

## Measuring and Modeling Primary Production in Marine Pelagic Ecosystems

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The measurement of primary production in the ocean is key to our estimates of ecosystem function and the role of the ocean and its biota in the planetary carbon (C) cycle. Accurate estimates are critical to a broad suite of biological questions across a wide range of space and time scales. The methods developed to measure primary production reflect the diversity of our research interests and encompass a range of approaches: from in situ to airborne and spaceborne observations, from intracellular to global systems, and from experimental to modeling.

A variable of interest in quantifying primary productivity is the rate of population increase within a pelagic community (McCormick et al. 1996). Growth rate ( $\mu$  [ $t^{-1}$ ]) can be expressed as the rate of change in the number of individuals ( $n$ ) per unit time ( $t$ ) or as a chemical constituent (C, nitrogen [N], etc.) within the community,

$$\mu = dn/dt (1/n). \quad (1)$$

In the field, the estimate of growth rates is limited by a number of factors because the terms  $dn$  and  $n$ , or alternatively  $dC$  and  $C$ , from phytoplankton are not readily measured. Several characteristics of plankton challenge the precision and accuracy of our present methods. One problem is that the target autotrophic algal population is suspended in seawater and has a spatial and size distribution which overlaps that of heterotrophic organisms. The plants in the plankton are microscopic (usually 2–200  $\mu\text{m}$ ) and multiply very quickly (from 0.1 to 2.0 divisions per day or a doubling rate of 0.5 to 10 days); the herbivores usually ingest whole cells and not parts; and the herbivores themselves are microscopic, with body size and division rate similar to the plants. In the absence of loss terms, these factors make measurements of primary production difficult (Waterhouse and Welschmeyer 1995). Also,

the plant eaters are mostly omnivores, so catabolic and anabolic reactions in both groups of organisms are difficult to differentiate, and often interact with each other.

Methods that are specific to autotrophic organisms are thus necessary to overcome the challenges in working with planktonic systems. There are numerous methods, such as the use of radioactive tracers, the determination of biophysical processes in photosynthetic pigments, and models aimed at the mechanistic estimation of photosynthesis. In this chapter the most common techniques used to estimate primary production in marine pelagic ecosystems are discussed, their strengths and limitations are described, and the comparability of the results from the different methods are considered. An important source of discrepancy among techniques originates from the different temporal and spatial scales that each method addresses (Li and Maestrini 1993). Our focus is a coastal marine ecosystem in the western Antarctic peninsula, the site of the Palmer Long-Term Ecological Research Program since 1990.

## General Considerations and Concepts

### *Gross and Net Primary Production*

Photosynthesis is often expressed in units of moles (or its mass equivalent) of carbon per unit cell (or volume of water containing cells) per unit time. This is an instantaneous rate (measured in milliseconds) which is integrated over time in order to be operational for estimations made in the field (Platt and Sathyendranath 1993). Over ecologically relevant periods (daily, annual, etc.), primary production is the organic C produced within that period that is made available to other trophic levels (Lindeman 1942). Methods of estimating primary production at the molecular and single-cell scale need to be scaled up in order to obtain a daily rate within a volume of seawater. When interest is aimed at primary production rates of a certain taxon, primary production rates are combined with cell size determinations or photosynthetic pigment complements (Gieskes et al. 1993).

Gross primary production (GPP) is the total number of electron equivalents originating from the photolysis of water (Fogg 1980; Falkowski and Raven 1997). Photosynthesis is defined as the conversion of light into metabolic energy (Fogg 1980); it is identical to gross photosynthesis,  $P_g$ . Net photosynthesis,  $P_n$ , is the difference  $P_g - R_l$ , where  $R_l$  is the respiratory loss in the light. Respiration is the conversion of metabolic energy into heat. These photosynthetic parameters are all rates; that is, time-dependent processes with dimensions of mass/time. Within planktonic communities, GPP is defined as photosynthesis not affected by respiration or the metabolism of heterotrophic organisms in the same body of water. Net primary production (NPP) is estimated as GPP corrected for algal respiration. Net ecosystem production (NEP) is GPP corrected for the metabolism of the entire autotrophic and heterotrophic community (community respiration, CR) and is defined as GPP minus CR (Williams 1993a). While the previous variables are based on C units, there exist parallel terms to express phytoplankton production in units of N (Dugdale and Goering 1967; Minas and Codispoti 1993).

