

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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Introduction

Primary production is the synthesis of organic material from inorganic compounds, such as CO₂ and water. The synthesis of organic carbon from CO₂ is commonly called carbon fixation: CO₂ 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 CO₂ 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

primary production with a broad variety of methods and for interpreting the measurements in a range of scientific contexts. It is nonetheless useful to define three components of primary production that can be estimated from measurements in closed systems:

- **Gross primary production** (P_g) is the rate of photosynthesis, not reduced for losses to excretion or to respiration in its various forms
- **Net primary production** (P_n) is gross primary production less losses to respiration by phytoplankton
- **Net community production** (P_{nc}) is net primary production less losses to respiration by heterotrophic microorganisms and metazoans.

Other components of primary production, such as new production, regenerated production, and export production, must be characterized to describe food-web dynamics and biogeochemical cycling. As pointed out by Platt and Sathyendranath in 1993, in any such analysis, great care must be taken to reconcile the temporal and spatial scales of both the measurements and the processes they describe.

Marine primary production is commonly expressed as grams or moles of carbon fixed per unit volume, or per unit area, of sea water per unit time. The timescale of interest is generally 1 day or 1 year. Rates are characterized for the euphotic zone, commonly defined as extending to the depth of 1% of the surface level of photosynthetically active radiation (PAR: 400–700 nm). This convenient definition of euphotic depth (sometimes simplified further to three times the depth at which a Secchi disk disappears) is a crude and often inaccurate approximation of where gross primary production over 24 h matches losses to respiration and excretion by phytoplankton. Regardless, rates of photosynthesis are generally insignificant below the depth of 0.1% surface PAR.

Photosynthesis and Growth of Phytoplankton

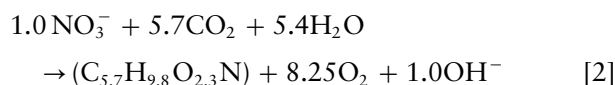
Primary production is generally measured by quantifying light-dependent synthesis of organic carbon from CO_2 or evolution of O_2 consistent with the simplified description of photosynthesis as the reaction:



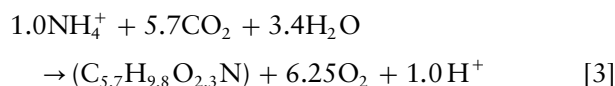
Absorbed photons are signified by $h\nu$ and the carbohydrates generated by photosynthesis are represent-

ed as CH_2O . Carbon dioxide in sea water is found in several chemical forms which exchange quickly enough to be considered in aggregate as total CO_2 (TCO_2). In principle, photosynthesis can be quantified by measuring any of three light-dependent processes: (1) the increase in organic carbon; (2) the decrease of TCO_2 ; or (3) the increase of O_2 . However, growth of phytoplankton is not so simple: since phytoplankton are composed of proteins, lipids, nucleic acids, and other compounds besides carbohydrate, both photosynthesis and the assimilation of nutrients are required. Consequently, many chemical transformations are associated with primary production, and eqn [1] does not accurately describe the process of light-dependent growth.

It is therefore useful to describe the growth of phytoplankton (i.e., net primary production) with a more general reaction that describes how transformations of carbon and oxygen depend on the source of nutrients (particularly nitrogen) and on the chemical composition of phytoplankton. For growth on nitrate:



The idealized organic product, $\text{C}_{5.7}\text{H}_{9.8}\text{O}_{2.3}\text{N}$, represents the elemental composition of phytoplankton. Ammonium is more reduced than nitrate, so less water is required to satisfy the demand for reductant:



The photosynthetic quotient (PQ; mol mol^{-1}) is the ratio of O_2 evolved to inorganic C assimilated. It must be specified to convert increases of oxygen to the synthesis of organic carbon. For growth on nitrate as described by eqn [2], PQ is $1.45 \text{ mol mol}^{-1}$; with ammonium as the source of N, PQ is 1.10. The photosynthetic quotient also reflects the end products of photosynthesis, the mixture of which varies according to environmental conditions and the species composition of phytoplankton. For example, if the synthesis of carbohydrate is favored, as can occur in high light or low nutrient conditions, PQ is lower because the reaction described in eqn [1] becomes more important. Uncertainty in PQ is often ignored. This can be justified when the synthesis of organic carbon is measured directly, but large errors can be introduced when attempts are made to infer carbon fixation from the dynamics of oxygen.

