LETTERS

Phytoplankton in the ocean use non-phosphorus lipids in response to phosphorus scarcity

Benjamin A. S. Van Mooy[1], Helen F. Fredricks[1], Byron E. Pedler[1]†, Sonya T. Dyhrman[2], David M. Karl[3], Michal Koblížek[4,5], Michael W. Lomas[6], Tracy J. Mincer[1], Lisa R. Moore[7], Thierry Moutin[8], Michael S. Rappé[9] & Eric A. Webb[10]

Phosphorus is an obligate requirement for the growth of all organisms; major biochemical reservoirs of phosphorus in marine plankton include nucleic acids and phospholipids[1–3]. However, eukaryotic phytoplankton and cyanobacteria (that is, 'phytoplankton' collectively) have the ability to decrease their cellular phosphorus content when phosphorus in their environment is scarce[1,4,5]. The biochemical mechanisms that allow phytoplankton to limit their phosphorus demand and still maintain growth are largely unknown. Here we show that phytoplankton, in regions of oligotrophic ocean where phosphate is scarce, reduce their cellular phosphorus requirements by substituting non-phosphorus membrane lipids for phospholipids. In the Sargasso Sea, where phosphate concentrations were less than 10 nmol l^{-1}, we found that only 1.3 ± 0.6% of phosphate uptake was used for phospholipid synthesis; in contrast, in the South Pacific subtropical gyre, where phosphate was greater than 100 nmol l^{-1}, plankton used 17 ± 6% (ref. 6). Examination of the planktonic membrane lipids at these two locations showed that classes of sulphur- and nitrogen-containing membrane lipids, which are devoid of phosphorus, were more abundant in the Sargasso Sea than in the South Pacific. Furthermore, these non-phosphorus, 'substitute lipids' were dominant in phosphorus-limited cultures of all of the phytoplankton species we examined. In contrast, the marine heterotrophic bacteria we examined contained no substitute lipids and only phospholipids. Thus heterotrophic bacteria, which compete with phytoplankton for nutrients in oligotrophic regions like the Sargasso Sea, appear to have a biochemical phosphorus requirement that phytoplankton avoid by using substitute lipids. Our results suggest that phospholipid substitutions are fundamental biochemical mechanisms that allow phytoplankton to maintain growth in the face of phosphorus limitation.

Linkages between phosphorus availability and phytoplankton productivity in the ocean have received renewed attention in recent years[7–11], yet there remains little direct evidence for instantaneous phosphorus limitation of primary production. For example, in the oligotrophic eastern Mediterranean Sea, where phosphate concentrations are sub-nanomolar and phosphate turnover times are only a few hours, a large-scale phosphorus-addition experiment did not stimulate net phytoplankton growth or the rate of total community photosynthesis[11]. A similar lack of stimulation by phosphate alone was recently reported in the oligotrophic Sargasso Sea[12], where the concentrations of phosphate are also quite low[7]. These observations are indicative of phytoplankton communities that are highly adapted to phosphorus scarcity and can simultaneously maintain both low cellular phosphorus requirements and effective rates of photosynthesis.

Phytoplankton communities in oligotrophic regions of the ocean are generally dominated by cyanobacteria[8], or, at times, small eukaryotic phytoplankton[13]. Phosphate is typically the preferred form of dissolved phosphorus for these organisms[8,14,15], but recent work has shown that many phytoplankton species can supplement their phosphorus demand by accessing dissolved organic phosphorus[16–18]. It has also been shown that phytoplankton have the ability to lower their physiological phosphorus demand by as much as 50% in response to phosphorus limitation[1,4,5]. This latter strategy is important because it essentially allows phytoplankton in oligotrophic marine environments to maintain growth in the face of phosphorus limitation. The physiological mechanisms for maintaining growth while lowering overall phosphorus demand are unknown, but the options are basically limited to reducing either nucleic-acid or phospholipid synthesis rates. Unlike nucleic acids, there are alternative, non-phosphorus membrane lipid molecules that may be substituted for phospholipids. These 'substitute lipids' have the same ionic charge as phospholipids, and thus serve similar biochemical purposes within cells[19,20]. Although it has been hypothesized that phytoplankton in the environment might synthesize substitute lipids in response to phosphorus limitation[2,19,20], this hypothesis has yet to be tested outside of cultures of a few model organisms.

