



Non-Redfieldian C:N:P ratio in the inorganic and organic pools of the Bay of Bengal during the summer monsoon

Deepika Sahoo^{1,2}, Himanshu Saxena^{1,2}, Nidhi Tripathi^{1,2}, Mohammad Atif Khan¹,
Abdur Rahman¹, Sanjeev Kumar¹, A. K. Sudheer¹, Arvind Singh^{1,*}

¹Physical Research Laboratory, Ahmedabad, Gujarat 380009, India

²Indian Institute of Technology, Gandhinagar, Gujarat 382355, India

ABSTRACT: Nitrogen (N) and phosphorus (P) determine the strength of the ocean's biological carbon (C) pump, and variation in the N:P ratio is key to phytoplankton growth. A fixed C:N:P ratio (106:16:1) in organic matter and deep-water nutrients was observed by Alfred C. Redfield. However, recent studies have challenged the concept of the Redfield Ratio, and its veracity remains to be examined in oceanic basins like the Bay of Bengal. For this purpose, we sampled the water in the Bay of Bengal for C, N, and P content in the organic and inorganic pools from the surface to 2000 m. Overall, the C:N:P ratio deviated greatly from the Redfield Ratio. The C:N:P ratio in particulate organic matter varied from 232:25:1 in the top layer (surface to the depth of the chlorophyll maximum) to 966:72:1 in the deep water (300–2000 m). In dissolved organic matter, the ratio varied from 357:30:1 in the top layer to 245:66:1 in the deep water. The N:P ratio in nutrients varied from 3 in the top layer to 12 in the deep water. The nutrient-depleted top layer (average $\text{NO}_3^- + \text{NO}_2^- \sim 0.7 \mu\text{mol l}^{-1}$) with a low N:P ratio coupled with reported low primary production rates in the Bay suggested that the production was N limited. Concurrent N_2 fixation rates were not sufficient to alter the observed C:N:P ratio. Eddies showed a mixed effect on the C:N:P ratio. Our C:N:P ratios in particulate organic matter are comparable to other tropical basins and supports the nutrient supply hypothesis for low latitude ecosystems.

KEY WORDS: Northern Indian Ocean · Elemental stoichiometry · Organic matter · Nitrogen limitation

— Resale or republication not permitted without written consent of the publisher —

1. INTRODUCTION

Until recently, it was believed that the molar carbon:nitrogen:phosphorus (C:N:P) ratio in phytoplankton (inferred from bulk organic matter) and deep ocean nutrients remained statistically uniform at 106:16:1 — a coincidence discovered by Alfred C. Redfield and thereafter known as the Redfield Ratio (Redfield 1934). Redfield provided 3 explanations for a fixed C:N:P ratio: (1) it is a mere geochemical coincidence, (2) microorganisms adapt to oceanic nutrient stoichiometry, and (3) biogeochemical processes regulate the ratio (Redfield 1958). However, a phyto-

plankton physiology model and an empirical data set suggested that the Redfield Ratio is not a universally optimal value; rather, it is the average stoichiometry of phytoplankton in the ocean (Klausmeier et al. 2004a). In addition, recent findings highlighted a global latitudinal variation in the C:N:P ratio from the canonical Redfield Ratio (Martiny et al. 2013a,b).

Elemental ratios of phytoplankton and nutrients are of paramount importance to our understanding of their biogeochemical cycling in the oceans (Weber & Deutsch 2012, Wang et al. 2019). Biologically, C is the backbone of all biomolecules, while N and P are proximate and ultimate limiting nutrients, respec-

*Corresponding author: arvinds@pml.res.in

tively, for oceanic primary production (Tyrrell 1999). The C:N:P stoichiometry in particulate and dissolved pools of the ocean has been fundamental to our understanding of marine biogeochemistry, as it allows us to estimate the approximate concentration of one nutrient through the knowledge of the other, leading to ease in calculations of various rate processes, such as export production and nutrient-based flux rate calculations (Geider & La Roche 2002, Tyrrell 1999). Deviations from the N:P ratio of 16:1 in nutrients are used to infer the net effect of various biogeochemical processes such as N_2 fixation ($>16:1$) and denitrification ($<16:1$) in the water column (Gruber & Sarmiento 1997, Tyrrell 1999, Lenton & Watson 2000, Deutsch & Weber 2012, Zehr & Capone 2020).

Most marine elemental stoichiometry studies are confined to particulate organic matter (POM) and dissolved inorganic matter (DIM) (Copin-Montegut & Copin-Montegut 1983, Martiny et al. 2013a, Singh et al. 2015a, Baer et al. 2019). Although dissolved organic matter (DOM) forms one of the largest reservoirs of C and N in the ocean (Ogawa & Tanoue 2003) and contributes 20–25 % in global export production, the elemental ratios in DOM are not well studied. A globally compiled data set on marine C:N:P ratio (810:48:1) in DOM, with little data from the Indian Ocean, suggested that it deviates greatly from the Redfield Ratio (Letscher & Moore 2015).

Several studies on the C:N:P ratio in phytoplankton and in nutrients have been reported from the Atlantic Ocean, and to an extent from the Pacific Ocean with limited studies in the Indian Ocean (Copin-Montegut & Copin-Montegut 1983, Karl et al. 2001, Martiny et al. 2013a,b, 2014, Singh et al. 2015a). In the Indian Ocean, these studies are mostly confined to the northwestern (Martiny et al. 2013b) and southwestern tropical regions (Copin-Montegut & Copin-Montegut 1983). Despite the fact that the northern Indian Ocean is distinct from other oceans in terms of the extent and magnitude of biogeochemical processes, particularly due to monsoonal wind forcing, less is known about mechanisms regulating elemental stoichiometry in this part of the Indian Ocean.

The Bay of Bengal (hereafter the Bay), the north-eastern part of the Indian Ocean, is an economically¹, ecologically, and culturally important basin as it forms a long coastline with the Indian subcontinent. It is surrounded by the Indian subcontinent in the north and

northwest, and the Andaman Nicobar Islands in the east. The prevalence of eddies are typical characteristics of this basin (Mukherjee et al. 2019); frequently occurring mesoscale eddies are associated with advective transfer of riverine water offshore. The Bay experiences semi-annual seasonality of the Asian monsoon system (Gadgil 2003). Strong southwesterly winds lead to high rainfall over the Indian subcontinent from June to September, whereas between December and February, northeasterly winds lead to heavy rainfall in the southern states of India. Large freshwater influx ($1.625 \times 10^{12} \text{ m}^3 \text{ yr}^{-1}$) from the Ganges-Brahmaputra river system drives a strong vertical density gradient leading to higher sea surface temperature than usual in the Bay (Subramanian 1993, Shetye et al. 1991). The influx of nutrients through riverine discharge, surrounding mangroves and wetlands enhances productivity in the coastal regions (Dutta et al. 2019) and leads to a considerable organic C export to the deeper Bay (Ittekkot et al. 1991, Kumar et al. 2004, Singh & Ramesh 2015).

The Bay shows high concentrations of dissolved organic C (DOC) $\sim 75\text{--}100 \mu\text{mol l}^{-1}$ in the surface waters due to high riverine flux (Shah et al. 2018). In addition, dissolved organic N (DON) and dissolved organic P (DOP) constitute about 70–99 % of the total dissolved nutrients in the waters above the thermocline (Sarma et al. 2019a). At the same time, the water column remains stratified, restricting the upward nutrient flux due to a strong halocline (Prasanna Kumar et al. 2010). In such cases, recycling processes and frequent eddies observed over the Bay could be of considerable importance for primary production (Prasanna Kumar et al. 2004, Singh et al. 2015b). In fact, eddies are known to enhance the primary production in the Bay (Prasanna Kumar et al. 2010, Singh et al. 2015b).

These hydrographic (e.g. riverine influx), physical (e.g. stratification and eddy-driven mixing), and biogeochemical (e.g. N_2 fixation) variables might have an influence on the C:N:P ratio in the Bay. However, there are only a few studies from the basin, and these are limited only to POM stoichiometry. The C:N ratio in POM was higher (8.0–17.2) in the coastal Bay during spring 2018 (Sarma et al. 2019b) than that (7.1) in the offshore Bay during spring 2016 (Garcia et al. 2018). In order to comprehensively explore the interplay of biogeochemical and physical processes on the C:N:P ratio, we sampled the water column at 8 locations in the Bay during the summer monsoon (July 2018). Our major objectives during this study were to (1) estimate the C:N:P ratio in organic and inorganic pools in the water column (surface to

¹The Bay of Bengal Initiative for Multi-Sectoral Technical and Economic Cooperation (BIMSTEC) supports international trade among India, Bangladesh, Bhutan, Myanmar, Thailand, Sri Lanka, and Nepal.

2000 m depth), (2) understand the impact of biogeochemical processes, such as N_2 fixation, on the elemental ratio, and (3) understand the role of physical processes, such as eddies, on elemental ratios in organic and inorganic pools.

2. MATERIALS AND METHODS

Sampling was performed in the Bay during the peak of the summer monsoon (12 July to 2 August 2018) on-board ORV 'Sagar Nidhi' (SN#132) (see Table 1). We sampled 8 different stations; 5 of which were along an 88° E transect while the rest were located from 85 – 87° E longitudinal range (Fig. 1). Water samples were collected using a Sea-Bird CTD rosette sampler from 12 different depths (10, 25, 50, 75, 100, 150, 200, 300, 500, 1000, 1500, and 2000 m) at each station. At times, one of the 2 subsurface sampling depths (i.e. 50 or 75 m) was changed to match the depth of the deep chlorophyll maximum (DCM). The CTD sensors provided data on water temperature, salinity, and density. Fluorescence data were obtained from a well-calibrated sensor mounted on the

CTD rosette sampler. Mixed layer depth was calculated using a 0.2°C deviation in potential temperature from the surface water (de Boyer Montégut 2004, Holte & Talley 2009).

For total organic C (TOC) and total N (TN) measurements, seawater samples were collected in 50 ml sterile centrifuge tubes. The samples were frozen immediately at -20°C until analysis in the onshore laboratory. The TOC measurements were performed using a high temperature catalytic oxidation method in a TOC analyser (TOC-L-CPH, Shimadzu Corporation) (Suratman et al. 2009, Pujo-Pay et al. 2011). Inorganic C was removed by acidifying the sample with 2 N HCl through purging of a carrier gas (zero gas, ultra-pure, 99.9995% purity) prior to the TOC measurement. The non-purgeable organic C was oxidised to CO_2 and measured using a Non Dispersive Infra-Red detector. TN concentrations were measured on a TN analyser (TNM-L-CPH, Shimadzu Corporation) by oxidising dissolved nitrogen to nitric oxide (NO) into the combustion tube at 720°C . The resultant NO was detected in a chemiluminescence detector (Chaichana et al. 2019). The accuracy of the results was ensured by routinely measuring a certified reference material (Batch 18, Lot#08-18 for deep seawater) provided by the University of Miami (Hansell 2005). Analysis was performed after ensuring that the absolute deviation of the measured value from the known value was within 5%. The coefficient of variation was 2% for total organic C (TOC) and TN measurements.

