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Influence of river discharge on zooplankton diet in the Godavari estuary (Bay of Bengal, Indian Ocean)

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ABSTRACT

In estuaries, detrital (*i.e.*, non-living) organic matter (OM) contributes significantly to the particulate organic matter (POM) pool and we hypothesize that it may be a major source of estuarine zooplankton diet. To test this hypothesis, the isotopic composition of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) of phytoplankton, zooplankton, and POM was assessed in the Godavari estuary (Bay of Bengal, Indian Ocean) during wet (November) and dry periods (January). As a result of higher riverine discharge, POM concentrations and values of the C/Chl-*a* ratio during the wet period were higher than those measured during the dry one. Relatively lower $\delta^{13}C_{POM}$ values were observed during wet than dry period and contrasting to that was found for $\delta^{15}N_{POM}$. Detritus from fresh water algae and C$_3$ plants contributed significantly to the POM pool during the wet and dry period, respectively. Based on isotopic mixing model, detrital OM and phytoplankton mostly characterized the POM pools during the wet and dry periods, respectively. Accordingly, our results suggest also that the zooplankton diet was mostly supported by detrital OM during the wet period and by both phytoplankton and detrital OM during the dry one. The zooplankton trophic level (TL, 2.7) during the wet period was relatively higher than that (1.9) during the dry one, suggesting a relative higher preference for detritus than phytoplankton during the wet period. The results of this study allowed us confirming that detrital OM can significantly support zooplankton production in the Godavari estuary.

Key words: Phytoplankton, Zooplankton, detritus, stable isotopes, river discharge, Godavari estuary.

INTRODUCTION

Estuarine and coastal environments are often characterized by energy sources for consumers which are heterogeneous and characterized by with large spatial and temporal variability (Stowasser *et al*., 2012). The trophic interactions are driven by a complex array of multiple biological, chemical and physical processes, which altogether make trophic linkages among different groups within the aquatic food web difficult to be defined (Layman *et al*., 2012; Stowasser *et al*., 2012). Such a difficulty in tracking the flow of energy along aquatic trophic webs is due to the fact that many species grow more than five orders of magnitude than others and some pass through several trophic levels during the different stages of their life cycle (Cushing, 1975; Pope *et al*., 1994; Post, 2002; Van Oevelen *et al*., 2012; Middelburg, 2014). Food web studies carried out previously relied on gut content analysis of higher trophic level organisms (Hall and Raffaelli, 1993), and this method has a limitation in assessing the assimilation of material in the gut (Stowasser *et al*., 2012).

Stable isotopic composition of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) can be used as complementary tools to evaluate the structure and dynamics of ecological communities (Peterson and Fry, 1987; France, 1995;

Vander-Zanden *et al*., 1997; Post, 2002; Middelburg, 2014; Hinz *et al*., 2017). These isotopes provide information about the source of material in the integrated temporal scale (Post, 2002), as $\delta^{13}C$ and $\delta^{15}N$ in the tissues of predators is enriched relative to their prey, and, thus, can be used to estimate trophic levels within a certain trophic web (Minagawa and Wada, 1984; Jennings *et al*., 2002). The $\delta^{13}C$ of consumers are usually close to that of their diet (<0.5‰; Post, 2002) whereas $\delta^{15}N$ is enriched in the consumers relative to their diet by 3.4‰ (DeNiro and Epstein, 1978, 1981; Minagawa and Wada, 1984; Post, 2002). Dissimilarity in isotopic composition of $\delta^{13}C$ and $\delta^{15}N$ of marine organisms are caused by selective uptake of nutrients, feeding (Meili *et al*., 1996; Matthews and Mazumder, 2003), and metabolic activities (DeNiro and Epstein, 1981; Hobson and Clark, 1992; Hobson *et al*., 2002; Matthews and Mazumder, 2006; Santer *et al*., 2006). Hence, the sensitivity of trophic position estimation carried out using stable isotope signatures depends on $\delta^{15}N$ and $\delta^{13}C$ of end-members, which, in turn, depends by several factors such as variation in source of nutrients, dissolved inorganic carbon (DIC), organic matter etc. Obtaining an appropriate baseline is therefore one of the most challenging methodological issues facing the effective application of stable isotopes to trophic food

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web dynamics (Post, 2002; Finlay and Kendall, 2007; Hussey *et al.*, 2014; Middelburg, 2014).

