PHYTOPLANKTON AND PRIMARY PRODUCTION

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Keywords: carbon dioxide, primary production, photosynthesis, photosynthetically active radiation, phytoplankton, photosynthesis-irradiance curves, upper mixed layer, ultraviolet radiation, vertical mixing.

Contents

Summary

Primary productivity in aquatic systems is mostly carried out by phytoplankton—unicellular organisms that move passively in the water column. Primary production is

dependent on the photosynthetic process in which cells use solar energy to combine water and carbon dioxide into organic compounds that will be available to higher trophic levels. There are a number of factors that regulate and limit primary production in aquatic ecosystems, being the most important solar radiation and nutrients. Particularly, solar radiation—quantity and quality—strongly affects the photosynthetic process. Solar radiation attenuates with depth (as a function of particulate and dissolved materials) so that there is delimited zone where phytoplankton photosynthesis can occur—the euphotic zone (conventionally, the depth of 1% surface irradiance). The general depth-distribution of phytoplankton photosynthesis may reflect a photo-inhibitory process at the surface because of high radiation levels; then a subsurface maximum is found and, at depth, photosynthesis is again reduced because of low radiation levels. The quality of solar radiation causes assorted responses in phytoplankton: While PAR (photosynthetically active radiation, 400-700 nm) is responsible for the bulk of photosynthesis, UVR (280-400 nm) is generally considered an inhibitor of this process. Still, it is very difficult to draw generalizations, as responses are clearly dependent on the species, the amount and quality of radiation, as well as on the time scale considered to assess phytoplankton primary production. The principal limiting nutrients in aquatic environments are nitrogen, phosphorous and silicon. It is generally seen that if their concentration is low, phytoplankton cannot increase their biomass and thus photosynthesis remains low. On the other hand, when nutrient concentrations increase (e.g. due to agricultural runoff in coastal areas or upwelling effect) total photosynthesis, and therefore phytoplankton biomass, will increase. Other limiting nutrients are trace metals such as iron, that seem to be responsible for limiting photosynthesis in large areas of the Southern Ocean and other areas such as the equatorial Pacific.

1. Introduction

Primary production depends on the photosynthetic process carried out by autotrophic organisms that in aquatic ecosystems include phytoplankton, phytobenthos and macroalgae. In this chapter we will focus mostly on phytoplankton, which are unicellular organisms (diatoms, dinoflagellates, silicoflagellates, coccolithophorids and autotrophic flagellates) that move passively in the water column and thus their distribution and physiology are strongly conditioned by changes of the physical environment (e.g. turbulence, currents). Although phytoplankton organisms account for only 1-2% of the total global biomass, they are responsible for producing 30-60% of the global annual fixation of carbon on Earth, thus they provide the necessary energy for consumers and ultimately, to human beings. Additionally, phytoplankton contributes to the "biological pump" through which atmospheric CO_2 is transported to the deep ocean and is sequestered in sediments, thus decelerating global warming.

During photosynthesis cells utilize solar radiation energy to combine water and carbon dioxide into organic compounds (e.g. as carbohydrates) with the release of oxygen to the atmosphere. The photosynthesis process essentially consists of a series of reactions that are dependent on light (the conversion of solar radiation into chemical energy, "light" reactions) and those independent of light ("dark" reactions) in which organic compounds are formed; the overall result of the photosynthesis reaction can be expressed as (Eq. 1):

$$6\,CO_2 + 6\,H_2O \xrightarrow{h\nu} C_6H_{12}O_6 + 6\,O_2 \quad (1)$$

The chemical conversion of energy is mediated by photosynthetic pigments (which absorb radiation, especially in the range 400-700 nm, PAR, photosynthetically active radiation) among which the most important are the chlorophylls contained in the chloroplasts. Other pigments associated with harvesting of solar radiation are carotenoids, xanthophylls and phycobilins. The common photosynthetic pigment present in all phytoplankton groups is chlorophyll a (chl-a) that has the basic structure of four pyrrole groups forming a porphyrin ring with a magnesium atom at the centre. A long unbranched hydrocarbon chain (i.e. a phytol tail) attached to one of the pyrrole groups characterize the pigments found in the different phytoplankton taxa.

