

Strong latitudinal patterns in the elemental ratios of marine plankton and organic matter

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Nearly 75 years ago, Alfred C. Redfield observed a similarity between the elemental composition of marine plankton in the surface ocean and dissolved nutrients in the ocean interior¹. This stoichiometry, referred to as the Redfield ratio, continues to be a central tenet in ocean biogeochemistry, and is used to infer a variety of ecosystem processes, such as phytoplankton productivity and rates of nitrogen fixation and loss^{2–4}. Model, field and laboratory studies have shown that different mechanisms can explain both constant and variable ratios of carbon to nitrogen and phosphorus among ocean plankton communities. The range of C/N/P ratios in the ocean, and their predictability, are the subject of much active research^{5–12}. Here we assess global patterns in the elemental composition of phytoplankton and particulate organic matter in the upper ocean, using published and unpublished observations of particulate phosphorus, nitrogen and carbon from a broad latitudinal range, supplemented with elemental data for surface plankton populations. We show that the elemental ratios of marine organic matter exhibit large spatial variations, with a global average that differs substantially from the canonical Redfield ratio. However, elemental ratios exhibit a clear latitudinal trend. Specifically, we observed a ratio of 195:28:1 in the warm nutrient-depleted low-latitude gyres, 137:18:1 in warm, nutrient-rich upwelling zones, and 78:13:1 in cold, nutrient-rich high-latitude regions. We suggest that the coupling between oceanic carbon, nitrogen and phosphorus cycles may vary systematically by ecosystem.

A. C. Redfield first noted the similarity between the particulate nutrient ratios of plankton living in the surface ocean and that of dissolved nutrients in the deep ocean¹. He predicted that deep-ocean nutrient ratios were controlled by the uniform nutrient requirements of sinking, and subsequently remineralized, surface plankton. This concept remains a central tenet in our understanding of ocean biogeochemistry. However, model, field and laboratory studies have shown that different mechanisms can explain both constant and variable C/N/P ratios among ocean plankton communities, but the range of ratios in the ocean and the relative importance of each mechanism are subject to much research^{5–10,13,14}. Despite this continued lack of understanding of global patterns, the N/P ratio is routinely used to draw conclusions about ocean ecosystem processes, particularly related to nutrient limitation of phytoplankton production and the net magnitude of N₂ fixation and denitrification^{2,3}. Alas, these ratios are of critical importance to study, model and predict ocean biogeochemical cycles. Equally important is the C/P ratio of ocean plankton

communities, which provides linkages between nutrient cycling, phytoplankton carbon fixation and the strength of the biological carbon pump. However, global-scale variations in this ratio are poorly resolved at present.

At least four mechanisms have been proposed to explain variability in C/N/P ratios in surface communities. The first mechanism suggests that the taxonomic composition of a community will influence its elemental stoichiometry. Indeed, several studies have measured low nutrient drawdown and C/P and N/P ratios for diatoms^{9,15,16}, whereas cultures of marine Cyanobacteria have C/P and N/P ratios greater than the Redfield ratio⁶. The second mechanism relates the nutrient supply ratio (that is, the stoichiometry of the environment) to cellular elemental stoichiometry. Depending on the nutrient supply ratio, laboratory phytoplankton strains exhibit a range of equilibrium cellular N/P ratios¹⁷, but the importance of this mechanism for open-ocean communities has yet to be determined. The third mechanism is that the elemental stoichiometry within a cell is controlled by the biochemical allocation of resources to different growth strategies and is referred to as the growth rate hypothesis^{18,19}. Fast-growing cells may have a lower N/P ratio due to a larger investment in P-rich ribosomes. The fourth mechanism is that dead plankton material or detritus can accumulate in ocean waters and thus influence the observed particulate elemental ratios. Unfortunately, our quantitative knowledge of detritus concentrations²⁰ and elemental composition²¹ in the open ocean is woefully inadequate.

Although these four different mechanisms might explain variance in C/N/P ratios among ocean plankton, little is known about the global patterns in C/P and N/P ratios. To improve our understanding of the fundamental importance of elemental ratios to ocean biogeochemistry, this study addresses the following questions: what are the global average C/P and N/P elemental ratios; and what are the global patterns of these elemental ratios in ocean plankton communities?