### *An Overview of Methods*

Methods and instrumentation for estimating primary production in the field are constantly evolving. Although the  $^{14}\text{C}$  incubation remains the standard method against which most other methods are compared or calibrated (Williams 1993b), a new suite of methods has been introduced since the mid-1980s. The traditional method of cell enumeration with microscopy (Hewes et al. 1990) has been extended to include flow cytometry (Li 1993) based on cell fluorescent and size-related properties of single cells, molecular techniques with emphasis on understanding gene expression and controlling mechanisms in photosynthetic processes (La Roche et al. 1993), and isotope tracers including not only  $^{14}\text{C}$  or  $^{13}\text{C}$  (Goes and Handa 2002), but also  $^{15}\text{N}$  (Le Bouteiller 1993) and  $^{18}\text{O}$  (Bender et al. 1987). For fieldwork these techniques require sampling of a parcel of water which is isolated from the environment and is considered representative of the target population. Other methods involve direct, noninvasive measurements in the water column, such as the use of cellular fluorescence, both solar-induced (Doerffer 1993) and active fluorescence (Falkowski and Kolber 1993); diel variability in optical properties in the water column affected by particle dynamics (Siegel et al. 1989); and remote sensing of ocean color based on water-leaving surface reflectance (Hovis et al. 1980; Gordon et al. 1980; Gordon and Morel 1983). These latter techniques scale from seconds to months and from cm to hundreds of km. Specific application of these methods is dependent upon their suitability to address a particular research question. Finally, the use of nonconservative tracers such as  $\text{O}_2$ ,  $\text{CO}_2$ , and  $\text{NO}_3^-$  on ocean mesoscales (Emerson et al. 1993; Robertson and Watson 1993; Minas and Codispoti 1993) is designed to integrate whole community processes over time scales of days to months. This chapter will focus on radioactive tracers, fluorescence, and remote sensing techniques which are widely used in biological oceanography.

### *Space and Time Scales in Marine Ecosystems*

The oceans cover nearly three-fourths of the earth's surface and exhibit physical and biological variability over a wide range of space and time scales (Steele 1978). The space/time scales of marine and terrestrial systems can be significantly different (Steele 1991), and these differences often influence both our approach to studying the system and our way of understanding how various components of the system are interconnected. One important difference includes sampling strategies; that is, the way we obtain data from the field. Phytoplankton are embedded in a continually changing environment that regulates factors controlling cell growth rates (temperature, light, and nutrients) as well as factors that control the accumulation rate of cells in the euphotic zone and, hence, population growth (grazing, water column stability, and sinking). A second important difference is the trophic structure of, as well as the related size and growth structure within, the system. Third, although physical processes of the ocean and atmosphere follow the same basic laws of fluid dynamics (Pedlosky 1987), they have very different temporal and spatial scales of their underlying processes. In marine systems the space/time scales of the physics and biology are close, and their interactions are tightly coupled (Steele 1985). Thus