Estuaries are among the most biogeochemically active zones on the surface of the Earth (Gattuso *et al.*, 1998; Cole *et al.*, 2007; Richey *et al.*, 2002; Bhavya *et al.*, 2015) and higher rates of biological production are observed due to large nutrient inputs (Nixon *et al.*, 1986; Kelly and Levin, 1986; Heip *et al.*, 1995; Caffrey, 2004; Gazeau *et al.*, 2004, 2005). Estuaries receive a considerable amount of inorganic nutrients, organic matter, contaminants from the land and exchange them with the coastal ocean (Nixon *et al.*, 1986; Howarth *et al.*, 1996). Besides the allochthonous sources, the active biological pump in estuaries produce significant amounts of organic matter that can accumulate both in the water column and sediments (Wollast and Mackenzie, 1989; Smith and Hollibaugh, 1993; Wollast, 1998). While it is clear that these two organic matter sinks play a key role in the trophic dynamics of estuaries, their relative importance is unclear and may be regional specific due to variable composition and (nutritional) quality of organic matter (Manini *et al.*, 2003).

Within this framework, a significant amount of work was carried out in lakes. For instance, Lammers *et al.* (2017) noticed that allochthonous organic matter can contribute significantly to bacterial diet during winter, whereas in summer and fall such a contribution is very low. Strong evidence for the support of allochthonous organic matter to herbivorous zooplankton production was reported in several lakes (Grey *et al.*, 2001; Brett *et al.*, 2009; Cole *et al.*, 2011). Suzuki *et al.* (2013), using stable isotopic composition of carbon, reported that the copepods diet in the Chikugo River estuary, Japan is supported by organic matter derived from phytoplankton ad their detrital remains. Matson and Brinson (1990), using stable isotopes of carbon, found that a significant fraction of zooplankton diet in the Pamlico and Neuse estuaries is contributed by terrestrial organic matter, and similar conclusions were made for some estuaries in Siberia (Doi *et al.*, 2006).

Indian estuaries are characterized by runoff episodes associated with monsoonal precipitation (Vijith *et al.*, 2009; Sridevi *et al.*, 2015). The estuary behaves like a freshwater lake during the peak discharge period whereas seawater contribution increases during the dry period (Sridevi *et al.*, 2015). Godavari is the largest monsoonal river in India and fed mainly by the southwest monsoonal precipitation during summer (June-September, wet period) (Acharyya *et al.*, 2012). During the wet period, freshwater brings large amounts of inorganic nutrients, organic matter and suspended matter to the estuary (Sarma *et al.*, 2009; 2010). During this period, despite the high nutrient concentrations, phytoplankton biomass is very low due to the high suspended load which limits light availability (Acharyya *et al.*, 2012). Based on the values

of the photosynthesis to respiration ratio, Sarma *et al.* (2009) estimated that 40-60% and 70-95% of the heterotrophic production is supported by organic matter of terrestrial orifin during the wet and dry periods, respectively (Gawade *et al.*, 2017). The contribution of different taxa to the phytoplankton assemblages in the Godavari estuary varies according to the magnitude of freshwater discharge rather than to nutrient concentrations (Bharati *et al.*, 2018). For instance, freshwater algae (*e.g.,* Chlorophyceae) dominate during the peak freshwater discharge period (July-August). A phytoplankton bloom (mainly due to Cyanophyceae) occurs in the estuary once the river discharge decreases below 2000 $m^3 s^{-1}$ and the suspended matter load is <200 mg L^{-1} (Bharati *et al.*, 2018). When the freshwater discharge completely stops (January-May) due to drying of the upstream river and closing of dam gates, estuarine phytoplankton are dominated by Bacillariophyceae (diatoms) (Sarma *et al.*, 2009, Bharati *et al.*, 2018).

We hypothesized that the contrasting conditions between wet and dry periods and the associated variations in the composition of the potential food items may influence the zooplankton diet in the Godavari estuary. To test this hypothesis, we investigated the sources of zooplankton diet in the Godavari estuary during wet and dry periods using stable isotopic composition of carbon and nitrogen in the live and dead organic matter.

METHODS

Study area

Godavari River is located between 16 and 18°N latitude and originates at an altitude of about 1600 m near Nasik city in the Western Ghats. It flows eastwards across peninsular India for about 1480 km and drains into the Bay of Bengal at Bhairavapalem, on the central east coast of India (Fig. 1). Godavari is the largest monsoonal river in India and has created an extensive delta on the east coast of India. The basin climate is generally dry with an average rainfall of 1512 mm y^{-1}. The catchment receives about 82% of the annual rainfall during the summer and the rest in the winter monsoon (Central Pollution Control Board, 1995). The discharge of freshwater into the Godavari estuary is controlled by century old low dam at Dowleiswaram (Fig. 1). Discharge occurs between June and December with a peak in July-August and reduces considerably from October. After the dam, the river bifurcates into two major distributaries; the eastward flowing major tributary is called Gautami-Godavari, while the other flowing southwards is Vasistha-Godavari and the former is the major branch of river in terms of discharge. The present study was conducted in the Gautami-Godavari estuary at Yanam during 2012-2013 (Fig. 1).

