

C:N stoichiometry and the fate of organic carbon in ecosystems of the northwest Pacific Ocean

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ABSTRACT

Phytoplankton elemental composition regulates the efficiency of energy and material transfer in the interface between phytoplankton and their consumers. The ratio of particulate organic carbon to particulate organic nitrogen (POC:PON) shows considerable regional deviations from the canonical Redfield ratio in the global surface ocean. However, in certain oceanic regions such as the northwest Pacific Ocean (NWPO) POC:PON distribution and its ecological significance remain uncertain. We investigated surface ocean POC:PON distributions at 66 stations in the NWPO, and quantified the correlations between POC:PON and multiple biotic and abiotic factors including sea surface temperature (SST), nutrient concentrations and multiple lipid biomarkers (fatty acids and sterols), by combining correlation analyses and generalized additive models. POC:PON (range: 3.53–14.18 M ratios; median: 6.89) was overall higher in the (sub)tropical biome than that in the high-latitude biome. In the entire study region, SST, nutrient concentration and lipid-derived phytoplankton community structure explained 41 %, 33 % and 26 % of the variance in POC:PON, respectively, while the respective importance of each factor differed between the (sub)tropical and high-latitude biomes. Furthermore, we calculated the percentage of primary production consumed by herbivores (PPC; 54–156 %), showing a higher mean value (117 %) in the high-latitude biome and a lower one (92 %) in the (sub)tropical biome. The spatial distribution pattern of PPC can be attributed to multiple factors, with PPC correlating negatively with SST and positively with lipid-based indicators of phytoplankton food quality and POC concentrations. The increase in SST may be associated with a reduced nitrogen content, resulting in lower PPC in the (sub)tropical biome. This study highlights the significance of SST and elemental and biochemical composition of phytoplankton in regulating the transfer of organic carbon to herbivores in the NWPO.

1. Introduction

The elemental stoichiometry of particulate organic matter, such as the ratio of particulate organic carbon (POC) to nitrogen (PON) (POC:

PON), provides a framework for estimating the pools and fluxes of energy and matter in the environment from an ecosystem perspective (Sternier and Elser, 2002). In the global upper ocean, the median POC:PON is overall close to the canonical Redfield ratio (Martiny et al.,

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2013b), while considerable regional deviations from this value have been also observed, e.g., below or near the Redfield ratio in the high-latitude and upwelling regions and above the Redfield ratio in most oligotrophic gyres (Crawford et al., 2015; Garcia et al., 2018; Martiny et al., 2013b). Including variable POC:PON in models of oceanic pelagic ecology has been considered to better represent ecosystem processes, e.g., predator–prey interactions and biogeochemical cycles of elements (Baklouti et al., 2021; Christian, 2005; Flynn, 2010).

There are complex interactive relationships between the regional variations in POC:PON, environmental factors, phytoplankton community, and carbon transfer in ecosystems (Cebrian and Lartigue, 2004; Galbraith and Martiny, 2015; Inomura et al., 2022; Isanta-Navarro et al., 2022; Manzoni et al., 2018; Martiny et al., 2016; Moreno and Martiny, 2018). The underlying controls of phytoplankton POC:PON have been studied in the North Atlantic Ocean, showing nitrogen availability as the main control, with temperature and grazing also playing important roles (Sauterey and Ward, 2022). The contributions of environmental factors to C:N:P stoichiometry have been quantified across major ocean basins, suggesting that sea surface temperature (SST) and macronutrient availability are strong predictors of C:N:P stoichiometry at high latitudes (Tanioka et al., 2022a). Furthermore, the variations in elemental stoichiometry show a strong relationship with the fate and processing of carbon in ecosystems, e.g., significant correlations between the percentage of primary production consumed by herbivores (PPC), autotroph turnover rate (i.e., the fate of autotroph biomass renewed per day) and autotroph nitrogen content (Cebrian, 1999; Sterner and Elser, 2002). More recently, the importance of elemental stoichiometry has been also reported in determining carbon use efficiency and ecosystem processes (Hillebrand et al., 2009; Isanta-Navarro et al., 2022; Manzoni et al., 2018; Pichon et al., 2023). These observations indicate that the fate of carbon such as PPC in ecosystems is predictable based on stoichiometric theories. However, understanding and predicting the effects of phytoplankton stoichiometric changes on marine ecosystems are still challenging, which is partially attributable to the difficulties to constrain regional variations in the relationship between variable factors and elemental stoichiometry. For example, the influence of warming on C:N:P stoichiometry remains unclear in regions with SST above 30 °C such as the western Pacific Ocean, causing uncertain model projections on future changes of C:N:P stoichiometry (Tanioka et al., 2022a).

The northwest Pacific Ocean (NWPO) encompasses a unique assemblage of dynamic marine processes, diverse ecosystems and a significant sea-air exchange of CO₂ under the influence of the strong western boundary current, the Kuroshio (Hu et al., 2015; Karl and Church, 2017; Nowicki et al., 2022; Takahashi et al., 2009), providing an environmental setting to deconvolute the relative importance of multiple abiotic and biotic factors that contribute to the variations in elemental stoichiometry. The low latitude regions include the Western Pacific Warm Pool (WPWP; SST > 28 °C) located at 10°N–20°N (Yan et al., 1992), and they are characterized by a warm water column, low productivity, small phytoplankton, and thus low carbon export (Nowicki et al., 2022). In contrast, the high latitude North Pacific is characterized by low SST, high productivity, large phytoplankton, and thus high carbon export (Nowicki et al., 2022). Moreover, high fishery production has been observed in the oligotrophic (lower productivity) Kuroshio region, i.e., the Kuroshio paradox, which can be explained by variable physicochemical processes and multiple biological trophic pathways (Saito, 2019). It should be acknowledged that the recent work of Tanioka et al. (2022a) provided a quantitative understanding of key environmental predictors for global surface ocean C:N:P, while there was no data from the NWPO. To our knowledge, only few POC:PON data (10 data points) have been reported in the open-ocean regions of the NWPO, with most of them located along 160 °E (Martiny et al., 2014). Therefore, our understanding on elemental stoichiometry and its controlling mechanisms and ecological implications in the vast area of the NWPO is still limited.

Certain lipids such as fatty acids (FAs) and sterols have been applied as biomarkers of nutritional quality of phytoplankton and tracers of

organic matter sources (Müller-Navarra et al., 2000; Straile and Martin-Creuzburg, 2022; Volkman et al., 1998). It is well established that polyunsaturated fatty acids (PUFAs) and sterols are essential for many animals and the presence of some of these lipids can be characteristic of particular algal classes (Cao et al., 2023; Dalsgaard et al., 2003; Müller-Navarra et al., 2004; Thomas et al., 2022). For example, the ratio of dinosterol to brassicasterol/epi-brassicasterol (D/B) has been proved to be a useful proxy for the biomass ratio of dinoflagellates to diatoms, and that of C₃₇ alkenones to brassicasterol/epi-brassicasterol (A/B) for the biomass ratio of haptophytes to diatoms in different oceanic regions including the NWPO (Bi et al., 2018a; Hernandez et al., 2008; Wang et al., 2022; Wu et al., 2016). Because sterols are carbon-rich molecules and contain neither nitrogen nor phosphorus (Sterner and Elser, 2002), sterol-derived biomass ratios of different phytoplankton groups refer to the relative amounts of carbon in each group. While these lipid ratios and carbon-normalized lipid contents (lipid:POC) in phytoplankton may change with environmental conditions and growth rate (Bi et al., 2014; Bi et al., 2021; Bi et al., 2020; Sachs and Kawka, 2015), characteristic profiles of FAs and sterols are relatively unique and stable for each algal class, showing the applicability of lipid ratios as proxies of phytoplankton community structure under highly variable environmental conditions (Bi et al., 2021; Galloway and Winder, 2015). As evidence for the significance of elemental stoichiometry and lipids in zooplankton nutrition continues to accumulate (Bi and Sommer, 2020; Relva et al., 2023; Saiz et al., 2023; Sommer, 2023; Twining et al., 2021), insight into the relationship between elemental stoichiometry and lipids is needed to understand the fate of organic carbon in the oceans.

Here, we provide new evidence for the spatial distribution of POC:PON and quantify the contribution of multiple factors to the variations in POC:PON based on observations in the surface layer at 66 stations in the NWPO. We also address the unknown connection between POC:PON and lipids in the NWPO via analyzing lipid biomarkers including PUFAs and sterols. This study region covers latitudes between 10.5°N and 41°N and longitudes between 130°E and 158°E, filling the spatial coverage of POC:PON data in the NWPO. We recently reported the spatial distribution of brassicasterol/epi-brassicasterol, dinosterol and C₃₇ alkenones in the NWPO, showing high biomarker-derived contributions of diatoms to eukaryotic phytoplankton community (73–90 %), followed by dinoflagellates (9–27 %) and haptophytes (0–19 %) (Wang, 2022). In the present study, the ratio of phytoplankton groups was estimated using lipid biomarkers, i.e., D/B indicating the biomass ratio of dinoflagellates to diatoms, and A/B indicating the biomass ratio of haptophytes to diatoms. We calculated PPC based on POC and PON, and applied lipid-based indicators of phytoplankton nutritional quality (PUFAs and sterols) to study the ecological role of lipids on the fate of organic carbon. A combination of correlation analysis and generalized additive models (GAMs) was conducted to determine the relative importance of multiple factors in explaining POC:PON and PPC. We aim to (i) reveal the spatial distribution patterns of POC:PON in the NWPO, (ii) connect environmental factors and lipid-derived phytoplankton community structure to POC:PON, and (iii) connect environmental factors, PUFAs and sterols to PPC.

