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A simple nutrient-dependence mechanism for predicting the stoichiometry of marine ecosystems

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It is widely recognized that the stoichiometry of nutrient elements in phytoplankton varies within the ocean. However, there are many conflicting mechanistic explanations for this variability, and it is often ignored in global biogeochemical models and carbon cycle simulations. Here we show that globally distributed particulate P:C varies as a linear function of ambient phosphate concentrations, whereas the N:C varies with ambient nitrate concentrations, but only when nitrate is most scarce. This observation is consistent with the adjustment of the phytoplankton community to local nutrient availability, with greater flexibility of phytoplankton P:C because P is a less abundant cellular component than N. This simple relationship is shown to predict the large-scale, long-term average composition of surface particles throughout large parts of the ocean remarkably well. The relationship implies that most of the observed variation in N:P actually arises from a greater plasticity in the cellular P:C content, relative to N:C, such that as overall macronutrient concentrations decrease, N:P rises. Although other mechanisms are certainly also relevant, this simple relationship can be applied as a first-order basis for predicting organic matter stoichiometry in large-scale biogeochemical models, as illustrated using a simple box model. The results show that including variable P:C makes atmospheric CO2 more sensitive to changes in low latitude export and ocean circulation than a fixed-stoichiometry model. In addition, variable P:C weakens the relationship between preformed phosphate and atmospheric CO2 while implying a more important role for the nitrogen cycle.

Author contributions: E.D.G. designed and performed the data analysis and model simulations; and E.D.G. and A.C.M. wrote the paper.

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Significance

The elemental ratios of nitrogen, phosphorus, and carbon in marine phytoplankton can diverge significantly from the “Redfield ratio,” but the underlying reasons have been hard to elucidate. As a result, global biogeochemical models often ignore this stoichiometric variability. Here we show that, hidden within the noise of a large dataset of particulate measurements, a surprisingly consistent relationship exists between community P:C and dissolved phosphate concentrations. The plasticity of ecosystem stoichiometry in the face of nutrient scarcity, with greater plasticity for P relative to N, appears to explain the main divergences from the Redfield ratio. When included in a simple model, the relationship implies a more important role for low latitude nutrient cycling in the biological pump than is commonly assumed.
cellular P:C ratio is more variable, due to the ability of organisms to substitute phosphorus compounds such as phospholipids (16), and ranges from ~1/50 to 1/500, or by about a factor of 10. Iron is even more variable, given the ability to substitute with other elements, such that Fe:C varies from about 1/1,000 to 1/1,000,000, or three orders of magnitude (17).

If we examine oceanographic data in terms of N:C and P:C, rather than the more commonly cited N:P ratio, some rather simple patterns emerge. Fig. 1 shows these ratios measured in hundreds of globally distributed organic particulate samples (locations shown in Fig. S1), binned by nutrient concentrations, and with the elemental ratios shown in permil units (‰) for ease of notation. As indicated by the large error bars, there is a broad range in the measured stoichiometry of particles found in waters of any given ambient nitrate or phosphate concentration, which partly reflects measurement error and the variable presence of nonliving detritus. Because these samples do not discriminate among particle types, they also include a significant fraction of heterotrophic plankton in addition to phytoplankton. However, the striking finding from this large dataset is that, despite wide variability among individual samples, the means of the bins display well-behaved trends with increasing ambient nutrient concentrations.

The robust linear correlation of P:C vs. PO₄ suggests that phosphorus frugality is an important consideration for phytoplankton everywhere in the ocean. Because this is an average expectation for the entire community, and because the samples probably include a significant fraction of heterotrophic biomass with less plastic stoichiometry (23), the underlying dependence of phytoplankton P:C on PO₄ may be stronger than implied by the empirical regression. This whole-community linear expectation could be locally modified by other factors such as water temperature and light intensity. Indeed, a regression of the P:C data vs. in situ temperature also shows a highly significant, although weaker, relationship (r² = 0.24), with a negative slope; part of this reflects the fact that cold waters typically have higher PO₄, but it has also been shown that more ribosomes are required to meet the same growth rate at low temperatures, exerting an additional effect on the P:C (11). Such modification could lead to small-scale spatiotemporal variability, or even cause large regions to diverge from the global “Line of Frugality.” However, the fact that the Line of Frugality explains 36% of the observed variability, despite measurement error, spatial and temporal patchiness, and non-steady-state conditions, suggests that the PO₄ concentration is a very important, and perhaps the most important single factor in determining community P:C at the ocean surface. In contrast, the absence of any dependence of