We analysed approximately 5,000 paired observations each of particulate phosphorus, nitrogen and carbon from 742 and 733 stations in time and space for N/P and C/P ratios, respectively (Supplementary Table S1). These measurement locations were distributed globally across a broad latitudinal range (Fig. 1) and included data from previously published studies augmented with observations from seven new cruises. The N/P ratios ranged from 5:1 to 316:1 with a global area- and biomass-weighted mean of ~20:1. The C/P ratios ranged between 27:1 and 1,702:1 with a global weighted mean of ~146:1 (Fig. 2a and Supplementary Table S2).

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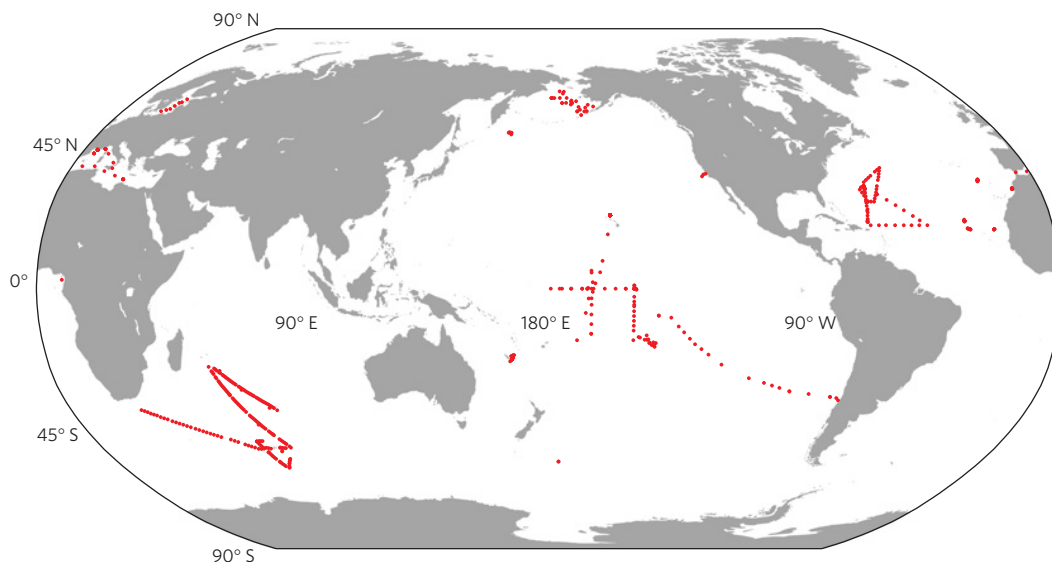


Figure 1 | Geographical locations of sample stations used in this study.

The observed variation in N/P and C/P ratios exhibits a strong latitudinal pattern (Fig. 2b and Supplementary Table S2). Between 45° N and 65° N, the C/N/P ratio ranged from 119:14:1 to 125:17:1, whereas at lower latitudes (15° N–45° N), the mean C/N/P ratio ranged from 171:15:1 to 226:37:1. A ratio of 137:18:1 was observed in the equatorial upwelling regions. This latitudinal pattern was largely mirrored in the Southern Hemisphere with a range from 66:11:1 to 74:13:1 at upper latitudes and 134:18:1 to 226:26:1 at lower latitudes. To account for differences in data redundancy at different stations, mean N/P and C/P ratios were also calculated for 1° × 1° grid cells. A similar latitudinal pattern was observed from this data treatment (Supplementary Table S3).

The oceans also exhibit a strong latitudinal gradient in environmental conditions, whereby high-latitude environments experience low temperatures and high nutrient concentrations and the opposite conditions at low latitudes. Equatorial regions are characterized by intermediate nutrient concentrations and temperatures due to upwelling. Thus, latitudinal variations in environmental conditions could explain the observed patterns in N/P and C/P ratios. This hypothesis was supported by a stepwise multiple regression, which revealed that temperature and nitrate concentration explained 33% and 36% of the variation (R^2) in N/P ratio, and 38% and 42% of the variation in C/P ratio (Supplementary Table S4), respectively. Nitrate concentration strongly correlated with phosphate and thus could be viewed as a proxy for nutrient availability², except in low-nutrient environments. At sites with low nitrate concentrations, we consistently found particulate N/P ratios >26:1. This ratio progressively declined to a mean of 13:1 in high-nitrate waters (Fig. 2c and Supplementary Table S2). This pattern was also observed for the C/P ratios. Elemental ratios were also high in regions with a temperature above 15 °C, whereas both N/P and C/P ratios declined in regions below 15 °C and reached a minimum in waters below 5 °C (Supplementary Fig. S1A and Table S2). In contrast to nutrient availability and temperature, we saw no significant relationship between the mixed-layer depth and the corresponding N/P and C/P ratios (Supplementary Fig. S1B and Tables S2 and S4). Together, our results suggest that the N/P and C/P ratios are lower in cold nutrient-rich environments in comparison with warm nutrient-depleted environments.