2. Materials and methods

2.1. Sampling and shipboard measurements

This study was conducted in the NWPO during cruises KH17-05 in November 2017, MEMEWS in May and June 2018, KK2003 in July and August 2020, KK2007 in December 2020 and February 2021, and 2021NWPO in May and June 2021 (Fig. 1; Fig. S1; Table S1).

Seawater samples for POC, PON, and lipid biomarker (FA and sterol) analysis were collected at the surface layer (depth: 0–5 m) using the onboard flow-through underway system, a submersible pump, or a trace-metal-clean towed sampling device (Table S1). The samples were filtered immediately onto pre-combusted (450 °C, 4 h) GF/F filters

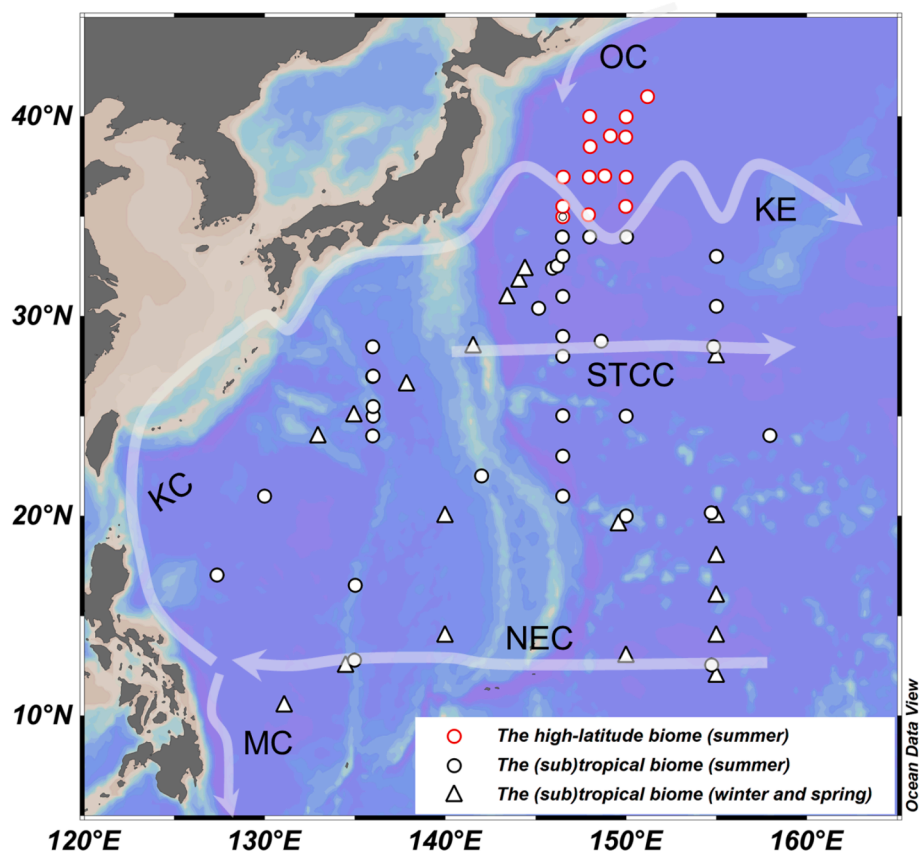


Fig. 1. Oceanographic setting and sampling locations in the Northwest Pacific region. Symbol colors refer to sampling locations in the two biomes, i.e., the (sub) tropical biome (10–34°N) and the high-latitude biome (34–41°N). Symbols indicate sampling locations and seasons. The arrows represent the directions of oceanic currents. KC: the Kuroshio Current; KE: the Kuroshio Extension; OC: the Oyashio Current; NEC: the North Equatorial Current; STCC: the Subtropical Counter Current; MC: the Mindanao Current. The locations and directions of the currents are adapted from [Ando et al. \(2021\)](#). Further details of the currents are given in Text S1.

(Whatman, manufactured in China) onboard and kept at -20°C after filtration. The samples for POC and PON measurements were collected at 66 stations (sample volume: 1–4 L), and those for FA and sterol analysis were obtained at 59 and 66 stations, respectively (sample volume: 100–500 L). All the stations were located > 500 km away from the land to exclude the influence of terrestrial organic matter delivered from rivers ([Hashihama et al., 2021](#); [Huang et al., 2018](#)). The data of FAs and sterols for cruises KH17-05, MEMEWSC, KK2003 and KK2007 were from [Wang \(2022\)](#), and those for the cruise 2021NWPO were measured in this study. The time (Greenwich Mean Time) in which the samples of POC, PON and lipids were collected is shown for most sampling stations in [Table S1](#), while that was not attainable for cruises MEMEWSC and KK2007.

The data of SST and salinity were obtained with shipboard CTD (Seabird SBE-9plus for the cruise KH17-05, Seabird SBE 917 plus for the cruises MEMEWSC, KK2003 and KK2007, and Seabird SBE 911 plus for the cruise 2021NWPO) for the surface layer (depth: 5 m). Nutrient water samples were collected by CTD and the depths of nutrient sampling were close to those of POC and PON samples (depth: 5 m at most stations; samples were obtained at 10 m when there were no surface samples at 5 m). Nutrient samples were filtered immediately onboard in cruises MEMEWSC (pre-cleaned cellulose acetate membranes with a pore size of $0.45\ \mu\text{m}$) and 2021NWPO (pre-combusted (450°C , 4.5 h) GF/F filters (Whatman, manufactured in China)) ([Chen et al., 2022](#); [Zhou et al., 2023](#)), while those were not filtered in cruises KK2003 and KK2007 (Text S1).

2.2. Sample analysis

The freeze-dried filters for POC and PON analysis were acidified with 6 mol/L HCl to volatilize inorganic carbon and then dried at 55°C before elemental analysis with a Thermo Flash 2000 Elemental Analyzer ([Sharp, 1974](#)). The precision was 0.02 % (wt%, $n = 6$) and 0.002 % (wt %, $n = 6$) in the measurements of POC and PON, respectively, determined by replicate analysis of laboratory standards of atropine (Thermo Fisher Scientific, Netherlands) and a low organic content soil (Elemental Microanalysis Ltd., UK). As total particulate nitrogen is almost wholly organic in the open ocean ([Sharp, 1974](#); [Worsfold et al., 2008](#)), the term PON is used in this study.

FAs, sterols and C_{37} alkenones were measured according to [Eglinton et al. \(1996\)](#), [Galy et al. \(2011\)](#) and [Zhao et al. \(2006\)](#), with the detailed methods described in [Bi et al. \(2021\)](#) and [Cao et al. \(2023\)](#). Briefly, freeze-dried material from filters was extracted with a solvent mixture (dichloromethane/MeOH, 3:1, v/v), and C_{19} *n*-alkanol and 19:0 nonadecanoic acid were added as internal standards. A polar fraction containing sterols and C_{37} alkenones was separated by silica gel chromatography and silylated using *N*, *O*-bis(trimethylsilyl)-trifluoroacetamide. An “acid” fraction containing FAs was derivatized with a mixture of methanol and HCl (95:5). Sterols and C_{37} alkenones were analyzed with an Agilent 7890 N gas chromatograph equipped with a HP-1 column ($50\ \text{m} \times 0.32\ \text{mm}$ i.d., $0.17\text{-}\mu\text{m}$ film thickness; Agilent J&W), and FAs were analyzed with an Agilent 8890 gas chromatograph equipped with the SP-2560 column ($100\ \text{m} \times 0.25\ \text{mm}$ i.d., $0.20\text{-}\mu\text{m}$ film thickness; Supelco). In this study, the ratio of dinosterol to brassicasterol/epi-brassicasterol (D/B) was applied as a proxy for the biomass ratio of dinoflagellates to diatoms, and that of C_{37} alkenones to

brassicasterol/epi-brassicasterol (A/B) for the biomass ratio of haptophytes to diatoms. Sterol concentrations (ng L^{-1}) and PUFA proportions (% of total fatty acids (TFAs); ng ng^{-1}) are used as nutritional indicators of phytoplankton food quality for other trophic levels.