To understand whether phytoplankton use phospholipid substitutions as a strategy to mitigate phosphorus limitation in the ocean, we examined the synthesis of phospholipids in the Sargasso Sea, a setting where phytoplankton appear to be stressed[16] by low concentrations of phosphate[7]. Our study sampled a mode water eddy, which is a physical oceanographic feature that can support very high rates of phytoplankton growth[13]. We found that the cycling of phosphorus was also particularly rapid: the turnover time of phosphate in surface waters ($n = 21$) was 1.4 ± 1.0 h (mean ± s.d.), which is nearly a factor of three shorter than previously reported[21]. This rapid turnover, compounded by concentrations that averaged 7.9 ± 2.4 nmol l^{-1}, indicated that phytoplankton were experiencing conditions where phosphate was scarce. We measured total community phospholipid synthesis rates, and found that they constituted only 1.3 ± 0.6% of the total phosphate uptake rate (Fig. 1). These observations contrast markedly with those we made in the surface waters of the oligotrophic North Pacific subtropical gyre ($n = 12$) and South Pacific subtropical gyre ($n = 18$), where the total planktonic community supported phospholipid synthesis rates that contributed 12 ± 8%

[1]Department of Marine Chemistry and Geochemistry, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543, USA. [2]Department of Biology, Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543, USA. [3]Department of Oceanography, University of Hawaii, Honolulu, Hawaii, USA. [4]Institute of Microbiology, Czech Academy of Sciences, Třeboň, Czech Republic. [5]Institute of Physical Biology, University of South Bohemia, Nové Hrady, Czech Republic. [6]Bermuda Institute of Ocean Sciences, St. George, Bermuda. [7]Department of Biological Sciences, University of Southern Maine, Portland, Maine, USA. [8]Laboratoire d'Océanographie Physique et Biogéochimique, Centre d'Océanologie de Marseille, Aix-Marseille University, France. [9]Hawaii Institute of Marine Biology, University of Hawaii, Kaneohe, Hawaii, USA. [10]Department of Biological Sciences, University of Southern California, Los Angeles, California, USA. †Present address: Scripps Institution of Oceanography, University of California at San Diego, La Jolla, California, USA.

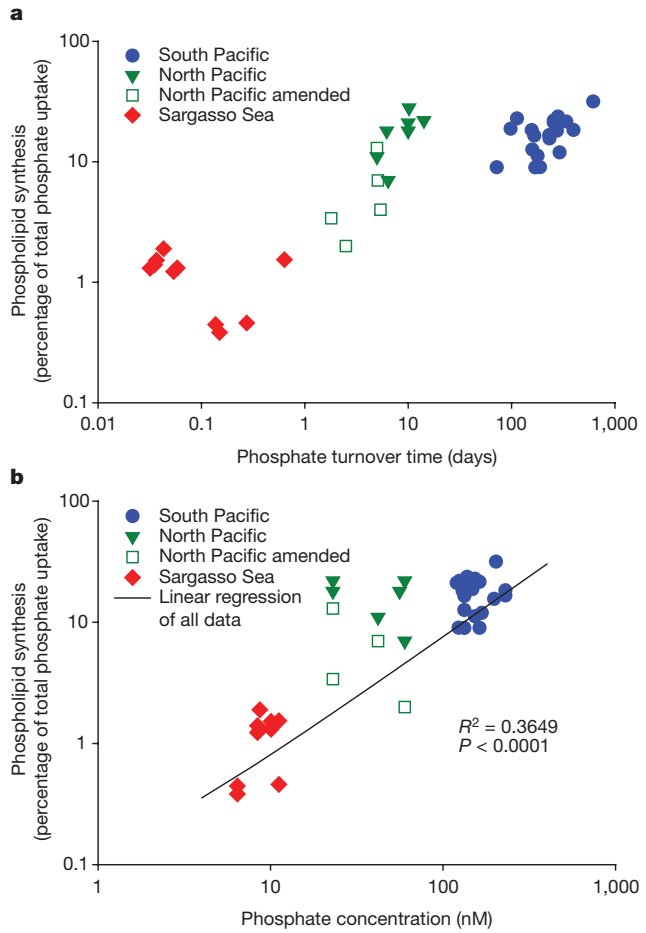

Figure 1 | Relationships between phosphate and phospholipid synthesis. Percentages of total phosphate uptake allocated to phospholipid synthesis and their relationships with phosphate turnover times (**a**) and phosphate concentrations (**b**). Solid symbols for South and North Pacific are data from refs 2, 6 and 22. Open symbols for the North Pacific are data from incubations, which were amended with NH_4^+ at a final concentration of 50 nmol l^{-1} (see ref. 3; ambient concentrations are generally of the order of 30 nmol l^{-1}) in an attempt to increase rates of phosphate uptake. The linear regression in the bottom plot indicates that 36% of the variation in the use of phosphate for phospholipid synthesis can be explained by the variation in phosphate concentrations. This suggests there is a strong, fundamental and global-scale control on phosphate allocation within the planktonic communities in response to variations in phosphorus availability.