Samples for nutrients (NO_3^- , NO_2^- , and phosphate [PO_4^{3-}]) analysis and total phosphorous (TP) were collected in 60 ml high density polyethylene bottles and frozen at -20°C . Nutrients were measured using an autoanalyser (SKALAR). The detection limits for NO_x ($\text{NO}_3^- + \text{NO}_2^-$), NO_2^- , and PO_4^{3-} were 0.16, 0.06, and $0.02 \mu\text{mol l}^{-1}$, respectively. NO_x and PO_4^{3-} are referred to as dissolved inorganic nitrogen (DIN) and dissolved inorganic phosphorus (DIP), respectively. The depth at which the NO_3^- concentration reached $1 \mu\text{mol l}^{-1}$ was considered the nutricline, which was used to infer the nutrient supply rate to the surface layer (Garcia et al. 2018). Dissolved inorganic C (DIC) samples were collected in 12 ml Exetainers (Labco) followed by addition of 0.2 ml

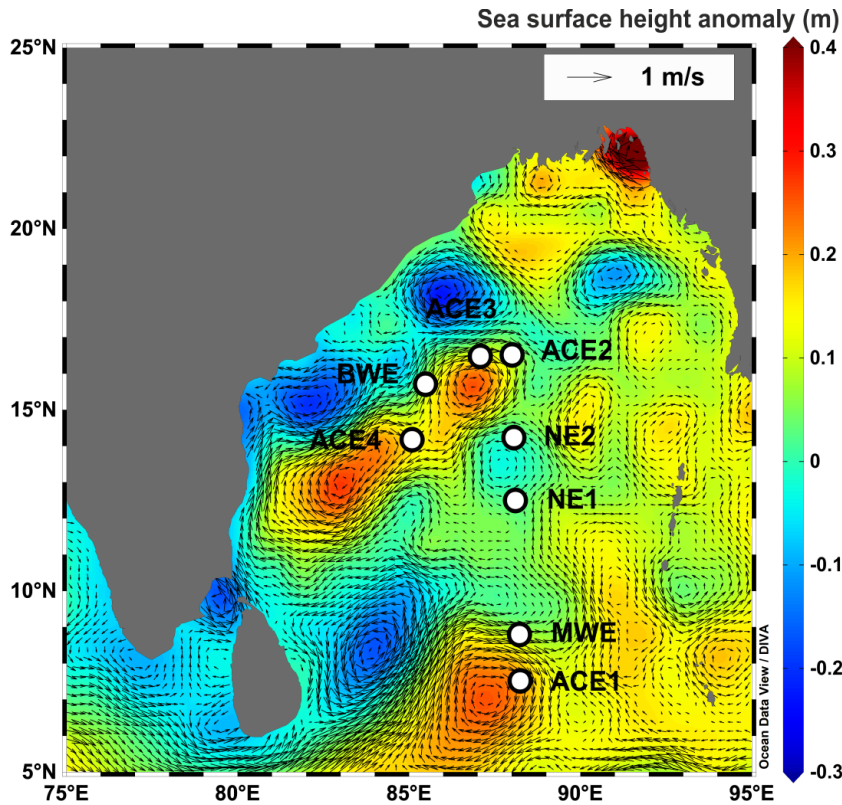


Fig. 1. Daily sea surface height anomaly overlaid by geostrophic currents on 12 July 2018. The eddies remained in the same position throughout the sampling period. Circles: sampling locations. Station abbreviations: ACE: anticyclonic eddy; MWE: mode water eddy; NE: non-eddy; BWE: boundary water eddy

mercuric chloride (100 % HgCl_2). DIC was measured using a coulometer (UIC; Model 5012) with an analytical precision of $\pm 2\%$.

Samples for particulate organic C (POC), N (PON), and P (POP) were collected by filtering seawater on precombusted (at 400°C for 4 h) Whatman glass microfiber filters (GF/F, 47 mm diameter, $0.7\ \mu\text{m}$ pore size). Around 3.7–4.7 l of water for depths up to 500 m and 5–8 l of water for depths from 1000–2000 m were filtered for POC and PON combined. For POP, 2.35 l of seawater was filtered for depths up to 500 m, whereas 3–4 l was filtered for depths from 1000–2000 m. Concentrations and isotopic compositions ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) for POC and PON were measured using an elemental analyzer (FLASH 2000; Thermo Scientific) coupled with an isotope ratio mass spectrometer (Thermo Delta V Plus; Thermo Scientific) connected via ConFlo interface. The analytical precision for both POC and PON for duplicate measurements was $<10\%$, while $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ had analytical precision of <0.1 and 0.3‰ , respectively. IAEA-N-2 ($(\text{NH}_4)_2\text{SO}_4$; 20.3‰) for N and IAEA-CH-3 (cellulose, -24.7‰) for C were used as standards in addition to the internal laboratory standards.

A high temperature oxidation method was adopted to estimate POP (Murphy & Riley 1962). Potassium persulfate ($\text{K}_2\text{S}_2\text{O}_8$) was used as an oxidising agent for digestion of the organic matter. Potassium dihydrogen phosphate (KH_2PO_4) standard was used for the calibration and adenosine-5'-triphosphate disodium (ATP-Na_2) standard was used to estimate the recovery percentage (80–85 %). Samples were digested in an autoclave at $1.055\ \text{kg cm}^{-2}$ (15 psi) for 80 min in the presence of $\text{K}_2\text{S}_2\text{O}_8$. Digested samples were analysed spectrophotometrically (Shimadzu Spectrophotometer UV-1800) at a wavelength of 880 nm. The detection limit of the measurements was $0.1\ \text{nmol l}^{-1}$. TON and total organic P (TOP) were estimated by subtracting inorganic matter from its total elemental pool as $[\text{TN}] - [\text{DIN}]$ and $[\text{TP}] - [\text{DIP}]$, respectively. DOC, DON, and DOP concentrations were quantified as the difference between TOC and POC, TON and PON, and TOP and POP, respectively. This method has limitations for DOP measurements in samples having $<10\%$ of total dissolved P. Our samples, however, had slightly higher than 10 % DOP in the total dissolved P pool. Nonetheless, the UV oxidation method is encouraged for the precise measurement of DOP in such waters (Foreman et al. 2019). All ratios were estimated in units of mol mol^{-1} .

We used published N_2 fixation and C uptake rates from a concurrent study performed on the same cruise (Saxena et al. 2020) to assess the role of these

2 biogeochemical processes on C:N:P ratios. Processed Automatic Weather Station data for wind speed was provided by the Indian National Centre for Ocean Information Services, India (Harikumar et al. 2013). To categorize the sample locations based on sea surface height anomaly, daily meridional and zonal geostrophic current ($0.25^\circ \times 0.25^\circ$) along with sea surface height anomaly ($0.25^\circ \times 0.25^\circ$) data were obtained from the Copernicus Marine Environmental Monitoring Service (<https://resources.marine.copernicus.eu/>; data retrieved on 17 August 2019). Cyclonic eddies were identified by anticlockwise geostrophic currents with $<-0.2\ \text{m}$ sea surface height anomaly. Anticyclonic eddies (ACE) were identified by a clockwise circulation with $>0.2\ \text{m}$ sea surface height anomaly. Features having increased sea surface height anomaly accompanied by lens shaped isopycnals were characterized as a mode water eddy (MWE) (Sweeney et al. 2003). Stations located along the boundary area of cyclonic and ACEs were categorised as a boundary water eddy (BWE). Stations with no significant sea surface height anomaly were considered non-eddy (NE) stations. We sampled 4 ACE (1–4), 2 NE (1–2) and one each MWE and BWE stations.

Linear regression analyses (significance level: $\alpha < 0.05$) were performed among C, N, and P concentrations in the different pools. One-way ANOVA was used to test the significant ($p < 0.05$) difference in the ratios of the different pools, using SigmaPlot 14.0 software. The Shapiro-Wilk test was performed to check the normality of the data for ANOVA analysis. Influence of environmental variables on the concentration of elements and their elemental ratios in the 3 different pools was investigated using principal component analysis (PCA) in R (R Core Team 2019). Elemental ratios, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ of POM were considered as dependent variables while others, such as the environmental parameters (temperature, salinity) and individual elemental concentrations in DIM, DOM, and POM were considered independent variables. Pearson's correlation coefficient at $\alpha < 0.05$ was used to estimate the strength of the relationships.

3. RESULTS

3.1. Hydrographic properties

Several eddy features were evident in the Bay during the study period. We observed strong southwesterly winds (average wind speed $\sim 11.5\ \text{m s}^{-1}$ with a maximum $\sim 24.5\ \text{m s}^{-1}$) throughout the sampling

Table 1. Details of environmental parameters at the 8 sampling locations during summer 2018 (error values: SD). See Fig. 1 for station locations. SST: sea surface temperature; SSS: sea surface salinity. Chl *a* values are averaged over the top layer; column-integrated (up to 75 m) N_2 fixation rates and primary production data are taken from Saxena et al. (2020)

Serial no.	Stn	Lat (°N)	Long (°E)	Date of sampling (dd-m-yyyy)	SST (°C)	SSS	Chl <i>a</i> (mg m ⁻³)	Depth of chl max (m)	Mixed layer (m)	Nutri-cline (m)	N_2 fixation (μmol N m ⁻² d ⁻¹)	Primary production (mmol C m ⁻² d ⁻¹)
1	ACE1	07°29.99'	88°14.23'	12-7-2018	28.8	34.19	0.29 ± 0.04	75	64	58	11 ± 5	30 ± 8
2	MWE	08°47.66'	88°13.44'	16-7-2018	28.1	34.39	0.89 ± 0.59	25	49	10	6 ± 6	87 ± 11
3	NE1	12°29.60'	88°06.52'	18-7-2018	28.8	33.11	0.38 ± 0.41	57	52	58	27 ± 16	39 ± 4
4	NE2	14°13.64'	88°03.63'	19-7-2018	28.5	32.78	0.23 ± 0.16	55	48	45	20 ± 4	24 ± 2
5	ACE2	16°30.49'	88°00.42'	24-7-2018	28.2	33.48	0.42 ± 0.21	47	43	51	4 ± 4	69 ± 5
6	ACE3	16°28.19'	87°05.02'	29-7-2018	28.7	33.44	0.20 ± 0.18	76	77	33	12 ± 8	58 ± 13
7	BWE	15°42.30'	85°28.94'	31-7-2018	28.7	33.62	0.23 ± 0.09	55	41	32	75 ± 98	81 ± 12
8	ACE4	14°10.33'	85°05.32'	02-8-2018	29.1	33.04	0.25 ± 0.28	78	66	66	41 ± 6	45 ± 4