The concentrations of nitrate, soluble reactive phosphate (SRP) and silicate acid (Si(OH)_4) were measured according to the methods described previously (Chen et al., 2022; Yuan et al., 2023). Briefly, nutrient concentrations were measured with a spectrophotometer (Xingsha 7230, Xiamen) during the cruise MEMEWSC, and they were determined using a nutrient auto-analyzer (AA3, SEAL, United Kingdom) for the cruise 2021NWPO. For nutrient samples from the cruises KK2003 and KK2007, a Four-channel Continuous Flow Technicon AA3 Auto-Analyzer was used, and micromolar samples (Si(OH)_4) were measured onboard and nanomolar samples ($\text{NO}_3^- + \text{NO}_2^-$ and SRP) were frozen onboard and measured in a shore-based laboratory. For the cruises KK2003 and KK2007, RMNS (KANSO CO., LTD.) and a deep-sea water reference were used as reference standards and run twice and every 10 samples, respectively. For the cruises 2021NWPO and MEMEWSC, reference standards were provided by National Marine Environmental Monitoring Centre of China and run every 20 samples. For the cruises KK2003 and KK2007, the sum of $\text{NO}_3^- + \text{NO}_2^-$ concentrations was measured because of the extremely low concentrations of nitrite. For example, at a station (K2) adjacent to the study area of the cruises KK2003 and KK2007 the integrated nitrite and nitrate inventory was $14.86 \text{ mmol N m}^{-2}$ and $0.09 \text{ mol N m}^{-2}$, respectively, at the upper 150 m water column (Wan et al., 2021). Thus, $\text{NO}_3^- + \text{NO}_2^-$ measured in the cruises KK2003 and KK2007 can be considered as the nitrate concentration (Shiozaki et al., 2009; Wan et al., 2021).

2.3. Biome partition

We divided our study region into the (sub)tropical biome and the high-latitude biome, based on the spatial distribution of lipid-derived biomass ratios of three phytoplankton groups (diatoms, dinoflagellates and haptophytes). This is consistent with the method based on phytoplankton biogeography in Elizondo et al. (2021), that was established using monthly biogeographic patterns of 536 phytoplankton species in the global open ocean and a clustering method (Elizondo et al., 2021). Biomes are biogeographical units and are used to classify global natural biodiversity. Considering the biogeographic patterns of phytoplankton, Elizondo et al. (2021) predicted a partitioning of the global open ocean into seven different biomes at the annual scale, with the largest differences in phytoplankton composition across three major regions, i.e., the high latitudes, the Pacific equatorial region, and the low latitudes. The strongest differences between biomes were well reflected by gradients of temperature and macronutrient availability. This biome partitioning based on phytoplankton biogeography rather than physico-chemical properties (e.g., temperature, salinity and chlorophyll concentration) can be especially used to investigate functional implications of phytoplankton community composition, and its impacts on zoogeographic partitionings.

The (sub)tropical biome partitioned in this study was located between 10°N and 34°N , showing a similar location with the tropical biome in summer and the winter subtropical biome in winter (Elizondo et al., 2021). The (sub)tropical biome was thus across two biomes identified at the annual scale, i.e., the tropical biome and the winter subtropical biome (Elizondo et al., 2021) (Fig. S2). The high-latitude biome in this study was located between 34°N and 41°N , showing a similar location with that in Elizondo et al. (2021). Moreover, Elizondo et al. (2021) showed that the relative taxon-specific richness for diatoms and dinoflagellates was similar between the tropical biome (diatoms: 42.5 %; dinoflagellates: 48.8 %) and the winter subtropical biome (diatoms: 43.8 %; dinoflagellates: 47.5 %), while the relative taxon-specific richness in these two biomes was clearly different from that in the high latitude biome (diatoms: 49.0 %; dinoflagellates: 43.3 %). This result suggests that it is reasonable to combine the tropical biome and the

winter subtropical biome as one biome, with unique phytoplankton community observed in the (sub)tropical biome and high-latitude biome identified in this study. Biome partitioning of this study region can help to better analyze the relationship between POC:PON distribution and multiple factors and to reveal the ecological implications of elemental stoichiometry.

2.4. Data analysis

The mixed layer depth (MLD; m) was defined as the depth where the potential density became 0.125 kg m^{-3} higher than the surface values (average: 23.27 kg m^{-3} ; range: $20.95\text{--}25.73 \text{ kg m}^{-3}$), and the potential density was calculated by temperature and salinity at each depth (Aita et al., 2007; Wang and Li, 2023). In addition, we obtained daily sea level anomaly (SLA; m) data on 14 May 2021 and 24 May 2021 to characterize the mesoscale eddies in this study area, with a $1/4^\circ \times 1/4^\circ$ horizontal resolution from the Copernicus Marine and Environment Monitoring Service (CMEMS) (available from: <http://marine.copernicus.eu/>).

We calculated the percentage of primary production consumed by herbivores (PPC) according to the following equations:

$$\text{LogPTR} = -2.6 + 1.9 \times \log[\text{Nitrogen content of dry weight (\%DW)}] \quad (1)$$

$$\begin{aligned} \text{LogPPC} &= 1.9 + 0.4 \times \log\text{PTR} \\ &= 0.86 + 0.76 \times \log[\text{Nitrogen content of dry weight (\%DW)}] \quad (2) \end{aligned}$$

where PTR stands for phytoplankton turnover rate (day^{-1}). PPC is a percentage estimate and does not carry rate units. POC content (g) was divided by 0.4 to convert into dry weight according to Cebrian (1999) and Sterner and Elser (2002), and nitrogen content per dry weight was then determined. Because carbon is 40–50 % of dry weight in most biological materials and biomass carbon content is relatively constant as a function of dry weight (Sterner and Elser, 2002), it is reasonable to calculate dry weight with the 0.4 multiplication factor in this study. In Eqs. (1) and (2), the relationships were obtained via fitting a data set across a range of aquatic and terrestrial plant communities (e.g., phytoplanktonic communities, macroalgal beds and forests) from over 200 published reports ($R^2 = 0.78$, $p < 0.00001$ for Eq. (1); $R^2 = 0.50$, $p < 0.00001$ for Eq. (2)) (Cebrian, 1999). Thus, this method of PPC calculation was developed and equations were derived empirically from samples collected across ecosystems with limited data from phytoplankton (Cebrian, 1999). PPC and absolute consumption of primary production by herbivores are not necessarily related (Cebrian and Lartigue, 2004), with the latter being best predicted by absolute productivity but not turnover rate (Cebrian, 1999; Sterner and Elser, 2002). It is also important to note the variability of PPC estimates that Cebrian (1999) reported for phytoplankton, i.e., approximately 10–90 % of PPC at a turnover rate of near 1.0 day^{-1} . This is a very wide range and thus would cause uncertainties in the PPC calculation in this study. While the level of consumption by herbivores was similar between different marine community types and primary production was identified as a robust control of the variability in herbivory among marine communities (Cebrian, 2002), caveats in the calculation of PPC should be still considered and detailed discussion is elaborated in Section 4.3.

To better understand the distribution of POC:PON over a large area of the North Pacific, we compiled 239 published data of POC:PON in surface water (0–6.2 m) at stations $> 500 \text{ km}$ away from the land in the North Pacific, including 10 and 229 data points from the NWPO and northeast Pacific Ocean (NEPO), respectively. POC:PON ratios below 2 and above 20 were considered unrealistic (Martiny et al., 2013b) and thus were excluded from this study. For the whole data set of POC:PON (239 published data + 66 new data from this study), we applied GAMs to test the effect of SST on POC:PON and visualize the relationship between SST and $\log_{10}(\text{POC:PON})$ in the NWPO and NEPO, respectively. Due to the lack of SST data at some stations in literature and two stations (k14

and XTW1-14) in our observations, we obtained daily 1/4° gridded SST between 2 May 1992 to 19 Aug 2020 from the CMEMS (<http://marine.copernicus.eu/>) to complement the SST data sets of Martiny et al. (2014) and Tanioka et al. (2022b) as well as our observations. We observed a significant positive correlation between satellite-derived and CTD-based temperature (Fig. S3) and non-significant differences between the two data sets of temperature (Wilcoxon signed-rank test: $p = 0.130$, $n = 91$), confirming that the two data sets could be combined to analyze the effect of SST on POC:PON.

Spearman's rank correlation analysis was conducted to test the relative importance of multiple factors (SST, nitrate, SRP, $\text{Si}(\text{OH})_4$, D/B and A/B) in explaining POC:PON in the whole study area, as well as in the two biomes. The same analysis was done to test the relative importance of SST, D/B, sterol and PUFAs/TFAs to explain PPC, and the correlations between multiple biotic and abiotic factors (Fig. S4). Because multiple factors are correlated to some degree (Fig. S5), Variance inflation factor (VIF) analysis was applied to test multicollinearity between biotic and abiotic factors (Table S2), with a high VIF value (>10) being suspected to have multicollinearity between different factors (Kumar et al., 2023). Based on the correlation analysis, VIF analysis (VIF value < 10) and previous understanding of ecological stoichiometry (Moreno and Martiny, 2018), the main biotic and abiotic factors were determined for the subsequent analysis of GAMs. These main factors were considered to be the ones behind the complex correlations with POC:PON. We conducted GAMs to quantify the relative strength of main biotic and abiotic factors in explaining POC:PON and PPC in the whole study area and the (sub)tropical biome (Tables 1, S3), respectively. Individual explained deviance (squared studentized residuals) of the main factors normalized to the total explained deviance was calculated.

Spearman's rank correlation analysis, VIF analysis and the Wilcoxon signed-rank test were conducted in IBM SPSS Statistics 25. GAMs were

conducted using the “gam” function from the package *mgcv* (Wood, 2017) in R version 4.2.2 (R Core Team, 2022). The significance level was $p < 0.05$ in all statistical tests. The figures were created in R using the *ggplot2* package (Wickham, 2016), the Ocean Data View, Origin 2021 and IBM SPSS Statistics 25.