and 17 ± 6% of total phosphate uptake, respectively[2,6] (Fig. 1). In the North Pacific and South Pacific, phosphate concentrations averaged 44.9 ± 19.9 and 151.2 ± 36.3 nmol l^{-1}, respectively, and phosphate turnover times averaged 6.8 ± 3.6 and 239 ± 74 days, respectively[14,22], which indicates that phosphate was much more readily available in these two environments than in the Sargasso Sea. Thus, our data unequivocally show a fundamental relationship between the availability of phosphorus and its biochemical allocation within planktonic cells on large geographic scales.

We also conducted a series of laboratory experiments with batch cultures of representative cyanobacteria and eukaryotic phytoplankton under phosphorus-replete and phosphorus-depleted conditions. Using a common approach, we grew these organisms in high- and low-phosphate media, and then harvested the cells once we observed a clear difference in growth rates under the two conditions. During these experiments we observed that non-phosphorus membrane lipids were substituted for phospholipids in all cases (Table 1). Cyanobacteria of the genera *Synechococcus*, *Prochlorococcus*, *Crocosphaera* and *Trichodesmium* all showed the ability to substitute the non-phosphorus membrane lipid sulphoquinovosyldiacylglycerol (SQDG; Supplementary Fig. 1) for the phospholipid phosphatidylglycerol (Supplementary Fig. 1) under conditions of phosphorus limitation (Table 1); both of these membrane lipids are anionic in the pH range of seawater and to a certain extent these lipids are biochemically equivalent[19]. The SQDG/phosphatidylglycerol ratios in phosphorus-limited cultures of *Synechococcus* and *Prochlorococcus* were higher than nitrogen-fixing *Trichodesmium* and *Crocosphaera*; this lack of biochemical flexibility on the part of the nitrogen-fixing genera is consistent with the observed susceptibility of these organisms to phosphorus limitation[9–11,18]. From the measured cellular phosphatidylglycerol content of *Synechococcus* and *Prochlorococcus* we determined that the substitution of SQDG for phosphatidylglycerol spared 0.3×10^6 to 5.2×10^6 atoms of phosphorus per cell, which, depending on the strain, equates to 10–86% of the phosphorus in their genomic DNA (Supplementary Table 1). Because the genes involved in SQDG synthesis[23] only contain about 5×10^3 phosphorus atoms, this metabolic pathway unequivocally confers a net phosphorus-sparing capability. Given that genomic DNA composes more than half of the total cellular phosphorus in phosphorus-limited cultures of *Synechococcus* and *Prochlorococcus*[4], we calculate that the ability to synthesize SQDG in place of phosphatidylglycerol spares an amount of phosphorus equivalent to 5–43% of their total cellular phosphorus demand.

In the phosphorus-limited cultures of eukaryotic phytoplankton, we observed that non-phosphorus 'betaine' lipids were substituted for phosphatidylcholine (Table 1 and Supplementary Fig. 1). There are three structurally related types of betaine lipid molecule (Supplementary Fig. 1), and, like phosphatidylcholine, they are all

Table 1 | Ratios of substitute lipids to phospholipids in phytoplankton cultures and environmental samples