Excretion of organic material would have a small influence on PQ and is not considered here.

Approaches

Primary production can be estimated from chlorophyll (from satellite color or *in situ* fluorescence) if carbon uptake per unit of chlorophyll is known. Therefore, 'global' estimates of primary production depend on direct measurements by incubation. The technical objectives are to obtain a representative sample of sea water, contain it so that no significant exchange of materials occurs, and to measure light-dependent changes in carbon or oxygen during incubations that simulate the natural environment. Methods vary widely, and each approach involves compromises between needs for logistical convenience, precision, and the simulation of natural conditions. Each program of measurement involves many decisions, each of which has consequences for the resulting measurements. Several options are listed in Tables 1 and 2 and discussed below.

Light-dependent Change in Dissolved Oxygen

The light-dark oxygen method is a standard approach for measuring photosynthesis in aquatic systems, and it was the principal method for measuring marine primary production until it was supplanted by the ^{14}C method, which is described below. Accumulation of oxygen in a clear container (light bottle) represents net production by the enclosed community, and the consumption of oxygen in a dark bottle is a measure of respiration. Gross primary production is estimated by subtracting the dark bottle re-

sult from that for the light bottle. It is thus assumed that respiration in the light equals that in the dark. As documented by Geider and Osborne in their 1992 monograph, this assumption does not generally hold, so errors in estimation of the respiratory component of P_g must be tolerated unless isotopically labelled oxygen is used (see below).

Methods based on the direct measurement of oxygen are less sensitive than techniques using the isotopic tracer ^{14}C . However, careful implementation of procedures using automated titration or pulsed oxygen electrodes can yield useful and reliable data, even from oligotrophic waters of the open ocean. Interpretation of results is complicated by containment effects common to all methods for direct measurement of primary production (see below). Also, a value for photosynthetic quotient must be assumed in order to infer carbon fixation from oxygen production. Abiotic consumption of oxygen through photochemical reactions with dissolved organic matter can also contribute to the measurement, primarily near the surface, where the effective ultraviolet wavelengths penetrate.

Light-dependent Change in Dissolved Inorganic Carbon

Changes in TCO_2 during incubations of sea water can be measured by several methods. Uncertainties related to biological effects on pH-alkalinity- TCO_2 relationships are avoided through the use of coulometric titration or infrared gas analysis after acidification. Measurement of gross primary production and net production of the enclosed community is like that for the light-dark oxygen

Table 1 Measurements that can be related to primary production

Measurement	Advantages	Disadvantages	Comments
Change in TCO_2	Direct measure of net inorganic C fixation	Relatively insensitive: small change relative to large background	Not generally practical for open-ocean work
Change in oxygen concentration (high precision titration)	Direct measures of O_2 dynamics can yield estimates of net and gross production	Small change relative to large background Interpretation of light-dark incubations is not simple	Very useful if applied with great care. Requires knowledge of PQ to convert to C-fixation
Incorporation of ^{14}C -bicarbonate into organic material (radioactive isotope)	Very sensitive and relatively easy. Small volumes can be used and many samples can be processed	Tracer dynamics complicate interpretations Radioactive – requires special precautions and permission	The most commonly used method in oceanography
Incorporation of ^{13}C -bicarbonate into organic material (stable isotope)	No problems with radioactivity	Less sensitive and more work than ^{14}C method Larger volumes required	A common choice when ^{14}C method is impractical
Measurement of $^{18}\text{O}_2$ production from H_2^{18}O	Measures photosynthesis without interference from respiration	Requires special equipment	A powerful research tool, not generally used for routine measurements

method, but there is no need to assume a photosynthetic quotient. However, precision of the analyses is not quite as good as for bulk oxygen methods. Extra procedures, such as filtration, would be required to assess precipitation of calcium carbonate (e.g., by coccolithophores) and photochemical production of CO₂. These processes cause changes in TCO₂ that are not due to primary production. The TCO₂ method is not used routinely for measurement of primary production in the ocean.