Fig. 1. Observed elemental ratios of suspended particles at the ocean surface. Stations were binned according to the NO₃ concentration (Upper) and PO₄ concentration (Lower). Squares show the log-transformed mean of the elemental ratios of all measurements within each bin. Error bars show 1 SD of the elemental ratios of all measurements within each bin. The solid orange line in Upper shows a hyperbolic approximation to the variability in the mean, optimized from all data, whereas the dashed orange line shows an alternative linear fit using the means of the binned data. The orange-shaded regions in both panels show the combined 95% confidence interval spanning the binned and unbinned regressions.
N:C on NO₃ above a NO₃ concentration of ~3 μM indicates that other environmental and ecological factors determine N:C at all but the lowest NO₃ concentrations. The saturation of average N:C at nitrate concentrations of about 3 μM does not indicate that nitrate is not limiting in the ocean. On the contrary, it is the most important limiting element, at least in a proximal sense, as clearly shown by nutrient assays everywhere outside of High Nitrate Low Chlorophyll (HNLC) regions (15). The observations here simply imply that higher N:C does not, on average, confer a consistent competitive advantage above a ratio of ~155 ‰.

It follows that the common observation that N:P increases under oligotrophy would arise simply due to low N:C plasticity compared with P:C plasticity. The observed particulate data suggest that the average N:C of planktonic communities increases by less than 30% above its minimum value of ~125 ‰ in response to an increase of NO₃, whereas community average P:C can increase by a factor of at least 3 above its minimum of ~5 ‰ under increasing PO₄, exhibiting an order of magnitude more response to nutrient availability than the N:C. Thus, moving from eutrophic waters that are rich in both NO₃⁻ and PO₄³⁻ to oligotrophic waters that are poor in both NO₃⁻ and PO₄³⁻ involves a small decrease of N:C but a very large P:C decrease. As a result, nutrient-dependent stoichiometric plasticity would tend to drive high N:P in oligotrophic regions and low N:P in eutrophic regions. In agreement with the underlying dynamic of chemostat models (10, 19), this mechanism suggests that N:P in phytoplankton is determined by the absolute concentrations of NO₃⁻ and PO₄³⁻, rather than their ratio, and explains why the NO₃⁻:PO₄ ratio of ambient waters is a poor predictor of phytoplankton N:P (24).

**Global Picture**

The simple predictive model proposed here can be used to generate global predictions of organic matter stoichiometry from observed surface nitrate and phosphate concentrations. The results are shown in Fig. 2. The predicted P:C agrees broadly with recent estimates from two global inverse models (Fig. S3), with the only significant discrepancy being that the inverse models suggest higher P:C in the subpolar North Atlantic than predicted here. The calculated N:C and P:C in Fig. 2 follow similar spatial patterns, given the strong correlation of NO₃ and PO₄ at the ocean surface. However, as expected from the reasoning laid out above, the N:P varies roughly inversely with the macronutrient concentrations, because N:C varies less than P:C. It should be emphasized that this result arises entirely from the elevated plasticity of P:C relative to N:C, and is not dependent on assumptions regarding the allocation of nutrient elements to cellular machinery or taxonomic groups.

That is not to say that this simple mechanism is inconsistent with either of these other hypotheses. It is entirely possible that frugal phytoplankton do, in fact, produce more resource-gathering molecules relative to RNA (1). Similarly, the taxonomic composition of ecosystems in different parts of the ocean could reflect the fit between phytoplankton elemental compositions and the available nutrients (7). Diatoms with high P:C flourish in phosphate-rich regions (which also happen to be nitrate-rich), and therefore diatom-dominated communities have low N:P.

