that allow for multiple sources but without explicit incorporation of source and consumer variability. The refining of the models has continued to progress through years with increasing capabilities and sophistication by various works. Recently, Bayesian mixing models have been developed that allow flexible model specification in a rigorous Bayesian statistical framework to incorporate some or all of these features such as uncertainties, concentration dependence, larger numbers of sources as well as others. These models include MixSIR (Moore and Semmens 2008; Ward et al. 2010), SIAR (Parnell et al. 2010, 2013), MixSIAR (Stock and Semmens 2013), IsotopeR (Hopkins and Ferguson 2012), FRUITS (Fernandes et al. 2014), and SIMMR (stable isotope mixing model with "R" package) (Parnell and Inger 2019) etc. SIMMR is designed as an upgrade to the SIAR package by Parnell et al. (2013). This new version contains a slightly more sophisticated mixing model, a simpler user interface, and more advanced plotting features.

Several researchers have employed stable isotope mixing models for illustrating the trophic structure of estuarine coastal ecosystems worldwide. The most important studies in this regard were undertaken by Abrantes and Sheaves, (2010) in Tropical North Queensland, Australia; Giarrizzo

et al. (2011) in Curuçá estuary, northern Brazil; Vaslet et al. (2012) in mangrove ecosystems of Florida and Belize of the Tropical western Atlantic region; Shahraki et al. (2014) in Qeshm Island, Persian Gulf, Northern Indian Ocean, Sepúlveda-Lozada et al. (2015) in Southern Gulf of Mexico; Contreras et al. (2018) in Central Coast of Colombia of the Tropical Eastern Pacific; Nelson et al. (2019) and Dillon et al. (2021) in the Northern Gulf of Mexico. However, there are no attempts so far has been reported from the Indian coastal waters and estuaries. Here we report one of the pioneer attempts in trophic structure study in a tropical estuarine ecosystem situated along the western coast of India, the Ulhas River Estuary (URE) using stable isotopic signatures. The present work aims to (1) characterize the food web structure of URE, based on the nodal links of the estuarine food web, by employing stable carbon and nitrogen isotopic signatures with the analytical tool of SIMMR; and (2) to elucidate how the isotopic trophic positions of selected fish species vary from the dietary trophic position and the reported estimates from the adjacent coastal waters.

Methods

Study area

The URE (URE) is one of the transitional ecosystems situated along Mumbai, (Maharashtra) along the western coast of India. The estuary connects the Ulhas River to the Arabian Sea through Vasai creek (Fig. 1). It is a macrotidal and well-mixed estuary, which shows well marked seasonal variations in the salinity attributed by the monsoon mediated freshwater influx (Rathod et al. 2003). The estuary is also characterized by considerable land runoff that carries huge amount of sediments from its catchment area (Rathod 2005). The ecosystem is experiencing declined productivity due to heavy discharge from urban and industrial activities along the banks. Heavy pollution due to anthropogenic activities from the surrounding areas and the resultant impact on the water quality has also been reported from URE (Nikam et al. 2008; Rathod and Patil

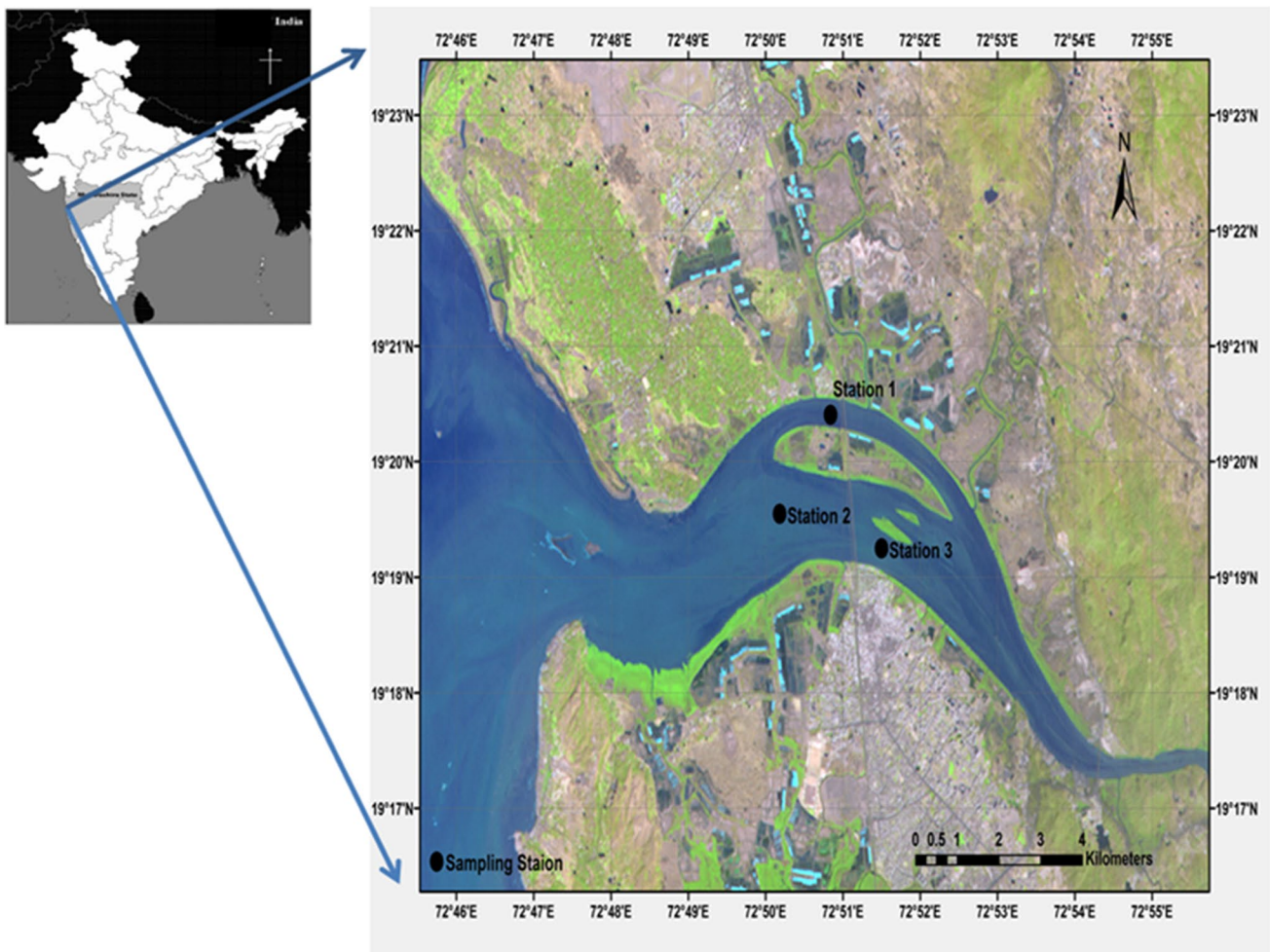


Fig. 1 Study area: location of the URE in the N-W Coast of India. Sampling sites are marked as shaded dots

2009). The industries situated along banks of the river acts as point sources of pollution in the Ulhas River and these pollutants are ultimately reaching the estuarine part (Mohapatra and Rengarajan 2000; Mishra 2002; Lad and Patil 2016). Sewage load from Thane city is also reported to be affecting the aquatic life and ecosystem health (Lala 2004). Moreover, the mangrove cover destruction in a greater extent along the banks due to urbanization has also adversely impacted the coastal ecosystems along the Mumbai waters in the last decades (Jagtap et al. 1994; Kantahrajan et al. 2018). Besides, Kumawat et al. (2015) reported that the fishery in the estuary is also in the wedge of damage due to the by-catch and discards from unsustainable gear operations.

Experimental fishing

Preliminary information of the seasonal patterns in the fish assemblage structure in the estuary was ascertained by experimental fishing trips conducted at three stations in the true estuarine zone (with annual average salinity range of 7.6 ± 5.5 ppt to 33.5 ± 0.70 ppt) between September 2017 and August 2018. Monthly sampling was carried out for an entire year in order to ensure the coverage of complete seasonal patterns in species diversity including all resident and the seasonal migrants in the estuary. Single day Dol net (stationary conical bag net) with a cod end mesh size of 10 mm was used throughout the sampling. The “dolnets” are long conical shaped bag nets with wide rectangular mouth and narrow cod-end. The length of the nets was 30 m, comprising four different segments of webbing. The mouth opening length and width were measured as 10 m and 4 m, respectively. Two wooden cylindrical spikes of 2–4 m length and 15 cm diameter driven to the bottom were used to fix the net. Two fishermen and a canoe are generally required to operate a net. For the experimental fishing, the dolnets were set against the tidal flow, moored at spikes fixed at identified stations, and operated according to the tidal pattern. The two corners of the lower end of the mouth of the dolnet were attached to the spikes, whereas the upper two corners of the mouth were tied to floats made of polystyrene to keep the mouth open. The operation was performed during the day time for a period of 3–4 h.

Un-sorted subsamples of fish catch (with catch to Sub-sample ratio-5:1) were brought to laboratory and care was taken to include all the fish species caught to be well represented in the sub-samples. In the laboratory, finfishes as well as shellfishes were identified up to species level based on the relevant taxonomic keys (Fischer and Bianchi 1984; Bianchi 1985). Mean trophic level of all the species were obtained from the FishBase database (Froese and Pauly 2016) as well as the information from the published literature (Vivekanandan et al. 2009). These data sources provided trophic level

values for 105 species, which included 81 species of finfishes, 21 species of crustaceans, and 3 species of cephalopods. Based on the mean trophic level values, the entire species were categorized to form feeding mode trophic guilds as per the criteria followed by Vivekanandan et al. (2009), as herbivores and detritivores (HRDR—trophic level (TL): 2–2.5), omnivores (OM-TL: 2.51–3), mid-level carnivores (MLCR-TL: 3.01–3.5), high level Carnivores (HLCR-TL: 3.51–4), and top predators (TPR- >4.01) (Supplementary Table 1).