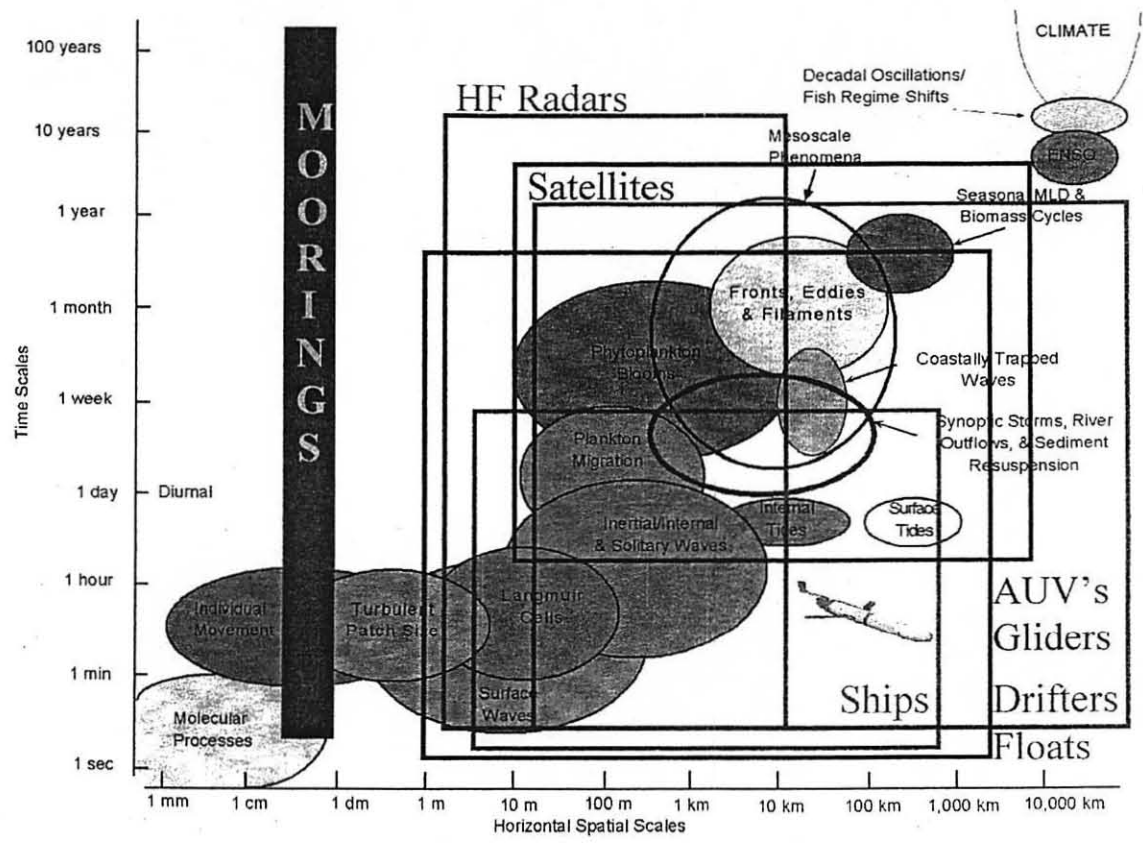
there can be a significant difference of emphasis, with focus on internal mechanisms in terrestrial studies and on external physical forcing in marine studies.

Multiplatform sampling strategies (Steele 1978; Esaias 1981; Smith et al. 1987; Dickey 2003) utilizing buoys, ships, aircraft, and satellites have been developed to meet the need to measure distributions of physical and biological properties of the ocean over large areas synoptically and over long time periods. Figure 9.1 compares the space/time domains of several physical and biological oceanic processes with space/time sampling regimes of various measurement platforms. Due to the wide range of space/time scales encompassed by marine organisms and the corresponding physical, chemical, and biological mechanisms that regulate their distributions, no single platform of data sensors is adequate to provide a comprehensive synoptic picture. With respect to estimates of primary production, ships can provide relatively accurate point data plus a wide variety of complementary physical, optical, chemical, and biological data, including water samples, from a range of depths in the water column. Ships, however, are disadvantaged by their limited spatial coverage. Moored buoys yield even less spatial coverage but have been utilized to provide long time series data at selected locations and to provide information as a function of depth. Aircraft and satellites permit regional and global coverage, and a wealth of horizontal detail impossible to obtain from ships and buoys alone, but these data are restricted to the upper few attenuation lengths in the water column.

Autonomous underwater vehicles (AUVs), drifters, and floats (Dickey 2003) are sampling platforms that have been developed to cover intermediate space/time scales. Optical sensors, providing proxy measures of various biological parameters, are typically deployed on in-water platforms such as buoys, AUVs, drifters, and floats, as well as aircraft and satellites. Indirect methods (discussed below) are used to estimate phytoplankton biomass and productivity from optical sensors deployed on these various platforms. The accuracy of NPP estimates, particularly in eutrophic coastal and upwelling areas, is hindered by the dynamic variability of the processes affecting production and the inability of a single-platform sampling strategy to provide the required synoptic data. Multiplatform sampling strategies and progress in more accurate quantification of remotely sensed observations have been used to lower the variances in estimates of NPP and have helped to identify the physical and biological factors responsible for these variances.