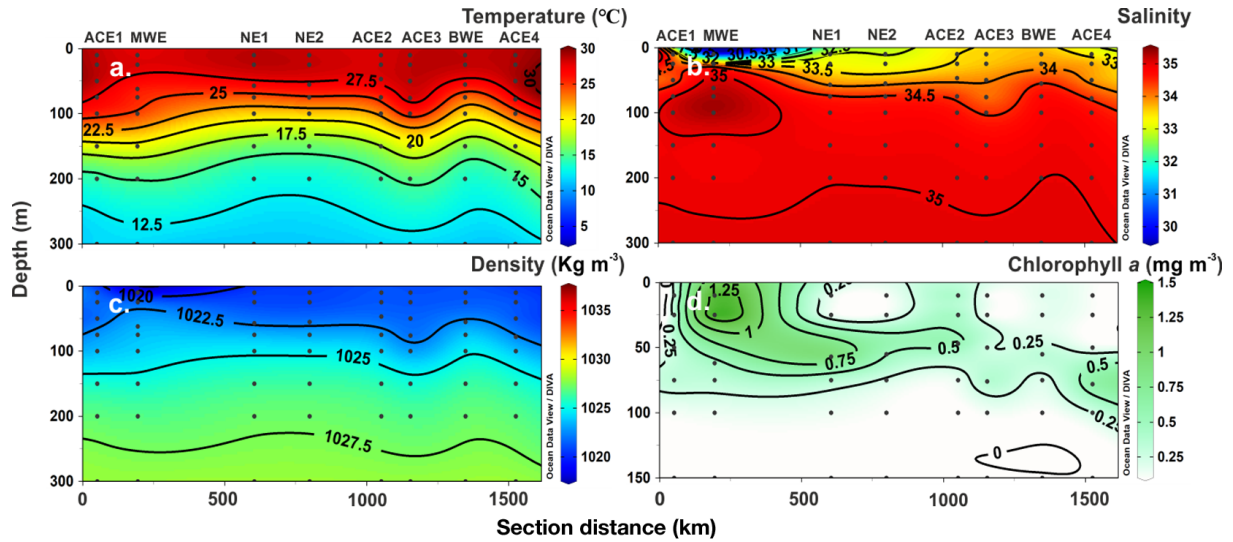


Fig. 2. Vertical section of (a) temperature, (b) salinity, (c) density, and (d) chl *a*. Section distance starts from Stn ACE1 (50 km) and ends at ACE4 (1500 km)

period. Sea surface temperature ranged from 28–29°C, while sea surface salinity varied from 33–34 (Table 1, Fig. 2). Sea surface salinity was the highest (34.39) at MWE and the lowest (32.78) at NE2. The mixed layer was deep (77 m) at ACE3 and shallow (41 m) at BWE. The nutricline varied between 10 m (at MWE) and 66 m (at ACE4) (Table 1).

3.2. Concentrations and ratios in the POM

To analyse the variability in elemental concentrations and ratios in the water column, we categorised our observations into 3 depth segments: (1) top layer (surface to DCM) where primary production is high, (2) subsurface layer (DCM to 300 m) where mineralisation is high, and (3) deep layer (300–2000 m). The

DCM varied between 25 m (MWE) and 78 m (ACE4). For calculation purposes, we considered the DCM depth in both the top and subsurface layers, and similarly 300 m depth in both the subsurface and deep layers.

POC, PON, and POP concentrations decreased with depth at all stations (Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m653p041_supp.pdf). The concentrations for POC, PON, and POP ranged from 3.5–6.5, 0.3–0.9, and 0.01–0.03 μmol l⁻¹, respectively, in the top layer at the ACE stations. High POC and POP concentrations were observed at ACE2, while POC and POP concentrations were low at ACE4. Among the ACE locations, the highest PON was at ACE1 and the lowest at ACE4. The MWE showed high POC, PON, and POP concentrations in the top layer compared to that at the other stations

Table 2. Average concentration ($\mu\text{mol l}^{-1}$, ± 1 SD; 8 stations), and % contribution of particulate organic C, N, and P (POC, PON, POP, respectively) from each pool to their respective total pools

	POC	PON	POP
Particulate organic pool			
Top layer	4.87 ± 1.83	0.54 ± 0.26	0.022 ± 0.011
	0.24	7.03	4.04
Subsurface water	2.37 ± 0.47	0.27 ± 0.14	0.008 ± 0.003
	0.11	0.98	0.40
Deep water	2.10 ± 0.55	0.15 ± 0.04	0.003 ± 0.001
	0.09	0.33	0.10
	DOC	DON	DOP
Dissolved organic pool			
Top layer	79.28 ± 10.67	6.40 ± 1.68	0.33 ± 0.09
	3.93	83.35	59.69
Subsurface water	64.78 ± 8.26	9.38 ± 4.95	0.39 ± 0.15
	2.95	34.45	20.11
Deep water	52.14 ± 11.05	11.95 ± 8.09	0.37 ± 0.18
	2.23	25.82	11.99
	DIC	DIN	DIP
Dissolved inorganic pool			
Top layer	1933.75 ± 70.74	0.74 ± 0.70	0.20 ± 0.09
	95.83	9.62	36.27
Subsurface water	2130.68 ± 80.41	17.57 ± 3.11	1.56 ± 0.22
	96.94	64.57	79.49
Deep water	2283.48 ± 71.38	34.17 ± 1.98	2.74 ± 0.11
	97.68	73.85	87.91

(Table S1). Overall, POC, PON, and POP constituted about 0.2, 7, and 4 % of their total elemental pools in the top layer (Table 2).

The C:N, N:P, and C:P ratios in POM were in every case higher than the Redfield Ratio in the top layer and increased further with depth (Figs. 3 & S2). Average POC:PON ratios in the top layers (~ 9) showed little variability, but showed deviations among stations in the deeper layer (Table S1). In the top layer, average POC:PON and PON:POP ratios were higher at ACE stations compared to most stations, whereas the POC:POP ratio was higher at NE stations in the subsurface and deeper layers. Overall, the C:N:P ratios in POM were 232:25:1, 457:35:1, and 966:72:1 in the top, subsurface, and deep layers, respectively (Fig. 4).

3.3. Concentration and ratios in the DOM

The DOC concentrations were higher in the top layer, with lower concentra-

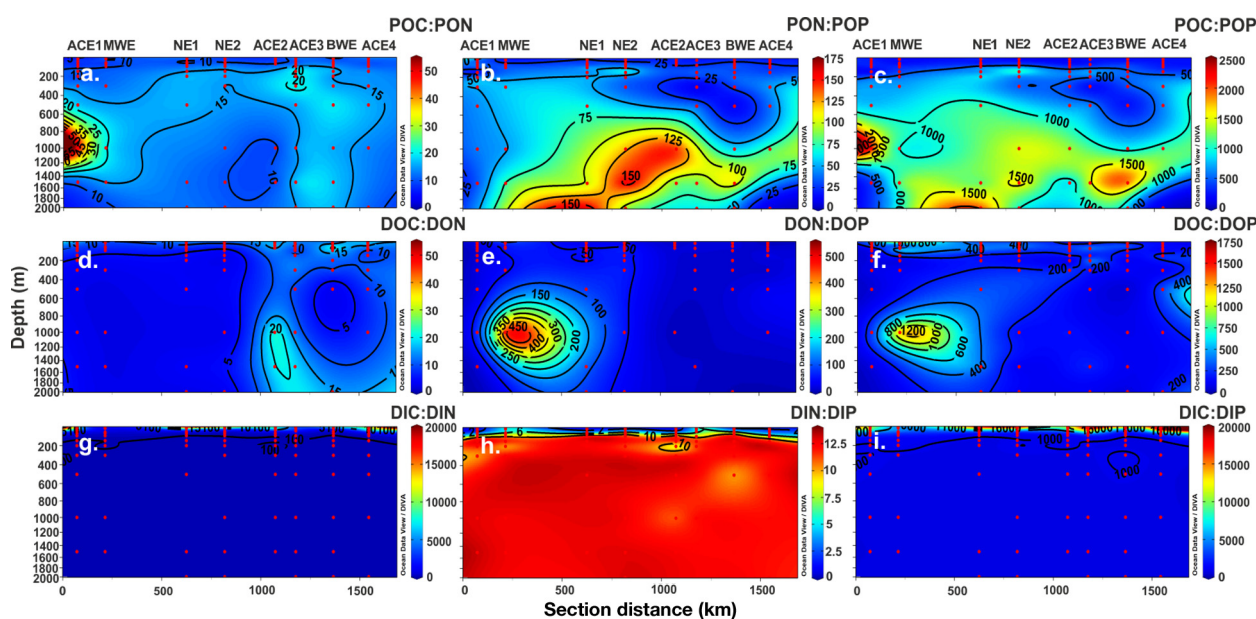


Fig. 3. Vertical section of (a) POC:PON, (b) PON:POP, (c) POC:POP, (d) DOC:DON, (e) DON:DOP, (f) DOC:DOP, (g) DIC:DIN, (h) DIN:DIP, and (i) DIC:DIP ratios. Section distance starts from Stn ACE1 (50 km) and ends at ACE4 (1500 km). POC, PON, POP: particulate organic C, N, P, respectively; DOC, DON, DOP: dissolved organic C, N, P, respectively; DIC, DIN, DIP: dissolved inorganic C, N, P, respectively

