PRIMARY PRODUCTION DISTRIBUTION

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doi:10.1006/rwos.2001.0204

Introduction

The study of the distribution of primary production in the world oceans preoccupied biological oceanographers for most of the twentieth century. Understanding the distribution remains a problem for which there is no facile answer; it is a many-faceted problem to which the approaches differ depending on the temporal and spatial scales at which understanding is sought. The issues relate to limitations of measurement techniques, interpretation of measurements that are available, and paucity of data.

In this context, the first point to bear in mind is that every method for the measurement of primary production has an intrinsic timescale associated with it (**Table 1**). Space and timescales are inextricably linked in oceanography, such that small timescales are always associated with small length scales, and large timescales with large length scales. Therefore, in studying the distribution of primary production in the ocean, one has to be careful that measurements are made at time and space scales appropriate for the problem at hand. Another important point is that all the available techniques do not measure the same quantity; the measured quantity may be gross primary production, net primary production, or net community production (if carbon-based methods are used), or total production, new production, or regenerated production (if nitrogen-based methods are used) (**Table 1**). A careful analysis quickly reveals that no methods are currently available for estimating the same component of primary production at all scales of interest in oceanography. It follows that, in comparing results (or in combining methods), one has to make sure that like things are being compared (or combined). Failure to do this can lead to perplexing results.

Precise measurements of primary production are time consuming, and paucity of data has been

Table 1 Various methods that can be used to estimate primary production in the ocean. The nominal timescales applicable to the results are also given. The components of primary production P_g (gross primary production), P_n (net primary production), and P_c (net community production) are based on rates of carbon uptake; P_T (total primary production), P_r (regenerated production) and P_{new} (new production) refer to nitrogen uptake rates. Sedimentation rate refers to the flux of organic particles from the photic zone

Method	*Nominal component of production*	*Nominal timescale*
In vitro		
^{14}C assimilation	P_T ($\equiv P_n$)	Hours to 1 day (duration of incubation)
O_2 evolution	P_T	Hours to 1 day (duration of incubation)
$^{15}NO_3$ assimilation	P_{new}	Hours to 1 day (duration of incubation)
$^{15}NH_4$ assimilation	P_r	Hours to 1 day (duration of incubation)
$^{18}O_2$ evolution	P_{new} ($\equiv P_c$)	Hours to 1 day (duration of incubation)
Bulk property		
NO_3 flux to photic zone	P_{new}	Hours to days
O_2 utilization rate (OUR) below photic zone	P_{new}	Seasonal to annual
Net O_2 accumulation in photic zone	P_{new}	Seasonal to annual
$^{238}U/^{234}Th$	P_{new}	1–300 days
$^3H/^3He$	P_{new}	Seasonal and longer
Optical		
Double-flash fluorescence	P_T	< 1 s
Passive fluorescence	P_T	< 1 s
Remote sensing	P_T, P_{new}	Days to weighted annual
Upper and lower limits		
Sedimentation rate below photic zone	P_{new} ($\equiv P_c$): (lower limit)	Days to months (duration of trap deployment)
Optimal energy conversion of photons absorbed	P_T (upper limit)	Instantaneous to annual
Depletion of winter accumulation of NO_3	P_{new} (lower limit)	Seasonal

a constant difficulty. This necessitates the use of extrapolation schemes to produce large-scale distributions from a small number of observations. When undertaking such extrapolations, it would be desirable to test the extrapolation schemes by comparing the estimated distributions at large scales against some other independent estimates. However, the lack of techniques for measuring the same component of primary production at different time scales confounds efforts to make independent validations of extrapolation protocols.

A profitable approach to dealing with these matters may be to begin by examining the factors that influence primary production. One may anticipate that the distribution of primary production would be influenced by the variability in the forcing fields.

Factors that Influence Variations in Primary Production

Primary production is the rate of carbon fixation by photosynthesis. The primary forcing variable is therefore light. The light field varies with depth in the ocean, with time of day, and with time of year. Correspondingly, primary production in the ocean exhibits a strong depth dependence and a strong time dependence. The temporal variations occur on several scales, ranging from seconds (response to clouds and vertical mixing) to diurnal, seasonal, and annual. Adaptations of phytoplankton populations to various light regimes also influence primary production. The adaptations may involve, for example, change in the concentration of chlorophyll-*a* per cell, change in the number of chlorophyll-*a* molecules per photosynthetic unit, or changes in the concentrations of auxiliary pigments, which may play either a photoprotective or a photosynthetic role. Understanding photo-adaptation requires that we know the light history of the cells, in addition to the current light levels.

