Factors controlling the C:N:P stoichiometry of dissolved organic matter in the N-limited, cyanobacteria-dominated East/Japan Sea

Tae-Hoon Kim, Guebuem Kim *  
School of Earth and Environmental Sciences/RIO, Seoul National University, Seoul, 151-747, Republic of Korea

Abstract

The vertical and horizontal distributions of dissolved organic carbon (DOC), nitrogen (DON), and phosphorus (DOP), together with dissolved inorganic nitrogen (DIN), phosphorus (DIP), silicate (DSi), and photosynthetic pigments, were measured in the euphotic layer (0–100 m) along the south–north transect of the East/Japan Sea (EJS) in May 2007. In the mixed layer, the DIN concentrations were lower than 3 μM, and the DIN:DIP ratios were lower than 10. Under this DIN-limited condition, cyanobacteria (20–65%) and diatoms (20–50%) dominated the phytoplankton community. The concentrations of DOC (60–83 μM) and DOP (0.1–0.4 μM) in the EJS fell into a range similar to those found in the major oceans, whereas the concentration of DON (2–7 μM) was lower than that in the Pacific Ocean (7–13 μM). The correlation analyses showed that the distributions of DOC, DON, and DOP in the study region were affected mainly by the physical characteristics of water masses. The lower DON concentrations, higher DOC:DON ratios, and lower DON:DOP ratios in the EJS, relative to the major oceans, together with a strong negative correlation between the concentrations DON and zeaxanthin, suggest that DON is preferentially taken up by cyanobacteria in this environment. Thus, our results show that the C:N:P stoichiometry of dissolved organic matter (DOM) in the EJS is controlled mainly by the physical and biological characteristics of water masses.

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1. Introduction

The dissolved organic matter (DOM) in the ocean is produced mainly by the solubilization of particulate organic matter (POM) by microbial activity (Jiao et al., 2010; Nagata et al., 2000) and by phytoplankton through at least three different mechanisms: direct extracellular release during growth (Collos et al., 1992), release via micro- and meso-zooplankton grazing (Strom et al., 1997), and release via cell lysis (Proctor and Fuhrman, 1992). In addition, there are terrestrial inputs (Cauwet, 2002) and atmospheric deposition (Buatmenard et al., 1989) of DOM. A major mechanism of DOM removal is consumption by microbial activity in the ocean (Azam and Malfatti, 2007; Kawasaki and Benner, 2006). DOM in the ocean is also removed by direct phytoplankton assimilation (Palenik and Morel, 1990), photochemical decomposition (Mopper et al., 1991), and sorption onto sinking particles (Keil and Kirchman, 1994). Because DOM can be remineralized to inorganic nutrients via the microbial loop or directly utilized by phytoplankton (Bronk, 2002; Karl and Björkman, 2002), DOM is an important source of nutrients for primary production, particularly in inorganic-nutrient-limited environments (Berman and Chava, 1999).

The DOM pool is often divided into three groups: dissolved organic carbon (DOC), nitrogen (DON), and phosphorus (DOP). Changes in DOC:DON:DOP ratios were observed during the enhancement of phytoplankton blooms in the ocean (Banse, 1974) and during phytoplankton growth in laboratory culture experiments (Dorch, 1982; Goldman et al., 1979; Sakshaug and Holm-Hansen, 1977). The decomposable portions of the bulk DOM in the photic zone generally increase in the order of DOC (30%), DON (40%), and DOP (81%) (Hopkinson et al., 2002) and are variable over time and space (Carlson et al., 1994; Sondergaard et al., 2000; Williams, 1995). As such, the average ratio of DOC:DON:DOP in labile DOM is 199:20:1 while that in refractory DOM is ~3511:202:1 (Jiao et al., 2010), which is much higher than the Redfield ratio (C:N:P = 106:16:1). Regardless, little is known about the factors controlling the C:N:P stoichiometry of DOM in the ocean (Hopkinson et al., 1997).