It is also important to emphasize that this prediction is suggested to hold only at large spatial and temporal scales, with important exceptions. Perhaps most importantly, *Phaeocystis*, a prymnesiophyte that tends to have relatively low P:C, frequently blooms in the PO₄-rich Southern Ocean (12). The suggestion here would be that the success of *Phaeocystis* reflects the relatively small advantage that less frugal phytoplankton gain by using more P such that, given other environmental factors (such as grazing pressures, temperature, light intensity, or iron availability), the more frugal *Phaeocystis* can be very successful without taking full advantage of the abundant PO₄. This wrinkle would appear to be given additional weight by the analysis of DeVries and Deutsch (25), which suggests that the domains of polar oceans with seasonal sea ice may be typified by low P:C despite high phosphate concentrations. If it turns out that seasonal sea ice zones are indeed typified by anomalously low P:C, this could be an important consideration for carbon cycling during ice ages as well as in the future (8). At the same time, the availability of silicate could potentially expand the range of P-rich diatoms in the Southern Ocean northward into lower-PO₄ waters, driving relatively high P:C export at relatively low phosphate concentrations as proposed by Weber and Deutsch (8). For the time being, we assume these other factors to be stationary with respect to the distribution of phosphate, and explore the impact of changes in P:C driven exclusively by phosphate cycling on ocean carbon storage.

**Implications for Carbon Export and Atmospheric CO₂**

The global oceanic phosphorus inventory is determined by the balance between the supply rate, ultimately derived from the weathering of minerals on land, and the removal by burial in seafloor sediments (26). If the P:C of organic matter were fixed, the maximum amount of C that could be stored in the ocean interior by the biological pump would simply be equal to the P inventory divided the P:C ratio. This concept led to some early
suggestions that glacial-interglacial changes in the global biological pump strength could have been caused by changes in either the global P inventory, or the P:C ratio (27). In addition, the use of preformed phosphate (i.e., phosphate that is transported physically to the ocean interior from phosphate-rich regions of the surface ocean, rather than being exported to the interior as an organic matter and subsequently remineralized) as a metric for the global strength of the biological pump is typically simplified to assume a constant P:C ratio, although the possibility that P:C varies is acknowledged (28-30). The theory associated with the concept of preformed phosphate suggests that the combined influences of ocean circulation and carbon export on atmospheric pCO₂ can be approximated quite well by the concentration of phosphate in the high-latitude regions that ventilate the deep ocean, most importantly the Southern Ocean.

The argument advanced here suggests that less-frugal phytoplankton in phosphate-rich regions actually use up P rapidly, without attaching much C to it. This profligate use of P makes for a relatively weak biological pump, for a given inventory of P. In contrast, more frugal phytoplankton attach a lot of C to every atom of P they export, storing a lot more respired carbon in the ocean interior per unit P exported. As such, in terms of carbon storage, not all use of a PO₄ molecule can be seen as equal.

We use a standard three-box ocean model coupled to a one-box atmosphere (Fig. S4), after Sarmiento and Toggweiler (31), to illustrate how P:C variability alters carbon export and atmospheric CO₂. Ref. S followed a similar approach to test the impact of a prescribed change in the P:C of export in the Southern Ocean. Although greatly simplified, the box model framework allows the rapid computation of a large number of experiments to plumb the main sensitivities of carbon storage to circulation and community export given different stoichiometries. The ocean boxes include a low-latitude surface box, high-latitude surface box, and a deep box, with realistic proportions (Methods). The box model predicts P:C as a function of PO₄, using the linear fit to the unbinned data shown by the solid line in Fig. 1. The model is then used to explore the impact of varying P:C, compared with fixed P:C, through a series of experiments. These experiments test the effect of variable high-latitude export Φₜ (which could vary due to iron supply to the Southern Ocean, or sea ice coverage), in combination with simultaneous changes in low-latitude phosphate concentration PO₄l (which might vary with changes in nitrogen fixation and denitrification rates), and the large-scale ocean circulation (varying the thermohaline overturning T and high-latitude vertical mixing fhd).