Light acts on the state variable, the biomass of phytoplankton. It has been a common practice, in this field, to treat the concentration of the main phytoplankton pigment, chlorophyll-*a*, as an index of phytoplankton biomass, because it (or a variant called divinyl chlorophyll-*a*) is present in all types of phytoplankton, because of the fundamental role it plays in the photosynthetic process, and because it is easy to measure. The tendency would be for primary production to increase with chlorophyll-*a* concentration, though the rate of increase would vary depending on other factors.

A third factor that determines the primary production in the ocean is the availability of essential nutrients such as nitrogen. In a stratified, oceanic water column, the upper illuminated layer is typically low in nutrients, with the deeper layers acting as a reservoir of nutrients. Mixing events bring these nutrients to the surface layer, enhancing primary production. In temperate and high latitudes, deep mixing events in winter, and subsequent stratification as the surface warming trend begins, lead to the well-known phenomenon of the spring bloom and more generally to a pronounced seasonal cycle in primary production. On the seasonal cycle are superimposed the effects of sporadic mixing events in response to passing storms. The short-term increases in primary production associated with these sporadic events are often missed by sampling schemes designed to record the seasonal cycle.

Temperature is another factor that influences primary production. It is believed that temperature controls the enzyme-mediated dark-reaction rates of photosynthesis. Thus, from laboratory experiments, it has been shown that photosynthetic rates in phytoplankton increase with temperature up to an optimal temperature, after which they decrease. However, the details of this response may differ with species. In nature, the tendency of primary production rates to increase with temperature is confounded by another effect: upwelling waters with high nutrients tend to have a low temperature, and the increase in primary production in response to the nutrient supply may in fact supersede the counteracting effect of temperature.

The recent years have seen an increasing appreciation of the role of micronutrients such as iron as limiting resources for primary production. The idea that iron limits production in certain marine environments was aired in the early twentieth century. However, it was in the 1980s that this idea gained renewed momentum, with the pioneering work by John Martin. It is now believed that iron limits primary production in large tracts of the ocean (the Southern Ocean, the Equatorial Pacific, the subarctic Pacific), leading to regimes known as the high-nutrient, low-chlorophyll regimes; these are environments where the nitrogen in the upper mixed layer is apparently never used up, and the phytoplankton biomass remains low throughout the year. Other contributing factors for the presence of high-nutrient, low-chlorophyll regimes include top-down control of phytoplankton biomass (and hence productivity) by zooplankton grazing, and the supply of nutrients by physical processes that exceeds the demands of biological production. It has been postulated that the variations in the distribution of primary production in response to changes in the availability of iron over geological timescales, and the consequent changes in the draw-down of carbon dioxide from the atmosphere into the ocean, may be implicated in climate change.

Species composition and species succession also influence rates of primary production. For example, the size distribution of the cells and the pigment composition of the cells can both change with species composition, thus influencing nutrient uptake and light absorption for photosynthesis.

In view of the large number of factors that influence the distribution of primary production at so many temporal and spatial scales, it is desirable to apply mathematical modeling techniques to organize and formalize the study of the distribution of primary production in the world oceans. Light-dependent models of primary production are particularly useful, not only because the models are based on the first principles of plant physiology, but also because of their direct applicability to remote sensing of primary production. According to such models, primary production P at a given location (x, y, z) and a given time (t) can be formalized as:

$$P(x,y,z,t) = B(x,y,z,t)f(I(x,y,z,t)) \qquad [1]$$

where B is the phytoplankton biomass indexed as chlorophyll-*a* concentration, and the function f describes the biomass-specific, photosynthetic response of phytoplankton to available light I. The response function f is known to have three phases: a light-limited phase at low-light levels when production increases linearly as a function of available light; a saturation phase at high-light levels, when production becomes independent of light; and a photoinhibition phase at extremely high light levels, when production is actually reduced by increasing light. At the most, three parameters (or only two, if the photoinhibitory phase is negligible, which is often the case) are required to describe such a response. Often, these are taken to be the initial slope α^B (typical units: mg C $(\mathrm{mg\,chl}a)^{-1}\,\mathrm{h}^{-1}$ $(\mathrm{W\,m^{-2}})^{-1}$); the saturation parameter P_m^B (typical units: mg C $(\mathrm{mg\,chl}a)^{-1}\,\mathrm{h}^{-1}$); and the photoinhibition parameter β^B (typical units: mg C $(\mathrm{mg\,chl}a)^{-1}\,\mathrm{h}^{-1}$ $(\mathrm{W\,m^{-2}})^{-1}$).