Sample collection for stable isotope analysis

The actual sampling for the stable isotope study was carried out in January 2019. The Winter season was chosen for the sampling because of two reasons. Firstly, the sediments brought by the river and terrestrial discharge remain in suspension during monsoon (July to September) and start settling down with the onset of the winter season (December to February) in the creeks and bays of the western coast of India (Rajawat et al. 2015). Secondly, along the west coast, sea level peaks during December and continue to prevail even in the subsequent months making the seasonal cycle more symmetric (Shankar 2000). Also, since the detritus pathways highly influence estuarine food webs (Mann 1998), January (winter season) is chosen as an ideal month, which is relatively stable period for the ecosystem as the impact of marine and riverine inputs in estuarine sediment sources are balanced.

Carbon sources of the estuarine food web were assumed to be the particulate organic matter (phytoplankton), detritus, and mangrove leaves and are collected during the sampling. Samples of green leaves of the mangroves of similar size and condition were collected by hand from the mangrove patches lining the estuary along the sampling stations. Detritus was taken along the mangrove system, sampling the greatest area possible. Particulate organic matter (phytoplankton) was obtained using a plankton net with a mesh size of 23 μ m. Zooplankton and fish larvae samples were collected using a bolting silk plankton net of 0.02 mm mesh size from the sampling sites of the estuarine system at high tide. Additionally, sediment sample was also collected with a PVC tube (of 9 cm in diameter \times 50 cm in length) at a depth of 5 cm from the fish sampling sites.

The most abundant fish species in the annual catch (pooled for 12 months) were assessed using the Relative Importance Index (RII) (De la Cruz-Aguero 1994), which represents the expression of importance of Individual species in the ecosystem estimated from the abundance values (% number of individuals, % catch weight and % frequency of occurrence of species in catch). Adult individuals of the most abundant species (species with maximum RII in the annual catches) from each trophic guild was chosen as the nodal consumer

species in the food web and considered for the isotopic study and to demonstrate the trophic structure of the URE ecosystem. The representative species are chosen because of the high degree of biodiversity as well as complexity of the ecosystem with dynamic assemblage patterns with respect to seasons and considering the difficulty in analyzing the stable Isotope signatures of all the available species in all the seasons. in the study area. As per the recent estimate, about 105 species of finfishes and shell fishes has been reported from URE (Lal et al. 2021). Two species are chosen from the MLCR trophic guild due to their equally higher RII values. The species selected for the study were *Nematalosa nasus* (HRDR), *Acetes indicus* (OM), *Johnius belangerii* (MLCR), *Escualosa thoracata* (MLCR), *Nemapteryx caelata* (HLCR), and *Lepturacanthus savala* (TPR) (Table 1).

At least four samples of both basal resources and consumer species of greater size and similar dimensions were used to avoid ontogenic variability. For small species like *A. indicus*, more samples were used to achieve the required sample weight for the stable isotope analysis. All the samples were carefully washed in the field and preserved in ice for their transportation to the laboratory, where they were stored in a vertical freezer at -21°C until further processing.

Sample preparation

The preparation of samples for the stable isotope analysis followed the protocol given by Contreras et al. (2018). Samples were carefully washed and thawed before processing. The dorsal white muscle of the finfishes were dissected out and used for the analysis due to the relatively higher consistency of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in the part compared to other tissues (Abrantes and Sheaves 2010). For the shellfish, *A. indicus*, abdominal segments were only used to analyze isotopic signatures (Contreras et al. 2018). The innervation of mangrove leaves was removed with scissors and fine blades. Water samples containing particulate organic matter were filtered using pre-combusted glass fiber filters (GC5047 mm, pore size: $0.5\ \mu$) to extract the solid part. All samples, including detritus and sediment, were dried at 60°C for a minimum of 48 hrs in a hot air oven and later homogenized

to form fine powder using a standard mortar and pestle and sieved through a $60\ \mu$ mesh screen to ensure homogeneity. From the powdered sample, lipids are extracted using methanol-chloroform (2:1 by volume), as lipids are depleted in $\delta^{13}\text{C}$ compared with the whole organism's tissue lipid content (Peterson and Fry 1987; Kling et al. 1992). For the estimation of carbon isotopic signature and total organic carbon (TOC) of the sediment and detritus samples, acid pre-treatment was carried out to remove the carbonates by centrifuging the dried and powdered samples with 5% HCl in 2000–3000 rpm for 5–10 min. The procedure was repeated about 4–5 times until the acid carbonate reaction stopped, followed by distilled water wash in the centrifuge until the sample turned neutral, which was checked using a pH paper. The supernatant was discarded each time, and the sample was dried again at $\sim 50^{\circ}\text{C}$. After drying, the samples were recovered and converted it into fine powder. From the homogenized sample, one milligram (mg) of tissue (both finfish and shellfish) samples and 10 mg of sediment samples were weighed using tin capsules in a microbalance.

Stable isotope analysis

The stable carbon and nitrogen isotopic ratios ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) were analyzed using an Isotope Ratio Mass Spectrometer (IRMS): MAT 253 (Thermo Finnegan, Germany). Stable carbon and nitrogen isotopic ratios were expressed in the delta notation ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) relative to the standard reference materials (V-PDB (Pee Dee Belemnite) for $\delta^{13}\text{C}$ and atmospheric N_2 for $\delta^{15}\text{N}$) as:

$$\delta X = \left[\left(\frac{R_{\text{sample}}}{R_{\text{standard}}} \right) - 1 \right] \times 1000 \quad (1)$$

where “X” is ^{13}C or ^{15}N , and “R” is the ratio of heavy to light isotopes, wherein “ δX ” expressed in ‰ (“Permil”).

From the stable Carbon isotopic ratios, the sources and links of the estuarine food web were predicted. From the Nitrogen isotopic ratios, the trophic positions and the food chain lengths were determined. The $\delta^{15}\text{N}$ values alone cannot be considered to represent the trophic position, since the

Table 1 Categorization criteria and the selected consumer representatives from various trophic guilds used for the study (Vivekanandan et al. 2009)

Trophic level category	Trophic guild	Abbreviation	Species selected	(N)	Trophic level (FishBase)
(2.00–2.5)	(HRDR)	Herbivores and Detritivores	<i>Nematalosa nasus</i>	5	2.2 ± 0.09
(2.51–3.00)	(OM)	Omnivores	<i>Acetes indicus</i>	> 25	2.51 ± 0.036
(3.01–3.5)	(MLCR)	Mid-level carnivores	<i>Escualosa thoracata</i>	6	3.2 ± 0.1
(3.01–3.5)	(MLCR)	Mid-level carnivores	<i>Johnius belangerii</i>	4	3.3 ± 0.32
(3.51–4.00)	(HLCR)	High-level carnivore	<i>Nemapteryx caelata</i>	4	4.0 ± 0.64
(> 4.01)	(TPR)	Top predator	<i>Lepturacanthus savala</i>	4	4.6 ± 0.76

$\delta^{15}\text{N}$ of primary producers (defined as organisms that convert inorganic N to organic N) are highly variable among systems (Kling et al. 1992; Cabana and Rasmussen 1996) and within systems through time (Toda and Wada 1990; Cabana and Rasmussen 1996). Hence, it is necessary to measure the isotopic signatures of each fish relative to an ecosystem-specific baseline $\delta^{15}\text{N}$ signature (Le Loc'h et al. 2008; Post 2002; Vander Zanden and Vadeboncoeur 2002). According to Vander Zanden et al. (1997), the species to be selected as the baseline should be relatively large and long-lived primary consumer species, which integrate temporal variability in primary producer's $\delta^{15}\text{N}$, thereby representing the average baseline $\delta^{15}\text{N}$ signature. In this study, the fish trophic positions were interpreted relative to that of Gizzard shad, *N. nasus*, which has been chosen to be the reference organism as per the criteria explained above.

The trophic position (isotopic) for each species was calculated using the formula given by Post (2002):

$$\text{Trophic position (TL)} = (\delta^{15}\text{N}_{\text{fish}} - \delta^{15}\text{N}_{\text{Base}}) / 3.4 + \lambda \quad (2)$$

Where 3.4 represents a 1.0 trophic level increment in $\delta^{15}\text{N}$ and λ is the trophic position of the organism used to estimate $\delta^{15}\text{N}$ base.

Comparison of dietary and isotopic trophic levels

Out of the 6 species chosen from each trophic levels, the dietary trophic positions were calculated for *Johnius belangerii* (MLC), *Nemapteryx caelata* (HLC), and *Lepturacanthus savala* (TPR) based on the gut content analysis.

For the rest of the species, the dietary trophic level was obtained from the published literature from Indian coastal waters (Vivekanandan et al. 2009). Calculation of fish trophic position required estimation of the trophic position of prey organisms. In the present study, the simplest possible assumptions together with the reported estimates were used. Primary producers and detritus were assigned a TL of 1.00, and for zooplankton 2.00, and so on.

Dietary TL was calculated using the following equation (Christensen and Pauly 1992):

$$\text{TL}_i = 1 + \sum \text{DC}_{ij} \times \text{TL}_j \quad (3)$$

Where “ TL_i ” is the trophic level of species “i”, “ DC_{ij} ” is the proportion of prey species “j” in the diet of species “i”, and “ TL_j ” is the trophic level of prey species “j”. Trophic levels for prey items used in dietary calculations of trophic position are obtained from literature, as shown in Table 2. The trophic level estimated from the stable isotopic ratios was compared with the dietary estimates and the published reports. The food chain length (FCL) was also enumerated, which is defined as the trophic position of the top predator estimated as the species or taxon with the highest *N* value.