### **Experimental Approaches to Primary Production: The Radiocarbon ( $^{14}\text{C}$ ) Method**

The most widespread experimental approaches to estimating primary production in marine systems are based on incubation of a water sample, spiked with a radioactive isotope, for a known period of time. Typically, samples are obtained over a range of depths within the water column, where solar radiation stimulates photosynthesis. There are various experimental approaches with respect to the number of depths sampled and how these depths are selected. Also, the design and physical setup of incubators varies, as does the timing of the incubation start and end point. For some field experiments, in situ (IS) incubations can be used, in which samples



are returned to the depth and light conditions from which they were obtained. Alternatively, incubations can be carried out elsewhere (such as on the deck of a ship), under diverse conditions, usually with the attempt to simulate in situ conditions, especially light and temperature. Under such simulated in situ (SIS) conditions, factors are needed to convert estimated production rates to in situ estimates. Finally, there are several approaches to data analysis and presentation.

### *In Situ and Simulated In Situ Experiments*

The  $^{14}\text{C}$  method was introduced by Steeman Nielsen (1952) and measures the  $\text{CO}_2$  incorporation by addition of trace amounts of  $^{14}\text{C}$  bicarbonate in seawater (Vollenweider 1965; Parsons et al. 1984; Rai 2002; Scott 2002). This method is specific for autotrophic photosynthesis and can be used in mixed populations. Large amounts of  $^{14}\text{C}$  data exist, and it has become the standard method in marine research against which other methods are compared.

Samples for the  $^{14}\text{C}$  method are obtained from the euphotic zone, defined as the layer where there is sufficient irradiance to support net primary production ( $\text{NPP} > 0$ ). The compensation depth, where photosynthetic fixation balances respiratory losses over a day, is the base of the euphotic zone (see Platt et al. 1989 for a review). Since the euphotic depth is seldom measured directly, it is often estimated to be equal to the 1% (or sometimes the 0.1%) depth of the incident photosynthetically available radiation (PAR), although it is recognized that the compensation depth is probably variable (Falkowski and Owens 1978; Platt et al. 1990). It is assumed that phytoplankton is freely mixed within the upper mixed layer and that the mixed layer is shallower than the euphotic zone, permitting cells to remain exposed to light and production to exceed respiratory losses. The term "critical depth" was introduced to characterize the depth in the water column where net carbon production ( $\text{NCP} > 0$ ) (Nelson and Smith 1991).

For primary production determinations at a given oceanographic station, samples are typically taken throughout the upper water column with Niskin or Go-Flo bottles attached to a conductivity-temperature-depth (CTD) rosette. A water sample is placed in an incubation bottle for a known period of time. A major limitation of this method is that it requires incubation of a sample in a confined volume that can introduce "bottle effects" (Gieskes et al. 1979). In the early 1980s "clean methods" (principally taking extreme care to exclude minute concentrations of toxic trace metals) were introduced (Fitzwater et al. 1982). Data prior to the introduction of these clean methods are generally considered to underestimate true photosynthetic rates (Martin 1992).

For shipboard observations, ideally and whenever possible, samples are taken before dawn for incubations to start at sunrise. Samples for productivity measurements need to be processed quickly after collection to avoid contamination and to minimize phytoplankton changes. These processes include filtering out larger zooplankton, transferring the sample to light and dark incubation bottles, spiking the incubation bottles with  $^{14}\text{C}$ , and incubating the spiked samples. For in situ incubations the incubation bottles are replaced at the depth from which they were sampled for the duration of incubation. Alternatively, samples are incubated on deck in a setup simulating in situ conditions for light and temperature (Lohrenz et al. 1992; Lohrenz 1993).

$^{14}\text{C}$  incorporation into the sample is measured in units of disintegration per minute (DPM). The intensity of the signal is proportional to the beta particle emission from the  $^{14}\text{C}$  incorporated into the cells. Primary production is calculated as

$$P_z = (\text{DPM in the light bottle} - \text{DPM in the dark bottle}) / \text{volume sample filtered} * 24,000 * 1.05 * \text{hrs of incubation} / (\text{specific activity in the sample} / \text{volume specific activity}) \quad (2)$$

in units of  $[\text{mg C m}^{-3} \text{ h}^{-1}]$ , where  $P_z$  is production at depth  $z$ , total  $\text{HCO}_3^-$  in the water is  $\sim 24,000 [\text{mg C kg}^{-1}]$  (Carrillo and Karl 1999), and 1.05 is the discrimina-