The ¹⁴C Method

Marine primary production is most commonly measured by the ¹⁴C method, which was introduced by Steemann Nielsen in 1952. Samples are collected and the dissolved inorganic carbon pool is labeled with a known amount of radioactive ¹⁴C-bicarbonate. After incubation in clear containers, carbon fixation is quantified by liquid scintillation counting to detect the appearance of ¹⁴C in organic form. Generally, organic carbon is collected as particles on a filter. Both dissolved and particulate organic carbon can be quantified by analyzing whole water after acidification to purge the inorganic carbon. It is prudent to correct measurements for the amount of label incorporated during incubations in the dark. The ¹⁴C method can be very sensitive, and good precision can be obtained through replication and adequate time for scintillation counting. The method has drawbacks, however. Use of radioisotopes requires special procedures for handling and disposal that can greatly complicate or preclude some field operations. Also, because ¹⁴C is added as dissolved inorganic carbon and gradually enters pools of particulate and dissolved matter, the dynamics of the labeled carbon cannot accurately represent all relevant transformations between organic and inorganic carbon pools. For example, respiration cannot be quantified directly. The interpretation of ¹⁴C uptake (discussed below) is thus anything but straightforward.

The ¹³C Method

The ¹³C method is similar to the ¹⁴C method in that a carbon tracer is used. Bicarbonate enriched with the stable isotope ¹³C is added to sea water and the incorporation of CO₂ into particulate matter is followed by measuring changes in the ¹³C:¹²C ratio of particles relative to that in the TCO₂ pool. Isotope ratios are measured by mass spectrometry or emission spectrometry. Problems associated with radioisotopes are avoided, but the method can be more cumbersome than the ¹⁴C method (e.g., larger volumes are generally needed) and some sensitivity is lost.

The ¹⁸O Method

Gross photosynthesis can be measured as the production of ¹⁸O-labeled O₂ from water labeled with this heavy isotope of oxygen (see eqn [1]). Detection is carried out by mass spectrometry. Net primary production of the enclosed community is measured as the increase of oxygen in the light bottle, and respiration is estimated by difference. In principle, the difference between gross production measured with ¹⁸O and gross production from light-dark oxygen changes is due to light-dependent changes in respiration and photochemical consumption of oxygen. Respiration can also be measured directly by tracking the production of H₂¹⁸O from ¹⁸O₂.

The ¹⁸O method is sufficiently sensitive to yield useful results even in oligotrophic waters. It is not commonly used, but when the measurements have been made and compared to other measures of productivity, important insights have been developed.

Methodological Considerations

Many choices are involved in the measurement of primary production. Most influence the results, some more predictably than others. A brief review of methodological choices, with an emphasis on the ¹⁴C method, reveals that the measurement of primary production is not an exact science.

Sampling

Every effort should be made to avoid contamination of samples obtained for the measurement of primary production. Concerns about toxic trace elements are especially important in oceanic waters. Trace metal-clean procedures, including the use of specially cleaned GO-FLO sampling bottles suspended from Kevlar™ line, prevent the toxic contamination associated with other samplers, particularly those with neoprene closure mechanisms. Frequently, facilitates for trace metal-clean sampling are unavailable. Through careful choice of materials and procedures, it is possible to minimize toxic contamination, but enrichment with trace nutrients such as iron is probably unavoidable. Such enrichment could stimulate the photosynthesis of phytoplankton, but only after several hours or longer.

Exposure of samples to turbulence during sampling can damage the phytoplankton and other microbes, altering measured rates. Also, significant inhibition of photosynthesis can occur when deep samples acclimated to low irradiance are exposed to bright light, even for brief periods, during sampling.

Method of Incubation

Samples of seawater can be incubated *in situ*, under simulated *in situ* (SIS) conditions, or in incubators illuminated by lamps. Each method has advantages and disadvantages (Table 2).