Stable isotope mixing model with SIMMR

Stable isotope mixing models are used to quantify the proportional contributions of various sources to a mixture (Parnel

Table 2 Trophic Levels of prey items used for dietary trophic level calculations of consumer species

Prey category	Species/group includes	Estimated trophic position
Finfishes		
Lesser sardines ^a	<i>Sardinella gibbosa</i>	3.15
White sardine ^a	<i>Escualosa thoracata</i>	3.2
White bait ^a	<i>Stolephorus indicus</i>	3.2
Uniconcod ^a	<i>Bregmaceros maclellandi</i>	3.3
Taper tailed anchovy ^a	<i>Coilia dussumieri</i>	3.35
Sciaenids ^a	<i>Otolithes cuvieri</i> , <i>Johnius belangerii</i> , <i>Johnius vogleri</i>	3.5
Unidentified fish matter		3.5
Decapods		
Penaeids ^a	<i>Parapenaeopsis stylifera</i> , <i>Metapenaeus affinis</i>	2.51
Non-penaeids ^a	<i>Nematopalaemon tenuipes</i> , <i>Acetes indicus</i>	2.51
Crabs ^a	<i>Charybdis callianassa</i>	2.7
Others		
Omnivorous zoo benthos ^b	Amphipoda	2.5
	Isopoda, Oligochaeta	
Zooplankton ^b	Cladocera, Copepoda	2.0
Detritus ^b	Detritus, plants, mud	1.0

^aTrophic position of prey items (as per Vivekanandan et al. 2009)

^bTrophic position of prey items (as per Vander Zanden and Rasmussen 1996)

et al. 2013). Isotopic values are determined for the tissues of a consumer and its food sources, and similarity in isotopic composition between the consumer's tissues, and its food sources (after adjustment for isotopic sorting or fractionation during digestion, metabolism, and assimilation) gives an index of the relative importance of each item in the consumer's diet. In the present study, a Bayesian mixing model employing two isotopes ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) has been developed that allows the estimation of contributions of three sources such as detritus, particulate organic matter, and mangroves to the assimilated diet of eight consumers. Other carbon sources like sediments with similar isotopic values to detritus were excluded from the analysis. The stable isotope mixing model, depicting the food web structure of URE, was developed with SIMMR-V: 0.4.2 (stable isotope mixing model with "R" package) (Parnell and Inger 2019). For the ease of running the model, the consumer species were represented as Group 1: ZP, Group 2: FL, Group 3: NN, Group 4: AI, Group 5: ET, Group 6: JB, Group 7: NC, and Group 8: LS.

This three-source mixing model is based on the fundamental linear mass balance equations (Phillips and Koch 2002):

$$\delta^{13}C_M = f_x(\delta^{13}C_x + \Delta^{13}C_{\text{tissue-x}}) + f_y(\delta^{13}C_y + \Delta^{13}C_{\text{tissue-y}}) + f_z(\delta^{13}C_z + \Delta^{13}C_{\text{tissue-z}}) \quad (4)$$

$$\delta^{15}N_M = f_x(\delta^{15}N_x + \Delta^{15}N_{\text{tissue-x}}) + f_y(\delta^{15}N_y + \Delta^{15}N_{\text{tissue-y}}) + f_z(\delta^{15}N_z + \Delta^{15}N_{\text{tissue-z}}) \quad (5)$$

$$1 = f_x + f_y + f_z \quad (6)$$

where the subscripts "x," "y," "z," and "M" represent three food sources and the mixture (i.e., the consumer), respectively; "f" represents the fractional contribution of "C" or "N" from each food source to the consumer's diet, and $\Delta^{13}\text{C}_{\text{tissue-x}}$ is the trophic fractionation (change in $\delta^{13}\text{C}$ during assimilation) between food source "x" and the consumer's tissue. "f" represents the proportion of C from a food source and not necessarily the proportion of the biomass. This standard linear mixing model is a system of three equations in three unknowns (f_x , f_y , and f_z), which can be solved to determine each food source's contribution to the diet. The present mixing model for two isotopes and three sources that do incorporate concentration variation in the sources for carbon and nitrogen, which has been enumerated separately using the Isotope Ratio Mass Spectrometer (IRMS): MAT 253 (Thermo Finnegan, Germany) before the analysis. Prior to running the mixing model, $\delta^{13}\text{C}$ of the consumers has to be corrected ($\delta^{13}\text{C}_{\text{corr}}$) for Trophic Enrichment Factor (TEF) and TL, using the following equation (Giarrizzo et al. 2011):

$$\delta^{13}\text{C}_{\text{corr}} = \delta^{13}\text{C} - (\text{TEF} \times (\text{TL} - 1)) \text{ for carbon} \quad (7)$$

$$\delta^{15}\text{N}_{\text{corr}} = \delta^{15}\text{N} - (\text{TEF} \times (\text{TL} - 1)) \text{ for nitrogen} \quad (8)$$

A standard TEF of $0.4 \pm 1.3\text{‰}$ for $\delta^{13}\text{C}$ and $3.4 \pm 1.0\text{‰}$ for $\delta^{15}\text{N}$ was used, as suggested by Post (2002). The present study analyses the source contributions in the assimilated diet of 8 different consumer species, considering the advantage that SIMMR can handle these data sets, provided they all share the same sources and concentration dependence values. The model has also enabled a comparison between these groups according to the relative contribution of various sources.

Estimation of isotopic niche

The ecological niche concept can provide insights into a wide variety of ecological and evolutionary problems (Martínez del Río et al. 2009). In the stable isotopic niche analysis, convex hull area (TA) describes the niche width of the organism (Quevedo et al. 2009) or community in question (Layman and Post 2008), which is used under two distinct situations, firstly, to describe individual components of the community and secondly applied to entire communities of different species or functional groups (e.g. Layman and Post 2008; Donázar-Aramendía et al. 2019). One of the shortcomings identified herein is that application of the metrics to single community group members is sensitive to sample size, particularly across the range of sizes frequently encountered in ecological studies ($n < 50$). Multivariate ellipse-based metrics are more suitable than Convex Hull methods when applied to single community members, which is unbiased with respect to sample size, allows robust comparison to be made among data sets comprising different sample sizes (Jackson et al. 2011). The total convex hull area (TA) and the standard ellipse area (SEAc) were also calculated for the URE community (c indicates that the SEA was corrected for a small sample size) using the SIBER package in R.

Results

Isotopic signatures of selected species

Isotopic carbon signatures of sources varied between -26.20‰ in mangrove leaves to -20.40‰ in phytoplankton, whereas in the consumers, the values ranged between -24.38‰ in *A. indicus* to -19.87‰ in zooplankton (Table 3). The isotopic nitrogen signatures reflected in the consumers' trophic level and showed substantial variation with respect to the trophic guilds considered. The ratio ranged from 6.71‰ in the primary consumer species to 15.07‰ in the top predator (Table 3). The values for

sediment $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were obtained as -25.3‰ and 8.70‰ , respectively.

Isotopic niche

The iso-space plot is divided into four quadrants to display the species distribution in the isotopic niche space (Fig. 2). The species that had enriched $\delta^{13}\text{C}$ and enriched $\delta^{15}\text{N}$ were distributed on quadrant (A); depleted $\delta^{13}\text{C}$ and enriched $\delta^{15}\text{N}$ in quadrant (B); depleted $\delta^{13}\text{C}$ and depleted $\delta^{15}\text{N}$ in quadrant (C), and enriched $\delta^{13}\text{C}$ and depleted $\delta^{15}\text{N}$ in quadrant (D). There were notable differences among the $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ niches of the dominant estuarine species, represented in different trophic guilds. The species, *L. savala* was found at the top of the niche map, occupied in the quadrant (A) with the enriched $\delta^{13}\text{C}$ and maximum $\delta^{15}\text{N}$ value

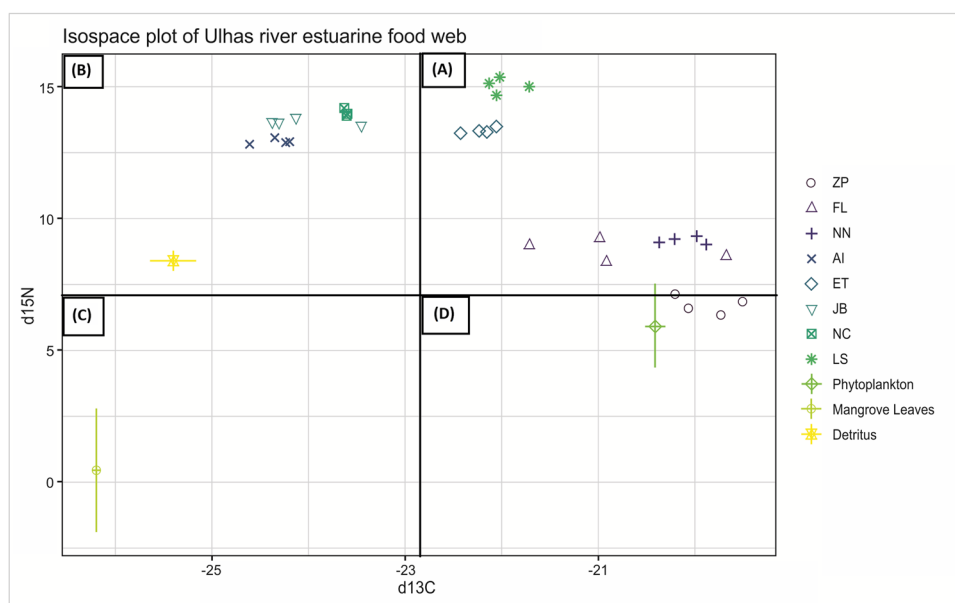
corresponding to the highest trophic level among the species. The groups like fish larvae, *N. nasus*, and *E. thoracata* were also included in the quadrant (A), with relatively enriched $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$. The species such as *A. indicus*, *J. belangerii*, and *N. caelata* occupied quadrant (B), indicating their utilization of depleted carbon sources compared to the other species. Concomitantly, the source detritus has also occupied in the quadrant (B) along with these species, confirming the higher utilization of more depleted carbon source, i.e. detritus. Mangrove leaves were grouped in quadrant (C) as expected, with the lowest $\delta^{15}\text{N}$, and the lowest trophic level with potentially depleted $\delta^{13}\text{C}$ sources. Phytoplankton and zooplankton were observed along quadrant (D) of the niche map constructed for URE.