Sampling

The samples were collected during November 2012 and January 2013, assumed to represent wet and dry conditions, respectively. At each sampling date, three water samples were collected at Yanam, middle of the estuary using 5L Niskin bottles operated onboard a hydrographic vessel, for the subsequent analyses of inorganic nutrients, phytoplankton biomass (in terms of chlorophyll-*a* - Chl-*a* - concentrations), content and isotopic composition of carbon and nitrogen in POM. About 1 L of water sample filtered through pre-combusted GF/F filter for either Chl-*a* concentrations or POM composition. An additional 1L of water sample was collected using plastic bottles for the taxonomic analysis of phytoplankton. Zooplankton samples were collected by horizontal towing using a bongo net (200 μm pore size).

Chlorophyll-a analysis

The Chl-*a* retained on the filter was extracted with dimethyl formamide (DMF) at 4°C for 12 hours in the dark and the extract fluorescence was measured with a spectrofluorophotometer (Varian Instruments, Palo Alto, CA, USA) (Suzuki and Ishimaru, 1990). POM retained on the filter was first dried at 60°C overnight, and then kept in HCl acid fumes for 12 hours to remove inorganic carbon for the subsequent measurement of content and isotopic composition of carbon ($\delta^{13}C_{POM}$). Acid treatment was not done on filters dedicated to the analysis of the content and isotopic composition of nitrogen ($\delta^{15}N_{POM}$) (Goering *et al.*, 1990; Bunn *et al.*, 1995; Pinnegar and Polunin, 1999).
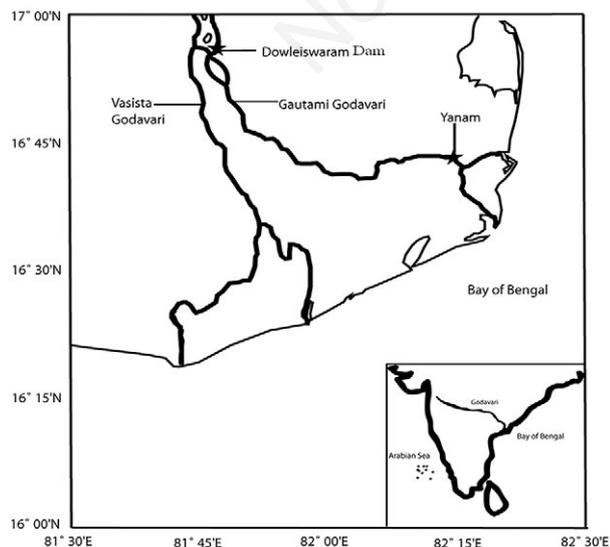
Fig. 1. The study site.

Phytoplankton and zooplankton taxonomy

Phytoplankton and zooplankton were separated under an upright microscope (4X magnification; Olympus DX 53) with the help of an injection syringe and fine needle. The specimens were cleaned with MilliQ water and subsequently transferred to tin cups and dried at 60°C for 12 h. The dried tin cups were introduced to the elemental analyzer attached to the Isotope Ratio Mass Spectrometer (IRMS).

Inorganic nutrient analyses

Nutrients were analyzed following standard procedures (Grashoff *et al.*, 1992) following colorimetric method using auto analyzer (Skalar San++, The Netherlands). The analytical precision, expressed as standard deviation, was ±0.02, 0.02, 0.01 and 0.02 μM respectively for nitrate+nitrite, ammonium, phosphate and silicate.

Stable isotope analyses

The content and isotopic ratios of carbon and nitrogen in the samples were measured using elemental analyzer (Thermo Electron, Germany) coupled with Isotope Ratio Mass Spectrometer (IRMS - Delta V Plus, Finnigan, Germany) through Conflo IV interface, with oxidized column kept at 1050°C and the reduced one at 650°C. The results are expressed as relative to conventional standards, i.e., PDB for carbon (Coplen, 1996) and atmospheric N_2 for nitrogen (Mariotti, 1983) as δ values, defined as:

$$\delta R = [X_{sample} - X_{standard}) / X_{standard}] * 1000\ (‰) \qquad (eq.\ 1)$$

where, $R = {}^{13}C$ or ${}^{15}N$, and $X = {}^{13}C/{}^{12}C$ or ${}^{15}N/{}^{14}N$. High-purity CO_2 and N_2 gases were used as working standards for carbon and nitrogen, respectively. These gases were calibrated with internal reference materials of glutamic acid, alanine and marine sediment and international standards obtained from the International Atomic Energy Agency (IAEA). The standard deviation on 20 aliquots of the same samples was < 0.2% for both $\delta^{13}C$ and $\delta^{15}N$.