	SQDG/PG ratio, P-replete	SQDG/PG ratio, P-limited	BL/PC ratio, P-replete	BL/PC ratio, P-limited
Cyanobacteria				
Synechococcus WH8102	**9.9 ± 2.0**	**120.5 ± 7.1**	0†	0†
Synechococcus WH7803	**10.3 ± 0.3**	**61.6 ± 15.4**	0†	0†
Synechococcus WH5701	**6.2 ± 0.5**	**132.0 ± 31.0**	0†	0†
Prochlorococcus MED4	**20.0 ± 1.3**	**34.1 ± 1.6**	0†	0†
Crocosphaera watsonii	4.0	5.8	0†	0†
Trichodesmium erythreum	**7.8 ± 1.0**	**18.5 ± 4.9**	0†	0†
Eukaryotic phytoplankton				
Thalassiosira pseudonana	**3.0 ± 0.9**	**394.8 ± 48.2**	<0.01‡	>500§
Chaetoceros affinis	**10.5 ± 3.6**	**26.3 ± 9.0**	**0.9 ± 0.2**	**27.8 ± 8.3**
Emiliania huxleyi	<0.01*	<0.01*	0.7	1.3
Communities				
South Pacific	**3.6 ± 0.8**	NA	**3.6 ± 1.7**	NA
Sargasso Sea	NA	**4.5 ± 1.1**	NA	**13.1 ± 4.0**

Bold type indicates significant differences between phosphorus-replete and phosphorus-limited conditions as indicated by directional Mann–Whitney *U*-tests ($P \leq 0.05$). Cultures were analysed in triplicate or greater except for *C. watsonii* and *E. huxleyi*, which were analysed once. In the South Pacific, five discrete samples of the total planktonic community (>0.2 μm) were collected and analysed; there were six samples from the Sargasso Sea. NA, not applicable; BL, betaine lipid; PC, phosphatidylcholine; SQDG, sulphoquinovosyldiacylglycerol; PG, phosphatidylglycerol. *SQDG not detected; analytical sensitivity is given. †BLs not detected and are not known to be produced by cyanobacteria. ‡BLs not detected; analytical sensitivity is given. §PC not detected; analytical sensitivity is given.

zwitterionic in the pH range of seawater. Furthermore, both phosphatidylcholine and betaine lipids contain one atom of nitrogen per molecule, and thus the substitution of betaine lipids for phosphatidylcholine does not require additional cellular nitrogen. Phosphorus-limited cultures of the diatom *Thalassiosira pseudonana* used betaine lipids to the complete exclusion of phosphatidylcholine. This substitution spared them $16 \pm 8\%$ of their total phosphorus demand compared with cells grown under phosphorus-replete conditions. The diatom *Chaetoceros affinis* and coccolithophorid *Emiliania huxleyi* also used betaine lipids, and we estimate that this substitution spared them approximately 10–30% of total phosphorus demand. Furthermore, as was observed in cyanobacteria, *T. pseudonana* and *C. affinis* also substituted SQDG for phosphatidylglycerol.

Based on the lipids we observed in phosphorus-limited cultures, we hypothesized that substitute lipids would be more prevalent in the Sargasso Sea than in the South Pacific. Indeed, we found that betaine lipids were the most abundant intact membrane lipids in the Sargasso Sea, reaching an average combined concentration of $2.4 \pm 0.2\ \mu g\,l^{-1}$. In contrast, the concentration of betaine lipids was only $0.2 \pm 0.1\ \mu g\,l^{-1}$ in the South Pacific. Furthermore, the betaine lipid/phosphatidylcholine ratio was 13.1 ± 4.0 in the Sargasso Sea, which is almost a factor of 4 higher than the 3.6 ± 1.7 we observed in the South Pacific (Table 1). Betaine lipids and phosphatidylcholine are by no means exclusive to the domain Eukarya (see ref. 26, and references therein), but they have yet to be reported in any cyanobacterium (see also Table 1), and, as discussed below, they do not appear to be abundant in heterotrophic bacteria from oligotrophic environments. Concentrations of SQDG were also higher in the Sargasso Sea than in the South Pacific (0.8 ± 0.3 compared with $0.3 \pm 0.1\ \mu g\,l^{-1}$), and this was reflected in the higher SQDG/phosphatidylglycerol ratios in the Sargasso Sea (Table 1). However, phosphatidylglycerol is not derived from phytoplankton alone but is also synthesized by heterotrophic bacteria[2], which confounds the interpretation of community SQDG/phosphatidylglycerol ratios; given the contribution of phosphatidylglycerol by heterotrophic bacteria, it is striking that we were able to observe a higher SQDG/phosphatidylglycerol ratio in the Sargasso Sea, the expected response of phytoplankton to lower phosphorus availability.