When the P:C is fixed, the prescribed changes modify atmospheric pCO₂ in a fairly strict relationship with preformed PO₄l as determined by the PO₄l concentration in the high-latitude box (Fig. 3) (31, 32). This strict relationship holds true over the range of changes in PO₄l, T, fhd, and Φₜ, and indicates that in a world with fixed stoichiometry, it is hard to change the strength of the biological pump without changing preformed PO₄. However, when P:C is plastic, the effects of PO₄l and T can diverge significantly from the strict preformed-PO₄l relationship, producing a range of pCO₂ for a given preformed PO₄l concentration. This divergence is particularly pronounced for PO₄l, which has a far greater impact on pCO₂ under variable P:C than under fixed P:C (Fig. 4).

The reason for these divergences is fairly straightforward: when P:C varies, export that occurs under low PO₄ concentrations stores more C for the same P inventory, thereby lowering pCO₂. Because the low-latitude export flux (Φₜ) has a lower P:C than Φₜ, increasing the fraction of total export that occurs at low latitudes leads to lower pCO₂. In the model, Φₜ is simply equal to T(PO₄d − PO₄l), where PO₄l is the phosphate concentration in the deep box, which is essentially fixed by the total PO₄ inventory. Therefore, increasing T drives a linear increase of Φₜ, causing pCO₂ to decrease. Similarly, decreasing PO₄l increases Φₜ, an effect that is compounded by decreasing the P:C of Φₜ as the ambient PO₄ concentration becomes more scarce. Altogether, this could produce more than a 20 ppm difference in atmospheric CO₂ for a change in PO₄l of only 0.1 μM (Fig. 4), such as might occur given a change in nitrogen limitation at low latitudes. Thus, the export of low P:C organic matter at low

![Fig. 3. Relationship between preformed PO₄ and pCO₂ in box model simulations. Top panels show results with fixed P:C, bottom panels show variable P:C following the Line of Frugality illustrated in Fig. 1. Each panel shows the pCO₂ predicted by 100 model simulations that simultaneously vary the high-latitude export flux (Φₜ, each value of which is shown by a single color) along a range of values for the other variable as indicated (shown as a continuous line for each value of high-latitude export), where PO₄l is low-latitude PO₄l. T is thermohaline overturning and fhd is high-latitude vertical mixing. For example, for the variable P:C model, varying PO₄l over the full range of values produces pCO₂ changes of more than 70 ppm, with little effect on the preformed PO₄l.](www.pnas.org/cgi/doi/10.1073/pnas.1423917112)
Fig. 4. Relationship between low-latitude PO₄ and pCO₂ in box model simulations. High-latitude export ϕₚ is held constant at an intermediate value for the simulations shown here. The variable P:C simulations (orange) show a much larger impact of low-latitude PO₄ on pCO₂ than the fixed P:C simulations (gray). The enhanced sensitivity of the variable P:C simulations arises from the greater carbon storage achieved by low-latitude export, per mol of P export, compared with high-latitude export. The range of possible CO₂, corresponding to the 95% confidence intervals of the Line of Frugality regression shown in Fig. 1, are indicated by the region of orange shading.

Conclusions

The stoichiometric ratios P:C and N:C are usually held constant in global biogeochemical models, despite evidence for significant variability from field and laboratory studies. Based on global suspended particulate measurements, it would appear that the community-averaged N:C varies linearly with the dissolved concentrations of NO₃ over low NO₃ concentrations, and that the community-averaged P:C varies linearly with PO₄ across the range of modern ocean PO₄ concentrations. We suggest that this is because the phytoplankton community tends to adjust to the available nutrient concentrations, either by intraspecific plasticity of elemental composition (e.g., ref. 37), or by shifting the species assemblage. All else being equal, the most frugal phytoplankton—those with the lowest requirements for a nutrient—dominate when the concentrations of that nutrient are lowest, and therefore most difficult to obtain. Because N is an integral component of many organic molecules, the N:C varies by less than 30% in response to changes in NO₃, whereas P:C varies by a factor of three in response to changes in PO₄. As a corollary, changes in the N:P ratio of phytoplankton communities are mostly due to changes in the concentration of PO₄ in the ambient waters, with little dependence on the ambient ratio of NO₃:PO₄.

A simple model based on these observations predicts the P:C export as a function of PO₄. When included in a classic box model, the flexible P:C model shows heightened sensitivity of atmospheric CO₂ to ocean circulation and the low-latitude PO₄ concentration. Significant variations in the P:C of nitrogenous material weaken the relationship between preformed PO₄ and CO₂ storage, suggesting that mechanisms of change in the biological pump could be better framed in terms of remineralized NO₃. The simple predictive model can be tested against future observations and laboratory study.