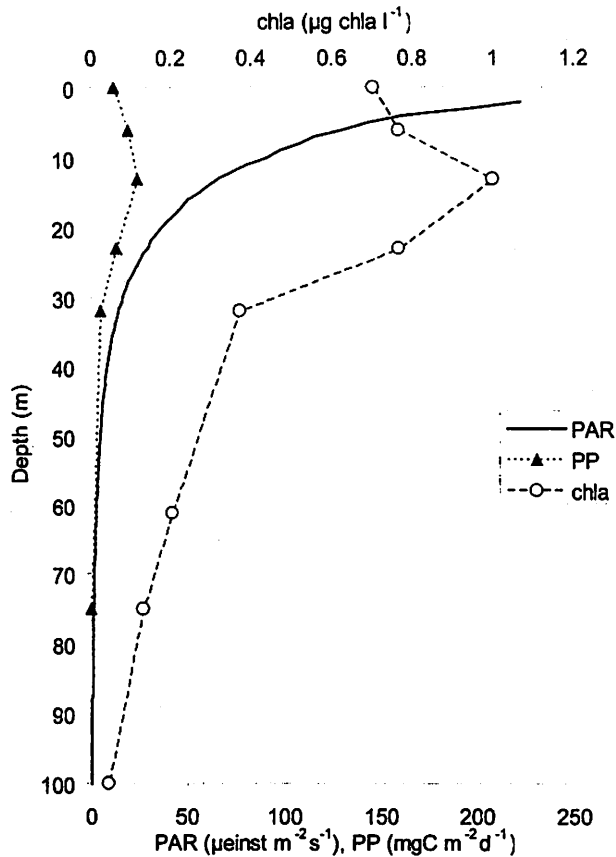


Figure 9.2. Profiles of phytoplankton biomass as chlorophyll  $a$  [ $\text{mg chla m}^{-3}$ ], photosynthetically active radiation (PAR) measured with a  $4\pi$  collector model QSP-200L4S from Biospherical Instruments, Inc. [ $\mu\text{Einst m}^{-2} \text{s}^{-1}$ ], and primary production [ $\text{mg C m}^{-3} \text{d}^{-1}$ ] measured with simulated in situ incubations on board ship for a coastal station in the western Antarctic peninsula (64.893S, 64.173W) in January 2003. Triangles and circles denote the depth of sampling at 100%, 50%, 25%, 10%, 5%, and 0.5% of incident radiation ( $E_0$ ). Euphotic zone was calculated as 1% of incident radiation at 61 m with corresponding integrated primary production of  $602 \text{ mg C m}^{-2} \text{d}^{-1}$  and integrated chlorophyll  $a$  of  $33 \text{ mg m}^{-2}$ .

tion factor between incorporation of  $^{14}\text{C}$  and  $^{12}\text{C}$ .  $P_z$  is the primary production expressed as C incorporated per unit volume of water per unit time (fig. 9.2). Daily  $P_z$  is calculated by converting the hours into a 24-hr day, and it is considered as NPP where the balance of photosynthesis – respiration is  $> 0$ . Furthermore,  $P^B$  [ $\text{mg C mg chl}a^{-1} \text{ h}^{-1}$ ] is defined as the assimilation number and is calculated as  $P_z$  per unit of biomass in the sample, usually chlorophyll *a*, in units [ $\text{mg chl}a \text{ m}^{-3}$ ]. The latter is used to standardize NPP when comparing different regions, and it is a measure of photosynthetic efficiency.

The  $^{14}\text{C}$  incorporation in the light bottle is considered to account both for biotic (i.e., photosynthesis and  $\text{CaCO}_3$  incorporation) and for abiotic (i.e., adsorption) processes (Banse 1993). Thus, the  $^{14}\text{C}$  incorporated is corrected by the dark bottle to account for biological  $^{14}\text{C}$  uptake that can occur outside photosynthesis. The incorporation of  $^{14}\text{C}$  into  $\text{CaCO}_3$  is corrected by sublimation with acid. Finally, a time-zero determination corrects for abiotic processes. In general, time-zero values should remain low (i.e.,  $< 5\%$ ) to indicate quality of the incubation.