We analysed in further detail the elemental composition at two ocean time-series located in warm nutrient-depleted environments (Supplementary Fig. S2). The plankton community at the Bermuda Atlantic Time-series Study (BATS) received an influx of water,

through vertical mixing, with a dissolved N/P ratio >24:1, whereas the opposite was true for the Hawaii Ocean Time-series (HOT; <10:1; refs 8,10). The average particulate C/N/P ratios were 229:37:1 at BATS and 172:25:1 at HOT. Thus, both sites had particulate ratios greater than the canonical Redfield ratio as previously observed^{8,10}. However, the ratios were significantly higher at BATS compared with HOT ($p < 0.001$) (Supplementary Fig. S2)—reflecting the higher nutrient supply ratio.

The biomass of plankton communities in the oligotrophic gyres was generally dominated by the cyanobacteria *Prochlorococcus* and *Synechococcus*, picoeukaryotes and the heterotrophic bacterium *Pelagibacter*^{10,22,23}. In contrast, diatoms and other large eukaryotes dominated plankton communities at higher latitudes. To directly assess the impact of community composition on particulate nutrient ratios, we first measured C/N/P ratios of 235:35:1 and 161:25:1 in flow cytometrically sorted natural *Prochlorococcus* and *Synechococcus* populations from warm nutrient-depleted stations in the subtropical North Atlantic Ocean. We found a high elemental ratio in marine Cyanobacteria that in part explains the overall elevated elemental ratios in this region (Fig. 3). In contrast, elemental ratios in eukaryotic phytoplankton from the same environmental samples were lower (C/N/P = 107:16:1). Thus, we observed consistent differences in elemental ratios between coexisting plankton lineages. The N/P and C/P ratios of *Prochlorococcus* were higher than *Synechococcus*, which in turn were higher than eukaryotic phytoplankton (Student's t -test, $p < 0.05$, $n = 6$). Second, we saw from our global data set a significant negative correlation between both the absolute and relative (normalized to chlorophyll a concentration) concentration of the pigment fucoxanthin and elemental ratios (Supplementary Fig. S3). As fucoxanthin was primarily found in diatoms²⁴, this observation supports the idea that communities dominated by diatoms had a lower N/P and C/P ratio compared with communities dominated by Cyanobacteria. We also evaluated the possibility that latitudinal differences in phytoplankton growth rate could explain the differences in N/P and C/P ratios but observed no obvious connection (Supplementary Information and Fig. S4).

Dead plankton material—especially in low-productivity regions—could influence the observed latitudinal stoichiometry of plankton communities. To investigate this, we calculated the summed contribution of *Prochlorococcus*, *Synechococcus*, eukaryotic phytoplankton and bacteria to the total particulate carbon (POC), particulate nitrogen (PON) and particulate phosphorus (POP) pools in the subtropical North Atlantic to be $60 \pm 17\%$,