Incubation *in situ* ensures the best possible simulation of natural conditions at the depths of sampling. Ideally, samples are collected, prepared, and deployed before dawn in a drifting array. Samples are retrieved and processed after dusk or before the next sunrise. If deployment or retrieval occur during daylight, deep samples can be exposed to unnaturally high irradiance during transit, which can lead to artifactually high photosynthesis and perhaps to counteracting inhibitory damage. Incubation of samples *in situ* limits the number of stations that can be visited during a survey, because the ship must stay near the station in order to retrieve the samples. Specialized systems both capture and inoculate samples *in situ*, thereby avoiding some logistical problems.

Ship operations can be much more flexible if primary productivity is measured using SIS incubations. Water can be collected at any time of day and incubated for 24 h on deck in transparent incubators to measure daily rates. The incubators, or bottles in the incubators, are commonly screened with neutral density filters (mesh or perforated metal screen) to reproduce fixed percentages of PAR at the surface. Light penetration at the station must be estimated to choose the sampling depths corresponding to these light levels. Cooling comes from surface sea water.

This system has many advantages, including improved security of samples compared with *in situ* deployment, convenient access to incubations for time-course measurements, and freedom of ship movement after sampling. Because the spectrally neutral attenuation of sunlight by screens does not mimic the ocean, significant errors can be introduced for samples from the lower photic zone where the percentage of surface PAR imposed by a screen will not match the percentage of photosynthetically utilizable radiation (PUR, spectrally weighted for photosynthetic absorption) at the sampling depth. Incubators can be fitted with colored filters to simulate subsurface irradiance for particular water types. Also, chillers can be used to match subsurface temperatures, avoiding artifactual warming of deep samples.

Artificial incubators are used to measure photosynthesis as a function of irradiance (P versus E). Illumination is produced by lamps, and a variety of methods are used to provide a range of light levels to as many as 24 or more subsamples. Temperature is controlled by a water bath. The duration of incubation generally ranges from about 20 min to several hours, and results are fitted statistically to a P versus E curve. If P versus E is determined for samples at two or more depths (to account for physiological differences), results can be used to describe photosynthesis in the water column as a function of irradiance. Such a calculation requires measurement of light penetration in the water and consideration of spectral differences between the incubator and natural waters. Because many samples,

Table 2 Approaches for incubating samples for the measurement of primary production

<i>Incubation system</i>	<i>Advantages</i>	<i>Disadvantages</i>	<i>Comments</i>
Incubation <i>in situ</i>	Best simulation of the natural field of light and temperature	Limits mobility of the ship Vertical mixing is not simulated Artifacts possible if deployed or recovered in the light	Not perfect, but a good standard method if a station can be occupied all day
Simulated <i>in situ</i>	Many stations can be surveyed Easy to conduct time-courses and experimental manipulations	Special measures must be taken to stimulate spectral irradiance and temperature Vertical mixing not simulated	Commonly used when many stations must be sampled. Significant errors possible if incubated samples are exposed to unnatural irradiance and temperature
Photosynthesis versus irradiance (P versus E) incubator (^{14}C)	Data can be used to model photosynthesis in the water column With care, vertical mixing can be addressed	Extra expenses and precautions are required Spectral irradiance is not matched to nature Results depend on timescale of measurement Analysis can be tricky	A powerful approach when applied with caution

usually of small volume, must be processed quickly, only the ^{14}C method is appropriate for most *P* versus *E* measurements in the ocean.

Containers

Ideally, containers for the measurement of primary production should be transparent to ultraviolet and visible solar radiation, completely clean, and inert (Table 3). Years ago, soft glass bottles were used. Now it is recognized that they can contaminate samples with trace elements and exclude naturally occurring ultraviolet radiation. Glass scintillation vials are still used for some *P* versus *E* measurements of short duration; checks for effects of contaminants are warranted. Compared with soft glass, laboratory-grade borosilicate glass bottles (e.g., PyrexTM) have better optical properties, excluding only UV-B (280–320 nm) radiation. Also, they contaminate less. Laboratory-grade glass bottles are commonly used for oxygen measurements. Polycarbonate bottles are favored in many studies because they are relatively inexpensive, unbreakable, and can be cleaned meticulously. Polycarbonate absorbs UV-B and some UV-A (320–400 nm) radiation, so near-surface inhibition of photosynthesis can be underestimated. The error can be significant very close to the surface, but not when the entire water column is considered. TeflonTM bottles, more expensive than polycarbonate, are noncontaminating and

they transmit both visible and UV (280–400 nm) radiation. When the primary emphasis is an assessing effects of UV radiation, incubations are conducted in polyethylene bags or in bottles made of quartz or TeflonTM.