An additional class of non-phosphorus lipids, ornithine lipids, has been reported in lineages of aerobic anoxygenic phototrophic (AAP) bacteria. However, with the exception of two samples from the South Pacific, we did not detect ornithine lipids in any of our samples from the field. We examined the AAP bacterium *Roseobacter* sp. strain COL2P originating from the oligotrophic Mediterranean Sea and found that although ornithine lipids were more prevalent in phosphorus-limited cultures, they did not appear to function as substitutes for phospholipids in this species (Supplementary Fig. 2). Given this observation, and the relatively low abundance of AAP bacteria in the oligotrophic North Atlantic[24], the absence of ornithine lipids in the Sargasso Sea is not particularly surprising.

Bacteria of the SAR11 clade dominate the heterotrophic bacterial community of the Sargasso Sea[8,25]. We found that a representative of this clade, *Pelagibacter ubique*, synthesized only the phospholipids phosphatidylglycerol and phosphatidylethanolamine. These results are consistent with those from marine bacteria isolated by classical methods[2]. The sum of these phospholipids in *P. ubique* amounted to 1.5×10^6 atoms of phosphorus per cell, which, for comparison, is 10 times more than the phospholipids in phosphorus-limited *Synechococcus* sp. strain WH8102 cells (0.16×10^6 atoms of phosphorus per cell). We were not able to examine *P. ubique* in phosphorus-limited cultures. However, known bacterial genes for SQDG[23], betaine lipid[26] and ornithine lipid[27] synthesis are absent from the *P. ubique* genome. The absence of these genes, which encode pathways that could spare *P. ubique* an amount of cellular phosphorus equivalent to almost half their entire genome, is a puzzling potential side effect of genome streamlining in this organism[28].

We tracked the lipid composition of resident heterotrophic bacteria from the Sargasso Sea ($n = 3$) in regrowth incubations[29], which are designed to allow heterotrophic bacteria to grow exponentially in the absence of other plankton. Even though concentrations of phosphate decreased from 6.4 ± 2.0 to $1.7 \pm 1.2\ nmol\,l^{-1}$ during the course of growth, we observed marked increases in phosphatidylglycerol and phosphatidylethanolamine only (Supplementary Fig. 3), whereas concentrations of substitute lipids decreased or remained low (Supplementary Fig. 4). Furthermore, the phospholipid content per cell of heterotrophic bacteria remained nearly constant throughout the incubation at $1.7 \pm 0.2 \times 10^6$ atoms of phosphorus per cell, which is essentially the same value we observed for *P. ubique* under phosphorus-replete conditions (Supplementary Fig. 5). Thus heterotrophic bacteria in the Sargasso Sea appeared not to use substitute lipids, which suggests that this group of organisms has a lipid-based requirement for phosphorus that could put them at a disadvantage against phytoplankton when phosphorus is scarce (Fig. 2). Indeed, phosphorus availability has been shown to play a role in affecting the growth rates of heterotrophic bacteria in the Sargasso Sea[30] and in the aforementioned phosphorus-addition experiment in the eastern Mediterranean Sea[11].

Phospholipid substitutions appear to be an important biochemical mechanism for cyanobacteria and eukaryotic phytoplankton to maintain photosynthesis in environments where phosphorus is scarce. Our data from the Sargasso Sea demonstrate that betaine-lipid-rich eukaryotic phytoplankton use this strategy to great effect in response to phosphorus-depleted conditions, and we hypothesize that this could contribute to the recent observation that phytoplankton in this environment are biologically nitrogen-limited[12] despite the chemical oceanographic observations suggesting otherwise[7,21]. However, it is important to recognize that eukaryotic phosphatidylcholine and betaine lipids both contain one nitrogen atom per molecule, whereas