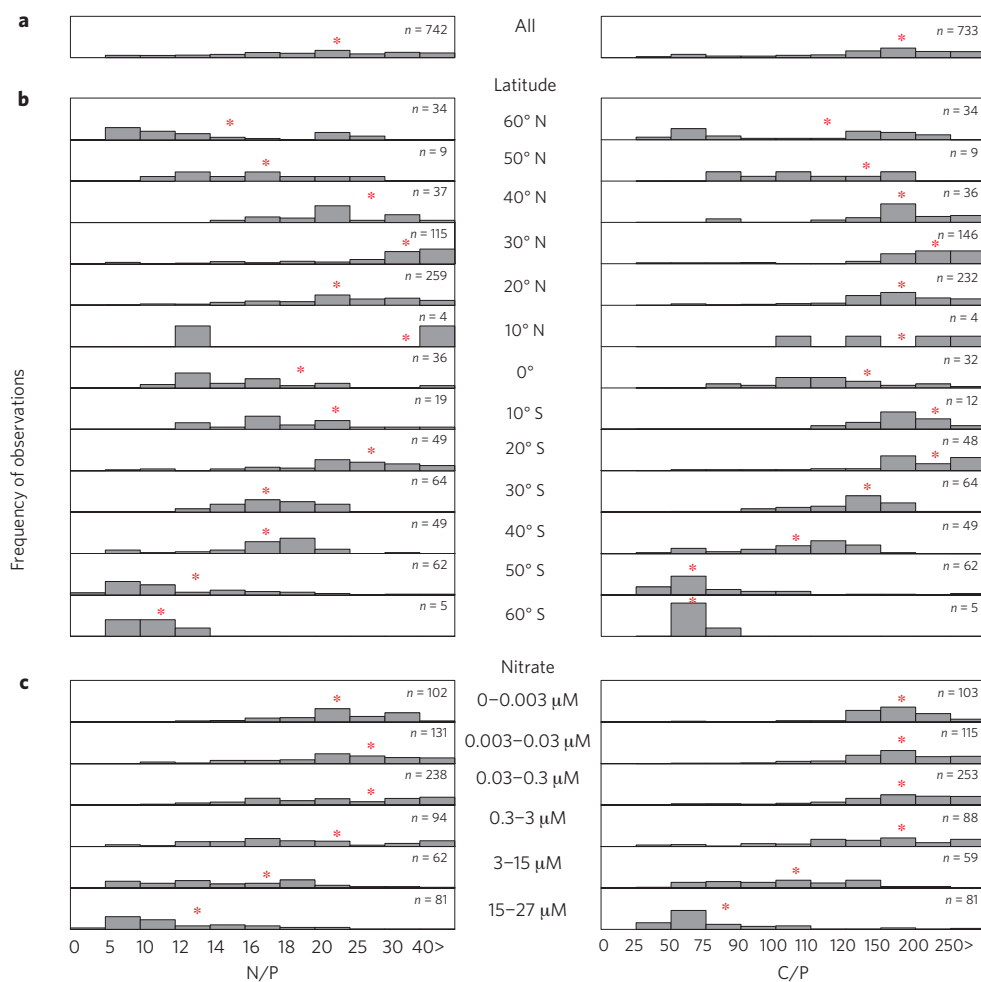


Figure 2 | Elemental stoichiometry of marine environments. Each histogram shows the frequency of stations (0–100%) with a N/P or C/P ratio within the specified range. The red asterisks specify the lognormal average and n specifies the number of stations in each histogram. **a**, The N/P and C/P ratios of all stations in this study. **b**, The N/P and C/P ratio binned by latitude. **c**, The N/P and C/P ratio binned by nitrate concentrations. The nitrate concentration is the average concentration in the top 50 m at a specific station. Please note the unequal bin size in the histogram.

$49 \pm 14\%$, and $98 \pm 21\%$, respectively (Supplementary Table S5). In combination with other planktonic lineages such as microzooplankton and heterotrophic nanoflagellates, we concluded that living planktonic material made up most of the particulate elemental pools in the surface oligotrophic ocean. Thus, it seemed unlikely that the observed latitudinal patterns in N/P and C/P ratios were due to differences in the detrital concentration.

In this study, we found that the global average C/P and N/P ratios were ~ 23 – 38% higher than the canonical Redfield ratio of 106:16:1. This is consistent with previous work using a much smaller and geographically limited data set²⁵. The observed variability in the C/N/P ratios was not random, but instead followed a strong latitudinal pattern driven by global variations in temperature, nutrients and biological diversity. This latitudinal gradient could be driven by changes in plankton assemblages as cold nutrient-replete environments commonly had a high abundance of diatoms with low N/P and C/P ratios¹⁶. In contrast, we directly measured high elemental ratios in marine Cyanobacteria from nutrient-depleted environments. This result was further supported by culture studies of *Prochlorococcus* and *Synechococcus*, where high ratios were observed—even under nutrient-replete conditions^{6,26}. Superimposed on this biodiversity effect, it further seemed that nutrient supply ratios can influence the elemental stoichiometry within nutrient-depleted environments. Laboratory, field and theoretical studies of marine microorganisms have suggested that

phytoplankton may express a range of elemental ratios^{5–7,15,16,19}, and this study shows how this variation results in global latitudinal patterns. Thus, we find a strong latitudinal variation in C/N/P ratios that at least in part is driven by changes in diversity of the plankton assemblage.