3. Results

3.1. Hydrological parameters and nutrients

SST decreased from the south to the north, ranging from 9.71 to 30.37 °C in our study region (Fig. 2a), while salinity (range: 32.77 to 35.28) was slightly lower around 12°N and lowest near 40°N (Fig. 2b). The MLD ranged between 4 and 138 m, decreasing first and then increasing northward. The shallowest MLD occurred between 24 and 32°N (6–67.73 m, and 19.84 m on average) (Fig. 2c).

The concentrations of nitrate, SRP and $\text{Si}(\text{OH})_4$ ranged from 0 to 3.95 $\mu\text{mol L}^{-1}$, 0.01 to 0.53 $\mu\text{mol L}^{-1}$ and 0.12 to 6.07 $\mu\text{mol L}^{-1}$, respectively, in the whole study region (Fig. 2d-f). For all nutrients, the concentrations were lower and did not change much south of the Kuroshio Extension (KE), while they were higher polewards of the KE (Fig. 1 and 2d-f).

3.2. POC:PON stoichiometry and lipid biomarkers

The concentrations of POC and PON ranged from 1.17 to 25.38 $\mu\text{mol L}^{-1}$ and 0.14 to 3.57 $\mu\text{mol L}^{-1}$, respectively, in our study region, showing high values at high latitudes (Fig. 3a, b). Specifically, in the (sub)tropical biome the concentrations of POC and PON ranged from 1.17 to 25.38 and 0.14 to 3.36 $\mu\text{mol L}^{-1}$, respectively (Fig. 3d, e). In the high-latitude biome, POC and PON ranged from 3.27 to 21.10 and 0.51 to 3.57 $\mu\text{mol L}^{-1}$, respectively (Fig. 3d, e). POC:PON (3.53 to 14.18)

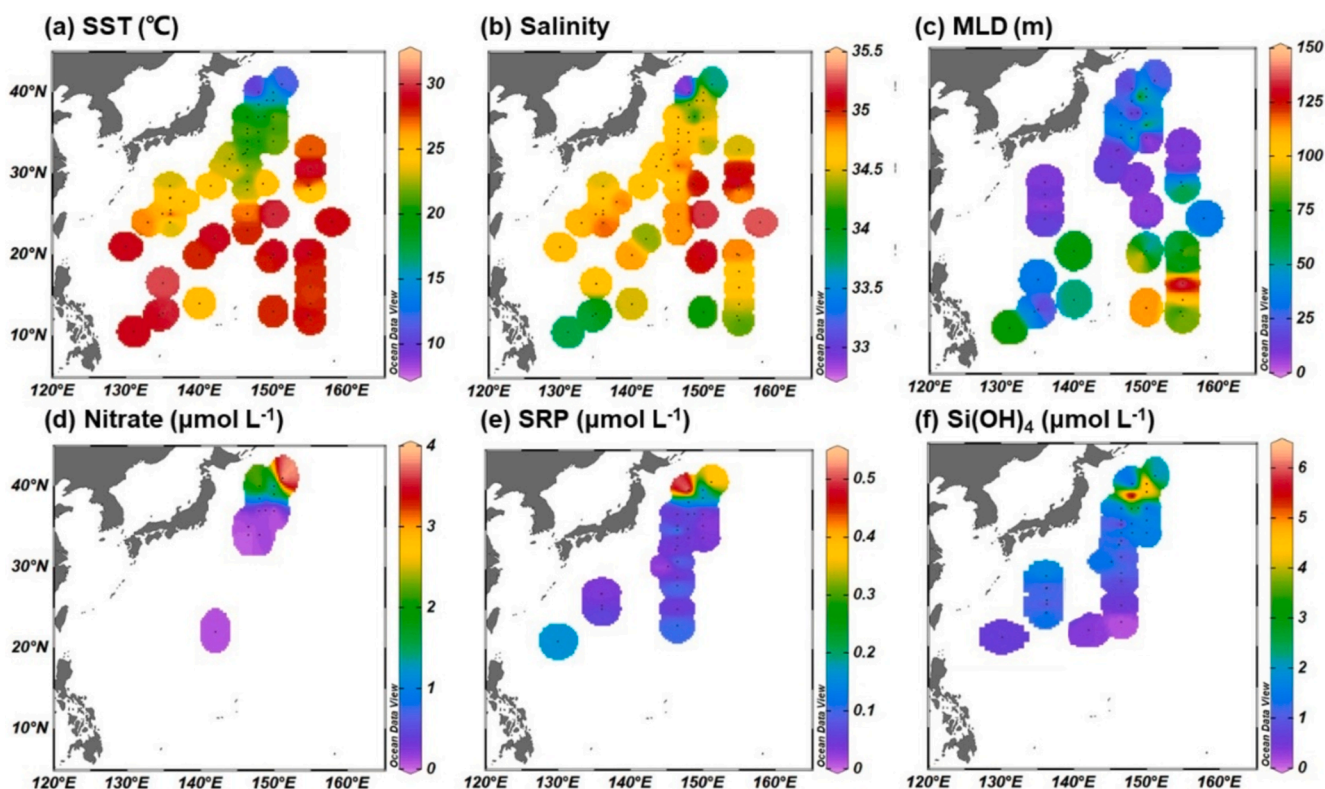


Fig. 2. Spatial distribution of (a) sea surface temperature (SST; °C), (b) salinity, (c) mixed layer depth (MLD; m), and (d-f) nutrient concentrations [nitrate ($\mu\text{mol L}^{-1}$), soluble reactive phosphate (SRP; $\mu\text{mol L}^{-1}$), $\text{Si}(\text{OH})_4$ ($\mu\text{mol L}^{-1}$)]. Unpublished data of nutrient concentrations in cruises KK2003 and KK2007 are not shown here according to the request of the data provider (see also Text S1). Nutrient concentrations at 16 out of 24 stations from the cruise 2021NWPO have been reported in a previous study (Zhou et al., 2023). Note the difference in color scales.

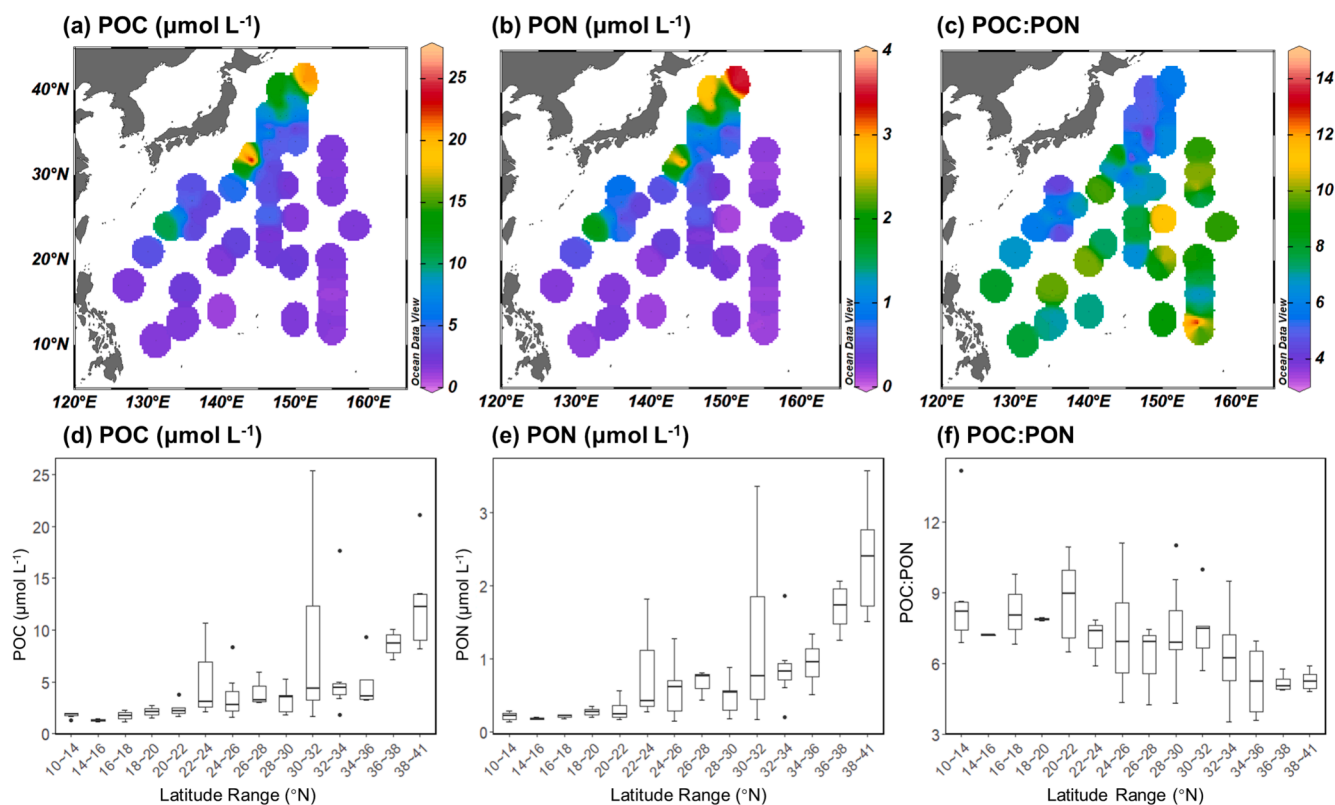


Fig. 3. Spatial distribution of (a) particulate organic carbon (POC; $\mu\text{mol L}^{-1}$), (b) particulate organic nitrogen (PON; $\mu\text{mol L}^{-1}$), (c) the molar ratio of POC to PON, and (d-f) the box diagrams of the changes of the three parameters with latitudes. The box charts in panels d-f show the median and 25th and 75th percentiles, with the top edge representing the maximum value and the bottom edge representing the minimum value. Dots represent values beyond 25th and 75th percentiles. Note the difference in color scales in panels a-c.