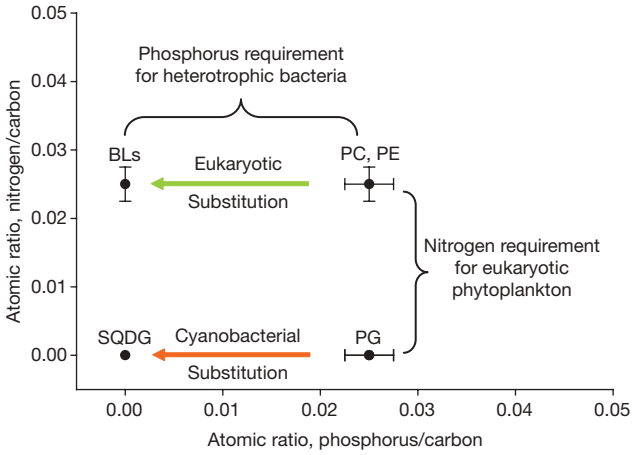

Figure 2 | Relative phosphorus and nitrogen contents of membrane lipids expressed as atomic ratios to carbon. Both cyanobacteria and eukaryotic phytoplankton have the ability to substitute non-phosphorus-containing lipids for phospholipids, whereas heterotrophic bacteria do not. Thus, heterotrophic bacteria are burdened with a phosphorus requirement for membrane lipid synthesis. In addition, betaine lipids and phosphatidylcholine contain nitrogen whereas SQDG and phosphatidylglycerol do not. Thus we posit that eukaryotic phytoplankton are burdened with an obligate lipid-based nitrogen requirement for membrane lipid synthesis; our data with nitrogen-limited *E. huxleyi* indicate that these nitrogen-containing lipids are not substituted with any other lipid (B.A.S.V.M. and S.T.D., unpublished observations). There is no evidence for the ability of heterotrophic bacteria to substitute phosphatidylglycerol for phosphatidylethanolamine in the data from the regrowth incubations (Supplementary Fig. 3). Error bars indicate the approximate range of carbon atoms in the indicated classes of lipid molecules. BLs, betaine lipids; PC, phosphatidylcholine; PE, phosphatidylethanolamine; SQDG, sulphoquinovosyldiacylglycerol; PG, phosphatidylglycerol.

cyanobacterial SQDG and phosphatidylglycerol do not. Thus eukaryotic phytoplankton, in contrast to cyanobacteria, appear to be burdened with a nitrogen requirement associated with membrane lipid synthesis (Fig. 2). We hypothesize that this difference could be a contributing factor to the dominance of cyanobacteria in all three of the oligotrophic regions of the ocean we studied, where, in addition to phosphorus, nitrogen is also scarce.

METHODS SUMMARY

Environmental samples were collected from the surface mixed layer (depth less than 60 m) using Niskin bottles. South Pacific stations were occupied during the BIOSOPE campaign approximately along 30° S between 110° and 90° W in November 2004; exact dates and locations have been described[6]. The Sargasso Sea cruise was conducted in April 2007 at approximately 31° N 63° W. The North Pacific data are from HOT cruises to 22° 45′ N 158° W (ref. 2). To determine the percentage phosphate incorporation into phospholipids, seawater samples were incubated with [^{33}P]phosphate, and lipids were extracted as previously described[2,6]. Membrane lipid molecules were extracted and analysed by high-performance liquid chromatography–mass spectrometry (HPLC–MS) as previously described[2]. Authentic standards for quantification of SQDG and betaine lipids (Supplementary Fig. 1) were isolated from phosphorus-limited cultures of *Synechococcus* sp. strain WH8102 and *C. affinis*, respectively, using preparative HPLC[2]. Phytoplankton were grown in batch cultures using standard methods and media (Supplementary Table 2); cells were harvested as soon as cultures in phosphorus-depleted media showed an attenuation in the increase in cell numbers or chlorophyll fluorescence compared with cultures in phosphorus-replete media. Cultures of *P. ubique* were grown in supplemented seawater as described[25]. Heterotrophic bacteria regrowth incubations were conducted as described[29] where seawater was filtered through acid-cleaned 0.2 μm pore-size membranes, re-inoculated with a 10% volume of whole seawater, and incubated in the dark at *in situ* temperatures. Total cellular phosphorus of *T. pseudonana* was determined after combusting cells in the presence of magnesium sulphate; the resultant phosphate was dissolved in dilute hydrochloric acid and quantified using a standard molybdate method. Total cellular phosphorus and lipid phosphorus of *E. huxleyi* and *C. affinis* were estimated based on data from ref. 1 and references therein. Mann–Whitney *U*-tests were applied to identify significant differences ($P < 0.05$) between samples because sample sizes were too small to assume normal distributions.

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Supplementary Information is linked to the online version of the paper at www.nature.com/nature.

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Author Contributions B.A.S.V.M. designed the study, conducted experiments and collected samples at sea, and wrote the manuscript. All of the other authors made essential, substantive contributions to the original and/or revised manuscripts. In addition, H.F.F. analysed lipids by mass spectrometry. B.E.P. assisted with lipid analyses and prepared samples in the laboratory and at sea. S.T.D., M.K., L.R.M., M.S.R. and E.A.W. each contributed to the design of the study and conducted experiments with cultures under phosphorus-limiting and -replete conditions. D.M.K., M.W.L. and T.M. provided data from the cruises and facilitated the work at sea.

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