The large impacts of variable P:C on ocean carbon storage illustrated by the simple box model suggest that global biogeochemical models should place a high priority on resolving P:C plasticity, in order to improve the understanding of past and present variability, and to account for this important aspect of the marine ecosystem in future projections of N₂ fixation, denitrification, ocean carbon uptake and oxygen distributions.

Methods

Data Analysis. The particulate data of ref. 7 is reanalyzed here as follows. For each station (i.e., geographic location at which samples were collected), all available measurements of particulate organic carbon (POC), particulate organic nitrogen (PON), particulate phosphorus (POP), nitrate, and phosphate within the upper 30 m of the water column were averaged. Wherever particulate data existed without corresponding nutrient measurements, the climatological nutrient concentration for the same location was taken from the monthly WOA climatology (7). The P:C and N:C were calculated for all stations at which the mean POP and PON concentrations were greater than 0.005 μmol g⁻¹. This selection process resulted in 610 stations with P:C and 4,064 stations with N:C data (Fig. S1).

A linear regression of P:C vs. PO₄ was calculated using all 610 (unbinned) data points, giving an intercept of 6.0 ± 0.2 % and a slope of 6.9 ± 0.4 % μmol g⁻¹. As shown by the solid orange lines in Figs. 1 and Fig. S2, referred to as the Line of Frugality. The linear regression coefficient (r², Pearson) against all 610 data points is 0.36 (P < 10⁻⁴). In addition, the log-transformed means of the binned data were used to generate an alternative linear regression, giving that the log-transformed values within each bin showed a more normal distribution. The binned-logged normal mean regression gives a significantly lower intercept of 4.8 ± 0.5 % and a slightly higher slope of 7.3 ± 0.6%μmol g⁻¹, shown by the dashed orange lines in Figs. 1 and Fig. S2. The linear regression coefficient of the binned-logged normal mean regression line against the nine binned means is 0.95 (r², Pearson, P < 10⁻⁷). To illustrate the full uncertainty in the Line of Frugality, the combined range of the 95% confidence intervals for both regressions is shown by the shaded areas in Figs. 1 and 4.

A linear regression of N:C vs. NO₃ using all 4,064 stations shows a weak (0.8 ± 0.1 % μmol g⁻¹), but highly significant (P < 10⁻⁴) linear increase over the full range of NO₃ concentrations. However, if only the stations with >5 μmol NO₃ are analyzed, the linear regression has a near-zero slope that is only weakly significant (P < 0.1), whereas a regression over the lowermost 3 μmol NO₃ range shows a strong slope (11 % μmol g⁻¹) with very high significance (P < 10⁻⁸). This rapid increase of N:C over low NO₃ concentrations, followed by negligible change, is consistent with a saturating hyperbolic relationship. An optimized fit using a Holling type 2 functional form is given by N:C = 125 % + 30 % × NO₃/0.32 μmol + NO₃, shown in Figs. 1 and Fig. S2 along with a shaded interval that spans the 95% confidence interval of the nonlinear fit using both the full unbinned dataset as well as binned log-transformed means.

Model. The biogeochemical model used here includes three ocean boxes and one atmospheric box, following ref. 31. The low-latitude surface PO₄ concentration is restored to a defined value, generating an export flux ϕₚ that depends on the physical supply of PO₄ to the low latitudes by the thermohaline circulation T, whereas the high-latitude surface export flux ϕₚ is imposed as an input parameter, representing iron-light-temperature-limited growth. A prescribed vertical mixing flux exchanges water between the high-latitude surface and the deep box, f_m. Carbonate exported from the surface by calcifying organisms is set to 20% of the organic carbon export flux, within the observational range given by Berelson et al. (38). Within the surface boxes, the carbonate equilibria are solved as a function of Dissolved Inorganic Carbon (DIC) and alkalinity concentrations, to determine the
saturation state of CO$_2$. Air-sea exchange is a linear function of CO$_2$ saturation state and a constant air sea exchange coefficient (the "piston velocity"), as described in ref. 39.