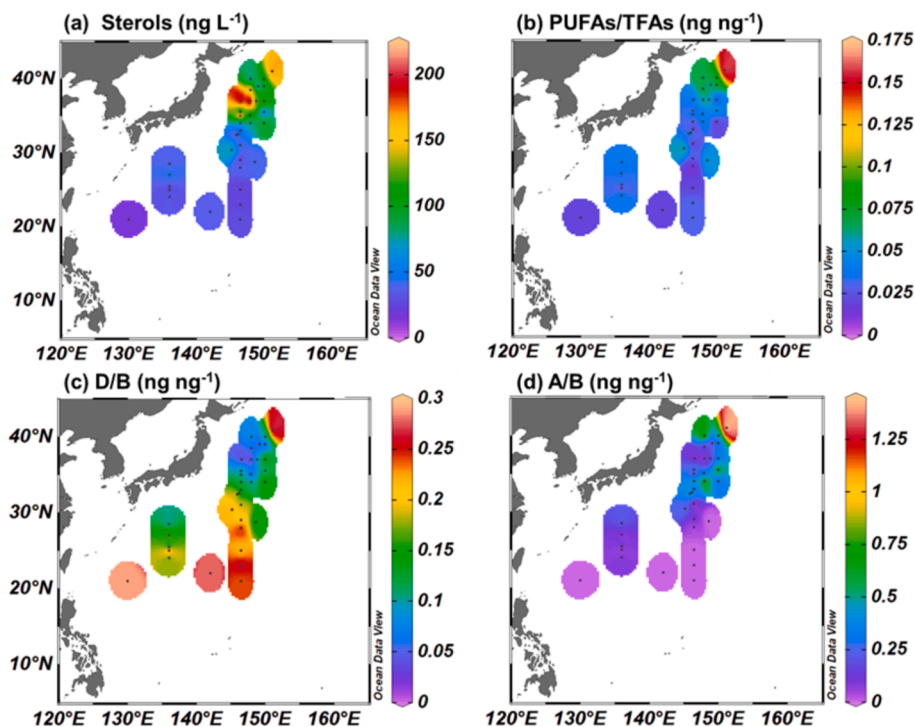


Fig. 4. Spatial distribution of (a) the concentration of total sterols (the sum of brassicasterol/epi-brassicasterol and dinosterol; ng L^{-1}), (b) the proportion of polyunsaturated fatty acids (% of total fatty acids (TFAs); ng ng^{-1}), (c) the ratio of dinosterol to brassicasterol/epi-brassicasterol (D/B; ng ng^{-1}), and (d) the ratio of C₃₇ alkenones to brassicasterol/epi-brassicasterol (A/B; ng ng^{-1}). Lipid data in cruises KH17-05, KK2003 and KK2007 are not shown here according to the request of the data provider. Note the difference in color scales.

showed the highest values at low latitudes (Fig. 3c). POC:PON ranged from 3.53 to 14.18 in the (sub)tropical biome and from 3.60 to 6.95 in the high-latitude biome (Fig. 3f). The highest POC:PON (14.18) was located at station k8a (12.53°N, 154.74°E) where PON concentration was the lowest (0.14 $\mu\text{mol L}^{-1}$).

The concentrations of total sterols (the sum of brassicasterol/epi-brassicasterol and dinosterol) ranged from 15.7 ng L^{-1} to 211.0 ng L^{-1} , showing higher values in the high-latitude biome than those in the (sub)tropical biome (Fig. 4a). Similarly, brassicasterol/epi-brassicasterol (12.2–205.6 ng L^{-1}), dinosterol (3.2–36.2 ng L^{-1}), PUFA proportions (1–16 %) and A/B (0–1.44) also showed higher values in the high-latitude biome (Fig. 4b, d; Fig. S6; Table S4). However, D/B (0.03–0.29) was overall higher in the (sub)tropical biome (Fig. 4c).

In the whole study area, SST and D/B had significant positive correlations with POC:PON (Fig. 5a; Table S5; Spearman's correlation: $p \leq 0.001$), suggesting that high SST and high relative biomass of dinoflagellates compared to diatoms had positive effects on POC:PON. In contrast, nutrient concentrations, A/B, total sterol concentrations and PUFA proportions showed significant negative correlations with POC:PON ($p \leq 0.001$), suggesting that high nutrient concentrations and high relative biomass of haptophytes compared to diatoms had negative effects on POC:PON. SST explained the highest variance for POC:PON (41 %), followed by nitrate concentrations (33 %) and D/B (26 %) (Fig. 5b; Table 1). Similarly, in the (sub)tropical biome SST and D/B had significant positive correlations with POC:PON ($p \leq 0.004$), Si(OH)_4 , A/B, total sterol concentrations and PUFA proportions correlated negatively with POC:PON ($p \leq 0.044$), and nitrate and SRP concentrations showed non-significant correlations with POC:PON. SST explained the highest variance for POC:PON (50 %), followed by nitrate concentrations (28 %) and D/B (23 %). In the high-latitude biome, only D/B showed significant positive correlations with POC:PON ($p = 0.036$), while other factors (SST, nutrient concentrations, A/B, total sterol concentrations and PUFA proportions) showed non-significant correlations. The relative contribution of multiple factors to POC:PON could not be quantified in the high-latitude biome due to the poor fitting results for most factors except D/B.

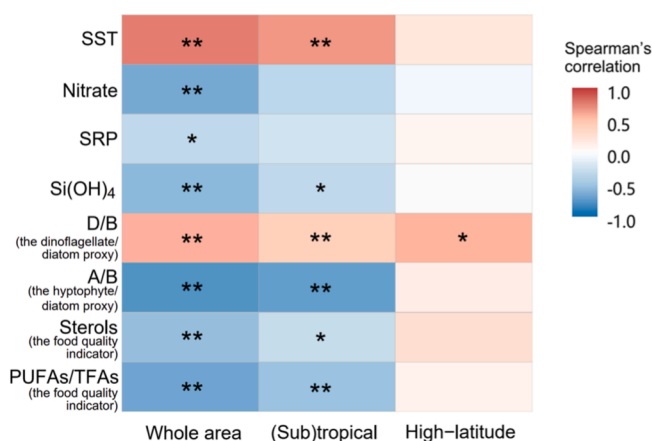
4. Discussion

4.1. Spatial distribution patterns of POC:PON in the North Pacific

In the large area of the North Pacific, the results of the compiled dataset showed that POC:PON decreased northward (Fig. 6), consistent with previous observations at the global scale (Huang et al., 2018; Martiny et al., 2013a; Martiny et al., 2013b; Tanioka et al., 2022a). The median POC:PON (6.77) in the North Pacific was higher than the global median of 6.5 (0–200 m) (Martiny et al., 2013b) (Table 2). Moreover, we observed a slightly higher median POC:PON (6.89) in the NWPO than that (6.75) in the NEPO, with SST explaining 47 % and 8 % of the individual deviance for POC:PON in the NWPO and NEPO, respectively (Table S6; Fig. S7). Obviously, mean SST (23.98 °C) was higher in the west where the WPWP is located than that in the east (21.38 °C) (Table 2; Fig. S8) (Yan et al., 1992). This study thus underscored the importance of SST in regulating POC:PON in the NWPO, and temperature interacted with other biotic and abiotic factors to further modulate the POC:PON spatial distribution, which is discussed in the next section. Moreover, ocean currents may influence POC:PON via transporting allochthonous particulate organic matter (Xiao et al., 2021), and it will be useful in future studies to systematically illustrate the effects of currents on POC:PON distribution in the North Pacific.