According to the methodology used (see below) phytoplankton photosynthesis can be expressed either as gross or net. Gross primary production refers to the total rate of CO_2 fixation without considering that some is lost during respiration. On the other hand, net primary production is the total rate of photosynthetic CO_2 fixation minus the rate of loss of CO_2 in respiration. In any case, phytoplankton primary productivity can be expressed as carbon fixed per unit chl-a per hour (i.e. assimilation number: mg C (mg chl-a) h^{-1}) or per unit area (e.g. from the surface to the bottom of the euphotic zone) per time (in mg C m^{-2} d^{-1}).

2. Methodological aspects

2.1. Techniques to measure phytoplankton production

There are several techniques that have been used to measure phytoplankton primary production. Most of the techniques measure some of the terms of Eq 1 (such as the production of carbohydrates or oxygen evolution) as outlined below:

2.1.1. Radiocarbon incorporation

The use of radiocarbon to measure photosynthetic rates assumes that fixation and reduction of $^{14}CO_2$ can be equated to the rate of utilization of $^{12}CO_2$, except for a slight isotope discrimination factor. Inorganic carbon exists in various species (CO_2, H_2CO_3, HCO_3^- and CO_3^{-2}) and their relative abundances in the water are dependent upon factors such as pH, temperature, and salinity. There is a rapid equilibrium between these carbon species, so that if one adds radiocarbon in any one form it equilibrates rapidly among the others. This is important as various phytoplankton species utilize different forms of inorganic carbon. In this technique, radiocarbon is generally introduced in the sample as bicarbonate ($H^{14}CO_3^-$) and, after the incubation period the amount of radiocarbon incorporated as carbohydrates is determined by liquid scintillation techniques. One of the main limitations of this method is that it usually estimates an intermediate value between gross and net photosynthesis.

2.1.2. Oxygen production

The oldest and most direct measurement of phytoplankton primary production involves the measurement of dissolved oxygen in light and dark bottles. The dark bottle provides the rate of respiratory consumption of organic substrates. Oxygen may be measured using the classic Winkler titration method, or an oxygen electrode (this latter if phytoplankton biomass is relatively high). One limitation of this method is that it requires long incubation periods and it also has low sensitivity for oligotrophic waters.

2.1.3. Carbon-13

The stable isotope ^{13}C may also be used in a similar way as described above for ^{14}C. Since the isotope is not radioactive the measurement of ^{13}C must be done using mass spectrometry.

2.1.4. Estimation from remote sensors

Sensors on remote platforms (airplanes or satellites) are capable of estimating the concentration of chl-a in surface waters by measurement of spectral changes of the upwelling light. From these data, in conjunction with other remotely sensed data, it is possible to use algorithms to estimate the rate of primary production in the water column. It should be noted though that there are many limitations in this methodology and the reliability of the estimates will depend on many factors, such as the distribution of phytoplankton in the euphotic zone, nutrient status of cells, carbon / chl-a ratio and mixing. As upwelling light recorded by remote sensors emanates mostly from the upper few centimeters of the water column, satellite estimates of primary production are more reliable for temperate and polar waters, where chl-a concentrations are generally highest in surface waters, as compared to tropical waters where maximal chl-a concentrations may be found at the so called deep chl-a maxima. Remotely sensed data however, has the advantage that it can cover large geographical areas and long periods of time.

2.1.5. Natural fluorescence at 683 nm

The reaction centers of photosystem II re-emit some of the absorbed radiant energy as fluorescence, with an emission peak at 683 nm. The measurement of 683 nm upwelling radiance in the euphotic zone can thus be used to estimate the rate of instantaneous photosynthesis. By using a profiling instrument which measures downwelling PAR and upwelling radiance at 683 nm as a function of depth, it is possible to estimate a profile of photosynthetic rates within the euphotic zone.

2.1.6. Measurements of pulsed fluorescence

This technique (and some variations of it) allows the estimation of photosynthetic rates from light-stimulated changes of photosystem II. The fluorescence of chlorophyll can be used as an indication of how the photosynthetic apparatus is working. Estimations of the capture of photons by light-harvesting pigments, light reaction, thylakoid electron transport rate (ETR), regulatory feedback processes, and other variables can be obtained using this technique and finally equated at least to oxygen evolution.