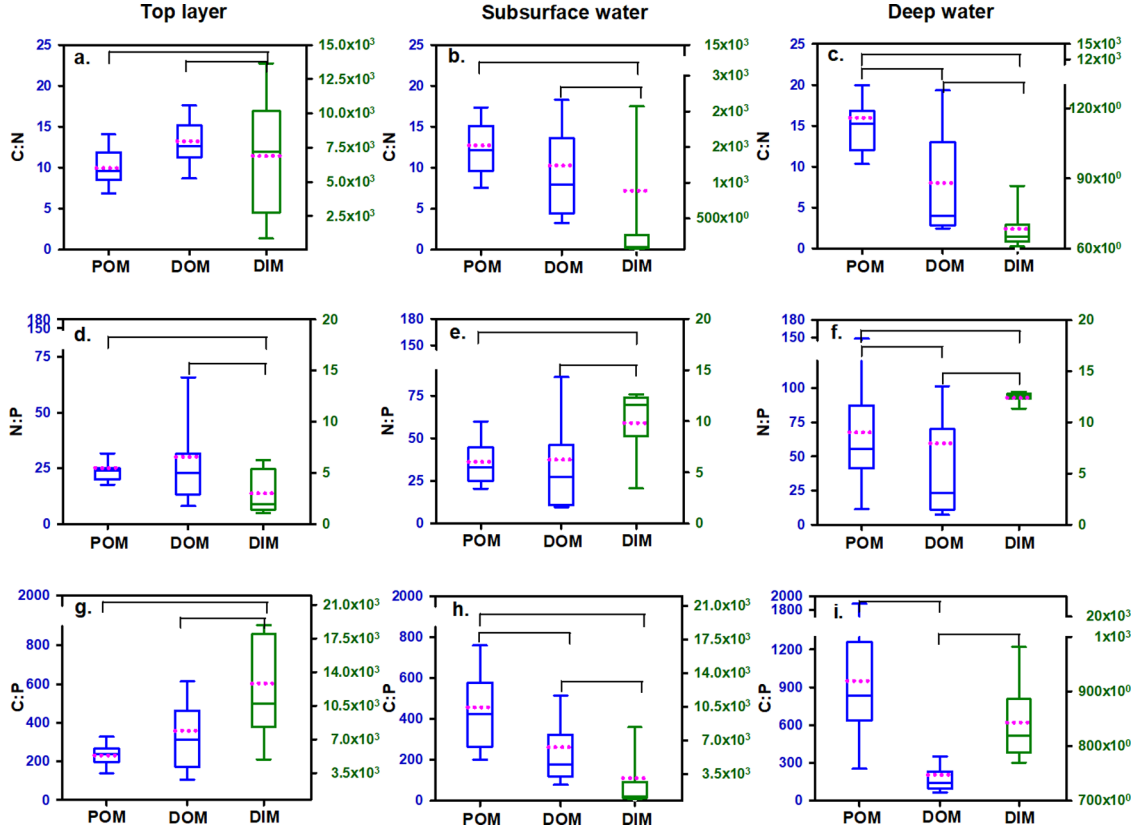


Fig. 4. C:N, N:P, and C:P ratios in top layer, subsurface water, and deep water. Pink dotted lines: mean; blue (POM, DOM: particulate organic, dissolved organic matter, respectively) and green (DIM: dissolved inorganic matter) solid lines: median. Black solid brackets: significantly different groups ($p < 0.05$) obtained from 1-way ANOVA; whiskers account for 10 and 90 % of distribution; box accounts for 25 and 75 %. Other abbreviations as in Fig. 3

tions measured in subsurface and deeper waters. The opposite vertical trend was observed for DON and DOP concentrations, with highest concentrations found in subsurface and deep waters (Table 2). Average DOC, DON, and DOP concentrations were 76.9 ± 5.8 , 5.3 ± 1.0 , and $0.4 \pm 0.1 \mu\text{mol l}^{-1}$, respectively, in the top layer of the ACE stations (Table S1). At MWE, the DOC, DON, and DOP concentrations were 76.0 ± 1.1 , 8.4 ± 0.8 , and $0.4 \pm 0.5 \mu\text{mol l}^{-1}$, respectively, in the top layer. The average concentrations of DOC, DON, and DOP in the top layers were 93.4 ± 5.1 , 8.2 ± 0.3 , and $0.3 \pm 0.03 \mu\text{mol l}^{-1}$, respectively, at the NE stations, while these values were 63.9 ± 2.9 , 5.1 ± 0.9 , and $0.3 \pm 0.1 \mu\text{mol l}^{-1}$, respectively, at the BWE. DOC, DON, and DOP constituted about 4, 83, and 60 %, respectively, of their total elemental pools in the top layers, while in the deeper waters their respective contributions were 2, 26, and 12 % (Table 2).

All the ratios in the DOM pool deviated greatly from the Redfield Ratio. In the top layer, the average DOC:DON ratio was higher at the ACE stations than others (Table S1). In contrast, DOC:DOP and DON:DOP ratios were the lowest in the top layer of the

ACE stations. The C:N and C:P ratios in DOM were lower in the subsurface and deep waters than in the top layer (Fig. 4). On average, C:N:P ratios in DOM were 357:30:1, 268:37:1, and 245:66:1 in the top, subsurface, and deep waters, respectively (Fig. 4).

3.4. Concentration and ratios in the dissolved inorganic pool

Average DIC, DIN, and DIP concentrations were 1910.3 ± 77.3 , 0.3 ± 0.1 , and $0.15 \pm 0.04 \mu\text{mol l}^{-1}$, respectively, in the top layer at the ACE stations (Table S1). DIN and DIP concentrations were high in the top layer at MWE and BWE (Table S1, Fig. S1). The average DIC, DIN, and DIP concentrations were 1973.1 ± 6.4 , 2.0 ± 0.5 , and $0.38 \pm 0.04 \mu\text{mol l}^{-1}$, respectively, in the top layer at the MWE station. At the NE stations, average DIC, DIN, and DIP concentrations in the top layer were higher than those observed at the ACE stations but lower than that at the MWE station. DIC, DIN, and DIP concentrations were 1916.6 ± 29.4 , 1.7 ± 2.5 , and $0.3 \pm 0.3 \mu\text{mol l}^{-1}$,

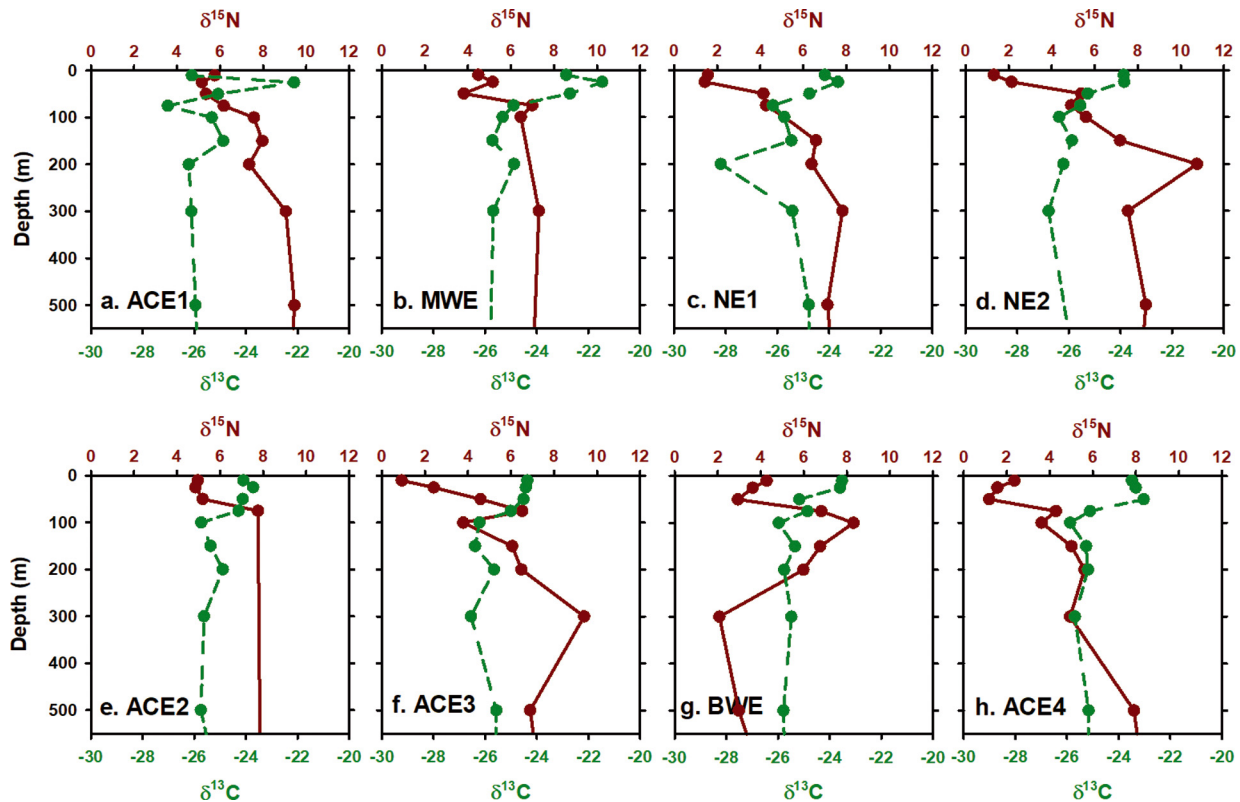


Fig. 5. Depth profile of $\delta^{13}\text{C}$ (green dashed line) and $\delta^{15}\text{N}$ (brown solid line) of POM at (a) ACE1, (b) MWE, (c) NE1, (d) NE2, (e) ACE2, (f) ACE3, (g) BWE, and (h) ACE4 stations. See Fig. 1 for abbreviations

respectively, in the top layer of the BWE. DIC, DIN, and DIP constituted about 96, 10 and 36 %, respectively, of their total elemental pools in the top layer (Table 2). There was large spatial variation in DIC: DIN and DIC:DIP ratios in the top and subsurface layers across the stations, with higher values at the ACE and NE stations (Table S1). However, DIC:DIN and DIC:DIP ratios were similar in the deeper layers across stations. The DIN:DIP ratios increased with depth with no significant spatial variability (Fig. 3). On average, the C:N:P ratios in dissolved inorganic nutrients were 12717:3:1, 3126:10:1, and 840:12:1 in the top, subsurface, and deep waters, respectively (Fig. 4).

3.5. Isotopic composition ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) of POM

The $\delta^{15}\text{N}$ of POM was positive throughout and increased with depth (Fig. 5). $\delta^{15}\text{N}$ ranged from 0.9–6.5‰ in the top, 1.2–9.4‰ in the subsurface, and 7–9.5‰ in the deep layers at the ACE stations. In the top layer, average $\delta^{15}\text{N}$ was 4.5 ± 0.7 , 2.7 ± 0.4 , and 3.6 ± 0.7 ‰ at the MWE, NE, and BWE stations, respectively. The ^{15}N enrichment in POM was higher in the deep waters of ACE and NE than that at the

BWE station. Contrary to $\delta^{15}\text{N}$, $\delta^{13}\text{C}$ decreased with depth. It varied between -22.1 and -26.1 ‰ in the ACE, and remained around -24.3 ± 0.1 ‰ in the top layer of the NE and -24.1 ± 0.9 ‰ in the top layer of the BWE stations. Comparatively less depleted ^{13}C signatures (-22.3 ± 0.8 ‰) in POM were observed at the top waters of the MWE.