In our study region of the NWPO, the average POC:PON (7.10) was broadly comparable with the global average of 7.06 (0–200 m), the Northern Hemisphere average of 6.88 (0–5 m), as well as the average of 6.96 in the global low latitude areas (in the top 50 m; 15–45°N) (Huang et al., 2018; Martiny et al., 2013a; Martiny et al., 2013b). It is noteworthy that POC:PON was lower than 4 at two stations (B1 and D3') between 32 and 41°N in our study area (Fig. 3f; Fig. S9). On the one hand, the NWPO is influenced by Asian dust events, which resulted in higher input of anthropogenic nitrogen relative to phosphorus to the North Pacific Ocean (Kim et al., 2014; Moon et al., 2020). This may have contributed to the high PON concentrations and the low POC:PON at stations B1 and D3', especially at B1 where $\delta^{13}\text{C}_{\text{POC}}$ (−25.19 ‰; Zhang et al., unpublished) was lower (indicative high terrestrial input) than most stations in our study area. On the other hand, the influence of anticyclonic eddies was stronger at the beginning of our cruise and became weaker on the sampling day at station D3' (Fig. S9), and more nutrients

(a) Spearman's correlation



(b) Explained deviance

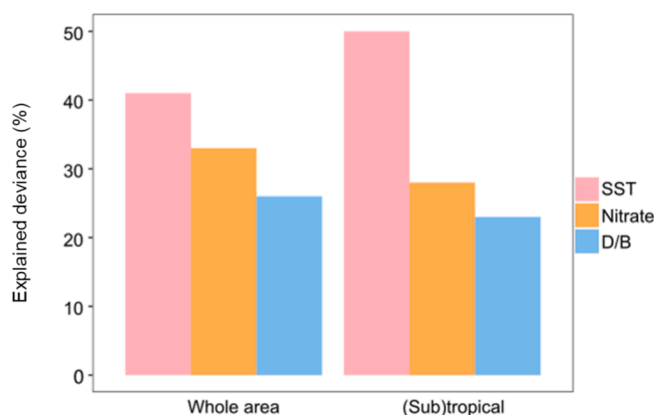


Fig. 5. Results of (a) Spearman's rank correlation analysis on the relationship between multiple factors and POC:PON in the whole study area (10–41°N) and the two biomes (the (sub)tropical biome: 10–34°N; the high-latitude biome: 34–41°N), and (b) individual explained deviance (squared studentized residuals) of the main variables normalized to the total explained deviance in GAMs for POC:PON in the whole study area and the (sub)tropical biome. The color in panel a represents the Spearman r correlation coefficient. Sea surface temperature (SST): °C; nitrate: $\mu\text{mol L}^{-1}$; SRP: soluble reactive phosphate ($\mu\text{mol L}^{-1}$); Si(OH)_4 : silicate acid ($\mu\text{mol L}^{-1}$); D/B: the ratio of dinosterol to brassicasterol/epi-brassicasterol (ng ng^{-1}); A/B: the ratio of C_{37} alkenones to brassicasterol/epi-brassicasterol (ng ng^{-1}); sterols: the sum of brassicasterol/epi-brassicasterol and dinosterol (ng L^{-1}); PUFAs/TFAs: the proportions of polyunsaturated fatty acids (% of total fatty acids (TFAs); ng ng^{-1}). *Significant correlation at $p < 0.05$; **Significant correlation at $p < 0.01$. Note that the relative contribution of multiple factors to POC:PON could not be quantified in the high-latitude biome due to the poor fitting results for most factors (Table 1).

Table 1

Generalized additive model (GAM) results on the strength of main biotic and abiotic factors in explaining POC:PON in the whole study area and the two biomes. Sea surface temperature (SST): °C; nitrate: $\mu\text{mol L}^{-1}$; D/B: the ratio of dinosterol to brassicasterol/epi-brassicasterol (ng ng^{-1}); edf: estimated degrees of freedom; GCV: generalized cross-validation; n : the number of observations. The lack of data in the high-latitude biome indicates poor data fitting ($R^2 < 0$).

	Intercept Estimate \pm SE	edf	p	R^2	Individual deviance explained	GCV	n
The whole study area (10–41°N)							
SST	7.0461 \pm 0.1808	2.224	<0.001	0.491	50.8 %	2.3	66
Nitrate	7.3529 \pm 0.4244	4.183	0.088	0.272	40.4 %	5.5	24
D/B	7.0461 \pm 0.2116	1	<0.001	0.302	31.3 %	3.0	66
The (sub)tropical biome (10–34°N)							
SST	7.5304 \pm 0.2205	0.2205	<0.001	0.381	39.6 %	2.6	52
Nitrate	8.4907 \pm 0.5681	1	0.076	0.162	22.2 %	5.6	15
D/B	7.5304 \pm 0.2563	1	<0.01	0.163	18.0 %	3.6	52
The high-latitude biome (34–41°N)							
SST	–	–	–	–	–	–	–
Nitrate	–	–	–	–	–	–	–
D/B	5.2471 \pm 0.2153	1.074	0.131	0.133	20.5 %	0.8	14

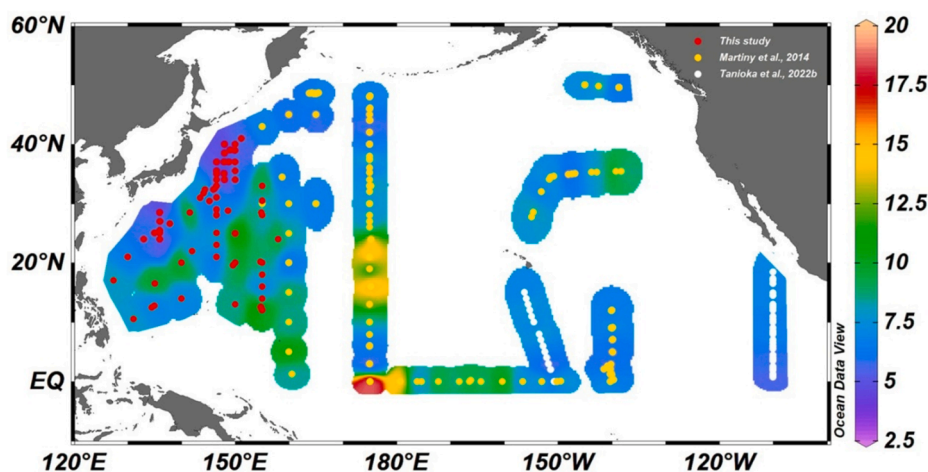


Fig. 6. Spatial distribution of POC:PON in the North Pacific (0–50°N) based on our observations (indicated by red dots), and published results of Martiny et al. (2014) (indicated by yellow dots) and Tanioka et al. (2022b) (indicated by white dots). Note that POC:PON values below 2 and above 20 were excluded, as they were considered unrealistic according to Martiny et al. (2013b). To make the high values of POC:PON in low latitude regions (i.e., 18.86 at 0.02°N, 175.03°E, 16.06 at 24°N, 175.25°E, 15.39 at 16°N, 175.25°E, and 15.24 at 21°N, 175°E) visible, 13 data points at adjacent stations or at the same stations collected from different years were excluded in this figure. POC:PON values of these 13 data points are shown in Table S7.

Table 2

POC, PON and sea surface temperature (SST) in the North Pacific. Data of POC:PON are from 305 stations, including 66 stations in the northwest Pacific from this study and 239 stations (10 and 229 stations in the northwest and northeast Pacific, respectively) from literature. Comparisons between our new data and the previously published data in the northwest Pacific are shown in Table S8.

	North Pacific				Northwest Pacific				Northeast Pacific			
	POC:PON ^{a,b,c}	POC ^{a,b,c}	PON ^{a,b,c}	SST ^{b,c,d}	POC:PON ^{a,c}	POC ^{a,c}	PON ^{a,c}	SST ^{c,d}	POC:PON ^{a,b}	POC ^{a,b}	PON ^{a,b}	SST ^{b,d}
Maximum	18.86	88.84	14.61	30.99	14.18	25.38	3.57	30.37	18.86	88.84	14.61	30.99
Minimum	3.53	0.35	0.07	4.19	3.53	1.17	0.14	9.71	4.37	0.35	0.07	4.19
Mean	7.17	5.42	0.83	21.99	7.10	4.91	0.79	23.98	7.20	5.59	0.84	21.38
SD	2.00	8.57	1.41	7.85	1.99	4.57	0.76	4.83	2.00	9.54	1.56	8.53
Median	6.77	3.11	0.43	25.41	6.89	3.35	0.55	24.53	6.75	2.91	0.43	25.86

^{a, b, c} and ^d Data are from Martiny et al. (2014), Tanioka et al. (2022b), this study and satellite observations (<https://data.marine.copernicus.eu/>), respectively.

may be transported to the euphotic layer and POC:PON thus became lower.

4.2. Controlling factors of POC:PON spatial variations

4.2.1. Overall relationships between POC:PON and multiple factors

Spatial variations in POC:PON are regulated by multiple environmental and biological factors (Garcia et al., 2018; Garcia et al., 2020;

Sauterey and Ward, 2022; Tanioka et al., 2022a; Tanioka and Matsu-moto, 2020), which are correlated to some degree. In the NWPO, our data suggest POC:PON was regulated to a large extent by SST, followed by nitrate concentration and D/B (Fig. 5b; Table 1). In global (sub) tropical regions (latitude < 45°; the western Pacific excluded), Tanioka et al. (2022a) showed that the interaction between nutricline and element-specific nutrient limitations had the highest contribution (54 %; calculated based on data in Tanioka et al. (2022a)) to the total explained

variance for POC:PON, followed by nutricline (20 %), SST (16 %) and nitrate concentration (10 %). It is clear that different factors were examined in different regions between this study and Tanioka et al. (2022a), making comparisons difficult between the two studies. However, both studies suggested the importance of SST and nitrate concentration in explaining POC:PON variability and showed a consistent order of the relative strength of the two factors, i.e., SST > nitrate concentrations. Similarly, Sauterey and Ward (2022) showed temperature and nitrogen availability as the main drivers of phytoplankton POC:PON in the North Atlantic. In the NWPO, the importance of SST may reveal characteristic environmental conditions, e.g., the higher SST due to the WPWP compared with other low-latitude ecosystems. We suggest to consider more variables and their interactions to further understand the regulation of POC:PON in the NWPO.