The East/Japan Sea (EJS) is a typical mid-latitude marginal sea with deep basins exceeding 2500 m. The EJS has various water-mass properties such as cold water originating from the Liman current, flowing south along the eastern coast, warm water originating from the subtropical Kuroshio current, entering through the Tsushima/Korea Strait (150 m depth), a sub-polar front formed by the confluence of the warm and cold currents positioned at approximately 40°N, and eddies in the surface ocean (Kim et al., 2010). Nitrogen is almost depleted in the surface water of the EJS, with a low N:P ratio (13) (Talley et al., 2004) relative to the Redfield ratio. Basin-scale observational results on phytoplankton composition showed that cyanobacteria (40–60%) dominated the phytoplankton community in the spring of 2004 in the EJS (Kim et al., 2010). In the present study, we determined the C:N:P stoichiometry of DOM in the euphotic layer of the EJS for the first time and evaluated the physical and biogeochemical factors controlling the C:N:P stoichiometry.
2. Materials and methods

2.1. Sampling

The hydrological and biogeochemical survey was conducted from 8 to 22 May 2007 on the R/V M.A. Gagarinsky of the Pacific Oceanological Institute (POI), Russia, through the East Asian Seas Time-series-1 (EAST-1) program (Fig. 1). This survey covered the entire transect from 42°N to 37°N of the EJS. Niskin bottles mounted on a rosette system (with CTD SBE 911+) were used for all of the vertical water samplings.

Seawater samples were collected at eight stations in the EJS to measure pigments, inorganic nutrients (NO₃+NO₂, DIN; PO₄, DIP; Si, DSi), DOC, total dissolved phosphorus (TDP), and total dissolved nitrogen (TDN). Approximately 1–2 L of the seawater samples were filtered through a GF/F filter (Whatman, 0.7 μm, 25 mm) for the pigment and nutrient determinations on board the ship. The GF/F filters were stored in a deep freezer (−80°C) immediately after filtration for the analysis of the pigments, and the solution samples (~100 mL) for the nutrient concentrations were collected in polyethylene bottles and frozen (−20°C) until the analysis. The samples for the DOC and TDN analyses were filtered on-board through a pre-combusted syringe glass fiber filter (Whatman, 0.7 μm, 25 mm). These samples were acidified with 6 M HCl in pre-combusted 20 mL glass ampoules (550°C for 5 h) and stored at 5°C until the analysis.

2.2. Analysis of inorganic and organic nutrients and pigments

In the laboratory, the concentrations of DIN, DIP, DSi, and TDP for the samples were measured using an auto analyzer (Futura Plus, Alliance Co.). Standard curves for potassium nitrate (KNO₃), potassium dihydrogen phosphate (KH₂PO₄), and sodium hexafluoride (Na₂SiF₆) were used for the DIN, DIP and TDP, and DSi standardization, respectively. The concentrations of TDP were also determined using this auto analyzer through UV oxidation, as described in Walsh (1989). The pigments in the frozen filters were extracted in 5 mL of 100% acetone with an internal standard (50 μL canthaxanthin) at −20°C for 24 h in the dark, sonicated for 30 s, and centrifuged for 10 min at 2000 rpm to remove the cellular and filter debris. The pigments in the acetone extracts were determined by HPLC using the modified method described by Wright et al. (1991). Briefly, the supernatant was filtered through a 0.45 μm PTFE syringe filter, and the clear extract (1 mL) was mixed with deionized water (0.3 mL). The mixed solution (0.1 mL) was injected into an HPLC system (Waters 2695, Waters Co.).

The HPLC solvent system consisted of the following: solvent A, 80% methanol and 20% 0.5 M ammonium acetate aqueous solution by volume; solvent B, 87.5% acetonitrile aqueous solution by volume; and solvent C, ethyl acetate. Each 100 mL of solvent A and solvent B included 0.01 g of butylated hydroxy toluene (BHT) as an antioxidant (Latasa and Bidigare, 1998). The binary linear gradient of min, solvent A%, solvent B%, solvent C% was as follows: 0, 90, 10; 11, 0, 100; 23, 0, 75; 30, 0, 30; 36, 0, 10, 90; and 40, 90, 10, 0. The flow rate was 0.5–1.0 mL min⁻¹. The authentic standards for chlorophyll a and other pigments were obtained from Sigma (UK) and DHI (Institute for Water and Environment, Denmark), respectively. The pigments in the organic solvents were quantified and identified using documented extinction coefficients (Jeffrey, 1997).

The DOC and TDN concentrations were measured using a TOC analyzer (TOC-VCPH, Shimadzu). Standard curves for acetonilide (C:N = 8)
were used for the DOC and TDN standardization. In this system, the acidified seawater sample is bubbled with high-purity air gas (purity: 99.999%) to completely purge inorganic carbon species from the injection system. Carrier gas is passed at a controlled flow rate of 150 mL min⁻¹ through a combustion tube that is filled with a thermal decomposition catalyst and heated to 720 °C. The DOC and TDN for the sample are oxidized to form CO₂ and NO, respectively. These gases are then simultaneously detected by an NDIR and chemiluminescence detector, respectively.