The size of the container is an important consideration. Small containers (≤ 50 ml) are needed when many samples must be processed (e.g. for *P* versus *E*) or when not much water is available. However, small samples cannot represent the planktonic assemblage accurately when large, rare organisms or colonies are in the water. Smaller containers have greater surface-to-volume ratios, and thus small samples have greater susceptibility to contamination. If it is practical, larger samples should be used for the measurement of primary production. The problems with large samples are mostly logistical. More water, time, and materials are needed, more radioactive waste is generated, and some measurements can be compromised if handling times are too long.

Duration of Incubation

Conditions in containers differ from those in open water, and the physiological and chemical differences between samples and nature increase as the incubations proceed. Unnatural changes during incubation include: extra accumulation of phytoplankton due to exclusion of grazers; enhanced inhi-

Table 3 Containers for incubations

Container	Advantages	Disadvantages	Comments
Polycarbonate bottle	Good for minimizing trace element contamination Nearly unbreakable Affordable	Excludes UV radiation Compressible, leading to gas dissolution and filtration problems for deep samples	Many advantages for routine and specialized measurements at sea
Laboratory grade borosilicate glass (e.g., Pyrex TM)	More transparent to UV Incompressible	More trace element contamination Breakable	A reasonable choice if compromises are evaluated
Borosilicate glass scintillation vials	Inexpensive Practical choice for <i>P</i> versus <i>E</i>	Contaminate samples with trace elements and Si Exclude UV radiation	Can be used with caution for short-term <i>P</i> versus <i>E</i> measurements
Polyethylene bag	Inexpensive Compact UV-transparent	More difficult to handle Requires caution with respect to contamination	Used for special projects, e.g., effect of UV
Quartz, Teflon TM	UV-transparent Teflon TM does not contaminate	Relatively expensive	Used for work assessing effects of UV
Small volume (1–25 ml)	Good for <i>P</i> versus <i>E</i> Samples can be processed by acidification (no filtration)	Cannot sample large, rare phytoplankton evenly Containment effects more likely	Used for <i>P</i> versus <i>E</i> with many replicates
Large volume (1–20l)	Some containment artifacts are minimized Potential for time-course measurements	More work Longer filtration times with possible artifacts	Required for some types of analysis, e.g., ^{13}C

bition of photosynthesis in samples collected from mixed layers and incubated at near-surface irradiance; stimulation of growth due to contamination with a limiting trace nutrient such as iron; and poisoning of phytoplankton with a contaminant, such as copper. When photosynthesis is measured with a tracer, the distribution of the tracer among pools changes with time, depending on the rates of photosynthesis, respiration, and grazing. All of these effects, except possibly toxicity, are minimized by restricting the time of incubation, so a succession of short incubations, or *P* versus *E* measurements, can in principle yield more accurate data than a day-long incubation. This requires much effort, however, and extrapolation of results to daily productivity is still uncertain. The routine use of dawn-to-dusk or 24 h incubations may be subject to artifacts of containment, but it has the advantage of being much easier to standardize.

Filtration or Acidification

Generally, an incubation with ^{14}C or ^{13}C is terminated by filtration. Labeled particles are collected on a filter for subsequent analysis. Residual dissolved inorganic carbon can be removed by careful rinsing with filtered sea water; exposure of the filter to acid purges both dissolved inorganic carbon and precipitated carbonate. The choice of filter can influence the result. Whatman GF/F glass-fiber filters, with nominal pore size $0.7\ \mu\text{m}$, are commonly used and widely (although not universally) considered to capture all sizes of phytoplankton quantitatively. Perforated filters with uniform pore sizes ranging from 0.2 to $5\ \mu\text{m}$ or more can be used for size-fractionation. Particles larger than the pores can squeeze

through, especially when vacuum is applied. The filters are also subject to clogging, leading to retention of small particles.