3.6. Statistical analysis

The POC concentrations were positively correlated with PON ($r^2 = 0.59$, $p < 0.05$) and POP ($r^2 = 0.71$, $p < 0.05$) (Fig. S3). In addition, PON concentrations were positively correlated with POP concentrations ($r^2 = 0.66$, $p < 0.05$). However, no significant correlations were detected between DOC and DON, DON and DOP, and DOC and DOP concentrations. The DIN and DIP concentrations were strongly correlated ($r^2 = 0.99$, $p < 0.05$) with a slope of 13.18 and negative intercept—suggesting N nutrients were exhausted before PO_4^{3-} . Although the generation of DIP and DIN through organic matter remineralisation is faster than DIC in the ocean, DIC was strongly correlated with DIN ($r^2 = 0.75$, $p < 0.05$) and DIP ($r^2 = 0.78$, $p < 0.05$).

The PCA analysis showed that the first 2 principal axes (PC) explained a total of ~60 % of the variability, with 49 % accounted by PC1 (Fig. 6). PCA is used to highlight the relationships between variables projected in a multidimensional space. We have shown only PC1 and PC2, as they explain the most variability among parameters. Each arrow in Fig. 6 represents a variable (as mentioned near the arrowheads); the distance of the arrows from the origin and their closeness to each other is proportional to correlation, i.e. when arrows are far from the centre and close to each other, they are positively correlated. When arrows are symmetrically opposite, they are anticorrelated. If the arrows are orthogonal, there is no correlation. If the variables are close to the origin, the relationship among these variables is inconclusive. The vectors for POC:POP and PON:POP were identical, and anticorrelated with POP ($r = -0.5$). DOC:DON was anticorrelated with DON ($r = -0.7$), while DOC:DOP was anticorrelated with DOP ($r = -0.6$). DIN:DIP was strongly correlated with both DIN and DIP ($r = 0.9$). Likewise, DIC:DIN was anticorrelated with DIC and DIN ($r = -0.7$). DIC:DIP was anticorrelated with DIC and DIP ($r = -0.7$). $\delta^{13}\text{C}$ was positively correlated with POC ($r = 0.7$) and negatively with DIC ($r = -0.6$), while $\delta^{15}\text{N}$ was positively correlated with DIN ($r = 0.7$). DOC:DOP and DON:DOP

were negatively correlated with DOP. DIC, DIN, and DIP were negatively and positively correlated with *in situ* temperature and salinity, respectively.

4. DISCUSSION

This comprehensive study on the elemental stoichiometry in the particulate and dissolved pools of the poorly studied Bay revealed significant deviations from the Redfield Ratio. This deviation is far more pronounced in the deeper than the upper layers, with variable role of eddies and biogeochemical processes such as N_2 fixation. Below, we examine the role of physical and biogeochemical influences in shaping the ecological stoichiometry in the Bay.

4.1. Role of environmental factors on C, N, and P concentrations and their ratios

Variations in elemental ratios are driven by environmental factors such as temperature, salinity, and nutrient concentrations (Körtzinger et al. 2001, Frigstad et al. 2011). Nutrients (DIN, DIP, and DIC) were anticorrelated with temperature in our PCA analysis (Fig. 6). This suggests that temperature might not play a direct role in nutrient concentration. Rather, it suggests that nutrient concentrations are high in deep (cold) waters, and the influx of cold waters through physical processes (such as eddies) might enhance the nutrient concentration in the surface Bay. Additionally, the positive correlation between nutrients and salinity indicates that the nutrients are of marine origin (Fig. 6). This is not surprising, as terrestrial nutrients are largely consumed within the Bay's estuarine ecosystem (Singh & Ramesh 2011, Dutta et al. 2019). Correlations between elemental ratios and temperature and salinity should be interpreted with caution, as neither of these parameters are known to directly affect the elemental ratios. However, temperature changes affect nutrient uptake and other biogeochemical processes (such as respiration/decomposition), in turn influencing elemental stoichiometry (Lomas et al. 2002, Spackeen et al. 2018). In addition, salinity gradients have been shown to change N uptake rates in mesocosm experiments (Kumar et al. 2018). In theory, temperature- and salinity-related influences could be both physiological and taxonomic (Barton & Yvon-Durocher 2019, Hernando et al. 2020). The N-uptake potential is a part of physiological change of phytoplankton driven by salinity and temperature (Kaur-Kahlon et

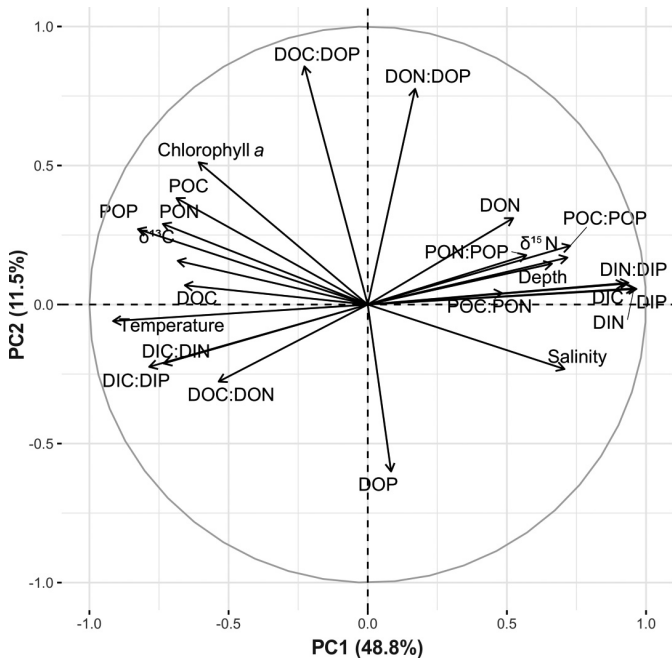


Fig. 6. Principal component analysis of depth, temperature, salinity, fluorescence, dissolved inorganic nutrients, particulate organic matter (POM), dissolved organic matter, elemental ratios, $\delta^{13}\text{C}$, and $\delta^{15}\text{N}$ of POM. Abbreviations as in Fig. 3

al. 2016, Kumar et al. 2018, Barton & Yvon-Durocher 2019, Hernando et al. 2020). Since our data are spatially distributed, these influences are likely to be taxonomical. The anticorrelation of salinity with POM concentrations could be attributed to the increase in elemental uptake potential due to the freshening of water at elevated temperatures (Hernando et al. 2020) or the relatively higher consumption (mineralisation) of POM at higher salinities. However, these mechanisms need to be experimentally verified in the Bay.

The overlapping of the PON:POP and POC:POP vectors suggest that these ratios are driven by variations in POP through similar processes, such as the POP remineralisation. Additionally, that there was no significant correlations of PON:POP and POC:POP with PON and POC, respectively, confirms that the variation of these ratios is due to oscillations in POP (Fig. 6).

4.2. Interlinking between the C:N:P ratios in POM, DOM, and DIM

The 3 elemental pools are interlinked among the depth layers through processes such as POM export, upward flux of nutrients, and exchange of DOM between the layers (Pujo-Pay et al. 2011). In the top layer, DIM and DOM are diffused to POM through biological consumption (Pujo-Pay et al. 2011). A part of POM gets recycled to DOM by excretion or lyses of organic matter; subsequently, DOM (and POM) remineralises to DIM, completing the cycle. In the subsurface and deep layers, POM and DOM are largely recycled to DIM (Krom et al. 2010).

The POC:PON ratio remains largely fixed in the water column, while increase in the C:P and N:P ratios in POM from the top to the subsurface layer (Fig. 3) suggests the preferential remineralisation of POP in sinking organic matter (Loh & Bauer 2000, Letscher & Moore 2015). In addition, the strong correlation ($r = 0.5$ and 0.7 and $p < 0.05$) of PON:POP and POC:POP ratios with nutrients confirms the recycling of POP (Fig. 6). During remineralisation, preferential removal of ^{13}C -enriched molecules such as protein and nucleic acids, and retention of ^{13}C -depleted, lipid-rich residual organic matter results in a decrease in $\delta^{13}\text{C}$ ($\sim 1.6\text{‰}$) of POM from the top layer to the subsurface and deep waters (Fig. 5) (Post et al. 2007). On the other hand, removal of N-rich biomolecules during degradation might have resulted in the increase in $\delta^{15}\text{N}$ (6‰ in the subsurface, and 7.5 ‰ in the deep water) of POM (Macko et al. 1994).

The very low N:P ratio in nutrients ($< 16:1$) in the top layer indicates N-stressed primary production in the Bay. This is confirmed from the negative intercept between DIN and DIP (Fig. S3e), which suggests that DIN gets exhausted before DIP. Unlike the N:P ratio, C:N and C:P ratios in DIM of the top layer were a thousand and a hundred times higher than the Redfield Ratio, respectively. The DIC pool is so large that it cannot be easily exhausted, and is considered here as unutilised. Therefore, when one looks at the change in DIC:DIN or DIC:DIP over time (i.e. consumption rate ratios), these ratios are likely to be close to the Redfield Ratio. However, the ratios in a static set of concentrations at a given time, as presented here, are roughly order of magnitudes higher.

The POM and DIM elemental proportions are primarily controlled by nutrient uptake and remineralisation processes. The remineralisation of POM to dissolved nutrients involves cycling through the DOM pool (Johnson et al. 2013, Singh et al. 2015a). Thus, DOM serves as an important intermediary link between POM and nutrients during remineralisation. In the NO_x -deficient top layer of the Bay, DON is an order of magnitude higher than DIN (Fig. S1e,h), suggesting that DON might be an alternative source of bioavailable N for phytoplankton in these waters (Church et al. 2002, Zubkov et al. 2003, Aldunate et al. 2020). A previous study in the Bay suggested a link between primary productivity and high DON and DOP concentrations during the spring intermonsoon of 2018 (Sarma et al. 2019a), but no such correlation was observed in our study (Fig. S4a,b). The absence of a correlation between primary production and DON in our study might be explained by the coupling between DON production and uptake, leading to a lack of DON accumulation. Another potential cause for no correlation may be the seasonal change in phytoplankton community composition. DON-consuming phytoplankton (cyanobacteria) are most abundant during summer in oligotrophic oceans (Huisman et al. 2018). Given that urea is one of the important sources of N for autotrophs in the surface water of the Bay (Baer et al. 2019), a study focused on DON uptake in different seasons is desirable to quantify the importance of DON as an alternative N source for phytoplankton in the Bay.