The reliability of the inorganic and organic nutrient data was obtained daily by measuring the certified reference materials (CRMs): MOOS-1 (23.7±0.9 μM for DIN, 1.56±0.07 μM for DIP, and 26.0±1.0 μM for DSI) from National Research Council, Canada and DSR (41–44 μM for DOC and 32–34 μM for TDN) from the University of Miami. Both of the CRM samples were measured for each batch of samples. The results were 22.8±0.5 μM for DIN, 1.51±0.03 μM for DIP, 25.2±0.2 μM for DSI (n=6), 42±2 μM for DOC, and 32.1±1 μM for TDN (n=15), which agreed with the certified value within 5%. However, we did not have a CRM for TDP. The analytical uncertainties for the inorganic and organic nutrients were <2%. The concentrations of DON and DOP were indirectly determined by subtracting the concentration of DIN from TDN and DIP from TDP, respectively. This subtraction method may produce large uncertainties when the total concentrations of dissolved nutrients are close to the concentrations of dissolved inorganic nutrients. However, the average concentrations of TDN and TDP were 9.3±0.8 and 0.46±0.07, respectively, in the study region, thus allowing a reasonable comparison of the overall ratios and trends of DON and DOP.

2.3. Estimating phytoplankton community structures using the CHEMTAX program

The HPLC pigment data were processed using CHEMTAX, a matrix factorization program, in order to estimate the contribution of different algal classes to the total chlorophyll a. The CHEMTAX program has been shown to be an effective tool for estimating phytoplankton community structures (Suzuki et al., 2002). Based on the pigment contents, we identified seven algal categories in our study: diatoms, cyanobacteria, pelagophytes, dinoflagellates, prymnesiophytes, prasinophytes, and cryptophytes. The initial pigment to chlorophyll a ratio for each marker used in the CHEMTAX calculation was obtained from the values in Mackey et al. (1996) and those modified by Lee et al. (2010) (Table 1). The final ratio results are from the best fit of the CHEMTAX program. The initial ratios of marker pigments to chlorophyll a for dinoflagellates, diatoms, and cyanobacteria were obtained from phytoplankton species isolated from offshore seawaters of the Korean Peninsula by the Korea Marine Microalgae Culture Center (KMMCC). However, the class-specific pigment compositions from the same environment need to be acquired through microscopic observations to obtain more accurate CHEMTAX results (Andersen et al., 1996; Jeffrey, 1997; Letelier et al., 1993; Mackey et al., 1996, 1998).

3. Results and discussion

3.1. Distributions of nutrients and phytoplankton community

The temperature and salinity in the 0–100 m layer ranged from 1 °C to 15 °C and 33.1 to 34.5, respectively, across the entire EJS in May 2007 (Fig. 2). The mixed-layer depth ranged from 10 to 30 m in the study region (Fig. 2). In this study, we define the mixed layer as a depth at which the temperature difference is lower than 0.2 °C from the surface as defined by Lim et al. (2012) in this region. The salinity was slightly lower (33.1–33.9) in the mixed layer of the northern sub-frontal zone (station 4) (Fig. 2) owing to the Liman and North Korean Cold Currents carrying cold and fresh waters southward (Talley et al., 2006).

The chlorophyll a concentrations, a phytoplankton biomass index, ranged from 10 to 1100 ng L⁻¹ in the 0–100 m layer. The highest concentration of chlorophyll a was observed at station 4, the site where the low salinity anomaly was observed. The concentrations of chlorophyll b, a marker pigment of green algae including prasinophytes, ranged from 30 to 550 ng L⁻¹ in the 0–100 m layer and were the highest at station 4 (Fig. 2). The contribution of prasinophytes to the total biomass of phytoplankton was <5% in the 0–100 m layer (Fig. 3). The concentrations of chlorophyll a and b in the mixed layer were relatively higher in the cold water mass than in the warm water mass as shown in Figs. 2 and 4.

