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Bouncing photons, underwater robots, and the ocean's green film

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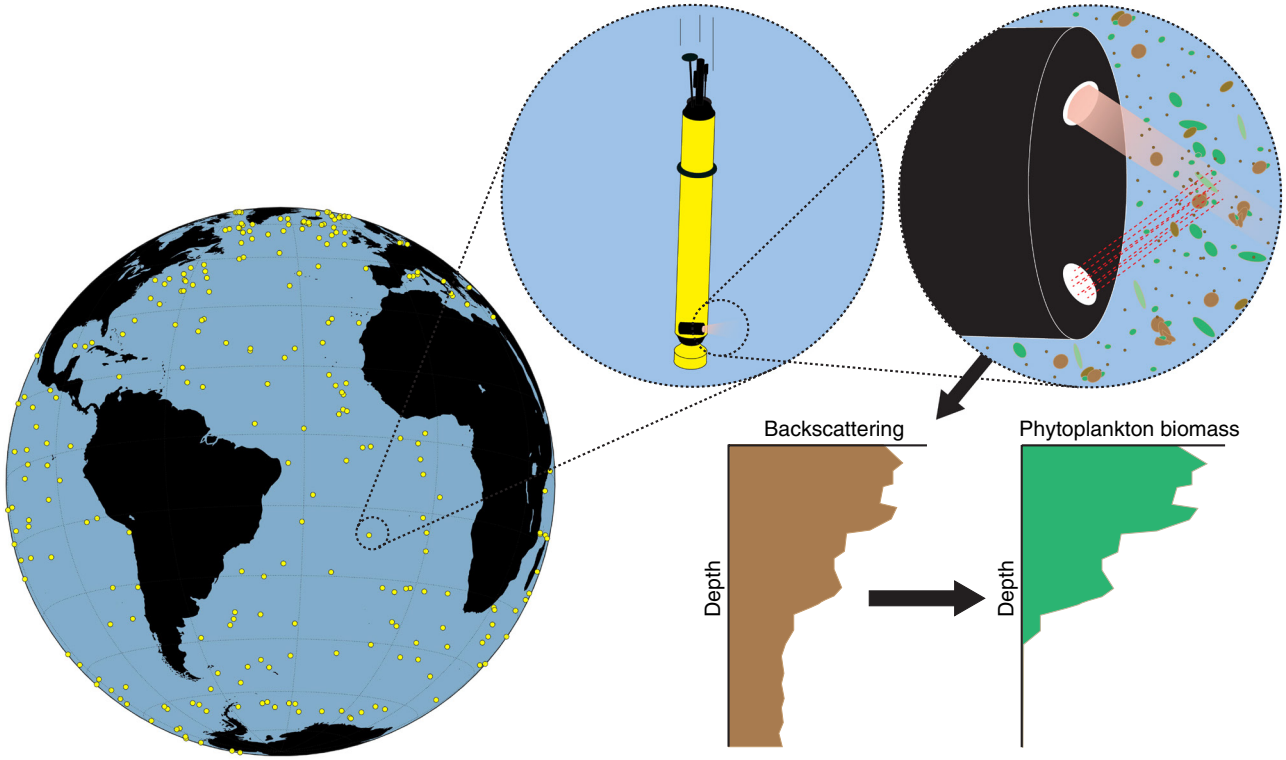

Fig. 1. The map on the *Left* depicts the position of the profiling floats that measured backscattering during the last year from the time of writing. The *Top Right* circles show a profiling float (*Left*) and a backscattering sensor (*Right*). *Bottom Right* panels depict idealized vertical profiles of the backscattering measurements (*Left*) and phytoplankton biomass calculated from these measurements (*Right*).