While ocean environmental variables are correlated, we observed that the direction of the links between SST and POC:PON (positive) and between nutrient concentrations and POC:PON (negative) are consistent with previous findings in the global ocean (Sauterey and Ward, 2022; Tanioka et al., 2022a) (Fig. 5a; Table S5). Temperature can affect the allocation of carbon and nitrogen resources in cells (Toseland et al., 2013). As temperature increases, more resources are invested in photosynthesis, increasing the efficiency of carbon synthesis to energy storage in the form of carbohydrates, thus elevating POC:PON (Talmy et al., 2016; Toseland et al., 2013). POC:PON is also known to vary with growth rate (Bi et al., 2012; Droop, 1983), and incorporation of these field measurements would reduce uncertainties in statistical models that aim to identify thermal effects.

Furthermore, POC:PON showed significant positive correlations with the lipid-derived biomass ratio of dinoflagellates to diatoms (D/B) (Fig. 5a; Table S5). There is compelling support in laboratory culture experiments and evolutionary hypothesis for the positive correlations between POC:PON and biomass ratios of dinoflagellates to diatoms. Systemic variations in C:N:P were observed between different eukaryotic phyla in marine phytoplankton, e.g., higher POC:PON in dinoflagellates compared to diatoms (Leonardos and Geider, 2004; Quigg et al., 2003). In the evolution of phytoplankton, diatoms arose in the secondary endosymbiotic event, while dinoflagellates arose in the secondary and tertiary endosymbiotic events (Quigg et al., 2011). It was thus hypothesized that the distinctive elemental composition across phytoplankton hierarchies under similar nutrient-replete conditions reflected their unique evolutionary history (Falkowski et al., 2004; Quigg et al., 2011; Quigg et al., 2003). The positive correlations between D/B and POC:PON in this study are in line with the findings in Quigg et al. (2003), providing evidence for the evolutionary inheritance hypothesis of elemental stoichiometry in diatoms and dinoflagellates.

Contrasting to D/B, A/B (a proxy for the biomass ratio of haptophytes to diatoms) showed significant negative correlations with POC:PON (Fig. 5a; Table S5). Previous studies observed a slightly higher POC:PON in diatoms compared to haptophytes (Finkel et al., 2010; Leonardos and Geider, 2004). For example, the mean value of POC:PON (12.91; range: 10.14–16.14) were higher in *Phaeodactylum tricornutum* (a model diatom species) than *Emiliania huxleyi* (the most widely distributed and abundant coccolithophores; mean: 11.74; range: 8.77–16.35) under the same culture conditions across large ranges of temperature, N:P supply ratios and $p\text{CO}_2$ (Bi et al., 2017; Bi et al., 2018b). Thus, the observed negative correlations between A/B and POC:PON are consistent with laboratory culture evidences.

We are aware that although diatoms, dinoflagellates and haptophytes contribute nearly half of organic carbon production in the oceans (Armbrust et al., 2004) and dominate in high-latitude regions (Chen et al., 2021; Isada et al., 2009; Wang et al., 2022), other phytoplankton groups such as picocyanobacteria also play an important role particularly in the oligotrophic gyres (Boyd et al., 2010). Indeed, large differences in elemental profiles were observed between cyanobacteria and lineages that arose as a result of primary and secondary endosymbiotic events (Quigg et al., 2011). However, the mean value of POC:PON in

cyanobacteria (~6) was clearly lower than those in other phytoplankton groups (~8–12) (Quigg et al., 2011), which could not explain the high POC:PON in the (sub)tropical biome in our study region. Nevertheless, studies on more open-ocean phytoplankton groups could help for a better understanding of the relationship between phytoplankton community and elemental stoichiometry.

4.2.2. Biome differences in the relationships between POC:PON and multiple factors

The correlations between multiple factors and POC:PON in each biome were overall comparable with those in the whole study area (Fig. 5a). However, there are also biome-specific characteristics, e.g., significant negative correlations between POC:PON and the haptophyte/diatom proxy (A/B) in the (sub)tropical biome, and non-significant correlations in the high-latitude biome where POC:PON showed significant correlations only with D/B (Fig. 5a; Table S5). This result is consistent with the distributions of diatom, dinoflagellate and haptophyte abundances in the oceans, i.e., high co-occurrence of diatoms and haptophytes in certain (sub)tropical biomes, but that of diatoms and dinoflagellates in the high-latitude biome (Elizondo et al., 2021). Interestingly, we observed that the (sub)tropical biome is characterized by a wide range of C_{37} alkenone concentrations (indicative haptophyte biomass; 0–44.68 ng L^{-1} (Wang, 2022)), especially in the boundary regions between the two biomes (~34°N, the Kuroshio Extension Front), also with significant variations in SST and MLD (Fig. 1 and 2a, c). It is known that the physical mechanism of cross-front convergence and the low salinity-cold water mass may be conducive to the growth of haptophytes (Harada et al., 2003; Pingree et al., 1975; Shin et al., 2002; Venables et al., 2012), which may also explain high C_{37} alkenone concentrations, as well as strong negative correlations between A/B and POC:PON in the (sub)tropical biome in this study.

Furthermore, the correlations between certain environmental factors (e.g., SST and nutrient concentrations) and POC:PON also differed between the two biomes (Fig. 5a; Table S5). The latitudinal patterns in the effects of SST and nitrate concentrations on POC:PON have been also found in recent models (Sauterey and Ward, 2022) and in situ observations (Lee et al., 2021; Tanioka et al., 2022a). Sauterey and Ward (2022) showed that phytoplankton C:N variation is overall controlled by nitrogen availability below 40°N in the North Atlantic Ocean, which is driven by eco-evolutionary shifts in the phytoplankton functional composition, while SST is one of prevalent factors in determining phytoplankton stoichiometry at high latitudes (polewards of 40°N). According to a global ocean observation, Tanioka et al. (2022a) suggested that nutricline depth and element-specific nutrient stress are the strongest predictors of C:N:P stoichiometry in (sub)tropical regions (latitude < 45°). Our results are consistent with the results above, showing a significant correlation between nutrient and POC:PON in the (sub)tropical biome (10–34°N), associating with significant contributions from phytoplankton community structure changes. However, we also found a significant correlation between SST and POC:PON in the (sub)tropical biome but not in the high-latitude biome (34–41°N). Higher spatial resolution sampling in the high-latitude biome would help to further test the latitudinal patterns in the relationship between multiple factors and POC:PON over the large area of the NWPO.

The samples of POC:PON from this study and compiled data from previous work were collected in different seasons. It has been observed that POC:PON showed significant seasonal variability at one open ocean station (31.7°N, 64.1°W) in the Northwestern North Atlantic Ocean, and non-significant seasonal variability at two open ocean stations located in the central North Pacific Subtropical Gyre (22.8°N, 158°W) and in the Cariaco Basin, north of Venezuela (10.5°N, 64.7°W), respectively (Talarmin et al., 2016). POC:PON may thus also show seasonal variability in the high-latitude biome of the NWPO, with lower values in winter and spring and higher ones in summer and autumn (Martiny et al., 2013b). Only a few samples were collected at the same stations in different seasons in this study, it was thus not possible to systematically

determine the seasonality of POC:PON. Nevertheless, the distribution pattern of POC:PON in this study is consistent with previous observations, indicating that seasonal variability of POC:PON in the high-latitude biome did not influence the overall distribution pattern of POC:PON in the NWPO observed in this study. Moreover, it has been observed that POC:PON fluctuates on a diel cycle in the surface Atlantic and Indian Oceans (Garcia et al., 2022), while we did not monitor the diel change in POC:PON in the present study. Thus, our results may reveal an overall spatial distribution pattern of POC:PON and its relationship with multiple factors in the NWPO, and further studies should focus on more detailed analyses on seasonal variability and the diel cycle in elemental ratios.

4.3. Potential implications on the fate of primary production

Ecological stoichiometric analyses often focus on chemical elements, and one reason is that the elements provide a framework for easily moving between levels of biological entities, ranging from organelles to the biosphere (Sterner and Elser, 2002). Key ecological players in food webs can be characterized in terms of their relative element demands by the stoichiometric approach, and their interactions in terms of consumption are thus constrained by ecological stoichiometry (Elser and Hessen, 2005). The compelling study by Cebrian (1999) indicated that autotroph stoichiometry well predicts trophic fate of primary production in diverse ecosystems. The percentage of primary production consumed by herbivores (PPC) is usually calculated by primary production and herbivorous grazing rate (Jiang et al., 2021; Schmoker et al., 2013), e.g., > 100 % of PPC when grazing rate is higher than primary production. We acknowledge that the utility of Eqs. (1)–(2) leads to caveats in the calculation of PPC. Our point in this study is not to give a quantitative measure of PPC, rather it is to infer what we can learn about stoichiometric properties of marine ecosystems based on the large scale data base of POC:PON in the NWPO.