The concentrations of fucoxanthin, a marker pigment of diatoms, ranged from 5 to 320 ng L⁻¹ in the 0–100 m layer. The concentrations of fucoxanthin were higher in the cold water mass (except for station 1) than in the warm water mass as shown in Figs. 2 and 4. The highest concentrations of fucoxanthin were found at station 4 (Fig. 2). Diatoms constituted approximately 40% of the phytoplankton community in the surface layer (0–20 m). In the deeper layer (20–100 m), the proportion of diatoms increased up to 90% (Fig. 3).

The concentration of zeaxanthin, a marker pigment of cyanobacteria, was less than 65 ng L⁻¹ in the 0–100 m layer. The concentrations of zeaxanthin were relatively higher in the warm water mass than in the cold water mass as shown in Figs. 2 and 4, opposite to the other pigments. The contribution of cyanobacteria to the total phytoplankton biomass

| Table 1 | The initial pigment to chlorophyll a ratios used for the CHEMTAX program and the final pigment ratios calculated from the program. |
|--------|---------|---------|---------|---------|---------|---------|---------|---------|---------|
| **Initial ratio** | Prasino | 0 | 0 | 0 | 0 | 0.3151 | 0.0616 | 0.0088 | 0 | 0.9452 |
| Dino | 0.6547 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Crypto | 0 | 0 | 0 | 0 | 0 | 0 | 0.2292 | 0 | 0 |
| Prynne | 0 | 0 | 0 | 1.7059 | 0 | 0 | 0 | 0 | 0 |
| Pelago | 0.2453 | 0.5849 | 0.5377 | 0 | 0 | 0 | 0.0321 | 0 | 0.2379 |
| Chloro | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.0076 | 0.3361 |
| Cyan | 0 | 0 | 0.5464 | 0 | 0 | 0 | 0 | 0 | 0.2808 |
| Diatoms | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **Final ratio** | Prasino | 0 | 0 | 0 | 0 | 0.3151 | 0.0616 | 0.0088 | 0 | 0.9452 |
| Dino | 0.6547 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Crypto | 0 | 0 | 0 | 1.7059 | 0 | 0 | 0 | 0 | 0 |
| Prynne | 0 | 0 | 0 | 0 | 0 | 0 | 0.2292 | 0 | 0 |
| Pelago | 0.4298 | 0.5849 | 0.5189 | 0 | 0 | 0 | 0 | 0 | 0.2379 |
| Chloro | 0 | 0 | 0 | 0 | 0 | 0 | 0.0076 | 0.3361 |
| Cyan | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0.2808 |
| Diatoms | 0 | 0 | 0.0792 | 0 | 0 | 0 | 0 | 0 | 0 |

Abbreviations: Prasino, Prasinophytes; Dino, Dinoflagellates; Crypto, Cryptophytes; Prynne, Prymnesiophytes; Pelago, Pelagophytes; Chloro, Chlorophytes; Cyan, Cyanobacteria; Perid, Peridinin; 19′-But, 19′-Butanoyloxyfucoxanthin; Fuco, Fucoxanthin; 19′-Hexa, 19′-Hexanoyloxyfucoxanthin; Pra, Prasinoxanthin; Viola, Violaxanthin; Allo, Alloxanthin; Lut, Lutein; Zea, Zeaxanthin; Chl b, Chlorophyll b.
ranged from 20% to 65% in the warm water mass and the surface frontal zone in the 0–20 m layer. This contribution decreased to <5% for the deeper layer (>20 m) (Fig. 3). The dominance of cyanobacteria in the warm water and frontal zone of the EJS could be due to the optimal temperature (>10 °C), relatively low DIN:DIP ratios (<12), and nitrogen depletion, which are favorable for the growth of cyanobacteria (Kim et al., 2010; Le Bouteiller et al., 1992; Odate et al., 1990).

The concentrations of 19′-butanoyloxy-fucoxanthin, a marker pigment of pelagophytes, were relatively higher in the subsurface layer of stations 1, 5, and 6 (Fig. 2) and showed a negative correlation against temperature in the mixed layer (Fig. 4). The distributions of pelagophytes, the pico-phytoplankton group, comprised 10–50% of the total biomass of the phytoplankton community in all of the stations in the 0–100 m layer (Fig. 3). The concentrations of 19′-hexanoyloxy-fucoxanthin, a marker pigment of prymnesiophytes, were relatively higher in station 3 (the cold water mass) and 5 (the warm water mass) than in the other stations as shown in Figs. 2 and 4. The contribution of prymnesiophytes to the total phytoplankton biomass was almost constant (>5%) in the entire layer (Fig. 3).