In such models, light and biomass are taken, justifiably, to be the principal agents responsible for variations in primary production. The effects of other factors (temperature, nutrients, micronutrients, species, light history and photoadaptation) may be accounted for indirectly, through their influence on the parameters of the response function (the photosynthesis–irradiance curve). The success of such models depends on how well we are able to describe, mathematically, the fields of biomass and light, as well as the parameters of the photosynthesis–irradiance curve. Such models could be taken to a higher level of sophistication if the photosynthesis parameters were in turn expressed as functions of the various factors that influence them. General relationships valid in the natural environment, that would account for the influences of all known factors on photosynthesis–irradiance parameters, have eluded scientists so far. Therefore, assignment of parameters has to rely heavily on direct observations.

With this background, we can look at what we know of the distribution of primary production in the world ocean.

Vertical Distribution

It is only the upper, illuminated part of the water column that contributes to primary production. A useful rule of thumb is that practically all the primary production in the water column occurs within the euphotic zone, commonly defined as the zone that extends from the surface to the photic depth at which light is reduced to 1% of its surface value (though there are some arguments for using 0.1% light level as a more rigorous boundary on the euphotic zone). However, it is important to realize that photosynthesis is a quantum process, which depends on the absolute magnitude of light available, rather than on relative quantities as indicated by the photic depth. Thus, regardless of the definition of photic depth that may be used, it will only tell us that the production below that particular depth horizon will be small compared with that above; it tells us nothing about the absolute magnitude of production in the water column. The 1% light level may occur at depths exceeding 100 m in oligotrophic open-ocean waters, whereas it may be less than 10 m in eutrophic or turbid waters. It is noteworthy that phytoplankton themselves are a major factor responsible for modifying the optical properties of sea water, and hence the rate of penetration of solar radiation into the ocean.

Another useful depth horizon that is relevant in the study of primary production is the critical depth. If production and loss terms of phytoplankton (grazing, sinking, decay) from the surface to some finite depth are integrated, then the integrated production and loss terms become equal to each other at some depth of integration, which is known as the critical depth. The concept of critical depth was formalized by Sverdrup in 1956. If the mixed-layer depth is shallower than the critical depth, then production in the layer will exceed losses, which is favorable for the accumulation of biomass in the layer, which would, in turn, further enhance mixed-layer production. If the mixed layer is deeper than the critical depth, the conditions would be unfavorable for the formation of blooms. Thus, the vertical distribution of production relative to the mixed-layer depth plays an important role in determining the potential for enhanced production.

The concept of critical depth is built on the fact that, within the mixed layer, production is typically a decreasing function of depth (because the available light decreases exponentially with depth), whereas the biomass and the loss terms are uniformly distributed within the mixed layer. However, it would be erroneous to suppose that the maximum primary production always occurs at the surface of the ocean. In fact, the maximum primary production may well occur at some subsurface depth, where the nutrient availability and light levels are optimal. In a stratified water column, several factors (species composition, photoadaptation, nutrient supply, and light levels) conspire to produce a deep-chlorophyll maximum. Depending on the physiological status of the phytoplankton in the deep-chlorophyll maximum, there may be a subsurface maximum in primary production, which may occur at the same depth as the chlorophyll maximum, or at a shallower depth. If the light levels at the surface are sufficiently high to induce photoinhibition, then also the maximum in production would occur at some subsurface level.

Horizontal Distribution

Primary production varies markedly with region and with season. Upwelling regions (e.g., waters off north-west Africa, the north-west Arabian Sea off Somalia, the equatorial divergence zone, the north-east Pacific off California and Oregon, the south-east Pacific off Peru, and south-west Africa) are typically more productive than the central gyres of the major ocean basins, because of the high levels of nutrients that are brought to the surface by upwelling. In general, coastal regions are more productive than open-ocean waters, also due to the availability of nutrients. Temperate and high latitudes show a pronounced seasonal maximum in spring (a consequence of the high supply of nutrients to the mixed layer during deep mixing events in winter, followed by a shallowing of the mixed layer and an increase in incoming solar radiation as the seasons progress). In summer, the depletion of nutrients in the mixed layer leads to reduced production and biomass, and to the migration of the chlorophyll maximum to below the mixed layer. This is often followed in fall by a secondary peak in production, as a result of increased nutrient supply as the mixed layers begin to deepen, and also perhaps a decrease in the grazing pressure. A notable exception to these seasonal cycles is the high-nutrient, low-chlorophyll regions mentioned earlier. Seasonal cycles are far less pronounced in tropical waters, unless they are influenced by seasonal upwelling, as is the case in the Arabian Sea. A summary of what we know of the distribution of primary production in the world's oceans, and of the physical and biological factors that influence it is available in the literature.