Labeled dissolved organic carbon, including excreted photosynthate and cell contents released through 'sloppy feeding' of grazers, is not collected on filters. These losses are generally several percent of total or less, but under some conditions, excretion can be much more. When ^{14}C samples are processed with a more cumbersome acidification and bubbling technique, both dissolved and particulate organic carbon is measured.

Interpretation of Carbon Uptake

Because the labeled carbon is initially only in the inorganic pool, short incubations with ^{14}C (≤ 1 h) characterize something close to gross production. As incubations proceed, cellular pools of organic carbon are labeled, and some ^{14}C is respired. Also, some excreted ^{14}C organic carbon is assimilated by heterotrophic microbes, and some of the phytoplankton are consumed by grazers. So, with time, the measurement comes closer to an estimate of the net primary production of the enclosed community (Table 4). However, many factors, including the ratio of photosynthesis to respiration, influence the degree to which ^{14}C uptake resembles gross versus net production. Consequently, critical interpretation of ^{14}C primary production measurements requires reference to models of carbon flow in the system.

Conclusions

Primary production is not like temperature, salinity or the concentration of nitrate, which can in

Table 4 Incubation times for the measurement of primary production

<i>Incubation time</i>	<i>Advantages</i>	<i>Disadvantages</i>	<i>Comments</i>
Short (≤ 1 h)	Little time for unnatural physiological changes	Usually requires artificial illumination Uncertain extrapolation to daily rates in nature	Closer to P_g
1–6 h	Convenient Appropriate for some process studies	Uncertain extrapolation to daily rates in nature	Used for <i>P</i> versus <i>E</i> , especially with larger samples
Dawn–dusk	Good for standardization of methodology	Limits the number of stations that can be sampled Containment effects Vertical mixing is not simulated, leading to artifacts	A good choice for standard method using <i>in situ</i> incubation Closer to P_{nc} near the surface; close to P_g deep in the photic zone
24 h	Good for standardization of methodology	Results may vary depending on start time. Longer time for containment effects to act	A good standard for SIS incubations. Close to P_{nc} near the surface; closer to P_g deep in the photic zone

principle be measured exactly. It is a biological process that cannot proceed unaltered when phytoplankton are removed from their natural surroundings. Artifacts are unavoidable, but many insults to the sampled plankton can be minimized through the exercise of caution and skill. Still, the observed rates will be influenced by the methods chosen for making the measurements. Interpretation is also uncertain: the ^{14}C method is the standard operational technique for measuring marine primary production, yet there are no generally applicable rules for relating ^{14}C measurements to either gross or net primary production.

Fortunately, uncertainties in the measurements and their interpretation, although significant, are not large enough to mask important patterns of primary productivity in nature. Years of data on marine primary production have yielded information that has been centrally important to our understanding of marine ecology and biogeochemical cycling. Clearly, measurements of marine primary production are useful and important for understanding the ocean. It is nonetheless prudent to recognize that the measurements themselves require circumspect interpretation.

See also

Carbon Cycle. Fluorometry for Biological Sensing. Ocean Carbon System, Modelling of. Network Analysis of Food Webs. Ocean Color from Satel-

lites. Primary Production Distribution. Primary Production Processes. Tracers of Ocean Productivity.

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PRIMARY PRODUCTION PROCESSES

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Introduction

This article summarizes the information available on the magnitude of and the spatial and temporal variations in, marine plankton primary productivity. The causes of these variations are discussed in terms of the biological processes involved, the organisms which bring them about, and the relationships to oceanic physics and chemistry. The discussion begins with a definition of primary production.

Primary producers are organisms that rely on external energy sources such as light energy (photolithotrophs) or inorganic chemical reactions (chemolithotrophs). These organisms are further characterized by obtaining their elemental requirements from inorganic sources, e.g. carbon from inorganic carbon such as carbon dioxide and bicarbonate, nitrogen from nitrate and ammonium (and, for some, dinitrogen), and phosphate from inorganic phosphate. These organisms form the basis of food webs, supporting all organisms at higher trophic levels. While chemolithotrophy may well have had a vital role in the origin and early evolution of life, the role of chemolithotrophs in the present ocean is minor in energy and carbon terms (**Table 1**), but is very important in biogeochemical element cycling, for example in the conversion of ammonium to nitrate.