The concentrations of alloxanthin, a marker pigment of cryptophytes, were relatively higher in the cold water mass than in the warm water mass (Figs. 2 and 4). The contribution of cryptophytes, one of the smaller nano-planktons, to the total phytoplankton biomass was less than 10% in the upper 50 m layer, except for in station 3 (~20%) (Fig. 3).
Fig. 3. Horizontal and vertical variations in the contribution of different phytoplankton groups to the total phytoplankton biomass in May 2007.

Fig. 4. Plots of temperatures versus (A) chlorophyll a, (B) chlorophyll b, (C) fucoxanthin, (D) zeaxanthin, (E) 19′-butanoyloxy-fucoxanthin, (F) 19′-hexanoyloxy-fucoxanthin, (G) alloxanthin, and (H) peridinin in the mixed layer of the East Japan Sea. The datum in parenthesis is the outlier.
Fig. 5. Plots of DOM (DOC, DON, and DOP) versus (A) temperature, (B) salinity, (C) chlorophyll a, (D) fucoxanthin, and (E) zeaxanthin in the mixed layer of the East-Japan Sea. The data in parentheses are the outliers.
concentrations of peridinin, a marker pigment of dinoflagellates, were relatively higher in the frontal zone (Figs. 2 and 4), without a distinct difference between the warm and cold water masses. The contribution of dinoflagellates to the total phytoplankton community was generally lower than 5% for the entire depth (0–100 m) (Fig. 3).

The phytoplankton community composition in the EJS at all of the stations was dominant in the order of diatoms, cyanobacteria, and pelagophytes in the 0–20 m layer, diatoms, pelagophytes, and dinoflagellates in the 20–50 m layer, and diatoms and pelagophytes the 50–100 m layer (Fig. 3). Our study showed that cyanobacteria and diatoms co-occurred in the 0–20 m layer of the EJS during the warm water season. This trend is similar to both the field and laboratory data of Chen et al. (2011) found in the low-latitude North Western Pacific in the Kuroshio Current flowing into the EJS in warm seasons.

The concentrations of dissolved inorganic nutrients (DIN, DIP, and DSI) gradually increased from the surface to the deeper layer and were relatively higher in the cold water mass than in the warm water mass (Fig. 2). In contrast, the concentrations of DOC, DON, and DOP gradually decreased from the surface to the deeper layer (Fig. 2). In general, the concentrations of DOC (64–83 μM) and DOP (<0.3 μM) in the 0–100 m layer fell into the range (60–80 μM for DOC and 0.1–0.4 μM for DOP) of the major oceans (Abell et al., 2000; Carlson and Ducklow, 1995; Doval and Hansell, 2000; Hansell and Carlson, 1998; Smith et al., 1986; Williams et al., 1980). However, the concentrations of DON (4–7 μM) in the EJS were slightly lower than those in the Pacific (7–13 μM) and Atlantic Oceans (4–11 μM) (Hansell and Carlson, 2001; Koike and Tuppy, 1993; Vidal et al., 1999).

The concentrations of DOC, DON, and DOP showed negative correlations against temperature and salinity (Fig. 5), indicating that their concentrations are primarily controlled by the physical characteristics of water masses (Fig. 5). In general, the lower-salinity water occurring in the northern part showed higher concentrations of chlorophylls a and b and higher DOC, DON, and DOP concentrations. Although the production mechanisms and sources of DOC, DON, and DOP can be determined on the basis of the available data, it is likely that the horizontal distributions of DOC, DON, and DOP in the EJS are controlled more effectively by physical mixing factor rather than by chemical and biological effects in each water-mass. As such, the index of biological production (i.e., chlorophyll a and fucoxanthin) correlated negatively with the temperature (Fig. 4) and positively with the DOM with large scattering (Fig. 5).

3.2. Factors controlling C:N:P stoichiometry in the East/Japan Sea

The DIN:DIP ratio in the entire EJS below 200 m was approximately 13 (Talley et al., 2004), a ratio that is lower than those in the Pacific Ocean (14–15), Atlantic Ocean (17), and Mediterranean Sea (22–24) (Table 2). The DIN:DIP ratios in the mixed layer of this study region were <10 (Fig. 2), which is considerably lower than the Redfield ratio (16). In general, the DIN:DIP ratios decreased as chlorophyll a concentrations increased (Fig. 2), though they showed no trend against temperature. This trend appears to be due to the rapid utilization of DIN, relative to DIP which has an excess fraction under a DIN-limited condition, as suggested by Kim et al. (2010). The higher DIN:DIP ratios relative to the chlorophyll a concentrations at the two stations seem to be associated with a more active mixing of the subsurface water, as indicated by the salinity distributions (Fig. 2), with higher nutrient concentrations and DIN:DIP ratios (Fig. 2).