Marra (1995) argues that the relevant time interval for estimation of ocean primary production is 24 hr. This time scale includes a whole photoperiod with maximum irradiance as well as night catabolism. In many instances, metabolic processes balance within a day. For experiments starting before dawn, production is positive during daylight and negative at night, and balancing daily primary production to initial values before dawn is recommended (Marra 2002). Cell division rates vary from hours to days; thus a 24-hr estimate fits with the ecology of most phytoplankton groups. Experimental approaches that last longer need to take into account biomass changes within the population and the efficiency of carbon transfer to other trophic levels. Shorter time scales will be more dependent on physiological properties of phytoplankton and will necessitate knowledge of physiological responses and how they vary within dominant groups in the sample.

### Determination of Light Field

In order to estimate water column productivity, it is necessary to sample as a function of depth. Typically, sampling depths are selected on the basis of the distribution of solar radiation within the water column. Light decreases exponentially, and sampling depths are defined as percentages of incident irradiance at the water surface, using the Lambert Beer law for predetermined light percentages:

$$E = E_0 \exp - (K_{\text{PAR}} * z), \quad (3)$$

where  $E$  is PAR [ $\mu\text{Einst m}^{-2} \text{ sec}^{-1}$ ] at depth  $z$ ,  $E_0$  is incident PAR just below the air-water interface,  $K_{\text{PAR}}$  is the attenuation coefficient in [ $\text{m}^{-1}$ ], and  $z$  [ $\text{m}$ ] is depth.  $K_{\text{PAR}}$  is estimated from measurement of PAR versus depth, where

$$K_{\text{PAR}} = - \ln (E_{z_2}/E_{z_1}) / (z_2 - z_1). \quad (4)$$

$E_{z_1}$  and  $E_{z_2}$  are irradiances at two different depths, and  $(z_2 - z_1)$  is the depth interval of the irradiance readings ( $z_2 > z_1$ ). To determine a sampling depth, for example, 50% of  $E_0$ ,



$$z = -\ln(E_z/E_0)/K_{PAR} = -\ln(0.5)/K_{PAR}$$

Ideally, incubations should replicate the light field from which a sample obtained. If incubations are done in situ, the light bottle is exposed to the and light quality at the depth sampled within the water column, and the  $\mu$  value is thus representative of environmental conditions at that depth. In in situ experiments, the different irradiance levels are simulated by the neutral density filters placed over the incubation bottles that screen surface to simulate the percent PAR from the depth sampled. Simulating the chan quality (i.e., spectral characteristics) with depth is not achieved by neutral filters. In general there is no consistent and accepted method to simulate characteristics with depth, but the difference in light exposure can be modeled (Barber et al. 1997). Depending on the body of water under study, or green filters have been recommended for the deep samples: green filters for productive waters and blue filters for more oceanic or oligotrophic environments. The addition of color filters increases primary production estimates at decreasing potential photoinhibition of cells suddenly exposed to white light (et al. 1993).

$^{14}\text{C}$  estimates of primary production usually lie somewhere between  $\mu$  and NPP. The degree to which the  $^{14}\text{C}$  incorporation approximates GPP is dependent on incubation time and photosynthetic rate (Williams 1993). Experiments of the  $^{14}\text{C}$  incorporation at varying photosynthetic and respiratory rates at different incubation show that at low respiration rates and short incubation times, the derived production is a reasonable approximation to GPP. In phytoplankton cultures under controlled conditions, when comparing  $^{14}\text{C}$  production and inorganic carbon (POC) accumulation (an index of NPP), experiments at low growth rates ( $<0.1 \text{ d}^{-1}$ ),  $^{14}\text{C}$  production is about 5 times higher than POC accumulation (Peterson 1978), and thus more closely approximates GPP. Under conditions of high respiration (rates similar to production),  $^{14}\text{C}$  production approximates GPP (Calvario-Martinez 1989). On the other hand, at high growth rates ( $>0.5 \text{ d}^{-1}$ ),  $^{14}\text{C}$  production and POC accumulation agree, indicating that under these conditions the  $^{14}\text{C}$  method more closely approximates NPP.