Our derivation of PPC varied between 54–156 % in the whole study region (Fig. 7). This result of PPC estimation is not only consistent with the Plankton Ecology Group (PEG) model, suggesting the importance of zooplankton grazing in regulating phytoplankton biomass in both meso- to eutrophic and oligotrophic water body (Sommer et al., 2012), but also in good accordance with previous observations in the NWPO. For example, in the high-latitude regions daily food requirements of the

herbivores accounted for 114 % of mean daily primary production in the Kuroshio Counter Current area in summer (the proportion is calculated based on data in Taniguchi (1973)). Similarly, high grazing proportions of phytoplankton by microzooplankton were observed in the Oyashio region (40°N – 41°N) (mean: 113 %; range: 69–157 %) (Shinada et al., 2000), and in three stations located at 34.4–38.1°N, 142.4–144°E of the NWPO (mean: 124 %; range: 104–155 %; at 5 m; the proportion is calculated based on data in Obayashi and Tanoue (2002)). A relatively low proportion was observed in the North Equatorial Current area (mean: 94 %; the proportion is calculated based on data in Taniguchi (1973)) and in the oligotrophic subtropical North Pacific (microzooplankton consuming on average 76 % (range: 30–119 %) of the daily phytoplankton production at 137°E–160°E, along 23°N) (Jiang et al., 2021). Despite the great variation in PPC, there was a very clear spatial distribution pattern of PPC, showing higher values (mean: 117 %) in the high-latitude biome than those in the (sub)tropical biome (mean: 92 %) in this study (Fig. 7), consistent with previous findings above. The spatial distribution pattern of PPC can be attributed to multiple factors such as algal diets and temperature, which may strongly influence the nutritional requirements of herbivores (Besiktepe and Dam, 2020; Danger et al., 2022; Garzio et al., 2013; Helenius et al., 2020; Hirst and Bunker, 2003; Mathews et al., 2018; Taniguchi, 1973).

Indeed, our results show significant correlations between PPC and multiple factors (Table S5). The negative correlation between PPC and SST suggests that the increase in SST may be associated with a reduced nitrogen content (%DW), leading to lower PPC, because PPC was calculated as a function of POC:PON in this study. Similarly, previous mesocosm and on-board experiments, modeling and in situ observations showed that rising SST caused an enhanced proportion of primary produced organic matter transferred to dissolved organic carbon, and a reduced proportion channeled to higher trophic levels (Kim et al., 2019; Kim et al., 2011; Scheibner et al., 2018; Vernet et al., 2017; Wohlers et al., 2009). Moreover, the significant positive correlations between PPC and lipid contents (PUFA proportions and sterol concentrations) in this study are in line with the findings in different types of ecosystems, suggesting that herbivores are major conduits in ecosystems with high-quality autotrophs but are minor players in those with low-quality autotrophs (Cebrian, 1999; Sterner and Elser, 2002). Apparently, in the high-latitude biome of the NWPO with high POC concentrations (i.e., high food quantity), herbivores feed on high-nutritious autotrophs and can then proliferate and consume more autotroph production, resulting in a large flux of organic carbon from autotrophs to herbivores (Sterner and Elser, 2002).

The caveats in our derivation of PPC are primarily due to the non-specificity of Eqs. (1) and (2) to marine plankton. First, data points for marine and freshwater phytoplankton were mostly above the fitted line of Eq. (1) (Fig. 3A in Cebrian (1999)), indicating that phytoplankton turnover rate, as well as PPC, might be underestimated for planktonic communities. Second, there was a low R^2 (0.50) in the relationship between phytoplankton turnover rate and PPC (Eq. (2)), which may also cause potential uncertainties in PPC calculations. Third, we did not consider several other factors that may be associated with PPC variability. For example, viral lysis can recycle as much as one quarter of the primary production in the ocean back to the organic matter pool (Fuhrman, 1999; Iversen, 2023; Moran et al., 2022; Wilhelm and Curtis, 1999), and this influence of viral lysis might shift across oceanic regions (Mojica et al., 2016). Primary production can be also consumed by detritivores (e.g., up to 60 % of primary production observed in the global ocean (Moran et al., 2022)) or be exported (~10 %) (Henson et al., 2022; Sterner and Elser, 2002). These fates and processing of primary production are highly variable in ecosystems (Mojica et al., 2016; Moran et al., 2022) and may be potentially associated with the variability in PPC. Overall, the values and spatial distribution patterns of PPC in this study are consistent with previous findings based on data compilation and modeling. We thus recognize caveats in the derivation of PPC and expect that our results would enhance the significance of the

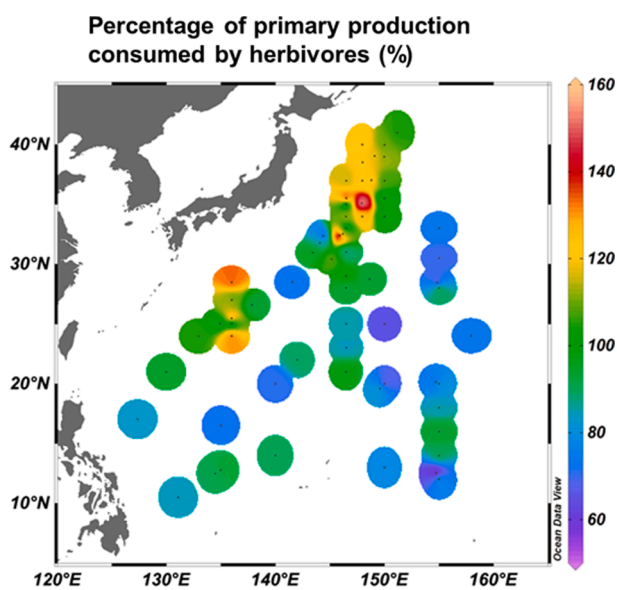


Fig. 7. Spatial distribution of the percentage of primary production consumed by herbivores (PPC; %). Note the uncertainty in PPC calculation, due to the variability of PPC estimates that Cebrian (1999) reported for phytoplankton.

strong relationship between the fate of primary production and stoichiometry. Furthermore, the novel approach of correlating PPC and lipid-based indicators of phytoplankton nutritional quality suggests that biochemical composition is an important determinant of the fate of primary production.

It is also worth noting that POC:POP is highly variable in different oceanic regions (Galbraith and Martiny, 2015; Martiny et al., 2013a). Previous studies showed that P-deficient diets could reduce growth rates, feeding and egg production rates of marine copepods (Bi and Sommer, 2020; Malzahn and Boersma, 2012; Saiz et al., 2023). Flexible POC:POP may also increase ocean carbon export in model simulations (Ödalen et al., 2020; Tanioka and Matsumoto, 2017). As we do not have data for POP in this study, there is a need in future studies to explore the full C:N:P variations and understand their ecological roles in the oceans. Moreover, we assume that the relative importance of metazoan grazing and protist grazing should differ between the two biomes of the NWPO according to field data compilations (Calbet and Saiz (2005); Calbet (2008); Saiz and Calbet (2007)) and the PEG model (Sommer et al., 2012), but this is beyond the scope of this study and should be addressed in future work.

5. Conclusion

This study reveals the spatial distribution of POC:PON and quantifies the contribution of multiple biotic and abiotic factors to the variations in POC:PON over a large area of the NWPO. Our results suggest that the strong latitudinal differences of POC:PON distribution (higher in the (sub)tropical biome and lower in the high-latitude biome) significantly correlated with multiple factors, with the following order of contribution: SST (41 %) > nitrate concentration (33 %) > lipid-derived phytoplankton community structure (26 %). Furthermore, the effects of multiple factors on POC:PON spatial distribution showed biome dependency, which can be attributed to the very high SST in the WPWP, characteristic MLD and associated phytoplankton community structure. PPC showed a higher mean value (117 %) in the high-latitude biome and a lower one (92 %) in the (sub)tropical biome. This distribution pattern significantly correlated with multiple factors such as SST and lipid-based indicators of phytoplankton quality for other trophic levels (PUFA proportions and sterol concentrations), indicating a reduced carbon flux to herbivores in ecosystems with low quality and quantity of phytoplankton, and high SST associated with nitrogen stress. Our findings underscore the significant roles of SST and elemental and biochemical composition of phytoplankton in regulating trophic transfer efficiency from primary producers to higher trophic levels, which is key to understanding the variability in marine ecosystem processes.

CRedit authorship contribution statement

Chuanli Zhang: Writing – original draft, Visualization, Investigation, Formal analysis, Data curation. **Yaoyao Wang:** Writing – original draft, Visualization, Investigation, Formal analysis, Data curation. **Rong Bi:** Writing – original draft, Validation, Supervision, Resources, Methodology, Funding acquisition, Conceptualization. **Ulrich Sommer:** Writing – review & editing, Methodology. **Guodong Song:** Writing – review & editing, Resources. **Zhaohui Chen:** Writing – review & editing, Resources. **Feng Lin:** Writing – review & editing, Resources. **Jing Zhang:** Writing – review & editing, Resources. **Meixun Zhao:** Writing – original draft, Validation, Supervision, Resources, Methodology, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.pocean.2024.103372>.

Data availability

Data will be made available on request.

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