Within the context of our data, a simple box model analysis demonstrated that one should still expect a largely uniform nitrate-to-phosphate ratio in the deep ocean, despite large differences in surface elemental ratios (Supplementary Information). In agreement with previous modelling studies¹¹, this was due to a relatively small downward flux compared with a large deep-ocean reservoir undergoing circulation averaging. However, biologically driven variability in plankton elemental ratios has important implications for ocean biogeochemistry. For example, variations in plankton N/P ratios will influence the competition between nitrogen fixers and the remaining autotrophic community and the resulting nitrogen fixation rate^{2,3}. In support hereof, a model study suggests that a realistic global nitrogen fixation rate can solely be achieved by allowing for latitudinal variations in planktonic N/P ratios¹². Our results support these models and provide a direct observational basis for linking plankton elemental ratios and the magnitude of ocean nitrogen fixation. The systematic variation in plankton elemental ratios also has implications for the future rate of biological carbon sequestration. Models predict that a future warming of the surface ocean will result in an expansion

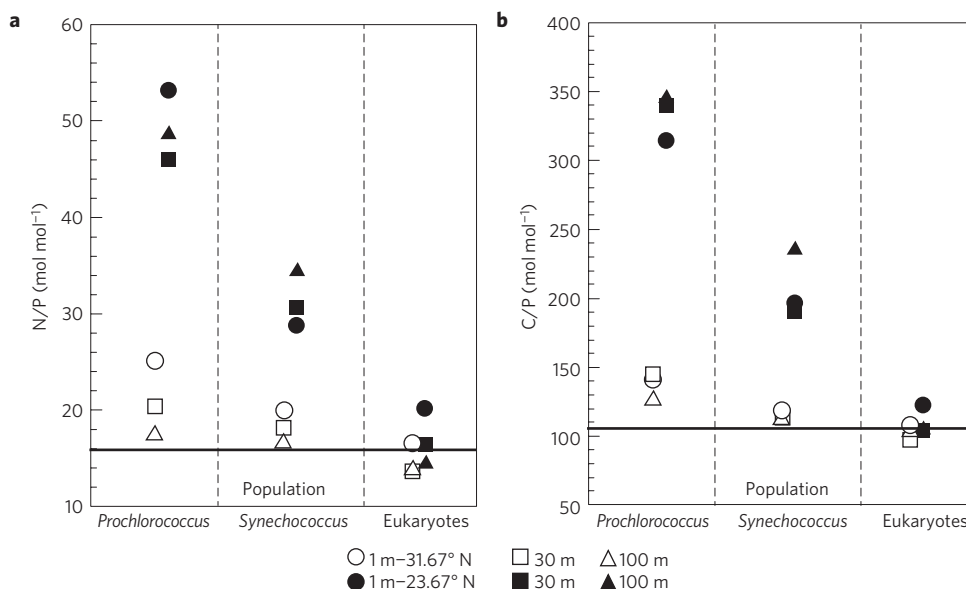


Figure 3 | Elemental stoichiometry of different taxa from natural North Atlantic Ocean plankton communities. a, b, The N/P ratio (**a**) and the C/P ratio (**b**) of *Prochlorococcus*, *Synechococcus* and combined pico- and nanoeukaryotes from six separate samples from the North Atlantic Ocean. The solid line represents the Redfield C/N/P ratio of 106:16:1.

of the warm nutrient-depleted oligotrophic gyres and thus an increase in the abundance of smaller at the expense of larger plankton. However, the elevated C/P ratio of small cyanobacteria could at least partly offset the negative impact this decline in cell size may have on carbon export. These examples show that the predictions of future cycles of nutrients in the ocean are intricately tied to the elemental ratios of plankton. Thus, biological controls on the elemental stoichiometry of ocean organic matter will have a large impact on global ocean biogeochemical cycles—now and in the future.