Given the highly dynamic nature of the distribution of primary production in the oceanic environment and the extreme paucity of measurements, it was only in the 1970s that compilations of measurements were first used to evaluate the distribution of marine primary production at the global scale. These studies had to combine observations from many years to maximize the number of measurements, so that it was impossible to examine interannual variability, or trends, in primary production. This inherent limitation to the study of the distribution of primary production at large scales was only addressed, at least partially, with the advent of remote-sensing techniques, which are examined briefly below.

The Use of Remote Sensing

The last two decades of the twentieth century saw the development of remote sensing to study the distribution of phytoplankton in the ocean. This technology uses subtle variations in the color of the oceans, as monitored by a sensor in space, to quantify variations in the concentrations of chlorophyll-*a* in the surface layers of the ocean. Since polar-orbiting satellites can provide global coverage at high spatial resolution (1 km or better), it became possible for the first time to see (cloud cover permitting) in great wealth of detail the variations in phytoplankton distribution at synoptic scales. The next logical step in the exploitation of ocean-color data was taken a few years later, when these fields of biomass were converted into fields of primary production.

The procedure that has met with the most success builds on models of photosynthesis as a function of available light. The light available at the sea surface can also be estimated using remote-sensing methods: geostationary satellites monitor cloud type and cloud cover, which are used in combination with atmospheric light-transmission models to estimate light available at the sea surface. Optical properties of the water, derived from ocean-color data are then used to compute light available at depth in the ocean. Thus, information on the variations in the forcing field (light), and the state variable on which light operates (phytoplankton biomass) in the process of photosynthesis, are directly available through remote sensing. If these satellite data are supplemented with best estimates of photosynthesis–irradiance parameters based on *in situ* observations, then all the major elements are in place for computations of primary production by remote sensing. These computations can be further refined by incorporating information on vertical structure in biomass, also derived from *in situ* observations. In regions where deep chlorophyll maxima are a consistent feature, ignoring their presence can lead to some systematic errors in the results.

The remote-sensing approach to computation of primary production has several advantages. It makes use of the vast database on light and biomass available through remote sensing, and in addition, makes use of all the available information on plant physiology obtained through *in situ* observations to define the parameters of the photosynthesis–irradiance curve. It has the potential to monitor the distributions of primary production at very large spatial scales, and over several timescales, ranging from the daily to interannual. It emerges as the method of choice for studying the distribution of primary production at large scales, especially when it is considered that remote sensing provides information on chlorophyll-*a* concentration, which can vary over four decades of magnitude, and on the highly variable light field at the surface of the ocean. In this method, the more sparse *in situ* observations are made use of only to define the parameters of the photosynthesis–irradiance curve and the parameters that are used to describe the vertical structure in biomass, which have a much lower range of variability compared with chlorophyll-*a* concentration.

The method is not without its problems, however. The major issues relate to differences in the time and space scales at which satellite and *in situ* measurements are made. This necessitates the development of methods for seamless integration of the two types of data streams. Ideally, the methods would bring to bear variations in the oceanographic environment and the physiological responses of phytoplankton to these variations. This is an active