The trophic level (TL) was estimated using $\delta^{15}N$ isotopic values using the expression proposed by Post (2002):

$$TL = \lambda + (\delta^{15}N_{consumer} - [\delta^{15}N_{base1}\ x\ \alpha + \delta^{15}N_{base2}\ x\ (1-\alpha)])/3.4 \qquad (eq.\ 2)$$

where, $\delta^{15}N_{consumer}$ is the nitrogen isotopic ratio of the zooplankton. $\delta^{15}N_{base1}$ and $\delta^{15}N_{base2}$ are the isotopic composition of base 1 (phytoplankton) and base 1 (detritus), respectively. l is trophic position of the organism used to estimate $\delta^{15}N_{base}$ and it is 1 for primary producers. α is the proportion of nitrogen derived from the base of food web one (base 1) to consumer (Post,

2002). When the movement of nitrogen and carbon through the food web is similar, α can be estimated using carbon isotopes - $\alpha=(\delta^{13}C_{consumer}-\delta^{13}C_{base2})/(\delta^{13}C_{base1}-\delta^{13}C_{base2})$ (Post, 2002).

Sources of the zooplankton diet

The relative contribution of variable sources of food to consumers was quantified using isotope mixing model 'SIAR' (Stable Isotope Analysis in R), an open source package (http://cran.r-project.org/), which resolves mixture within a Bayesian framework (Parnell *et al*., 2008, 2010). This model includes standard deviation as a residual error term to compute the variability (Jackson *et al*., 2009; Parnell *et al*., 2010). A detailed description of the model is given elsewhere (Sarma *et al*., 2014). The selection of isotopic composition of the source is critical for the estimation of proportional contributions to consumers. Mean isotopic ratios of $\delta^{13}C$ and $\delta^{15}N$ of several end members (C_3 and C_4 terrestrial plants, soil organic matter, fresh water algae, marine phytoplankton, estuarine phytoplankton, zooplankton) from drainage basin of the Godavari river were measured (Tab. 1) to separate and determine the percentage contribution of the live (autochthonous/*in situ* phytoplankton) and the detrital fractions (allochthonous/*ex situ*, dead organic matter) to the POM (Krishna *et al*., 2015). The freshwater algae were separated under the microscope from water samples collected from the upstream Godavari estuary (close to the dam) for fixing end members of *in-situ* sources. The end member values are close to those estimated elsewhere in other estuaries (Hamilton and Lewis, 1992; Middelburg and Nieuweuwenhuize, 1998; Barth *et al*., 1998; Hellings *et al*., 1999; Kao and Liu, 2000; Boschker *et al*., 2005; Bontes *et al*., 2006).

RESULTS

Water column variables

Due to variable river discharge, hydrographic conditions varied considerably between the wet (June-December) and dry (January-May) periods. During the

wet period, the mean river discharge to the Godavari estuary was relatively weak (~825 m^3 s^{-1}, on average), whereas no discharge at all occurred during the dry period (January). As a result of the weak discharge during the wet period, a strong stratification occurred in the estuary with low salinity waters (9.236) constrained at the surface and high salinity waters at the bottom (27.631). In contrast, during the dry period, high salinity (27.236) values characterized the entire water column. The highest concentrations of nutrients (nitrate, ammonium, phosphate and silicate of 10.9, 15.30, 2.91 and 52.82 μM respectively) were observed during the wet period, whereas values measured during the dry period were up to 5-10 times lower (1.8, 1.4, 0.9 and 10.3 μM, respectively). Particulate organic C (POC) concentrations were significantly higher (*t*-test, t=245.1; P<0.001) during the wet period (3608±117 μgC L^{-1}) than during the dry one (1284±67 μgC L^{-1}). The C:N ratio values of POM were significantly (*t*-test; t=31.6; P<0.001) higher during the wet (19.4±3) than the dry period (14.6±2; Tab. 1).

Phytoplankton abundance, biomass and assemblage composition

Phytoplankton abundance was lower (*t*-test; t=-70.4; P<0.001) during the wet period (44253 cell L^{-1}) than during the dry one (63684 cell L^{-1}; Tab. 2), the phytoplankton biomass was significantly higher (*t*-test; t=25.8; P<0.001) during the wet period (10.5±2 μg Chl-*a* L^{-1}) than during the dry one (4.7±1 μg Chl-*a* L^{-1}) (Tab. 2). Values of the POC/Chl-*a* ratio were higher during the wet (343) than the dry period (271) (*t*-test; t=34.6; P<0.001). During the wet period, the phytoplankton assemblage was dominated by Cyanophyceae (mostly *Merismopedia sp.* and *Gleocapsa sp.*; overall 47% of the total phytoplankton abundance), followed by Chlorophyceae (33%; mostly *Actinastrum sp.*, *Scenedesmus sp.*, *Pediastrum sp.*), small (<10 μm) diatoms (19%, *Leptocylindrus sp.*, *Coscinodiscus sp.*) and Dinophyceae (1%). During the dry period small size diatoms (mostly *Coscinodiscus sp.*, *Chaetoceros sp.* and *Ceratium sp.*) represented up to 95% of the total phytoplankton abundance.

Tab. 1. The isotopic composition of different sources of organic matter used in the SIAR model.