Scaling up daily primary production estimates measured on a per volume basis includes interpolation of data points. First, to estimate integral water column primary production in units of  $[\text{mg C m}^{-2} \text{ d}^{-1}]$ , individual sample depths are integrated by polynomial interpolation. It is assumed that the production between consecutive depths changes linearly and that any incubation less than 24 hours is prorated to a full day. Second, time integration is carried out by interpolation between sampling dates, as is done when calculating seasonal primary production. This provides a seasonal or annual estimate in units of  $[\text{mg C m}^{-2} \text{ mo}^{-1}]$  or  $[\text{mg C m}^{-2} \text{ y}^{-1}]$ . Finally, when estimating primary production in a region such as an embayment or a continental shelf, sampling stations are interpolated spatially and divided by the time interval under analysis, providing a measure in  $[\text{mg C m}^{-2} \text{ d}^{-1}]$ .

The frequency of sampling is determined by the question to be addressed. The dominant process controlling primary production in the biome of interest

termine the seasonal evolution and the interannual variability, sampling is carried out twice weekly (Vernet, unpubl. data). Thus, determining factors in scales less than 1 week is not possible. Mixing events that control the phytoplankton accumulation within surface waters are driven by large storms that on average pass through the region every few weeks. Each bloom is then characterized by an average of 5–7 data points, which provides detail on productivity increase, peak value, and decrease within each cycle. Within one growth season, defined by sun angle and ice cover to last between October and April, tens of sampling points provide definition of the bloom events within a season. Similar sampling carried out during the next season provides the additional data to compare annual NPP among seasons as well as the difference in frequency, intensity, and timing of the bloom events within each season.

### Laboratory Incubations

Photosynthesis versus irradiance curves (P vs. E curves) have been recommended over in situ or simulated in situ experiments as the best method to estimate NPP in predictive models of photosynthesis in ocean waters (Coté and Platt 1984). Estimates of productivity are based on determination of the response of phytoplankton incubated over a range of irradiances at in situ temperature. Two parameters are necessary to describe the P vs. E relationships: alpha ( $\alpha$ ), the initial slope of the light-limited portion photosynthesis, and  $P_{\max}$ , the light-saturated rate of photosynthesis. The photosynthetic response is modeled by curve-fitting. By transferring the modeled curve into the vertical gradient of the underwater light field, the vertical distribution of photosynthesis can be estimated.

Three models of curve-fitting have been the most commonly used in the literature, but care must be taken to recognize their intrinsic differences (Frenette et al. 1993). When no photoinhibition is present, production can be modeled as suggested by Webb et al. (1974):

$$P^B = P_M^B * (1 - \exp(-\alpha * E / P_M^B)), \quad (6)$$

or, as given by Platt and Jasby (1976):

$$P^B = P_M^B \tanh(\alpha * E / P_M^B), \quad (7)$$

where  $P^B$  is photosynthesis per unit biomass (or chlorophyll *a*) in units of [mg C (mg chl*a*)<sup>-1</sup> h<sup>-1</sup>],  $P_M^B$  is maximum rate of photosynthesis per unit chl *a*,  $\alpha$  is the initial slope in units of [mg C (mg chl*a*)<sup>-1</sup> h<sup>-1</sup> ( $\mu$ Einst m<sup>-2</sup> sec<sup>-1</sup>)<sup>-1</sup>], and *E* is irradiance in units of [ $\mu$ Einst m<sup>-2</sup> sec<sup>-1</sup>].

When photoinhibition is present, photosynthesis can be modeled as an extension of equation (6) (Platt et al. 1980):

$$P^B = P_S^B * (1 - \exp - (\alpha * E / P_S^B)) * \exp - (\beta * E / P_S^B), \quad (8)$$

where all variables are defined as before and beta ( $\beta$ ) is the photoinhibition parameter with the same units as  $\alpha$ , and where

$$P_{\max} = P_s [\alpha / (\alpha + \beta)] [\beta / (\alpha + \beta)]^{\beta / \alpha}. \quad (9)$$