Methods

Data analysis. To assess the variation in plankton community elemental stoichiometry, we compiled POC, PON and POP measurements from 18 previously published and publically available cruises or time series and collected data during seven further cruises (~19% of the total data set; Supplementary Table S1). When available, we also collected information about *in situ* temperature, nitrate concentration, mixed-layer depth and net primary production. Unless otherwise stated, all mathematical operations were done in Matlab (Mathworks). Our combined data set covered 5,631, 5,318 and 4,965 measurements of POC, PON and POP but we excluded all observations with <5 nM POP, as that was set as our practical detection limit. The data covered both open-ocean and coastal samples. We calculated the mean elemental ratio in the top 50 m for each station in two ways—as the mean ratio for each observation pair or as the ratio of the 50 m integrated mean POP and PON or POC. The two ways gave comparable results ($R^2 = 0.99$) so we report only the mean of ratios here. A station was defined as a unique depth profile in time (± 1 day) and space (within a $1^\circ \times 1^\circ$ box). This margin was provided to allow for measurements of different environmental parameters on separate casts at the same station. If temperature or nitrate data were missing for specific stations, we attempted to substitute for missing values with monthly average values from the World Ocean Atlas²⁷.

To visualize the relationship between latitude, environmental variation and the N/P or C/P ratios, we separated stations into bins. We found the mean of each bin by using a logarithmic transformation, because it produced an approximate Gaussian distribution for the total data set. Using a custom script²⁸, we also estimated whether the total data set, as well as each bin, was best represented by one or more individual Gaussian distributions. We determined that 82% and 91% of the bins for N/P and C/P ratios, respectively, were best represented by a single Gaussian distribution (Supplementary Table S2). Thus, a single mean was generally an appropriate representation of the data.

Some samples were collected from the same spatial location but at different time points. To evaluate the possible influence of spatial autocorrelation, we took the mean of each $1^\circ \times 1^\circ$ grid cell, which resulted in 303 and 291 unique stations for N/P and C/P ratios, respectively (Supplementary Table S3). We then re-estimated the global biomass-weighted mean and latitudinal trends with this data set

(Supplementary Table S3). The trends were similar to those presented and thus it seems that spatial autocorrelation was not a problem in our data analysis. We also determined the best environmental predictors of elemental variation by stepwise multiple linear regression. As we did not have all environmental values for each station, we also carried out Pearson and Spearman correlation for each variable against logarithmically transformed N/P and C/P ratios.

Particulate carbon, nitrogen and phosphorus measurements. POC and PON samples were filtered on precombusted (450 °C, 4 h) Whatman GF/F filters and frozen until analysis²⁹. Samples were analysed on a Control Equipment 240-XA or 440-XA elemental analyser standardized to acetanilide. The POC analysis included an acidification step so that the measurement did not include inorganic carbonate. POP was analysed using an ash-hydrolysis method¹⁰. Oxidation efficiency and standard recovery were tested with each sample run using an ATP standard solution and a certified phosphate standard (OSIL Phosphate Nutrient Standard Solution). Method precision is 1–2% at 5 nmol kg⁻¹.

Taxon-specific particulate carbon, nitrogen and phosphorus measurements.

Samples were collected from two stations within the subtropical North Atlantic gyre and three depths at each station (total of 6 discrete samples). The stations were the BATS station at $31^\circ 40' N 064^\circ 10' W$ and at $23^\circ 40' N 065^\circ 22' W$. Samples were collected from near surface (<5 m), 30 and 100 m in an acid-cleaned Niskin bottle. From the same Niskin bottle, subsamples were taken for taxon-specific elemental content (method below) and for whole-community elemental content as previously described. For taxon-specific elemental content, seawater samples (1–2 l) were gently concentrated on 0.4 μm polycarbonate filters and kept at 4 °C until they could be sorted, within several hours. From the concentrated samples, replicate *Prochlorococcus*, *Synechococcus* and combined pico/nanoeukaryote populations were sorted using standard protocols³⁰ and immediately filtered onto 0.2 μm silver filters. Samples were stored at $-20^\circ C$ until analysis. Analyses for POC, PON and POP content were as described for whole particulate samples. Average cellular elemental content was determined by dividing the elemental content of the sample by the number of sorted cells.

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Author contributions

All authors participated in the analysis and interpretation of results. M.W.L. collected the newly presented cruise data and taxon-specific plankton elemental data. A.C.M. and M.W.L. designed the study and wrote the paper.

Additional information

Supplementary information is available in the [online version of the paper](#). Reprints and permissions information is available online at www.nature.com/reprints. Correspondence and requests for materials should be addressed to M.W.L.

Competing financial interests

The authors declare no competing financial interests.