Modern models of the Earth system include the interaction among physical, chemical, and biological components to predict the consequences of our changing climate. These numerical simulations rely on global observations to constrain the magnitude of key ecosystem processes and of the populations responsible for them (1). One of the most important processes is the flux of carbon between the mineral and the biological realms that is mediated by photosynthesis. In order to improve our understanding of photosynthesis, we need to quantify the biomass (living mass in terms of carbon content) of photosynthetic organisms including plants, macroscopic algae, and phytoplankton. In the ocean, this task is particularly challenging because the majority of photosynthesis is carried out by microscopic phytoplankton cells that are present in suspension with particles of similar dimension including other organisms, detritus, and mineral particles. In the early days of modern biogeochemistry, a century ago, E. Vernadsky pointed out that even though the ocean is thousands of meters deep, a large part of the biochemical activity takes place in the top few tens of meters, where a thin green film contains almost the entirety of phytoplankton biomass (2). He emphasized that this layer was responsible for most photosynthesis on Earth [more recent estimates put it at ~46% (3)] and he believed that it contained the large majority of the biomass of photosynthetic organisms on the planet. Even though we now know that the biomass of land plants is more than two orders of magnitude larger than phytoplankton biomass (4), Vernadsky was ahead of his time in highlighting the importance of the living matter suspended near the ocean surface, whose quantification still presents difficulties nowadays. In the current issue of PNAS, Stoer and

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Fennel (5) addressed this long-standing challenge and obtained a new estimate of global phytoplankton biomass by leveraging underwater observations collected by a large fleet of autonomous profiling floats in the last couple of decades. Stoer and Fennel (5) took advantage of recent improvements in our understanding of the optical properties of seawater to estimate the biomass of natural phytoplankton communities from relatively simple measurements.

When we consider a single phytoplankton cell, its biomass can be estimated using available relationships linking carbon content to cell volume. This approach is commonly applied to large phytoplankton cells, but many regions of the ocean are dominated by phytoplankton whose diameter is on the order of only ~1 μm and it cannot be measured using traditional microscopy. For this reason, the most accurate estimation of phytoplankton biomass in natural environments is obtained when the phytoplankton community in seawater is separated from other kinds of suspended particles (in virtue of its fluorescence properties) and its carbon content is measured after combustion (6, 7). Unfortunately, this method is labor intensive and it has only been utilized in a few regions of the ocean so that other approaches need to be explored to obtain global biomass estimates.

Stoer and Fennel took advantage of recent improvements in our understanding of the optical properties of seawater to estimate the biomass of natural phytoplankton communities from relatively simple measurements.

An estimate of the global phytoplankton biomass can be obtained from measurements of cell abundance separated by taxon, which are converted into carbon by applying constant carbon cellular content for each different population. The major limitation of this approach lies in the documented variability in the cellular carbon content within a phytoplankton population. For example, the average cellular biomass of the most abundant photosynthetic organism on Earth, the cyanobacterium *Prochlorococcus*, varies by a factor of 6 with depth and season at the same open ocean location in the North Atlantic (6). Besides the large uncertainty linked with the use of a constant cellular carbon content, current observations of phytoplankton abundance are more common in coastal and productive environments and this likely leads to an overestimation of phytoplankton biomass with this method (8).

Historically, the most used proxy for phytoplankton biomass has been the concentration of chlorophyll *a*, which is the main photosynthetic pigment and it has the advantage of being uniquely contained in photosynthetic organisms. Furthermore, chlorophyll *a* concentration is relatively easy to estimate from oceanographic ships, autonomous underwater platforms, and even satellites. Satellite chlorophyll *a* observations have very good spatial coverage and they have been used to obtain estimates of global phytoplankton carbon after using an empirical formula to calculate how much chlorophyll *a* is contained in the subsurface layer not visible from satellite, and after assuming a ratio between chlorophyll *a* and carbon in phytoplankton biomass (9). The main uncertainty in this calculation derives from the latter assumption because the chlorophyll *a* to carbon ratio is very variable both physiologically and phylogenetically, with a reported range spanning more than one order of magnitude (10).