Source	δ¹³C (‰)	δ¹⁵N (‰)	Reference
C_3 plants	-25.9±1.2	5.1±2.1	Krishna *et al*., 2015
C_4 plants	-13.1±1.2	4.4±2.1	Krishna *et al*., 2015
Marine phytoplankton	-23.6±0.3	9.2±0.8	Krishna *et al*., 2015
Soil organic matter	-19.2±2.4	10.3±2.7	Krishna *et al*., 2015
Freshwater algae	-33.1±2.3	6.8±0.8	This study

Zooplankton abundance and community composition

Mesozooplankton abundance was relatively lower during the dry (105 ind. m^{-3}) than the wet period (188 ind. m^{-3}). During the wet period the mesozooplankton assemblage consisted mostly of copepods (85% of the total zooplankton abundance) and other, less abundant, taxa were Cladocera, Gastropod veliger, Nauplii, *Tellina* sp, and Zoea (cumulatively representing 15% of the total abundance). Calanoida represented up to 90% of the total zooplankton abundance, followed by Cyclopoida (5%), Harpacticoida (3%) and Polycheate larvae (2%). During the dry period, Copepods (Calanoida, Cyclopoida and Harpacticoida) were the most abundant (92% of the total mesozooplankton abundance), followed by Zoea, Decapoda, and Harpacticoid Copepoda (cumulatively 8%).

Isotopic composition of phytoplankton and zooplankton

The isotopic composition of carbon in the different phytoplankton taxa ranged between -28.1 and -24.9‰ and a relatively higher value characterized Cyanophyceae (-28.1‰) during the wet period (Tab. 3). The mean δ^{13}C (δ^{15}N) of phytoplankton was significantly lower (higher) (*t*-test; t=-8.9; P<0.01 and t=53.21; P<0.01, respectively) during the wet (-26.1±1.4‰ and 15.9±2.5‰ respectively) than the dry period (-24.6±0.6‰ and 4.6±1.0‰ respectively) (Tab. 2). The isotopic composition of δ^{13}C and δ^{15}N of mesozooplankton ranged from -29.3 to -29.1‰ and 13.9 to 15.2‰, respectively during wet period (Tab. 3), and from -23.8 to -22.2‰ and 6.9 to 8.4‰ during the dry one (Tab. 3). The δ^{13}C (δ^{15}N) of mesozooplankton during the dry period was significantly higher (lower) during the wet one (*t-Test*; t=-44.3; P<0.001 and t=140.5; P<0.001, respectively; Tab. 2).

Sources and isotopic composition of POM and detritus

The δ^{13}C and δ^{15}N of POM was relatively lighter during the wet (-31.2‰ and 4.9‰) than the dry period (-25.6‰ and 6.4‰). The results obtained from the SIAR model suggest that 17 and 25% of POM was contributed by live organic matter during the wet and dry periods, respectively (Tab. 4). During the wet period freshwater algae contributed the most 69%) to detritus, followed by C$_3$ plants (9%), whereas during the dry periods C$_3$ plants (60%) were the most important contributors to detritus, followed by estuarine phytoplankton (14%) and freshwater algae (12%) (Tab. 4).

During the wet period the isotopic composition of carbon in detritus (δ^{13}C$_{det}$), resembling that of freshwater algae, was significantly (*t*-test; t=-56.5; P<0.001) depleted (-31.7±1.4‰), when compared to that measured during the dry one (-25.9±1.3‰; Tab. 2). The isotopic composition of nitrogen in detritus (δ^{15}N$_{det}$) was significantly higher (*t*-test; t=5.9; P<0.01) during the wet period (6.5±3.7‰) than the dry one (5.3±1.3‰; Tab. 2).

Trophic levels and food web structure

During the wet period, due to the higher δ^{15}N$_{phytoplankton}$, the δ^{15}N$_{base}$ values for consumers were enriched (10.3 and 7.5‰) when compared to those estimated during the dry one (4.9 and 6.2‰ respectively). During the wet period, the estimated TL for Calanoida and Cyclopoida was 2.6 and 2.7, respectively and decreased (1.8 and 2.0, respectively) during the dry period (Tab. 5). The mean TL

Tab. 2. Mean concentrations and isotopic values of several components of the Godavari estuary ecosystem during wet and dry.

Property	Wet period	Dry period	*t*-test and P-value
Discharge (m^3 s^{-1})	825±80	0	142.04; <0.001
Chlorophyll-a (µg L^{-1})	10.5±2	4.7±1	25.88; <0.001
POM (µgC L^{-1})	3608±117	1284±67	245.15; <0.001
PON (µgN L^{-1})	238±3.2	210±2.9	11.17; <0.001
C/N	19.4±3	14.6±2	31.64; <0.001
Phytoplankton abundance (cells/L)	44253	63684	-70.40; <0.001
POC/Chl	343±18	271±12	34.60; <0.001
Dominant group	Cyanophyceae	Bacillariophyceae	—
δ^{13}CDetritus (‰)	-31.7±1.4	-25.9±1.3	-56.51; <0.001
δ^{15}NDetritus (‰)	6.5±3.7	5.3±1.3	5.87; <0.01
δ^{13}CPhytoplankton (‰)	-26.1±1.4	-24.6±0.6	-8.96; <0.01
δ^{15}NPhytoplankton (‰)	15.9±2.5	4.6±1.0	53.21; <0.001
δ^{13}CZooplankton (‰)	-29.1±0.1	-23.3±0.8	-44.31; <0.001
δ^{15}NZooplankton (‰)	14.5±0.6	7.9±0.7	140.48; <0.001

for zooplankton was 2.7 and 1.9 during the wet and dry periods, respectively.