Low concentrations of DON and DOP in the top layer may be attributed to the photochemical breakdown of organic matter (Chari et al. 2016) and faster remineralisation of DOP and DON over DOC (Church et al. 2002, Letscher & Moore 2015, Chaichana et al. 2019). DOC is freshly produced in the sunlit surface ocean via phytoplankton degradation and food web

processes (grazing by microzooplankton), and the labile components are generally rapidly consumed by heterotrophic prokaryotes (Calleja et al. 2019). The semi-labile portion of DOC escapes rapid microbial consumption and accumulates in surface waters during high stratification. The accumulation of DOC in the top layer might have resulted in a high C:P ratio of ~357, and a C:N ratio ~13 in DOM (Ogawa & Tanoue 2003). Bacteria (mostly heterotrophs) use DOM as a substrate (Granéli et al. 1999). They require more N per unit biomass (C:N = 3–7; Nagata 1986) than phytoplankton (C:N = 6–20). In the present study, DOM had a high C:N ratio (13.2) in the top layer, thus bacteria may retain the same DOM proportion. Bacteria also consume more N than P compared to the Redfield Ratio (Bertilsson et al. 2003), hence they might also change DOM stoichiometry at the surface if DOM concentrations are low.

Accumulated semi-labile DOM in the surface water can be transported down by vertical mixing and by ballasting of terrestrially derived lithogenic matter in sinking particles, thereby increasing the organic C export to the deep sea (Rixen et al. 2019). This subducted fraction of DOC can be remineralised by subsurface heterotrophic communities (Calleja et al. 2019), thereby decreasing the DOC concentration in the subsurface and deep waters. The depth profile of DOC in this study is consistent with observations elsewhere in tropical regions (Santinelli et al. 2006). DON is more resistant to remineralisation than DOP. The downward transport of refractory DON (>50% of DON; Roussenov et al. 2006, Vidal et al. 2018) results in an enhanced accumulation below the surface layer of the ocean. Overall, this may have resulted in decreased C:N and C:P, along with increased N:P ratio in DOM in the subsurface and deep waters. These observations are consistent with the negative correlation of DON:DOP with DOP (Fig. 6). The average C:N:P ratio in the DOM in the top layer is 357:30:1 in the Bay, lower than the global average 640:44:1 for bulk DOM in the surface ocean (Letscher & Moore 2015). However, the DON:DOP ratio in the top 100 m ranged from 5–237 among stations, higher than that (1.1–16.6) reported for the coastal Bay during spring 2018 (Sarma et al. 2019a).

Usually $\delta^{13}\text{C}$ in POC varies from –24 to –18‰ (Fry & Sherr 1989, Middelburg & Nieuwenhuize 1998) and $\delta^{15}\text{N}$ in PON from 5–8‰ in marine phytoplankton (Minagawa et al. 2001). Although the Bay receives enormous terrestrial influx (33–51.2 g m⁻² yr⁻¹) (Ittekkot et al. 1991, Unger et al. 2003), the mean C:N ratio (~10), $\delta^{13}\text{C}$ (–21.5 to –26.2‰, average –24.6 ± 1.2‰), and $\delta^{15}\text{N}$ (0.9–8.3‰, average 4.4 ± 1.9‰) of

POM in the top 100 m in our study indicates that the POM in the surface layer of the Bay is largely derived from *in situ* production rather than external supply.

4.3. The role of strong winds and eddies on the C:N:P ratios

Overall, eddies showed a mixed effect on the C:N:P ratios in the top layer. Strong southwesterly winds (up to 24.5 m s⁻¹) and eddies were identified in our sampling area during the study period. A relatively deep mixed layer (41–77 m) and shallow nutricline (10–66 m) (Table S2) were observed during the sampling period, which might be due to the strong winds and eddy-induced mixing of the water column. Although there were differences in DIM and POM concentrations, little variability in C:N:P ratios of POM between eddy and non-eddy stations was observed. DOC and DON concentrations were lower at the ACE compared to that at the NE stations, while DOP was slightly higher at the ACE stations in the top layer. Due to this difference, the DOC:DOP and DON:DOP ratios were lower in the ACE locations compared to the NE locations. A study conducted to understand the influence of eddies on nutrients and POM during spring 2018 (Sarma et al. 2019b) reported POC and PON concentrations higher than our study, but the C:N ratio in POM remained the same. Similarly, primary production estimates reported in a concurrent study (288–1044 mg C m⁻² d⁻¹; Saxena et al. 2020) are consistent with that (758 ± 220 mg C m⁻² d⁻¹) reported by Sarma et al. (2019a). These primary productivity estimates are much higher than an earlier estimate of primary productivity conducted during N-stressed conditions in April 2016 (primary productivity: 3–7 nmol C l⁻¹ h⁻¹; N:P flux ratio <14; Baer et al. 2019). Overall, these studies suggest a role of eddies in supplying nutrients to the photic layer and consequently increasing primary production leading to an elevated elemental ratio in POM (Sarma et al. 2019a,b). On an average, the C:N:P ratio in POM in the top layer is higher than reported earlier in the Bay during spring inter-monsoon (Garcia et al. 2018) (Table S2).

4.4. Impact of biogeochemical processes on the C:N:P ratio

Marine biogeochemical processes have the potential to change the plankton and nutrient elemental ratios, and vice versa (Klausmeier et al. 2004b, Mills

& Arrigo 2010, Jabir et al. 2020). Despite PO_4^{3-} excess (N:P ~3) in the top layer with adequate dry deposition flux of Fe ($0.02\text{--}1.2 \mu\text{mol m}^{-2} \text{d}^{-1}$; Srinivas & Sarin 2013), low N_2 fixation rates were observed in the Bay (Saxena et al. 2020). Assuming photoautotrophs require 1 mol N to fix 6.6 mol C (Redfield 1958, Orcutt et al. 2001), the contribution of N_2 fixation to phototrophic C fixation remains below 1 % (Saxena et al. 2020). Apart from the low N_2 fixation in surface waters during our study, heterotrophic N_2 fixation rates are below detection limits in the oxygen minimum zone of the Bay (Löscher et al. 2020). Such low rates of N_2 fixation are unlikely to change the C:N:P ratios. No correlation between N_2 fixation rates and different elemental ratios confirms the same (Fig. S4e,f).

The observed PON:POP ratio (~25) could be attributed to the presence of smaller non-diazotrophic cyanobacteria, such as *Prochlorococcus* and *Synechococcus*, which are ubiquitous in the surface waters (Bertilsson et al. 2003, Martiny et al. 2013a, Baer et al. 2019). *Prochlorococcus* tend to be dominant in high-temperature and low-nutrient waters.

The N:P ratios in nutrients act as a proxy for biogeochemical processes leading to N loss (such as denitrification and anammox) in the subsurface low oxygenated waters. The N:P ratio of dissolved inorganic nutrients in the water column (<16:1) suggests the occurrence of N loss processes in the Bay, with low but detectable rates of anammox (5.5 nM N d^{-1}) and denitrification (0.9 nM N d^{-1}) measured in the oxygen minimum zone (Bristow et al. 2017). However, an extensive study is required to understand the effect of N loss processes of this magnitude on nutrient stoichiometry of the Bay.

Considering the observed deviations in the C:N:P ratio from the Redfield Ratio in the dissolved and particulate matter pools, we examined whether the Bay supports the nutrient supply hypothesis for tropical ecosystems proposed by Rhee (1978). This hypothesis states that the absolute concentration of nutrients such as DIN and DIP, rather than their ratio, determines the POM stoichiometry. Based on this hypothesis, expected C:N:P ratios in oligotrophic basins are higher than the Redfield Ratio, and the reverse holds for nutrient-rich basins (Galbraith & Martiny 2015). This happens because slow growing cyanobacteria, with a high N:P ratio in their biomass/nutrient uptake requirements, grow in oligotrophic waters whereas fast growing microorganisms (with a low N:P ratio) flourish in nutrient-rich waters (Singh et al. 2017, Sharoni & Halevy 2020). Poor supply of nutrients due to stratification makes the Bay oligotrophic

during most seasons (Prasanna Kumar et al. 2010, McCreary et al. 2013). We observed that the C:N, C:P, and N:P ratios in the POM at surface waters are higher than the Redfield Ratio, and this seems to favour the nutrient supply hypothesis for tropical systems.

The average C:N:P ratio (232:25:1) of POM in the top layers of the Bay is similar to observations in other tropical oceans, such as the subtropical North Atlantic Ocean (210:36:1) (Singh et al. 2015a) and subtropical North Pacific Ocean (172:25:1) (Martiny et al. 2013a). The subtropical North Atlantic is considered a P-limited (DIN:DIP ~30) basin, and exhibits a high C:N:P ratio in the POM (Wu et al. 2000). However, the Bay and the subtropical North Pacific Ocean are N-limited, and both possess high N:P ratios (25) in POM and low N:P ratios (<16) in subsurface nutrients. Our overall analysis suggests that the nutrient availability in the Bay is likely governed by N loss processes (such as denitrification), whereas N gain processes (such as N_2 fixation) exert control in the subtropical North Atlantic Ocean (Deutsch & Weber 2012).

5. CONCLUSIONS

We presented a comprehensive study of C:N:P ratios in the inorganic and organic pools of the Bay water column covering depths from the surface to 2000 m. Overall, C:N:P ratios deviated greatly from the Redfield Ratio (C:N:P = 106:16:1) in all the biogeochemical pools and at all depths. In the POM, C:N:P ratios were 232:25:1, 457:35:1 and 966:72:1 in the top, subsurface, and deep water layers, respectively. Our estimated C:N:P ratios in POM are comparable to that observed in other tropical basins such as the North Pacific Ocean and North Atlantic Ocean. On the other hand, the C:N:P ratio in the DOM in the top layer (357:30:1) is lower than the global average of 640:44:1 for bulk DOM in surface water.

Despite being a peak summer monsoon period, relatively low concentrations of nutrients with a low N:P ratio suggest that primary production was limited by bioavailable N. Concurrently estimated low N_2 fixation rates suggest that diazotrophic organisms had a minimal impact on nutrient or POM stoichiometry. Instead, a low supply of nutrients governed the observed higher N:P ratio in the POM. The POC:PON ratio and $\delta^{13}\text{C}$ of POM in the top 100 m of the Bay indicate that the POM was mostly derived from *in situ* processes, and that there is a relatively small influence of terrestrial influx in the open Bay. Over-

all, the higher C:N:P ratio than the Redfield Ratio in POM in surface waters supports the nutrient supply hypothesis for tropical oceans with low inorganic nutrient concentrations. The low N:P ratio in nutrients in the subsurface waters suggests a potential role of N loss processes in regulating nutrient stoichiometry.