Besides chlorophyll *a* concentration, satellite measurements of the reflection of sunlight on the ocean surface can be used to retrieve other useful information on the plankton ecosystem. One important parameter that is routinely calculated is the amount of light that is scattered (bounces) backward after interacting with the particles suspended in seawater, or backscattering, which has been proposed to provide an alternative proxy for the estimation of phytoplankton biomass (11). However, as for chlorophyll *a*, satellites only detect backscattering from the ocean surface and further assumptions need to be adopted to estimate backscattering in the subsurface ocean. In their novel assessment, Stoer and Fennel (5) circumvented the limitations of satellite observations by using backscattering measurements collected at different depths by autonomous floats. The authors then converted backscattering into phytoplankton biomass using an empirical procedure that addresses a bio-optical problem first noticed 90 y ago (Fig. 1).

The first backscattering measurements date back to 1934, when Hans Pettersson deployed a submersible instrument that used a car headlight lamp to shine light in the seawater and an actinometer that measured the amount of light that was scattered in the opposite direction of the light beam (12). Pettersson noticed that maxima in the amount of scattered light were associated with clouds of particles, but he remarked that these measurements alone could not be used to ascertain what kind of particles were responsible for the scattering. This was the main problem faced by Stoer and Fennel (5): scattering measurements alone cannot be used to disentangle the signal caused by phytoplankton from the signal caused by nonliving particles and heterotrophic organisms. Furthermore, when phytoplankton scattering is measured in isolation from monospecific laboratory cultures, there is severalfold variability in the biomass-normalized scattering, highlighting the presence in nature of populations with varying degrees of scattering efficiency (13). But there is reason for optimism.

Experiments from different environments helped determine that the size of phytoplankton cells is in the range of the particles that contribute most of the backscattering signal (14). Furthermore, the variability observed in backscattering is consistent with physiological changes causing adjustments in phytoplankton biomass (14). A more recent survey of the surface waters of different ocean basins also found good empirical correspondence between scattering and the biomass of natural phytoplankton communities, which led the authors to propose a linear regression model to convert one into the other (7). Stoer and Fennel (5) leveraged this improved understanding of the backscattering properties of seawater to convert their autonomous measurements into phytoplankton biomass. This procedure consists in two steps: First, the authors subtracted a constant background scattering assumed to be caused by nonalgal particles; and then they obtained phytoplankton biomass by multiplying backscattering by an empirical conversion factor (7). Considering that this conversion factor derives from surface measurements, this procedure could lead to a bias in the determination of the subsurface biomass. However, Stoer and Fennel (5) verified that this was

not the case by showing that the vertical biomass distributions are consistent with abundance-based estimates, which increases the confidence in their results.

As emphasized earlier, one of the strengths of the approach adopted by Stoer and Fennel (5) is the use of observations from different vertical layers in the ocean interior. These vertically resolved data not only improve the accuracy of the global estimates of plankton biomass, but they also allow to understand what portion of phytoplankton is contained in waters that cannot be monitored from satellite. The subsurface ocean often contains a maximum in chlorophyll *a* concentration associated with a shade-adapted community that interacts with the nutrient reservoir of the deep ocean (15). The dynamics of this subsurface ecosystem can be decoupled from those observed at the sea surface and the results by Stoer and Fennel (5) indicate that only about half of the total phytoplankton biomass is represented in the observations obtained from satellites.

While the uncertainty associated with the conversion of backscattering into phytoplankton biomass is still large, it must be reiterated that the alternative approaches available to calculate the global phytoplankton stock rely on proxies (chlorophyll *a* or cell abundance) that are affected by similar, if not larger, uncertainties. To increase the accuracy of these estimates, we need more direct measurements of phytoplankton biomass from different environments both near the surface and in deeper ocean layers. These measurements should be used to formulate more accurate procedures to convert our different proxies into phytoplankton biomass. Despite the current limitations, our improved understanding of the optical properties of seawater and the increased number of vertically resolved observations are advancing our quantitative understanding of the ocean as demonstrated by the analysis by Stoer and Fennel (5). Their new global estimate indicates that the ocean contains less phytoplankton than we previously expected. This finding reinforces the idea that a very small amount of living matter is responsible for the intense biochemical activity of the green film that covers our oceans.

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