DISCUSSION

Variable sources of POM during the wet and dry periods

The carbon to nitrogen (C:N) ratio is a trace to identify source of organic matter as it varies for variable sources such as plankton (6-7), bacteria (4-5), and organic matter

from higher plants (>20) (Hedges *et al.*, 1997). However, several diagenetic processes can modify C:N ratios which lower its viability to identify the actual sources of organic matter. For instance, C:N ratio of higher plant litter typically decreases due to bacterial colonization, and increases in senescent or dead algae due to the preferential removal of nitrogen by consumers (Hedges *et al.*, 1997; Herman and Heip, 1999). Nonetheless, though such biases do not allow identifying the exact source of organic matter, variations in the C:N ratio values can provide some indication on changes occurring in OM origin and

Tab. 3. Isotopic composition of sources, primary, secondary and tertiary consumers and trophic level of primary and secondary consumers during the wet and dry periods.

Source/consumer	Groups	δ13C (‰)	δ15N (‰)	TL
	Wet period			
Source	Phytoplankton*	-26.1±0.9	15.9±2.5	
	Detritus	-31.7±1.4	6.5±3.7	
	Soil organic matter	-23.5±1.1	6.0±0.9	
Zooplankton	Calanoida (10)	-29.3±1.2	13.9±2.5	2.6
	Cyclopoida (21)	-29.1±0.6	14.5±3.4	2.7
	Cladocera (11)	-29.2±0.5	15.2±0.3	2.9
	Dry period			
Source	Phytoplankton (100)	-24.6±0.4	4.6±1.0	
	Detritus	-25.9±1.2	5.3±1.3	
	Soil organic matter	-23.1±0.8	6.3±0.5	
Zooplankton	Harpacticoida (14)	-22.5±0.3	7.4±0.6	1.8
	Cyclopoida (25)	-24.2±0.6	6.9±0.8	1.6
	Zoea (25)	-22.2±0.5	8.0±0.5	2.0
	Calanoida (25)	-23.8±0.5	8.2±0.3	2.0
	Decapoda (16)	-23.4±0.8	8.1±0.4	2.0

TL, Trophic level; *nearly 100 number of phytoplankton cells were analyzed.

Tab. 4. Proportion (%) of source contributors to the particulate organic matter pool in the Godavari estuary based on the outputs of the SIAR model.

POM	Period	Wet period	Dry period
Live fraction	Phytoplankton	7	14
Zooplankton		8	7
Marine algae		3	3
Detrital fraction	Freshwater algae	69	12
	C3 plants	9	60
	C4 plants	4	4

POM, Particulate organic matter.

Tab. 5. Contribution (%) of detritus and phytoplankton to the zooplankton diet in the Godavari estuary based on SIAR model.

Consumers	Period	Detritus	Phytoplankton
Zooplankton	Wet	60	40
Zooplankton	Dry	40	60

diagenetic status (Middelburg and Herman, 2007). The higher values of the C:N ratio values of POM observed during the wet period (Tab. 1) suggest that during this period the Godavari estuary was characterized by a relevant fraction of non-living organic matter.

The POC:Chl-*a* ratio (C:Chl-*a*) can also be used to delineate the sources of organic matter as relatively lower values are associated with freshly derived organic matter by *in situ* biological production, whereas higher values are associated with older and degraded OM (Cifuentes *et al*., 1988; Richard *et al*., 1997; Bentaleb *et al*., 1998). In fact, the C:Chl-*a* ratio of fresh organic matter produced by marine phytoplankton varies from ~40 (Montagnes *et al*., 1994), <70 (Geider, 1987) <100 (Head *et al*., 1996), <140 (Thompson *et al*., 1992) to <200 (Cifuentes *et al*., 1988; Bentaleb *et al*., 1998) also according to regional temperature and irradiance regimes, as well as species growth rates and composition (Heath *et al*., 1990; Montagnes *et al*., 1994; Geider *et al*., 1998). In our study, the C:Chl-*a* ratio during the wet (343 ± 18) and dry (271 ± 12) period were consistently >200, suggesting the presence in both periods of a relevant fraction of terrestrial OM sources, more evidently during the wet period (Tab. 2), as previously reported from other Indian estuaries (Sarma *et al*., 2014).