On the other hand, the iso-space plot of mean $\delta^{13}\text{C}$ versus $\delta^{15}\text{N}$ values (\pm SD) of basal resources and consumers

Table 3 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (mean $\text{‰} \pm$ SD) of sources and the consumer species

Species	Mean $\delta^{13}\text{C}$ (‰)	SD	Mean $\delta^{15}\text{N}$ (‰)	SD
Phytoplankton	-20.40	0.12	5.90	1.61
Mangrove leaves	-26.20	0.02	0.40	2.36
Detritus	-25.40	0.24	8.40	0.11
Sediment	-25.30	0.99	8.70	0.09
Zooplankton	-19.87	0.32	6.71	0.35
Fish larvae	-20.82	0.85	8.79	0.40
<i>Nematalosa nasus</i>	-20.11	0.22	9.18	0.15
<i>Acetes indicus</i>	-24.38	0.17	12.93	0.12
<i>Escualosa thoracata</i>	-22.22	0.16	13.42	0.14
<i>Johnius belangerii</i>	-24.07	0.42	13.70	0.12
<i>Nemapteryx caelata</i>	-23.61	0.02	14.04	0.12
<i>Lepturacanthus savala</i>	-21.98	0.18	15.07	0.29

Fig. 2 Scattergram of showing the food web structure in URE based on nodal species. (Colored icons represent each species. The lines divide the niche map into four quadrants. The intersection of the lines represents the central point of the niche map)



from URE ecosystem indicated the dependence over the phytoplankton sources by the groups ZP, FL, NN, and ET as indicated by their closer positions occupied in the isotopic space with respect to the $\delta^{13}\text{C}$ of POM. The sources, mangrove leaves and detritus showed close $\delta^{13}\text{C}$ isotopic values, indicating that the detritus component has a high dependency over mangrove leaves, which might generally be sourced from the decomposition of mangrove leaves in the ecosystem. The trophic structure of URE, measured with the standard ellipse area corrected for a small sample size (SEAc) was 11.08, and the total area (TA) was 24.2. The fairly larger values of SEA in the URE suggest a much broader food web structure and high trophic diversity in the ecosystem (Fig. 3).

Stable isotope mixing model with SIMMR

The summary outputs of the isotope mixing model generated for URE based on three sources and eight consumer species (representing trophic guilds), are shown in Table 4. The SIMMR output table represents the mean values and the credible intervals (2.5 to 97.50%) containing the proportions

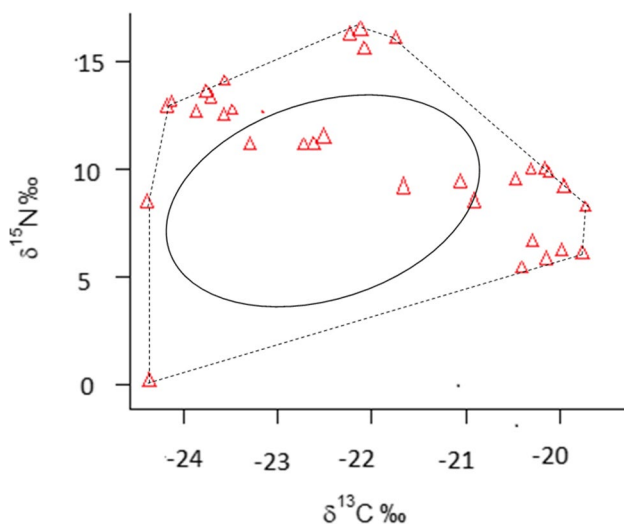


Fig. 3 Trophic niche width according to the convex hull area (dotted lines) and standard ellipse areas corrected for a small sample size (SEAc) for the URE (solid lines). Triangles represent individuals of all the species measured in the URE

Table 4 Summary outputs of the isotope mixing model generated for Ulhas River estuary

	Mean	sd	2.50%	25%	50%	75%	97.50%
Phytoplankton	0.274	0.071	0.161	0.224	0.266	0.316	0.438
Mangrove Leaves	0.051	0.031	0.010	0.028	0.045	0.067	0.130
Detritus	0.674	0.092	0.460	0.622	0.688	0.741	0.816
sd [$\delta^{13}\text{C}$]	1.778	0.243	1.386	1.604	1.755	1.921	2.335
sd [$\delta^{15}\text{N}$]	4.902	0.677	3.770	4.429	4.838	5.295	6.425

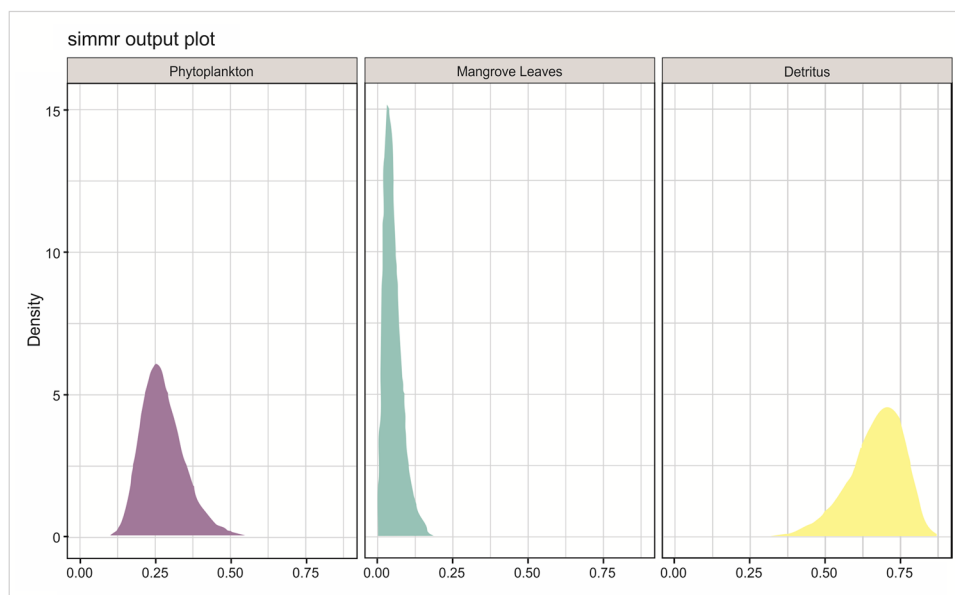
of each sources in the consumer species (combined) analyzed in the study. In the Bayesian model, the credible interval is just the range containing a particular percentage of probable values. The results suggest that the dietary proportions for this model are quite certain. However, the credible interval for mangrove leaves was the narrowest, running from approximately 1 to 13% to the overall contribution of the estuarine fish diet. The density plot of source contributions (Fig. 4) has also indicated that all the three sources chosen in the present study are fairly separated from one another.

Source contribution to consumers

The multiple consumer-source isotopic values could be combined in SIMMR based on “multi-group data” function which yield the tracers plot representing the positioning of the consumers on the iso-space (Parnell and Inger 2019). The outputs from SIMMR depicted the contribution of various sources to consumers from different trophic guilds. Among the three sources analyzed in this study, detritus contributed maximum to the assimilated diet in the fish fauna of URE, followed by phytoplankton (Fig. 5). However, the diet sourced from mangrove leaves contributed the least to the food web. The sources analyzed in the study, such as phytoplankton, detritus, and mangrove leaves together contributed only around 30% of the assimilated diet of the consumers combined, indicating the possibility of missing food sources in the present study. When the consumers were analyzed separately for their assimilated diet contributions, the primary trophic guild such as Group 1 (zooplankton) (Fig. 6A), Group 2 (fish larvae) (Fig. 6B), and Group 3 (*N. nasus*) (Fig. 6C) were found to utilize the localized food sources in the estuary. The sources evaluated in this study, such as detritus, phytoplankton, and mangrove leaves together, contribute about more than 70% of their assimilated diet. For all these three primary consumer groups, source phytoplankton showed maximum contribution to the assimilated diet.

The source contribution plots of *A. indicus* indicated that its assimilated diet is mainly sourced from detritus and mangrove leaves (Fig. 6D). However, all three sources together contributed only about 35% of the diet components, indicate the possibilities of utilizing allochthonous dietary sources. Phytoplankton was found to be the major diet source for *E. thoracata*. Where the local sources considered in the study

Fig. 4 Density plot for trophic chain-source contributions in URE



together accounted for nearly 30% of the assimilated diet (Fig. 6E). While, the isotopic source contribution plot of *J. belangerii* (Fig. 6F) and *N. caelata* (Fig. 6G) showed similar trends, dominated by detritus and mangrove leaves that contributed about 50% of their assimilated diet. In addition, the phytoplankton source also showed a minor influence on the diet of *J. belangerii* and *N. caelata*.

The source contribution plot for the top predator species, *L. savala*, indicated that only over 30% of its assimilated diet is accounted by the local sources, in which phytoplankton based sourced were the major contributors (Fig. 6H). The summarized results of the stable isotope mixing model is provided at Fig. 7. The entire trophic space is divided into 3 isotopic trophic zones with (a) higher phytoplankton influence, (b) mangrove-detritus influence, and (c) mixed influence. Five out of the eight consumer species chosen in the present study occupied in the mixed influence zone. Within

the mixed influence zone, the species *L. Savala* and *E thoracata* showed more phytoplankton influence and *A. indicus*, *J. belangerii*, and *N caelata* showed more detritus influence.

Comparison of dietary and isotopic trophic levels

Among the six species chosen from each trophic guild based on the highest RII for the stable isotopic ratio analysis, the dietary trophic positions were calculated for three species such as, *J. belangerii* (MLCR), *N. caelata* (HLCR), and *L. savala* (TPR) for comparison. The dietary data summarized by calculating the average diet percentage (percentage of stomach volume \pm 1SD) for every three species (Table 5). *A. indicus*, *E. thoracata*, and *S. indicus* were found to be the major diet components for all three species. A clear affinity towards the zoobenthic prey types such as polychaetes was evident for *N. caelata*, compared to the other two species. The dietary TL values obtained were 3.35 ± 0.77 , 3.97 ± 0.49 , and 4.27 ± 0.19 for *J. belangerii*, *N. caelata*, and *L. savala*, respectively. The trophic levels of fish species corresponding to different trophic guilds based on isotopic signatures varied between 2.00 in *N. nasus* to 3.75 in *L. savala* (Table 6). While comparing the TL estimates of these species between the diet data, stable isotope data and the available literature, the species *J. belangerii* showed the highest consistency between the three estimates of trophic positions (TL=3.35, 3.34, and 3.3 respectively). However, the dietary TL values for *N. caelata* and *L. savala* were more or less close to the earlier records than the isotopic TL values. The comparison of the isotopic and earlier estimates of the trophic positions revealed the relationship such that: $\delta^{15}\text{N}$ trophic position = $0.67 \times$ reported

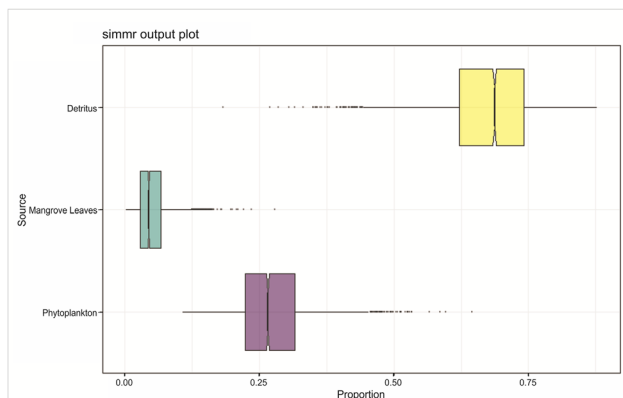


Fig. 5 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ -based contribution of various sources to the trophic web of URE constructed with the nodal species