2.2 Incubations

A wide variety of approaches are used to assess phytoplankton primary production. These include incubations where samples are exposed to either solar or artificial radiation and/or those where samples are incubated under *in situ* or simulated *in situ* conditions. A brief explanation of these incubations is presented below:

2.2.1. *In situ* incubations

In this type of incubation, samples are taken from different depths, placed in transparent tubes and exposed to solar radiation in their natural habitat and at the depth from where they were collected. If considering also the effects of UVR (280-400 nm) phytoplankton will be exposed to the *in situ* radiation field by using UV-transparent tubes placed in trays which are incubated at different depths in the water column. Different treatments can be implemented (i.e. by the use of selective filters) to assess the effects of UV-B (280-315 nm) and UV-A (315-400 nm) in addition to that of PAR. The principal disadvantage of *in situ* incubations is that cells are kept at a fixed depth throughout incubation period (e.g. a few hours) thus receiving a constant proportion of the surface incident radiation. In the water column however, cells move within the upper mixed layer (UML) and thus they are exposed to a variable irradiance field. In fact, relatively few studies have addressed the importance of mixing on phytoplankton photosynthesis, not only due to fluctuations in PAR but also in UVR. These studies have determined a wide range of responses, with vertical mixing enhancing, reducing or having no effects on primary production. Although *in situ* incubations will result in the most realistic responses of phytoplankton exposed to various depths, they are strongly conditioned by weather conditions; as a result, certain areas of the World Ocean (i.e. polar) are relatively under-sampled.

2.2.2. Simulated *in situ* incubation

Considering the practical difficulties of *in situ* incubation, outdoor incubation in temperature-controlled containers (e.g. on the deck of a research vessel, or in flow-through systems on land sites) have been used as an alternative approach. Neutral density filters are often used to approximately simulate the attenuation of solar radiation in the water column. These filters, however, do not mimic the differential spectral attenuation that actually occurs in the water column, and samples are generally exposed to higher UV-B / UV-A / PAR ratios than they would normally experience. Nevertheless, this approach is widely used and very convenient at the time to obtain photosynthesis versus irradiance (P vs. E) curves for different phytoplankton populations (see below).

2.2.3. Radiation sources

The most realistic approach will be the evaluation of phytoplankton primary productivity under solar radiation levels. However, in many mechanistic studies, it has been preferable to use artificial sources (i.e. different lamps), although one should be careful at the time to extrapolate the results obtained in this way to the natural environment. Various artificial radiation sources have been used to determine primary production and, in the particular case of studies assessing UVR effects on phytoplankton primary production, an assorted range of lamps are commercially

available, such as fluorescent and halogen. So far, most studies carried out with artificial radiation sources have been done with the main objective of obtaining P vs E curves and the impact of UVR at fixed irradiances, or in combination with neutral density screens and cut-off filters to obtain biological weighting functions (BWFs).

3. Phytoplankton primary production in the oceans

As phytoplankton distribution and position in the water column is highly dependent on physical forcing, the physical environment conditions primary production in the oceans. One of the most evident features, when looking at the World Ocean from space, is the heterogeneous distribution of phytoplankton as viewed by color images (Figure 1).

Five areas of low chl-a concentration (and also low phytoplankton abundance) are observed in these satellite images, which correspond to the five central gyres of the oceans. In these areas the ocean circulation (i.e. surface currents) piles water to the center of the gyres (Coriolis' effect) and isolate it. Due to thermal stratification, the water is also isolated vertically and the end result is that nutrients are depleted and thus productivity is low.