The output of the SIAR model suggests that 18 and 24% (wet and dry period, respectively) of the POM was contributed by live OM, also that the contribution of detrital OM was high during both study periods (Tab. 4). Such low contribution of live OM was caused by the minimal photic depth (0.1 to 2 m; Sarma *et al*., 2009) which likely limited primary production. During the wet period, the $\delta^{13}C_{detritus}$ (-31.7 ± 1.4 ‰) is close to that of freshwater algae (-33.2‰; Tab. 1), suggesting that dead freshwater algae contributed significantly to the detritus pool. During the wet period, apart from estuarine phytoplankton, the estuary received organic matter also from terrestrial sources, such as C_3, C_4 land plants and soil OM (Sarma *et al*., 2014). Moreover, the output of the SIAR model suggests that, during the wet period, 69% of the detritus was contributed by freshwater algae and 9% by C_3 plants (Tab. 4).

The accumulation of detritus in the water column depends also upon the residence time of water in the estuary. The residence time of water in the Godavari estuary is <1 d during the peak discharge and increases up to >30 d during the dry period. However, also when a moderate discharge occurs (November, wet period) the residence time of estuarine water is >20 d (Sridevi *et al*., 2015). Moreover, during November, freshwater phytoplankton blooms have been also reported in the Dowleiswaram dam reservoir waters (Prasad *et al*., 2013), which could have been injected into the estuary along with freshwater discharge during the wet period. The combination of varying residence times and the potential input of waters from the dam can be reasonably invoked to explain the relative importance of dead freshwater contribution to the detritus pool during the wet period. On the other hand, during the dry period, ~60% of detritus was contributed by C_3 plants and 12% by freshwater algae. Despite the negligible amount of discharge during the dry period a certain amount of terrestrial OM, brought during discharge period, might have been trapped in the estuary due to high residence time of water and recirculation through tidal mixing.

Thus, the results of our study suggest that during both wet and dry periods the contribution of *in situ* phytoplankton to POM in the Godavari estuary is very small when compared to allochthonous OM sources, like terrestrial OM or freshwater algae.

Potential sources of nutrients for phytoplankton

The $\delta^{15}N_{phytoplankton}$ was significantly heavier (15.9 ± 2.5 ‰) during wet period than earlier reports from the Godavari estuary (5.1 to 7.8 ‰; Sarma *et al*., 2012, 2014). Such heavier $\delta^{15}N_{phytoplankton}$ were normally observed in highly polluted estuaries (up to 23‰; Middelburg and Herman, 2007; Kromkamp *et al*., 1995) and were at times attributed to the high chemoautotrophic production rates by nitrifiers (Soetaert and Herman, 1995a, 1995b). Owens (1985) noticed enriched $\delta^{15}N$ of PN (14.7‰) in the suspended matter at the turbidity maximum zone and attributed it to intense biological processing of OM. Seasonal enrichment of $\delta^{15}N_{POM}$ (18-24‰) has been also reported repeatedly during spring in several other estuaries (Middelburg and Herman, 2007), and attributed to the utilization of isotopically enriched nitrogen, especially residual ammonium resulted from nitrification (Mariotti *et al*., 1984) or extensive algal uptake of nitrogen, leading to enrichment of leftover nitrogen.

The occurrence of phytoplankton blooms associated with rapid decrease in DIN concentrations was reported a month prior to our sampling (Sarma *et al*., 2009). Based on previous studies conducted in other estuaries, we can hypothesize that in our study $\delta^{15}N_{DIN}$ might be enriched in October due to the extensive utilization of lighter inorganic nitrogen available in association with the phytoplankton bloom and that the uptake of such enriched $\delta^{15}N_{DIN}$ might have increased isotopic value of phytoplankton during the wet period.

Though the detritus pool includes phytoplankton biomass, during the dry period the $\delta^{15}N_{POM}$ were lower than $\delta^{15}N_{phytoplankton}$ suggesting that the contribution of the latter may be less than the former. On the other hand, during the dry period, $\delta^{15}N_{Phytoplankton}$ (4.6 ± 1.0‰) was close to that of the nutrients derived from regeneration of marine organic matter (4.8‰; Sigman *et al*., 2000) suggesting that regenerated nutrients might have supported phytoplankton biomass during the dry period.

Potential sources for the zooplankton diet

The output of the SIAR model suggests that zooplankton based for their diet preferentially (60%) on detritus than phytoplankton (40%) during the wet period, and inverted such preference during the dry one (Tab. 5). Despite during the wet period higher phytoplankton biomass was observed (10.5±2 µg Chl-*a* L^{-1}) zooplankton preferred detritus as a food source. In this regard, however, it is worth noting that the detritus pool during the wet period contained an important fraction of freshwater dead/senescent algae, likely providing a labile source of food as the one provided by phytoplankton biomass. During the dry period, instead, the preference of zooplankton for phytoplankton (60%) depended most likely by the availability of larger size phytoplankton.