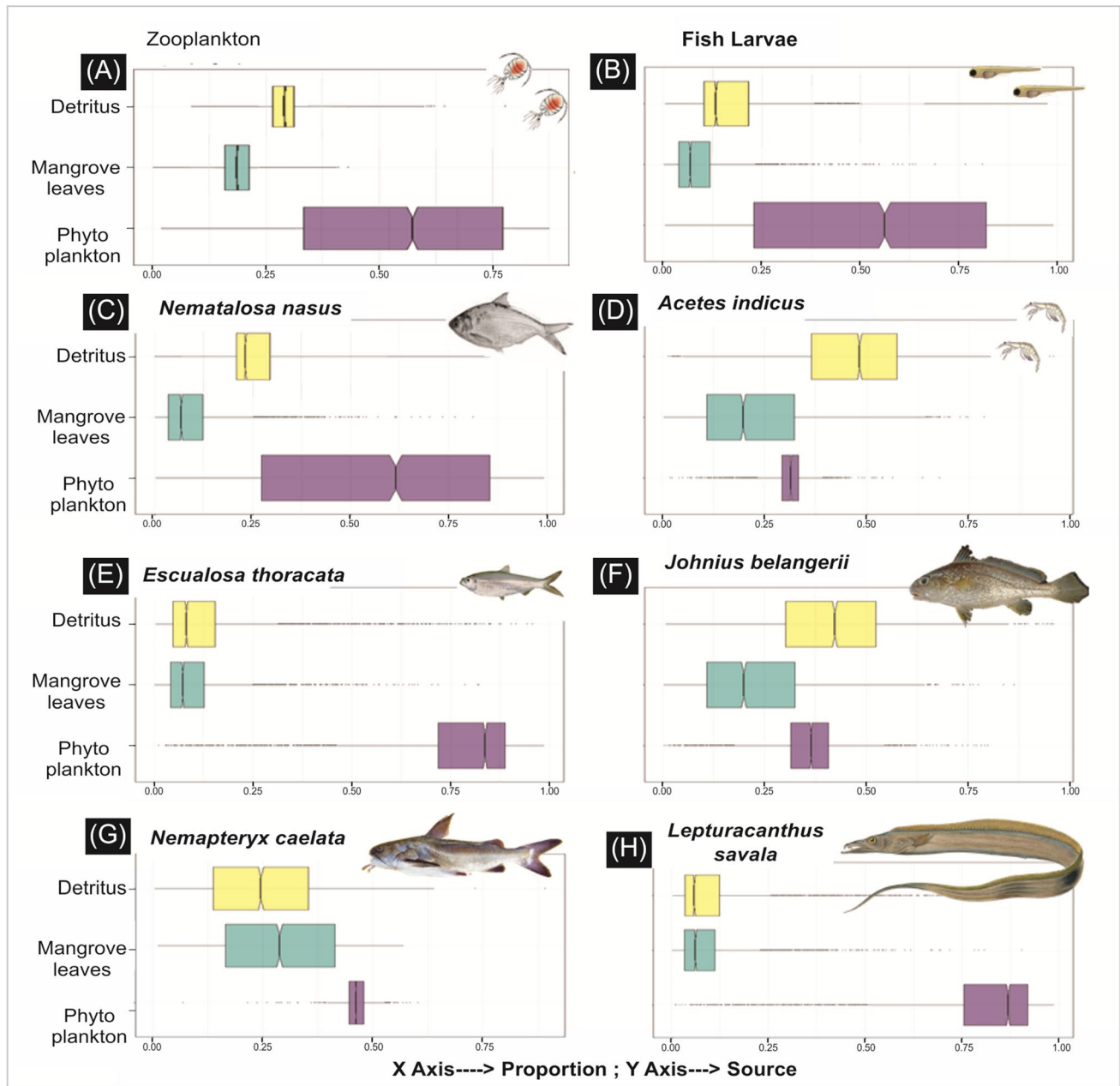


Fig. 6 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ -based contribution of various sources to the assimilated diet of consumers of URE: **A** zooplankton, **B** fish larvae, **C** *Nematalosa nasus*, **D** *Acetes indicus*, **E** *Escualosa thoracata*, **F** *Johnius belangerii*, **G** *Nemapteryx caelata*, and **H** *Lepturacanthus savala*

trophic position + 0.27; $R^2 = 0.67$) (Fig. 8). Trophic position of fishes using isotope ratios demonstrated variations from the generally reported estimates for the majority of species; however, a few were more or less close to the estimates. The species such as *A. indicus* was the major outlier, where the isotopic TL showed significantly higher value than the published reports. At the same time, the predatory carnivorous species such as *L. savala* and *N. caelata* showed lower isotopic TL values compared to the literature estimates.

Discussion

Food webs are recognized as the functional components of an ecosystem and have been structured by complex species interactions (Summerhayes and Elton 1923). Characterization of food web functioning is still challenging due to the complexity in precisely measuring species interactions within a food web. Novel tracing methods that estimate species diet uptake and trophic positions are therefore required to determine food

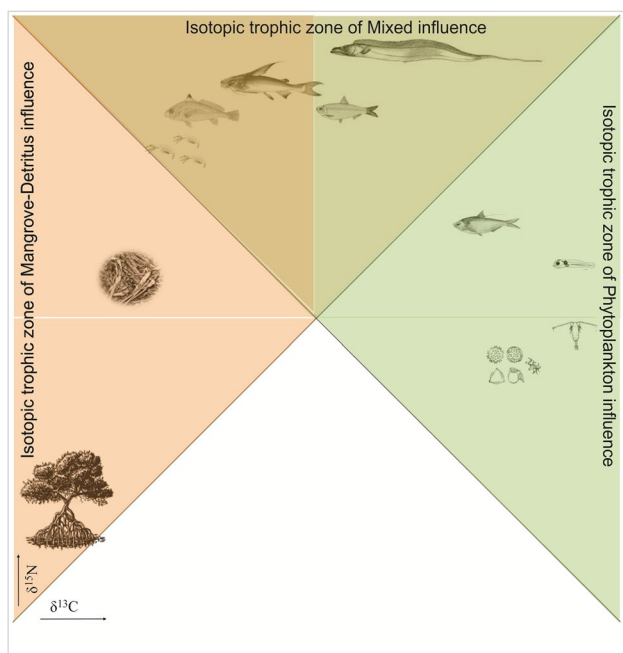


Fig. 7 Summarized results of the stable isotope mixing model of URE

web features. The application of stable isotope analysis in the characterization of food webs has improved the understanding of sources and niche properties along with the quality of trophic level (TL) estimations, especially for the aquatic

ecosystems, which are less amenable to the traditional tracing methods (Boecklen et al. 2011).

Source variations

The wide range of $\delta^{13}C$ values indicates the diverse use of carbon sources in the estuarine habitat (Bouillon et al. 2008). In riverine ecosystems, the existence of diverse carbon sources is reported to be the result of size, the degree of seasonal fluxes, and fluvial dynamics (Caraco et al. 2010; Babler et al. 2011). Similar effects are also expected to affect the source variations in the estuarine systems. Stable isotope compositions of particulate organic matter (POM) have been used as a powerful tool to understand the sources and cycling of carbon in aquatic ecosystems (Popp et al. 1989, 1997, 1998; Bidigare et al. 1997; Rau et al. 1996). Particulate organic matter of various types, including those generated from forests, primary production in rivers, and human activity, is supplied to coastal waters via rivers. However, the nature and role of river-supplied POM in coastal waters is not universal, as the source and course characteristics shows wide range of regional variability (Komatsu et al. 2019). Since there are more than 10,000 small rivers originating from monsoon-dominated and/or mountainous regions globally, it must be appreciated that their total organic carbon contribution to the coastal system must be substantial (Shynu et al. 2015).

Table 5 Dietary data and trophic level calculated for each selected species

Species	(N)	Prey items found	Dietary trophic position	± SE
<i>Johnius belangerii</i>	45	<i>A. indicus</i> , <i>E.thoracata</i> , <i>S.indicus</i> <i>P.stylifera</i> , <i>N.tenuipes</i> , unidentified fish matter, <i>C. callianassa</i>	3.35	0.77
<i>Nemapteryx caelata</i>	51	<i>A. indicus</i> , <i>E. thoracata</i> , <i>B. mccllellandi</i> <i>S. indicus</i> , <i>P. stylifera</i> , <i>N. tenuipes</i> Polychaete worm, Amphipods, isopod, Cladocera, Copepoda, unidentified fish matter, Detritus	3.97	0.49
<i>Lepturacanthus savala</i>	35	<i>E.thoracata</i> , <i>S. gibbossa</i> , <i>S.indicus</i> <i>A.indicus</i> , <i>P.stylifera</i> , <i>M.affinis</i> , Sciaenids, <i>C.dussumeiri</i> , unidentified fish matter	4.27	0.19

Table 6 Comparison of trophic levels of various species obtained from Diet analysis, $\delta^{15}N$ values, and literature estimates

Species	Trophic level (dietary) ^a	Trophic level (isotopic)	Trophic level (reported) ^b
<i>Nematalosa nasus</i>	-	2 ± 0.19	2.2 ± 0.09
<i>Acetes indicus</i>	-	3.24 ± 0.06	2.51 ± 0.036
<i>Escualosa thoracata</i>	-	3.12 ± 0.21	3.2 ± 0.1
<i>Johnius belangerii</i>	3.35 ± 0.77	3.34 ± 0.24	3.3 ± 0.32
<i>Nemapteryx caelata</i>	3.97 ± 0.49	3.44 ± 0.33	4.0 ± 0.64
<i>Lepturacanthus savala</i>	4.27 ± 0.19	3.75 ± 0.52	4.3 ± 0.76

^aTrophic level estimated by diet analysis from the present study

^bTrophic level reported using dietary data of fishes along the Indian coast (Vivekanandan et al. 2009)