In the 0–100 m layer, the DOC: DON and DON:DOP ratios ranged from 13 to 30 (average: 17 ±3) and from 10 to 36 (average: 22 ±5), respectively (Fig. 2). These DOC: DON:DOP ratios (374:22:1) in the EJS were considerably higher than the Redfield ratio (C:N:P = 106:16:1) but were similar to those in the northeastern Pacific Ocean and North Pacific Ocean (HOT), which are DIN-limited, with the DIN:DOP ratios of approximately 14–15 (Table 2). However, the DOC:DON ratios were higher and the DON:DOP ratios were much lower in the EJS than those in the Mediterranean Sea and Atlantic Ocean, which are DIP-limited (Table 2). The concentrations of DOP are <0.08 μM in the Mediterranean Sea (Aminot and Kérouel, 2004; Santinelli et al., 2012) which has the DIN:DIP ratios of approximately 22–24. The production of DON under N-limited conditions is relatively much lower than that under P-limited conditions, resulting in relatively higher DOC:DON ratios (>22) in N-limited conditions (Conan et al., 2007; Normann et al., 1995; Sonderegger et al., 2000).

In the study region, the concentrations of DON, and DOP showed significant negative correlations with the concentrations of zeaxanthin, though large scattering were observed for chlorophyll a and fucoxanthin (Fig. 5). This result seems to indicate that DON is effectively utilized by cyanobacteria as shown in other areas of the ocean and laboratory experiments (Berg et al., 2001, 2003; Gilbert et al., 2004; Paerl et al., 1993; Vonshak et al., 2000). More significant correlations between the concentrations of zeaxanthin and DON (r² = 0.68), relative to DOC (r² = 0.44) and DOP (r² = 0.13), seem to be due to preferential uptake of DON by cyanobacteria under a DIN-limited condition. Both N₅-fixing and non-N₅-fixing cyanobacteria use DON (including urea, uric acid, alanine, glycine, and serine) as an important nitrogen source (Mulholland and Capone, 2000; Sakamoto and Bryant, 2001).

4. Conclusions

The EJS is extremely DIN limited, with DIN concentrations <3 μM and DIN:DIP ratios <10 in the mixed layer. The DIN:DIP ratios in the mixed layer of the EJS decreased as the chlorophyll a concentrations increased due to the presence of excess DIP in the water column. In the mixed layer, diatoms (25–60%) and cyanobacteria (20–65%) dominated the biological production. In the EJS, the distributions of DOC, DON, and DOP were controlled mainly by the physical characteristics of water masses. The relatively lower DON concentrations, higher DOC: DON ratios, and lower DON:DOP ratios in the EJS, relative to the major oceans, together with significant negative correlations between the DON and zeaxanthin concentrations, seem to be due to effective utilization of DON by cyanobacteria under DIN-limited EJS conditions. Thus, further extensive studies are necessary in order to examine the role of cyanobacteria under extremely DIN-limited conditions with regard to the C:N:P stoichiometry of DOM in the ocean.

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Table 2

<table>
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<th>Location</th>
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<th>DOC: DON</th>
<th>DON: DOP</th>
<th>DIN: DIP</th>
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<tr>
<td>East/Japan Sea</td>
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<td>17 ±3</td>
<td>22 ±5</td>
<td>13</td>
<td>This study</td>
</tr>
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<td>19 ±3</td>
<td>13b</td>
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</tr>
<tr>
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<td>layer</td>
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<td>0.4</td>
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<td>layer</td>
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<td>13</td>
<td>84–120</td>
<td>22–24</td>
<td>Pujo-Pay et al. (2011)</td>
</tr>
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</table>

a These values obtained below the 200 m layer.

b Value was taken from Wu et al. (2000). These DIN:DIP ratios were measured at Bermuda Atlantic time series (BATS) and Hawaii Ocean time-series (HOT).

c Value was taken from Bethoux et al. (1998).

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