Trophic level of food web during wet and dry periods

The computed TL for zooplankton (Calanoida, and Cyclopoida) was 2.6-2.9 during the wet period and decreased (1.6-2.0) during the dry one (Tab. 3). Such a difference can be attributable to variations in the base of the food web. In fact, during the dry period, when phytoplankton represented a relevant proportion of the zooplankton diet, the TL for primary consumers was low, whereas the more important contribution of detritus during the wet period resulted in a higher TL (Tab. 3). These results are also consistent with the variations in the relative importance of detritus *vs* phytoplankton to the zooplankton diet between the two sampling periods. Variations in the relative importance of detritus (40% *vs* 60% in the dry and wet periods, respectively), were also associated with changes in the relative importance of detritus from C$_3$ plants (prevailing during the dry period) and freshwater algae (prevailing in the wet period) (Tab. 4).

CONCLUSIONS

Our results confirm previous findings showing that mesozooplankton can modify their TL in response to natural environmental changes, resulting, in turn, in expansions or contractions in trophic linkages within the food web and, as a consequence, affecting the efficiency of energy transfer in food webs (Decima *et al.*, 2013). For instance, Landry (1981) reported that several species may alter their dietary compositions and TL within the food web as a consequence of changes in the size structure and availability of phytoplankton with a preference for larger cells (Frost, 1972; Landry, 1981; Ohman and Runge, 1994), either as a passive response to relative availability of alternate prey or an active switching tendency toward omnivory, when mean phytoplankton size is smaller (Calbet and Landry, 1999).

As changes in TL of primary consumers affect, by cascade, the trophic position of consumers at higher
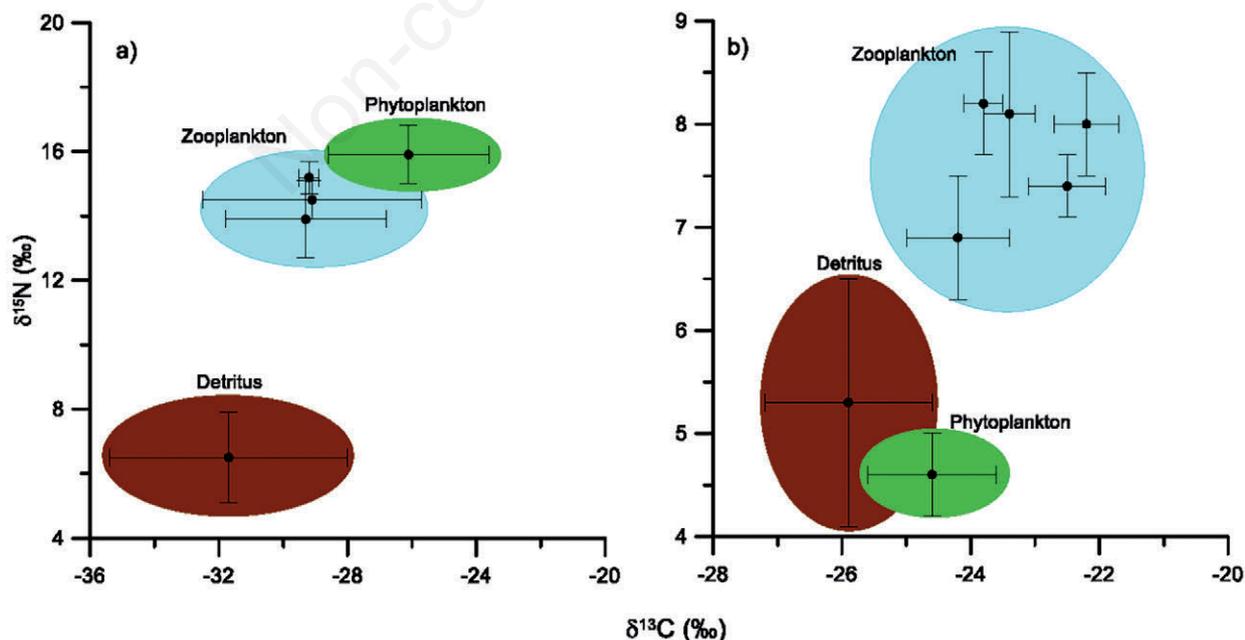
Fig. 2. The isotopic composition of carbon and nitrogen of phytoplankton, detritus and zooplankton during wet (a) and dry (b) periods in the Godavari estuary.

trophic levels, our results, based on the estimates of the trophic position through $\delta^{15}N$ isotopic values, suggest the presence of a food chain that is longer during the dry than the wet period (Fig. 2).

Although based on an under-replicated study, we conclude that changes in the structure (length) of the food chain in the Godavari estuary reported here were plausibly determined by variations in the array of environmental factors, which, in turn, affected the origin, composition and food availability of POM at the base of the food web and, by cascade, the zooplankton diet.

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