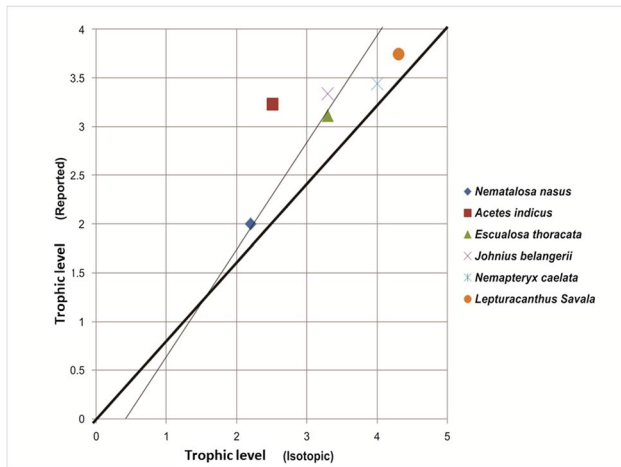


Fig. 8 Comparison of mean trophic positions (TL's) of the species obtained from literature estimates and $\delta^{15}\text{N}$ method. The bold diagonal line represents the 1:1 line

A study from the Mandovi-Zuari Estuaries by Shynu et al. (2015) indicated the dominance of terrestrial plant-derived organic matter and terrestrial soil-derived organic matter respectively, in the Mandovi and Zuari estuaries during wet season. It is estimated that each river contributed at least ~20% terrestrial organic carbon (TOC) to the coastal system during wet season and received similar quantity of TOC during dry season. Samanta et al. (2015) reported that $\delta^{13}\text{C}$ values in the Ganga (Hooghly) River estuary are a result of the combined influence of seawater-river water mixing, chemical weathering, biological production, precipitation or dissolution of minerals such as calcite, and respiration and degradation of organic matter, which may be supplied via both natural as well as anthropogenic processes.

As per Kelly et al. (1998) and Coffin and Cifuentes (1999), the $\delta^{13}\text{C}$ values are lighter (-34 to -23‰) for C3 plants and heavier (-17 to -9‰) for C4 plants (Deines 1980), whereas those derived from the marine phytoplankton range (-22 to -18‰) in between C3 and C4 plants sources. As the $\delta^{13}\text{C}$ value for the detritus was about -25.4 , and was found very close to the values of the mangrove leaves (-26.2), it is clear that the detritus in URE during the study period was of terrestrial-mangrove based origin. Also, the $\delta^{13}\text{C}$ of the phytoplankton (-20.40) lies within the range of value that of the marine phytoplankton.

A comparison of the $\delta^{13}\text{C}$ values of the carbon sources from various tropical mangrove/coastal ecosystems is given in Table 7. The carbon sources analyzed in this study (-26.20 to -20.40‰) are found to be more enriched than the carbon sources reported from the majority of the tropical coastal ecosystems (Abrantes and Sheaves 2010; Giarrizzo et al. 2011; Vaslet et al. 2012; Shahraki et al. 2014; Sepu'lveda-Lozada et al. 2015; Contreras et al. 2018; Nelson

et al. 2019). The basal source, mangrove leaves showed the most depleted carbon isotopic signature among the others and found within the range of $\delta^{13}\text{C}$ values reported from the other ecosystems. Being C3, a plant (plants that follow C3 photosynthetic pathway), mangroves are reported to have low $\delta^{13}\text{C}$ values because of the photosynthesis with high stomatal conductance leading to depletion in $\delta^{13}\text{C}$ values (Brugnoli and Lauteri 1991). The particulate organic matter (POM), including the phytoplankton analyzed in this study, was close to the estimates from Qeshm Island, Persian Gulf of northern Indian Ocean (Shahraki et al. 2014), and Northern Gulf of Mexico (Nelson et al. 2019). However, there exist large regional variations among the $\delta^{13}\text{C}$ values of the POM between the study areas, which will be more of a function of the prevailing environmental conditions and composition of the plankton community and hence cannot be generalized in a broader scale (Bouillon et al. 2002).

The $\delta^{13}\text{C}$ signal for detritus was closer to the isotopic values of mangroves in the URE, possibly indicating that these are the predominant source of detritus in the area. These results are in agreement with the values from the mangrove ecosystems of tropical Eastern Pacific (Contreras et al. 2018) as well as the southern Gulf of Mexico (Sepu'lveda-Lozada et al. 2015). However, for Qeshm Island, Persian Gulf of Northern Indian Ocean (Shahraki et al. 2014), the detrital $\delta^{13}\text{C}$ signal was closer to that of the POM and phytoplankton. This indicating that the source of detritus carbon in the coastal ecosystems also shows region-specific variations.

Several studies reported the impact of the mangrove-seagrass sourced detritus to be the persistent source of organic matter in the soft sediments of estuaries and coastal bays (Bishop et al. 2007; Taylor et al. 2010). The sediments in the Indian estuaries are also reported to be constituted by high levels of detrital load (Chakraborty et al. 2014; Irudhayanathan et al. 2011; Rao et al. 2011). Moreover, increase of organic matter with decreasing the particle size has been reported from many areas, around the world, and is attributed to co-sedimentation of particulate organic matter with clay and mineral particles (Carter and Mitterer 1978; Sheu and Presely 1986). Nikam et al. (2008) also recorded high organic carbon load in the fine surface sediments from the URE. Hence, the closer values of the stable carbon and nitrogen isotopic signatures of the detritus and sediments observed in the present study substantiates these results. Similar pattern in the detritus-sediment isotopic composition were also reported by Contreras et al. (2018) in a Riverine Mangrove System at the Central Coast of Colombia.

Source consumer relationships

The omnivorous invertebrate representative, *A. indicus*, exhibited the most depleted value of $\delta^{13}\text{C}$ among the consumer species (-24.38‰), which was highly close to the

Table 7 A comparison of the $\delta^{13}\text{C}$ values of the carbon sources from various tropical mangrove/ coastal ecosystems

Study area	Author	Food sources studied						
		Mangrove leaves	Particulate organic matter (POM)	Phytoplankton (Separately)	Detritus	Benthic algae	Marsh plants	Seagrass
Tropical North Queensland, Australia	Abrantes and Sheaves 2010	-28.9‰	--	--	--	--	--	-18.6‰
Curuçá estuary, northern Brazil	Giarrizzo et al. 2011	27.8 to -29‰	-28.2 ± 1.7‰	--	--	-21.5 ± 0.8‰	--	-14.6 to -7.0‰
Tropical Western Atlantic region	Vaslet et al. 2012	-28.9 to -27.1‰	--	21.6 to -21.1‰	--	-19.8 to -16.4‰	--	--
Qeshm Island, Persian Gulf, Northern Indian Ocean	Shahraki et al. 2014	-28.2 ± 1.1‰	-22.8 ± 0.8‰	-22.3 ± 1.6‰	-19.5 ± 2.1‰	-17.8 ± 2.1‰	--	--
Southern Gulf of Mexico	Sepu'lveda-Lozada et al. 2015	-25.1‰	-29.1 to -28.3‰	-12.5‰	-29.7 to -28.1‰	-33.2 to -22.4‰	-32.4‰	--
Tropical Eastern Pacific	Contreras et al. 2018	-30.2 to -26.9‰	--	-30.6 ± 0.4‰	-28.5 ± 0.6‰	--	--	--
Northern Gulf of Mexico	Nelson et al. 2019	-26.3 ± 1.1‰	-22.1 ± 0.8‰	--	--	-16.1 ± 2.1‰	-14.5 ± 0.3‰	--
Ulhas River Estuary, Tropical Eastern Indian Ocean region	Present study	-26.20 ± 0.02‰	-20.40 ± 0.12‰	--	-25.40 ± 0.24‰	--	--	--

detrital $\delta^{13}\text{C}$ values (-25.40‰). This similarity in values indicated a strong linkage of *A. indicus* with its benthic feeding niche. Also, the shallow coastal waters of the Northwest coast of India have been reported to have a good amount of detritus, the magnitude of which is more pronounced along the Mumbai waters (Babenerd et al. 1973). Deshmukh (2002) suggested that the phenomenal abundance of paste shrimp, *A. indicus* in Mumbai coastal waters compared to the other regions, is, in fact, supported by this huge detrital load in the region. Therefore, the present study clearly concurring the theories behind the detritus-paste shrimp trophic relationship. A majority of the studies that investigated the estuarine food web sources has widely used some generic factors to explain the higher productivity of estuarine consumers (Currin et al. 1995; Deegan and Garritt 1997; Ansari et al. 1995; Sreekanth et al. 2020). These factors include the marine sediments carried by tides, terrestrially derived organic matter carried by rivers, phytoplankton or benthic microalgae, and abundant biomass of marsh plants cycled through detrital pathways. Vingare et al. (2012) have also

reported the high reliance of all top-level consumers towards benthic prey in the estuarine waters of Europe. Similar inferences can be made from URE ecosystem also as, *A. indicus* forms the primary source of prey for about 80–90% of the consumer fish species along the north western coast of India (Jaiswar and Chakraborty 2005).

Stable isotope mixing model

A Bayesian isotope mixing model has been developed using SIMMR to estimate the assimilated diet proportions of the selected consumer species representing various trophic guild in the URE. The results of the present study were in agreement with the existing hypothesis on the estuarine food webs that different trophic pathways in the system result from the diversity of resources, connectivity with other ecosystems, and trophic guild diversity of consumers. Also, the system is supported by multiple primary sources, as previously suggested by other authors (Bouillon et al. 2002, 2008; Abrantes and Sheaves 2010). Phytoplankton, detritus, and

mangrove leaves together contributed only around 30% of the assimilated diet of the all consumers combined, with a slightly higher share from detritus sources. When consumers are considered separately, about 70% of the assimilated diet of lower trophic level groups, such as zooplankton, fish larvae, and *N. nasus*, were found to be contributed by localized sources such as phytoplankton, detritus, and mangrove leaves. However, the contribution of these sources to the assimilated diet was comparatively lower in the consumers along the higher trophic levels.