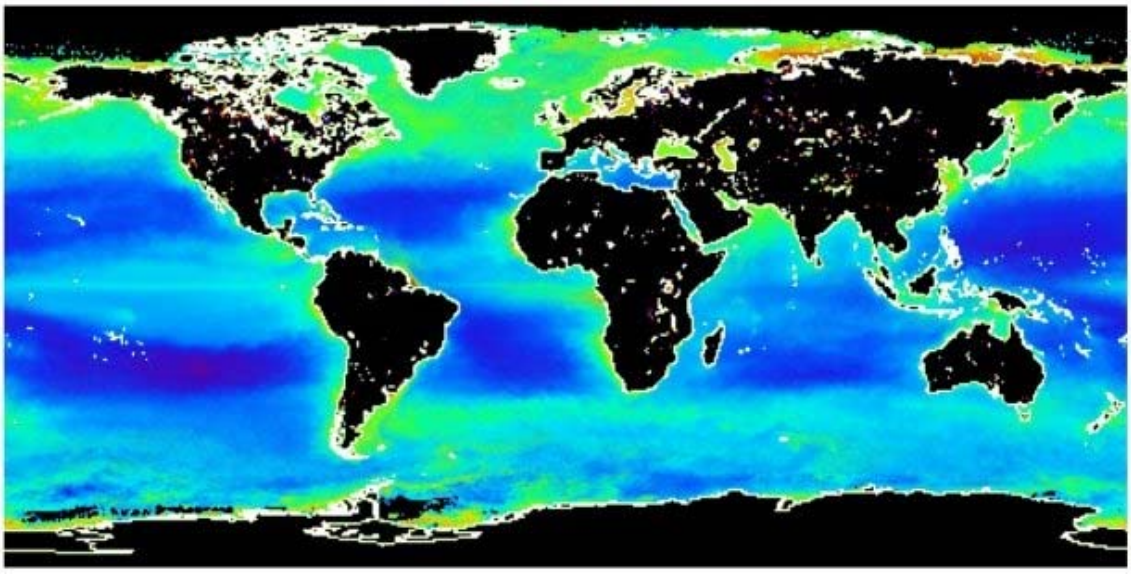

Figure 1: SeaWifs chlorophyll global distribution (Data from NASA, www.nasa.gov). The blue areas represent the gyres of the oceans which are characterized by low chl-a concentration. The green and red areas (with high chl-a concentrations) are considered high productive systems.

Circulation patterns of the oceans also cause the surface water on the western side of continents to be moved away from land, and thus to be replaced by low-temperature, high-nutrient water from the deeper part—a phenomenon that is referred to as upwelling. In these areas, phytoplankton production is consequently very high. These areas also sustain high secondary production and fisheries, like for example, the very productive Humboldt Current System (HCS) along the coast of Chile. A clear evidence of the importance of the upwelling system in the Pacific Ocean can be gathered during El Niño events. During El Niño, the upwelling is interrupted and the high-temperature,

low-nutrient waters that are normally piled on the western side of the Pacific Ocean, are spread towards the American continent and thus fisheries and phytoplankton production collapse.

Other areas of high phytoplankton primary production are the extended continental shelves (depth < 200 m) as for example in the Argentinean Sea that supports very important fisheries around the Malvinas Islands. In these areas, vertical mixing is important at the time to re-suspend bottom material and bring nutrients to the upper layer; also, inputs from land contribute to the observed pattern.

Polar areas are also special from the point of view of phytoplankton primary production. In the northern hemisphere the phytoplankton bloom develops in conjunction with the retreat of the icepack (polynya) and thus high primary and secondary production (including fisheries) are sustained. In the southern hemisphere (south of the Polar Front) there is an area with relatively low phytoplankton abundance (and low chl-a concentration) in spite of the high nutrient concentration (HNLC area). This area has received special attention and many studies were devoted to understand what causes low phytoplankton primary production. Particularly, and even though light, mixing and grazing have been proved to limit phytoplankton primary production in relatively shallow areas of Antarctica (over the shelf), it was determined that iron (Fe) was the limiting factor over the deep and open parts of the Southern Ocean. Thus the addition of Fe not only increased phytoplankton biomass and production, but also resulted in a shift of the community towards large phytoplankton. Fe limitation of primary production, however, is not exclusive for the Southern Ocean, as experiments demonstrated that this micronutrient limited phytoplankton in oceanic areas where terrestrial input was negligible (i.e. tropical Pacific).

The general pattern of primary production in the oceans seems to be tied to the observed differential size distribution of phytoplankton. While in the central gyres small nano-picoplankton (cells < 20 μm in effective diameter) dominate the phytoplankton assemblages, large microplanktonic cells (> 20 μm in effective diameter) dominate the blooms at mid-latitudes and in polar areas. This seems to be related not only to the utilization of light but also to the effective uptake of nutrients. Small cells have a higher surface-to-volume ratio and thus they have a faster acclimation dynamics and so they tend to dominate when nutrients are the limiting factor.

Finally, there are other oceanic areas that deserve attention when addressing phytoplankton primary production, such as the frontal systems. Basically, frontal systems are characterized by large gradients of temperature or salinity over relatively small distances. Fronts normally occur when two water masses with different characteristics and origins meet, and one (the denser and heavier) sinks, while the lighter overrides. In these areas high productivity may occur due to the accumulation of phytoplankton and particles and/or *in situ* growth due to stratification in one of the sides of the front. Several important frontal zones can be identified in the ocean but not all of them result in a net "benefit". For example, it has been seen that fronts may be related to the outbreak of red tide species, with an obvious drawback for secondary production, such as clams, mussels, and others invertebrates of commercial interest.

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Biographical Sketches

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