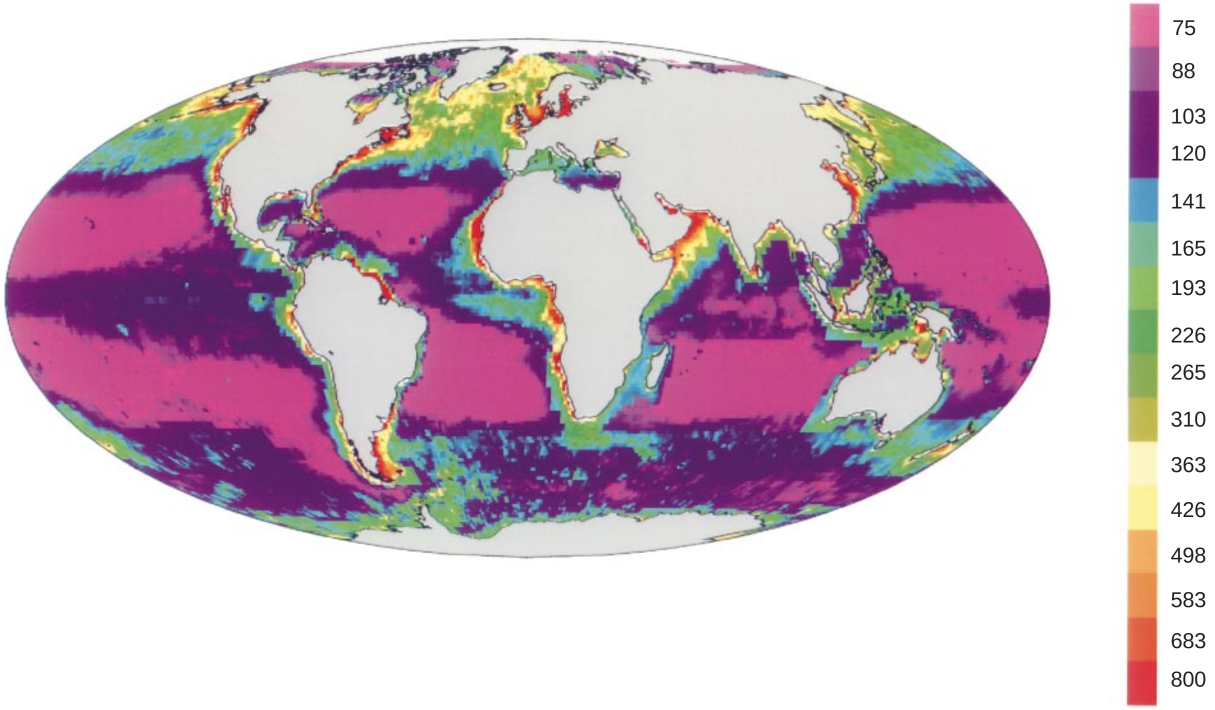

Figure 1 Distribution of primary production ($\mathrm{g\,C\,m^{-2}\,year^{-1}}$) in the world oceans, as estimated using remotely sensed ocean-colour data (Longhurst *et al.*, 1995). Areas of high production are seen in northern high latitudes; these reflect the impact of spring blooms on the distribution of production integrated over an annual cycle. Areas of upwelling (e.g., equatorial upwelling, the Benguela upwelling, the Somali upwelling, the California upwelling and the Peru upwelling) also emerge as areas of high production. The coastal shelf regions are also locations of high production. However, it is recognized that the remote-sensing method used in this calculation could overestimate the biomass, and hence the production in some coastal areas. Recent improvements in ocean-color technology offer the potential to reduce this type of error in the computation.

area of research. The first computation of global oceanic primary production using the remote-sensing approach appeared in the literature in 1995 (**Figure 1**). Other, similar computations have since appeared in the literature. It is a method that will continue to improve, with improvements in satellite technology as well as in the techniques for extrapolation of local biological measurements to large scales.

See also

Microbial Loops. Network Analysis of Food Webs. Ocean Gyre Ecosystems. Pelagic Biogeography. Primary Production Processes. Primary Production Methods.

Further Reading

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PRIMARY PRODUCTION METHODS

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doi:10.1006/rwos.2001.0203

Introduction

Primary production is the synthesis of organic material from inorganic compounds, such as CO_2 and water. The synthesis of organic carbon from CO_2 is commonly called carbon fixation: CO_2 is fixed by both photosynthesis and chemosynthesis. By far, photosynthesis by phytoplankton accounts for most marine primary production. Carbon fixation by macroalgae, microphytobenthos, chemosynthetic microbes, and symbiotic associations can be locally important.

Only the measurement of marine planktonic primary production will be discussed here. These measurements have been made for many decades using a variety of approaches. It has long been recognized that different methods yield different results, yet it is equally clear that the variability of primary productivity, with depth, time of day, season, and region, has been well described by most measurement programs. However, details of these patterns can depend on methodology, so it is important to appreciate the uncertainties and built-in biases associated with different methods for measuring primary production.

Definitions

Primary production is centrally important to ecological processes and biogeochemical cycling in marine systems. It is thus surprising, if not disconcerting, that (as discussed by Williams in 1993), there is no consensus on a definition of planktonic primary productivity, or its major components, net and gross primary production. One major reason for the problem is that descriptions of ecosystems require clear conceptual definitions for processes (e.g., net daily production of organic material by phytoplankton), whereas the interpretation of measurements requires precise operational definitions, for example, net accumulation of radiolabeled CO_2 in particulate matter during a 24 h incubation. Conceptual and operational definitions can be reconciled for particular approaches, but no one set of definitions is sufficiently general, yet detailed, to serve as a framework both for measuring planktonic