The reasons for the same can be interpreted in two ways: firstly, due to the probability that other C-enriched sources not evaluated in this study are being exploited by these consumers (Contreras et al. 2018), secondly due to the mobility of organisms in the highly dynamic estuarine environment (Costanza et al. 1993). Some of the earlier reports from mangrove ecosystems suggested that microphytobenthos as an important food source for the consumer groups (Abrantes and Sheaves 2010; Giarrizzo et al. 2011; Shahraki et al. 2014). Hence, one of the most probable missing primary carbon sources in the present study area could be the microphytobenthos. A carbon isotopic enrichment is also observed in the lower trophic level group like zooplankton (-19.87‰) compared to the sources analyzed in the present study. As per Al-Zaidan et al. (2006), the microbenthic biota are dominated by Cyanobacteria typically show the most enriched $\delta^{13}\text{C}$ values among aquatic autotrophs by virtue of its CO_2 concentrating mechanism (Price et al. 2008). This could probably explain the role of microphytobenthos in the base of the food chain, which have been missed in the present study. It is also to be noted that some of the sources considered in the earlier works such as marsh plants close to the shoreline (Sepu'lveda-Lozada et al. 2015; Nelson et al. 2019), seagrasses (Abrantes and Sheaves 2010) as well as epiphytes (Sepu'lveda-Lozada et al. 2015), marine POM or marine phytoplankton, which are not considered in the present study. The $\delta^{13}\text{C}$ values of these higher aquatic vegetation shows high regional variability. For instance, the marsh plants with $\delta^{13}\text{C}$ values about 32.4‰ in Southern Gulf of Mexico (Sepu'lveda-Lozada et al. 2015) and -14.5‰ along Tropical Eastern Pacific (Contreras et al. 2018) and Seagrass with -14.6 to -7.0‰ in Curuçá estuary (Giarrizzo et al. 2011) and -18.6‰ in Tropical Northern Queensland (Abrantes and Sheaves 2010). Hence, the conclusions about the missing carbon sources in the present study could not be correctly drawn out unless a detailed region specific isotopic analysis of all the available carbon sources in the ecosystem is been carried out.

The consumer species belong to lower TLs, including the larval forms with limited life cycle and mobility, may probably utilize the readily available resources in their diet and thus justifies the higher contribution values of the localized sources analyzed in the study. The studies from elsewhere on the food and feeding of fish larvae substantiate these results

as planktonic preys such as mysids and copepods are often the main prey for fish larvae (Rakocinski et al. 1996; Ramos et al. 2006; Pasquaud et al. 2010). When the source contributions analyzed separately, phytoplankton was the most dominant dietary source for the groups such as zooplankton, fish larvae, and *N. nasus* over the other two sources. In these three consumers, phytoplankton sources alone contributed more than 50% of the assimilated diet. *N. nasus* is considered to be a generalized feeder on microplankton (80%), with specialization on foraminiferans and green algae in Chilika Lagoon, eastern coast of India (Mukherjee et al. 2016). The present results also strongly suggest phytoplankton based foraging habitat of the species in the URE.

Similarly, for the mid-level carnivore, *E. thoracata* and predatory species *L. savala*, the phytoplankton contribution was dominant over the other sources, although these species recorded a clear indication of the external carbon sources in their assimilated diet. Raje et al. (1994) reported that zooplankton, such as copepods, cladocerans, and crab larvae, formed the main food items of *E. thoracata*, whereas *L. savala* is principally a pelagic carnivore, feeding mainly on small pelagic fish (*Stolephorus* sp., *Sardinella* sp., *Dussumieria acuta*, and carangids) (Pakhmode and Mohite 2014). In the present study also, the major gut contents of *L. savala* were observed to be the species like *E. thoracata*, *Sardinella gibbosa*, and *S. indicus*, with a notable proportion of *A. indicus* as well. Hence a phytoplankton-based trophic pathway taken forward by zooplankton linkages, including the pelagic prey species such as *E. thoracata* reaching up to the top predator *L. savala* was evident in this study.

The contribution of mangrove leaves and detritus was dominant over the groups *A. indicus*, *J. belangerii*, and *N. caelata*. These results indicated their dependence on the detritus-based carbon sources, wherein more than 50% of their assimilated diet was contributed by the detritus and mangrove sources together. Also, in the niche map, *J. belangerii* and *N. caelata* exhibited more or less enriched and close values of $\delta^{13}\text{C}$ compared to others. This observation could be a result of their dietary overlap, as suggested by Abrantes and Sheaves (2010). The dietary overlap for *J. belangerii* and *N. caelata* is reasonable, as crustaceans chiefly *A. indicus* was recorded to be the principal food item for both the species in the coastal and estuarine waters around Mumbai (Chakraborty et al. 2000; Raje 2006). Also, *J. belangerii* and *N. caelata* are demersal inhabitants (Chakraborty 1988) in the marine coastal waters. Therefore, a mangrove-detritus sourced pathway driven by *A. indicus* particularly reaching up to the demersal species such as *J. belangerii* and *N. caelata* was also could be clearly delineated from the results of the stable isotope mixing model developed in the present study. Similar results were found from the studies from a mangrove ecosystem of the Tropical Eastern Pacific, Central Coast of Colombia, where a trophic route based on mangrove-derived carbon (including detrital material) was evident (Contreras et al. 2018).

The largest negative correlation is between mangrove leaves and detritus obtained in the matrix plots (-77) has clearly indicated the least degree of segregation between these sources in the consumer diets in the present model. However, a remarkable contribution of mangrove leaves in the mid trophic level groups other than the detritus was observed for groups such as *A. indicus*, *J. belangerii*, and *N. caelata* from the URE. These results strongly point towards the existence of a trophic link that missed out in the present study that converts the mangrove leaves to the assimilated diet of these consumer species in the ecosystem. Shahraki et al. (2014) suggested that bacteria would play an important role in the incorporation of mangrove carbon after colonizing and increasing the nitrogen values of the organic matter. Hence, the results are indirectly identifying the role played by the bacterial component in the system as an important connecting link at the base of the aquatic food web. The present results clearly point towards a phytoplankton based pelagic food chain and detritus-based benthic food chain in the URE. Whereas, there were also clear signs that these pathways are never independent, but with interconnecting trophic linkages as evident from the occurrence of both the detrital and plankton sources in varying proportions in the assimilated diet of all the consumers analyzed for the stable isotope mixing models (Bouillon et al. 2002, 2008; Contreras et al. 2018). Also, the fish catch data of URE has indicated that the biomass of benthic groups (mainly contributed by the *Acetes indicus* and *Sciaenids*) is significant in the estuary over the pelagic sources. Therefore, the importance of a detritus-based food chain is highly evident from these results.

Food chain length

The food chain length (FCL) has long been recognized as a fundamental ecosystem attribute (Elton 1927; Pimm 1982) to characterize the food chain dynamics (Fretwell 1987), trophic cascades (Carpenter et al. 1985; Pace et al. 1999), ecosystem functions (Worm et al. 2002; Emmett Duffy et al. 2005), fish productivity (Pauly and Christensen 1995), and contaminant bioaccumulation in top predators (Kidd et al. 1995). A food chain length of 3.75 was yielded in the current study based on the isotopic signatures ($\delta^{15}\text{N}$) of dominant consumer fish species, indicating a food web structure with at least four trophic guilds. According to Vander Zanden and Fetzer (2007), the average trophic chain length of the marine/coastal and freshwater ecosystems is in the tune of ~ 4.00 and ~ 3.50 , respectively. The results from URE defined an intermediate value compared to those reported in marine and freshwater ecosystems demanding a more detailed explanation for the interface ecosystems such as estuaries. The FCL variability between ecosystems is generally explained either by “productivity hypothesis” (Jenkins et al. 1992), productive space hypothesis (Schoener 1974), and/or dynamic stability hypothesis (Sterner et al. 1997a, b). The latter suggests that long food chains tend to be dramatically fragile towards environmental perturbation resulting in

shorter food chains in ecosystems subjected to disturbances. However, Vander Zanden, and Fetzer (2007) demonstrated that although the stream and estuaries are equally subjected to disturbances, the freshwater streams will be more consistent with the dynamic stability hypothesis than estuaries. This inference is based on their observation of relatively similar and higher TCL for coastal, and marine ecosystems compared to streams in the global literature. On the other hand, Vander Zanden et al. (1999) opined that marine food chains are longer than the other aquatic systems, attributed by the inclusion of marine mammals, which results in a rise of an additional 0.6 trophic level in the overall food chain. Hence, the intermediate trophic chain length obtained in the current study may be due to the missing nodes in the higher trophic position like marine mammals in the ecosystem or their limited habitat capacity in these ecosystems (Sreekanth et al. 2019).

According to Winemiller (2005), shallow lotic and estuarine systems tends to have food webs with three or four trophic levels. Among these ecosystems also food chain length is constrained by various factors such as: energetic constraints (Odum and Smalley 1959), productivity (Pimm 1982; Briand and Cohen 1987), ecosystem size (Post et al. 2000), predator–prey population constraints (Sterner et al. 1997a, b; Pimm 1982; Holt 2002), and environmental fluctuations and disturbance (Pimm 1982). Akin and Winemiller (2006) conducted studies on Mad Island Marsh, an ecosystem situated at further south of the Mumbai megacity experiencing similar geo-climatic and disturbance situations as that of URE. They reported low trophic positions of top predators and hence the trophic chain length and inferred that it is probably due to high incidence of feeding on herbivores and detritivores (i.e., mullet, menhaden, and crabs). Also, the Mad Island Marsh tidal estuary is a relatively small and dynamic habitat subject to frequent disturbances, and hence, the ecosystem size and disturbance could be the main factors limiting food chain length. Similarly, the moderate trophic chain length observed in the study area may also be considered in line with the case of Mad Island Marsh tidal estuary.

It is also to be noted that the mean trophic level of catches can be considered to be a function of the trophic chain length in an exploited ecosystem. Pauly et al. (1998) have suggested that the mean trophic level of the fish landed can be used as a tool for ecosystem status, where the series must extend into the past to cover major changes in the relative biomass of key ecosystem components. Lal et al. (2021) have reported a mean trophic level of catch from URE to be 3.01, indicating a fishery exploiting lower to medium trophic level groups. Similar results were observed from the recent studies from the estuarine and coastal waters of India such that; 2.72 for Sundarbans mangroves (Dutta et al. 2017), 3.12 for Bay of Bengal ecosystem (Das et al. 2018), 2.34 for Hooghly Matlah estuarine System (Mukherjee et al. 2019), and 2.91 for Zuari estuary (Sreekanth et al. 2018). According to Pauly et al. (1998), globally trophic levels of

fisheries landings have declined at a rate of 0.1 per decade. The present trends will lead to widespread collapse of fisheries due to a relaxation of the top-down control (Power 1992).