Eddies have mixed effects on C:N:P ratios in the top layer. DIM concentrations are lower in ACE locations compared to that in the NE locations. Conversely, POM concentrations are higher in ACE locations compared to that in the NE locations. However, there is not much difference in the C:N:P ratios of DIM and POM at eddy and non-eddy stations. This study provides a detailed insight of elemental dynamics in organic and inorganic pools during the summer monsoon in the Bay, which can be used in biogeochemical models for this region.

Acknowledgements. We acknowledge ISRO–Geosphere Biosphere Programme (GBP) and Department of Space for the financial assistance and National Institute of Ocean Technology (NIOT), Chennai for the allotment of ship time. We express our gratitude to the research technicians, captain and crew of ORV ‘Sagar Nidhi’ for their support throughout the expedition. We are thankful to S. Nazirahmed for his help during sample processing. Three anonymous reviewers and Allannah Paul are thanked for critically reviewing the manuscript.

LITERATURE CITED

- ✦ Aldunate M, Henríquez-Castillo C, Ji Q, Lueders-Dumont J and others (2020) Nitrogen assimilation in picocyanobacteria inhabiting the oxygen-deficient waters of the eastern tropical North and South Pacific. *Limnol Oceanogr* 65:437–453
- ✦ Baer SE, Rauschenberg S, Garcia CA, Garcia NS, Martiny AC, Twining BS, Lomas MW (2019) Carbon and nitrogen productivity during spring in the oligotrophic Indian Ocean along the GO-SHIP IO9N transect. *Deep Sea Res II* 161:81–91
- ✦ Barton S, Yvon-Durocher G (2019) Quantifying the temperature dependence of growth rate in marine phytoplankton within and across species. *Limnol Oceanogr* 64: 2081–2091
- ✦ Bertilsson S, Berglund O, Karl DM, Chisholm SW (2003) Elemental composition of marine *Prochlorococcus* and *Synechococcus*: implications for the ecological stoichiometry of the sea. *Limnol Oceanogr* 48:1721–1731
- ✦ Bristow LA, Callbeck CM, Larsen M, Altabet MA and others (2017) N₂ production rates limited by nitrite availability in the Bay of Bengal oxygen minimum zone. *Nat Geosci* 10:24–29
- ✦ Calleja MLI, Al-Otaibi N, Morán XAG (2019) Dissolved organic carbon contribution to oxygen respiration in the central Red Sea. *Sci Rep* 9:4690
- ✦ Chaichana S, Jickells T, Johnson M (2019) Interannual variability in the summer dissolved organic matter inventory of the North Sea: implications for the continental shelf pump. *Biogeosciences* 16:1073–1096
- ✦ Chari NVHK, Sarma NS, Rao PS, Chiranjeevulu G, Kiran R, Murty KN, Venkatesh P (2016) Fluorescent dissolved organic matter dynamics in the coastal waters off the central East Indian Coast (Bay of Bengal). *Environ Ecol Res* 4:13–20
- ✦ Choudhury AK, Pal R (2010) Phytoplankton and nutrient dynamics of shallow coastal stations at Bay of Bengal, eastern Indian coast. *Aquat Ecol* 44:55–71
- ✦ Church MJ, Ducklow HW, Karl DM (2002) Multiyear increases in dissolved organic matter inventories at Station ALOHA in the North Pacific Subtropical Gyre. *Limnol Oceanogr* 47:1–10
- ✦ Copin-Montegut C, Copin-Montegut G (1983) Stoichiometry of carbon, nitrogen, and phosphorus in marine particulate matter. *Deep-Sea Res A Oceanogr Res Pap* 30: 31–46
- ✦ de Boyer Montégut C (2004) Mixed layer depth over the global ocean: an examination of profile data and a profile-based climatology. *J Geophys Res* 109:C12003
- ✦ Deutsch C, Weber T (2012) Nutrient ratios as a tracer and driver of ocean biogeochemistry. *Annu Rev Mar Sci* 4: 113–141
- ✦ Dutta MK, Kumar S, Mukherjee R, Sanyal P, Mukhopadhyay SK (2019) The post-monsoon carbon biogeochemistry of the Hooghly–Sundarbans estuarine system under different levels of anthropogenic impacts. *Biogeosciences* 16:289–307
- ✦ Foreman RK, Björkman KM, Carlson CA, Opalk K, Karl DM (2019) Improved ultraviolet photo-oxidation system yields estimates for deep-sea dissolved organic nitrogen and phosphorus. *Limnol Oceanogr Methods* 17:277–291
- ✦ Frigstad H, Andersen T, Hessen DO, Naustvoll LJ, Johnsen TM, Bellerby RGJ (2011) Seasonal variation in marine C: N:P stoichiometry: Can the composition of seston explain stable Redfield ratios? *Biogeosciences* 8:2917–2933
- ✦ Fry B, Sherr EB (1989) $\delta^{13}\text{C}$ measurements as indicators of carbon flow in marine and freshwater ecosystems. In: Rundel PW, Ehleringer JR, Nagy KA (eds) *Stable isotopes in ecological research*. Springer, New York, NY, p 196–229
- ✦ Gadgil S (2003) The Indian monsoon and its variability. *Annu Rev Earth Planet Sci* 31:429–467
- ✦ Galbraith ED, Martiny AC (2015) A simple nutrient-dependence mechanism for predicting the stoichiometry of marine ecosystems. *Proc Natl Acad Sci USA* 112: 8199–8204
- ✦ Garcia CA, Baer SE, Garcia NS, Rauschenberg S, Twining BS, Lomas MW, Martiny AC (2018) Nutrient supply controls particulate elemental concentrations and ratios in the low latitude eastern Indian Ocean. *Nat Commun* 9: 4868
- ✦ Geider R, La Roche J (2002) Redfield revisited: variability of C:N:P in marine microalgae and its biochemical basis. *Eur J Phycol* 37:1–17
- ✦ Granéli E, Carlsson P, Legrand C (1999) The role of C, N and P in dissolved and particulate organic matter as a nutrient source for phytoplankton growth, including toxic species. *Aquat Ecol* 33:17–27
- ✦ Gruber N, Sarmiento JL (1997) Global patterns of marine nitrogen fixation and denitrification. *Global Biogeochem Cycles* 11:235–266
- ✦ Hansell DA (2005) Dissolved organic carbon reference material program. *Eos (Wash DC)* 86:318

- ✦ Harikumar R, Balakrishnan Nair TM, Bhat GS, Nayak S, Reddem VS, Shenoi SSC (2013) Ship-mounted real-time surface observational system on board Indian vessels for validation and refinement of model forcing fields. *J Atmos Ocean Technol* 30:626–637
- ✦ Hernando M, Varela DE, Malanga G, Almandoz GO, Schloss IR (2020) Effects of climate-induced changes in temperature and salinity on phytoplankton physiology and stress responses in coastal Antarctica. *J Exp Mar Biol Ecol* 530-531:151400
- ✦ Holte J, Talley L (2009) A new algorithm for finding mixed layer depths with applications to Argo data and sub-antarctic mode water formation. *J Atmos Ocean Technol* 26:1920–1939
- ✦ Huisman J, Codd GA, Paerl HW, Ibelings BW, Verspagen JMH, Visser PM (2018) Cyanobacterial blooms. *Nat Rev Microbiol* 16:471–483
- ✦ Ittekkot V, Nair RR, Honjo S, Ramaswamy V, Bartsch M, Manganini S, Desai BN (1991) Enhanced particle fluxes in Bay of Bengal induced by injection of fresh water. *Nature* 351:385–387
- ✦ Jabir T, Vipindas PV, Jesmi Y, Valliyodan S, Parambath PM, Singh A, Abdulla MH (2020) Nutrient stoichiometry (N:P) controls nitrogen fixation and distribution of diazotrophs in a tropical eutrophic estuary. *Mar Pollut Bull* 151:110799
- ✦ Johnson MT, Greenwood N, Sivyer DB, Thomson M, Reeve A, Weston K, Jickells TD (2013) Characterising the seasonal cycle of dissolved organic nitrogen using Cefas SmartBuoy high-resolution time-series samples from the southern North Sea. *Biogeochemistry* 113:23–36
- ✦ Karl DM, Björkman KM, Dore JE, Fujieki L and others (2001) Ecological nitrogen-to-phosphorus stoichiometry at station ALOHA. *Deep Sea Res II* 48:1529–1566
- ✦ Kaur-Kahlon G, Kumar S, Rehnstam-Holm AS, Rai A and others (2016) Response of a coastal tropical pelagic microbial community to changing salinity and temperature. *Aquat Microb Ecol* 77:37–50
- ✦ Klausmeier CA, Litchman E, Daufresne T, Levin SA (2004a) Optimal nitrogen-to-phosphorus stoichiometry of phytoplankton. *Nature* 429:171–174
- ✦ Klausmeier CA, Litchman E, Levin SA (2004b) Phytoplankton growth and stoichiometry under multiple nutrient limitation. *Limnol Oceanogr* 49:1463–1470
- ✦ Körtzinger A, Koeve W, Kähler P, Mintrop L (2001) C:N ratios in the mixed layer during the productive season in the northeast Atlantic Ocean. *Deep Sea Res I* 48:661–688
- ✦ Krom MD, Emeis KC, Cappellen PV (2010) Why is the Eastern Mediterranean phosphorus limited? *Prog Oceanogr* 85:236–244
- ✦ Kumar S, Ramesh R, Sardesai S, Sheshshayee MS (2004) High new production in the Bay of Bengal: possible causes and implications. *Geophys Res Lett* 31:L18304
- ✦ Kumar S, Bhavya PS, Ramesh R, Gupta GVM and others (2018) Nitrogen uptake potential under different temperature–salinity conditions: implications for nitrogen cycling under climate change scenarios. *Mar Environ Res* 141:196–204
- ✦ Lenton TM, Watson AJ (2000) Redfield revisited. 1. Regulation of nitrate, phosphate, and oxygen in the ocean. *Global Biogeochem Cycles* 14:225–248
- ✦ Letscher RT, Moore JK (2015) Preferential remineralization of dissolved organic phosphorus and non-Redfield DOM dynamics in the global ocean: impacts on marine productivity, nitrogen fixation, and carbon export. *Global Biogeochem Cycles* 29:325–340
- ✦ Loh AN, Bauer JE (2000) Distribution, partitioning and fluxes of dissolved and particulate organic C, N and P in the eastern North Pacific and Southern Oceans. *Deep Sea Res I* 47:2287–2316
- ✦ Lomas MW, Glibert PM, Shiah FK, Smith EM (2002) Microbial processes and temperature in Chesapeake Bay: current relationships and potential impacts of regional warming. *Glob Change Biol* 8:51–70
- ✦ Löscher CR, Mohr W, Bange HW, Canfield DE (2020) No nitrogen fixation in the Bay of Bengal? *Biogeosciences* 17:851–864
- ✦ Macko SA, Engel MH, Qian Y (1994) Early diagenesis and organic matter preservation—a molecular stable carbon isotope perspective. *Chem Geol* 114:365–379
- ✦ Martiny AC, Pham CTA, Primeau FW, Vrugt JA, Moore JK, Levin SA, Lomas MW (2013a) Strong latitudinal patterns in the elemental ratios of marine plankton and organic matter. *Nat Geosci* 6:279–283
- ✦ Martiny AC, Vrugt JA, Primeau FW, Lomas MW (2013b) Regional variation in the particulate organic carbon to nitrogen ratio in the surface ocean. *Global Biogeochem Cycles* 27:723–731
- ✦ Martiny AC, Vrugt JA, Lomas MW (2014) Concentrations and ratios of particulate organic carbon, nitrogen, and phosphorus in the global ocean. *Sci Data* 1:140048
- ✦ McCreary JP, Yu Z, Hood RR, Vinayachandran PN, Furue R, Ishida A, Richards KJ (2013) Dynamics of the Indian-Ocean oxygen minimum zones. *Prog Oceanogr* 112: 15–37
- ✦ Middelburg JJ, Nieuwenhuize J (1998) Carbon and nitrogen stable isotopes in suspended matter and sediments from the Schelde Estuary. *Mar Chem* 60:217–225
- ✦ Mills MM, Arrigo KR (2010) Magnitude of oceanic nitrogen fixation influenced by the nutrient uptake ratio of phytoplankton. *Nat Geosci* 3:412–416
- ✦ Minagawa M, Ohashi M, Kuramoto T, Noda N (2001) $\delta^{15}\text{N}$ of PON and nitrate as a clue to the origin and transformation of nitrogen in the subarctic North Pacific and its marginal sea. *J Oceanogr* 57:285–300
- ✦ Mukherjee A, Chatterjee A, Francis PA (2019) Role of Andaman and Nicobar Islands in eddy formation along western boundary of the Bay of Bengal. *Sci Rep* 9: 10152
- ✦ Murphy J, Riley JP (1962) A modified single solution method for the determination of phosphate in natural waters. *Anal Chim Acta* 27:31–36
- ✦ Nagata T (1986) Carbon and nitrogen content of natural planktonic bacteria. *Appl Environ Microbiol* 52:28–32
- ✦ Ogawa H, Tanoue E (2003) Dissolved organic matter in oceanic waters. *J Oceanogr* 59:129–147
- ✦ Orcutt KM, Lipschultz F, Gundersen K, Arimoto R, Michaels AF, Knap AH, Gallon JR (2001) A seasonal study of the significance of N_2 fixation by *Trichodesmium* spp. at the Bermuda Atlantic Time-series Study (BATS) site. *Deep Sea Res II* 48:1583–1608
- ✦ Post DM, Layman CA, Arrington DA, Takimoto G, Quattrochi J, Montaña CG (2007) Getting to the fat of the matter: models, methods and assumptions for dealing with lipids in stable isotope analyses. *Oecologia* 152:179–189
- ✦ Prasanna Kumar S, Nuncio M, Narvekar J, Kumar A and others (2004) Are eddies nature's trigger to enhance biological productivity in the Bay of Bengal? *Geophys Res Lett* 31:L07309
- ✦ Prasanna Kumar S, Murukesh N, Narvekar J, Nagappa R and others (2010) Seasonal cycle of physical forcing and