For the purposes at hand, we assume that the P:C of sinking particulate export follows the same relationship with surface phosphate as the measured surface particles. The real world is undoubtedly more complex, given preferential export by specific taxa (such as diatom aggregates) at particular times of year, and the consumption of phytoplankton by heterotrophs, producing rapidly sinking fecal pellets with P:C that differs from that of the food source (40). Additionally, it has been observed that P disappears more rapidly than C from sinking particles within the upper water column, implying preferential remineralization of P that would add a vertical dimension to differential P:C cycling (41–43). Nonetheless, two recent global inverse models incorporating ocean circulation and chemical data (25, 44) found a close match across ocean basins between the stoichiometry of net organic matter export and the suspended particulate data used here, as well as with the Line of Frugality prediction (Fig. S3). The good agreement between these alternative methods suggests that the Line of Frugality predicts captures the first order variability in P:C of exported organic matter.

The low-latitude PO$_4$ concentration PO$_4$ is restored to a prescribed value that is varied between 0–0.6 μM. The export flux of carbon from the high-latitude box $\Phi_h$ is prescribed to vary from 0.25 to 4 Pg C yr$^{-1}$, as might occur under large changes of iron fertilization. The thermohaline overturning $T$ is varied over a range of 10–45 Sv. The high-latitude vertical mixing $\Phi_m$ is varied over a range of 30–130 Sv. Varying each of PO$_4$, T, and $\Phi_m$ over 10 values with simultaneous variations in $\Phi_h$ over 10 values results in a total of 300 simulations, each of which was repeated with both fixed and flexible P:C, run to equilibrium (20,000 y).

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Supporting Information

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Fig. S1. Map showing locations of particulate data used in the analysis. Black symbols indicate stations with N:C data, whereas blue symbols indicate stations with P:C data.

Fig. S2. All particulate data vs. nutrient concentrations. Analogous to Fig. 1, but showing all data as individual points, without binning. The orange lines show the regression and 95% confidence intervals for the regression using all stations, whereas the blue lines show the regression and 95% confidence intervals for the binned, log-transformed data. The overall 95% confidence interval for the P:C Line of Frugality, shown in the lower panel of Fig. 1 and used in the calculations of Fig. 4 and Fig. S3, spans from the upper orange line to the lower blue line.
Fig. S3. Line of Frugality P:C prediction vs. P:C estimates from two global inverse models. All P:C values are calculated in the 11 regions defined by Teng et al. (1). Symbols show the P:C of organic matter export estimated by the global inverse models of Teng et al. (blue) and DeVries et al. (red; ref. 2) vs. the P:C predicted from the in situ PO₄ concentrations (black). The error bars for the inverse model estimates are as reported by the original authors, whereas the error bars for the frugal prediction reflect the 95% confidence intervals of both regressions. Note that the DeVries estimate was made for O₂:P, and has been multiplied here by the stoichiometric ratio 106/150 to give units of C:P, introducing an additional error. The only ocean region that suggests a consistent, significant difference between the Line of Frugality prediction and the inverse models is the subarctic North Atlantic.


Fig. S4. Schematic diagram of the box model. The ocean consists of high-latitude surface (h), low-latitude surface (l), and deep (d) boxes. Tracers (PO₄, DIC, and ALK) are transported by the thermohaline overturning (T) and by vertical mixing between d and h (f.hd). Sinking particulate fluxes of organic matter and calcium carbonate transfer P, C, and alkalinity from the low-latitude (Φ_l) and high-latitude (Φ_h) surface boxes to the deep. Air-sea exchange transfers CO₂ between the surface boxes and the atmospheric reservoir (a).

<table>
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<th>Vol (m³)</th>
<th>PO₄ mmol m⁻³</th>
<th>NO₃ mmol m⁻³</th>
<th>DIC mmol m⁻³</th>
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<tr>
<td>h</td>
<td>9.3 x 10¹⁶</td>
<td>1.5</td>
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<td>3.02 x 10¹⁶</td>
<td>2.26</td>
<td>32.3</td>
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The high-latitude box is 250 m deep, whereas the low-latitude box is 100 m deep.