Trophic level variations

The $\delta^{15}\text{N}$ values have clearly defined the trophic level of the consumer species. The herbivorous species like *N. nasus* confirmed the evidence of its consumption of basal sources by showing the least value of $\delta^{15}\text{N}$. Hence, this species would be one of the first links between the primary producers and the second-order consumers, along with the zooplankton acquaintances in the estuary. Besides *N. nasus*, the white sardine, *E. thoracata* that represented the MLCR trophic guild, also showed its isotopic trophic level, which is consistent with its dietary estimates obtained from the present study as well as that from published reports (Hajisamae et al. 2004). For other consumer species, remarkable deviations in isotopic TLs were observed from the dietary estimates and those reported from the literature. Out of these species, *A. indicus* was the major discrepant with a $\delta^{15}\text{N}$ -based TL that was highly dissimilar to its feeding habits reported in the literature. The isotopic TL of *A. indicus* (which is considered to be an omnivore) was obtained as 3.24, made it classified under the trophic guild, MLCR as per the species segregation criteria (Vivekanandan et al. 2009). Crustaceans along the estuarine and mangrove areas show diverse grazing patterns compared to other ecosystems, comprising benthic microalgae, plant epithelial cells, detritus, and cyanobacteria (Bouillon et al. 2002). Therefore, the close association of these species with the benthic feeding habitats coupled with the incidental prey types such as; animal tissue-enriched detritus, fish larvae, or holoplanktonic organisms could explain the elevated $\delta^{15}\text{N}$ values for *A. indicus* as of an MLCR or zoobenthivore.

On the other hand, the species from the higher trophic guilds (*N. caelata* and *L. savala*) showed remarkably low isotopic TLs compared to that obtained from the reported values as well as from dietary estimates. As a result, the trophic guild of *L. savala* and *N. caelata* could be downgraded to the MLCR-HLCR trophic guild from the HLCR-TPR guild based on the isotopic TL. The hierarchical demotion of TL from the literature estimates indicated a different prey consumption pattern for these species in URE compared to the other marine coastal waters. The adults of *L. savala* is considered to be a piscivore with a wide range of prey preference with occasional crustacean diet in Brazilian waters (Martins et al. 2005). However, on the northwestern coast of India, the species has been reported as a predator feeding principally on crustaceans, along with fish and cephalopods (Khan 2006). Among crustaceans, sergestid, *Acetes* spp. is the most frequently encountered prey item in the gut contents of *L. savala* (Khan 2006; Jaiswar and Chakraborty 2005). Thus, the unique abundance of sergestid shrimps in the area has molded the species to be a crustacean feeder regardless of other geographical areas, where it has occupied the piscivorous

niche position. This trophic positioning might be the clear justification of the significantly lower $\delta^{15}\text{N}$ and hence, the isotopic TL of the species in the estuary. Vander Zanden et al. (1997) have attempted to verify the $\delta^{15}\text{N}$ measure of trophic position using within-system comparisons between dietary data and $\delta^{15}\text{N}$. They have reported some degree of inability of dietary data to represent temporal variation in feeding and errors in trophic position estimates of the prey item. The differences in the way that the dietary and $\delta^{15}\text{N}$ methods integrate trophic position may cause problems while attempting a direct comparison of the estimates (Vander Zanden et al. 1997). Also, use of dietary data provides a snapshot in time of an organism's diet, which certainly does not represent the average trophic position of a species for larger temporal scales. The deviation from the dietary estimates can possibly be justified by this reason. Hence this study clearly projects the importance of $\delta^{15}\text{N}$ -based TL calculations over dietary estimates in predicting the average trophic position of fish species over larger temporal scales in dynamic ecosystems like estuaries.

The variation in the isotopic trophic Level with the dietary and literature estimates may also be due to the constant fractionation factor used in the present study. Hussey et al. (2014) revealed that practically, the fractionation factor ($\delta^{15}\text{N}$) cannot be a constant, and determined an empirical linear relationship with $\delta^{15}\text{N}$ of consumer through meta-analysis. Following this, the TL analysis used a scaled $\delta^{15}\text{N}$ trophic framework that was a narrowing discrimination with increasing trophic levels, which provided a more accurate representation of species structuring (Reum et al. 2015). The use of the constant fractionation factor may either under estimate or overestimate the actual trophic level, based on the basal resource which may have far reaching consequences in a managerial perspective. That means, the elevated trophic levels of large apex predators indicates 1 to 2 orders of magnitude less energy available to support these fish than previously thought, assuming a transfer efficiency of approximately 10% (Trebilco et al. 2013). This suggests that for highly exploited large predators, the population numbers or biomass estimates could be much smaller than current theoretical estimates, emphasizing the need for proactive precautionary fisheries management to ensure viable populations (Hussey et al. 2014).

Stable isotopic signature as pollution indicators

It has been considered that high levels of $\delta^{15}\text{N}$ in basal sources can be used as an alternative method to establish the level of human eutrophication since anthropogenic sources of nitrogen are generally enriched in the heavy isotope when compared to natural sources (Cole et al. 2006; Bannion and Roman 2008; Baeta et al. 2009a, b; Baeta et al. 2017). In URE the $\delta^{15}\text{N}$ (‰) for the basal sources such as phytoplankton (5.90), and detritus (8.40) were remarkably higher compared to that for mangrove leaves (0.40). Hence, the possibility of nitrogen enrichment in the detritus and the POM/phytoplankton due to human eutrophication cannot be snubbed. Apart from that, isotopic signatures of zooplanktivorous fish and fish larvae also

reflect anthropogenic pressures in the estuarine eco systems, and function as an exposure indicator of nitrogen pollution (Baeta et al. 2017). Thus, the mean $\delta^{15}\text{N}$ (‰) of 6.71 ± 0.35 for zooplankton observed from URE is also substantiating a possibility of nitrogen pollution in the ecosystem.

Conclusion

The present study clearly illustrated the food web structure of the URE ecosystem in terms of the major sources and links explained based on the stable carbon and nitrogen isotopic signatures. Although the study has been conducted based on the nodal species of the food web regardless of the huge diversity in the estuarine ecosystems, it could clearly delineate the trophic pathways and the connecting links steered by the detritus and

phytoplankton sources. Furthermore, the study points towards a possibility of nitrogen enrichment in the detritus and the POM/phytoplankton due to human eutrophication in URE. Hence, the present study throws light for more investigations in this line using such advanced and reliable methods for studying complex coastal ecosystems. Investigations of other spatio-temporal scales of environmental variations, including estuarine hydrography and other biotic factors in context of the heavy pollution pressure in the area, might further illustrate the dynamics of basal sources and trophic functioning of the estuary. Since the advanced tools such as stable isotopic signatures are poorly utilized for ecosystem analysis in the Indian coastal waters, future research is encouraged to further disclose the underlying facts of trophic organization in these unique tropical ecosystems.

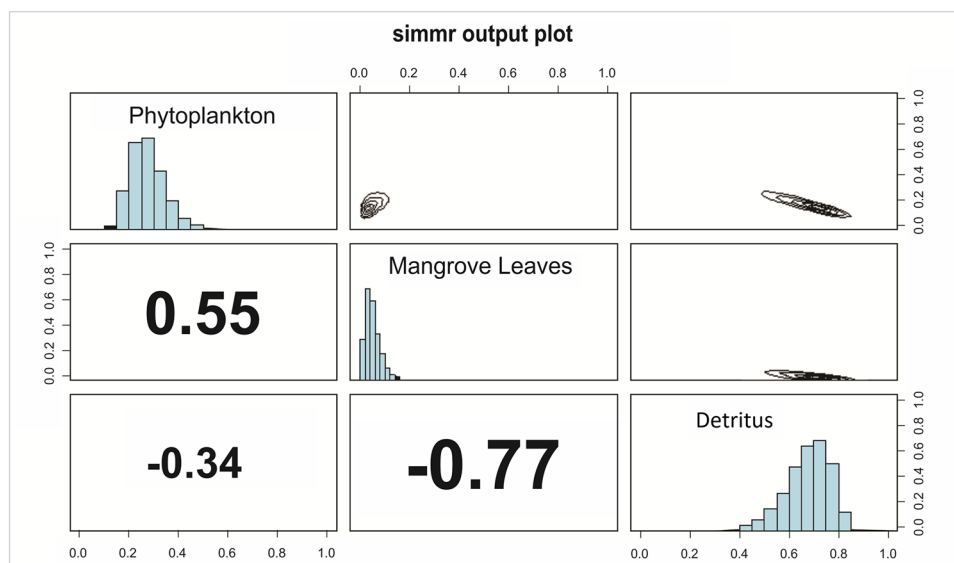
Appendix

Matrix plots

The matrix plots obtained from the SIMMR analysis from the URE represented the source histograms on the diagonal, correlation between the sources on the lower diagonal, and contour plots of the relationship between the sources on the

upper diagonal (Fig. 9). Large negative correlations indicate that the model cannot discern between the two sources; they may lie close together in iso-space. In the present study, the largest negative correlation is found between mangrove leaves and detritus since they are closer in the iso-space than the other sources. These relations indicate that the model is constrained with some degree of difficulty in segregating the contribution of these sources to the overall food web.

Fig. 9 Matrix plots for trophic chain-source contributions in URE



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Author contribution Dhanya Mohan Lal: conceptualization; data collection, data analysis, and original draft preparation. Giri Bhavan Sreekanth: conceptualization, data analysis, and manuscript preparation. Chitra Soman: data collection and analysis. Anupam Sharma: methodology, laboratory supervision, and data interpretation. Zeba Jaffer Abidi: overall supervision and manuscript editing.

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Data availability All the data involved in the present study are provided in the manuscript and the supplementary material.

Declarations

Ethical approval The authors declare that preparation of this manuscript has been duly considered the ethical aspects of manuscript publication. The authors also declare that the manuscript is prepared strictly according to the Journal format as provided in the instruction to authors.

Consent to participate The present research does not involve any human participants.

Consent for publication All the co-authors have agreed for submission of this manuscript to “Environmental Science and Pollution Research.”

Competing interests The authors declare no competing interests.

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