- biological response in the Bay of Bengal. *Indian J Geo-Mar Sci* 39:388–405
- ✦ Pujo-Pay M, Conan P, Oriol L, Cornet-Barthaux V and others (2011) Integrated survey of elemental stoichiometry (C, N, P) from the western to eastern Mediterranean Sea. *Biogeosciences* 8:883–899
- R Core Team (2019) R: a language and environment for statistical computing (Version 3.0. 2). R Foundation for Statistical Computing, Vienna
- Redfield AC (1934) On the proportions of organic derivatives in sea water and their relation to the composition of plankton. In: Daniel RJ (ed) *James Johnstone Memorial Volume*. University Press of Liverpool, Liverpool, p 176–192
- Redfield AC (1958) The biological control of chemical factors in the environment. *Am Sci* 46:205–221
- ✦ Rhee GY (1978) Effects of N:P atomic ratios and nitrate limitation on algal growth, cell composition, and nitrate uptake. *Limnol Oceanogr* 23:10–25
- ✦ Rixen T, Gaye B, Emeis KC, Ramaswamy V (2019) The ballast effect of lithogenic matter and its influences on the carbon fluxes in the Indian Ocean. *Biogeosciences* 16: 485–503
- ✦ Roussenov V, Williams RG, Mahaffey C, Wolff GA (2006) Does the transport of dissolved organic nutrients affect export production in the Atlantic Ocean? *Glob Biogeochem Cycles* 20:GB3002
- ✦ Santinelli C, Manca BB, Gasparini GP, Nannicini L, Seritti A (2006) Vertical distribution of dissolved organic carbon (DOC) in the Mediterranean Sea. *Clim Res* 31:205–216
- ✦ Sarma VVSS, Rao DN, Rajula GR, Dalabehera HB, Yadav K (2019a) Organic nutrients support high primary production in the Bay of Bengal. *Geophys Res Lett* 46: 6706–6715
- ✦ Sarma VVSS, Yadav K, Behera S (2019b) Role of eddies on organic matter production and *f*-ratios in the Bay of Bengal. *Mar Chem* 210:13–23
- ✦ Saxena H, Sahoo D, Khan MA, Kumar S, Sudheer AK, Singh A (2020) Dinitrogen fixation rates in the Bay of Bengal during summer monsoon. *Environ Res Commun* 2: 051007
- ✦ Shah C, Sudheer AK, Bhushan R (2018) Distribution of dissolved organic carbon in the Bay of Bengal: influence of sediment discharge, fresh water flux, and productivity. *Mar Chem* 203:91–101
- ✦ Sharoni S, Halevy I (2020) Nutrient ratios in marine particulate organic matter are predicted by the population structure of well-adapted phytoplankton. *Sci Adv* 6: eaaw9371
- ✦ Shetye SR, Shenoi SSC, Gouveia AD, Michael GS, Sundar D, Nampoothiri G (1991) Wind-driven coastal upwelling along the western boundary of the Bay of Bengal during the southwest monsoon. *Cont Shelf Res* 11:1397–1408
- ✦ Singh A, Ramesh R (2011) Contribution of riverine dissolved inorganic nitrogen flux to new production in the coastal northern Indian Ocean: an assessment. *Int J Oceanogr* 2011:983561
- ✦ Singh A, Ramesh R (2015) Environmental controls on new and primary production in the northern Indian Ocean. *Prog Oceanogr* 131:138–145
- ✦ Singh A, Baer SE, Riebesell U, Martiny AC, Lomas MW (2015a) C:N:P stoichiometry at the Bermuda Atlantic Time-series Study station in the North Atlantic Ocean. *Biogeosciences* 12:6389–6403
- ✦ Singh A, Gandhi N, Ramesh R, Prakash S (2015b) Role of cyclonic eddy in enhancing primary and new production in the Bay of Bengal. *J Sea Res* 97:5–13
- ✦ Singh A, Bach LT, Fischer T, Hauss H and others (2017) Niche construction by non-diazotrophs for N₂ fixers in the eastern tropical North Atlantic Ocean. *Geophys Res Lett* 44:6904–6913
- ✦ Spackeen JL, Bronk DA, Sipler RE, Bertrand EM, Hutchins DA, Allen AE (2018) Stoichiometric N:P ratios, temperature, and iron impact carbon and nitrogen uptake by Ross Sea microbial communities. *J Geophys Res Biogeosci* 123:2955–2975
- ✦ Srinivas B, Sarin M (2013) Atmospheric deposition of N, P and Fe to the northern Indian Ocean: implications to C- and N-fixation. *Sci Total Environ* 456–457:104–114
- Subramanian V (1993) Sediment load of Indian rivers. *Curr Sci* 64:928–930
- ✦ Suratman S, Weston K, Jickells T, Fernand L (2009) Spatial and seasonal changes of dissolved and particulate organic C in the North Sea. *Hydrobiologia* 628:13–25
- ✦ Sweeney EN, McGillicuddy DJ, Buesseler KO (2003) Biogeochemical impacts due to mesoscale eddy activity in the Sargasso Sea as measured at the Bermuda Atlantic Time-series Study (BATS). *Deep Sea Res II* 50:3017–3039
- ✦ Tyrrell T (1999) The relative influences of nitrogen and phosphorus on oceanic primary production. *Nature* 400: 525–531
- Tyrrell T (2019) Redfield ratio. In: Cochran JK, Bokuniewicz HJ, Yager PL (eds) *Encyclopedia of ocean sciences*, Vol 1: marine biogeochemistry. Elsevier, Amsterdam, p 461–472
- ✦ Unger D, Ittekkot V, Schäfer P, Tiemann J, Reschke S (2003) Seasonality and interannual variability of particle fluxes to the deep Bay of Bengal: influence of riverine input and oceanographic processes. *Deep Sea Res II* 50:897–923
- ✦ Vidal M, Aspillaga E, Teixidor-Toneu I, Delgado-Huertas A (2018) Lateral transport of N-rich dissolved organic matter strengthens phosphorus deficiency in Western Subtropical North Atlantic. *Global Biogeochem Cycles* 32: 1350–1366
- ✦ Wang WL, Moore JK, Martiny AC, Primeau FW (2019) Convergent estimates of marine nitrogen fixation. *Nature* 566:205–211
- ✦ Weber T, Deutsch C (2012) Oceanic nitrogen reservoir regulated by plankton diversity and ocean circulation. *Nature* 489:419–422
- ✦ Wu J, Sunda W, Boyle EA, Karl DM (2000) Phosphate depletion in the Western North Atlantic Ocean. *Science* 289: 759–762
- ✦ Zehr JP, Capone DG (2020) Changing perspectives in marine nitrogen fixation. *Science* 368:eaay9514
- ✦ Zubkov MV, Fuchs BM, Tarran GA, Burkill PH, Amann R (2003) High rate of uptake of organic nitrogen compounds by *Prochlorococcus* cyanobacteria as a key to their dominance in oligotrophic oceanic waters. *Appl Environ Microbiol* 69:1299–1304