Unlike IS and SIS, where one determination is taken at each depth, in P vs. E curves a suite of light and dark bottles are incubated at different irradiances for each depth sampled. All incubations are thus done *in vitro*, and neutral filters are used to simulate varying irradiances (but see Lohrenz et al. 1992). Incubations are usually short, from 1 to 4 hr, because the response curve is determined before photoacclimation. Most recently, P vs. E curves have been determined with increased numbers of light treatments (e.g., 25) and decreased volume of incubation (e.g., 2 ml; fig. 9.3). Sensitivity of the determination is preserved by increasing the specific activity of the sample. Irradiance levels usually range from 0 to

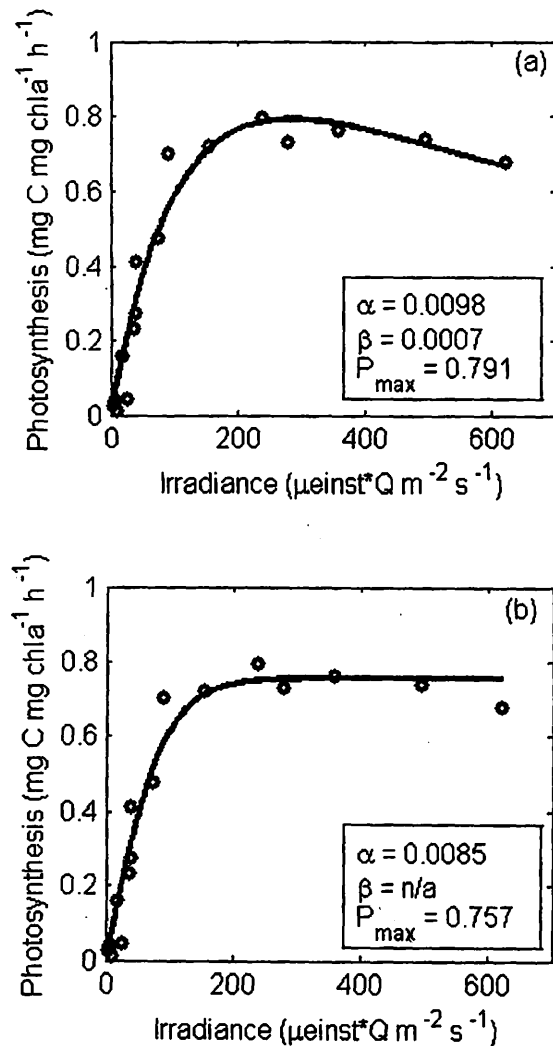


Figure 9.3. Photosynthesis [mg C chl a<sup>-1</sup> h<sup>-1</sup>] versus irradiance [μEinst m<sup>-2</sup> s<sup>-1</sup>] determined with <sup>14</sup>C incubations in the western Antarctic peninsula. Curvefitting with (a) equations (8) and (9) (Platt et al. 1980) and (b) equation (7) (Platt and Jasby 1976).

1000  $\mu\text{Einst m}^{-2} \text{sec}^{-1}$ , although adjustments in the light range are necessary in different geographic locations and depend on the time of the year. For example, Antarctic samples are usually exposed to 0–600  $\mu\text{Einst m}^{-2} \text{s}^{-1}$ , while open ocean samples in the North Pacific are exposed to 0–2000  $\mu\text{Einst m}^{-2} \text{s}^{-1}$ . Relatively high irradiances are needed to determine the photoinhibition factor ( $\beta$ ).

Value of the modeled productivity is dependent on the analytical quality of the P vs. E curves and their accuracy with respect to in situ production rates. It is recommended that incubators also simulate in situ light quantity with the addition of neutral filters. Similar to SIS incubations, determination of the light quality can be achieved through the use of colored filters. More accurate determination can be achieved with the use of solar simulators. Furthermore, the value of  $P_{\text{max}}$  is a function of ambient temperature (Geider and MacIntyre 2002). Acclimation is sufficiently fast that  $P_{\text{max}}$  may differ for the same sample incubated at several temperatures (fig. 9.4). It is recommended that incubations be carried out at in situ temperatures. Alternatively, if the temperature in both the water and the incubator is known, a predetermined  $Q_{10}$  can be applied for correction (Tilzer et al. 1993). Finally, the accuracy of the P vs. E determination is compromised if the natural variability of  $\alpha$  or  $P_{\text{max}}$  is not included in the primary production estimate. Changes in irradiance with depth determine the value of  $\alpha$  in situ. The value of  $\alpha$  is proportional to the light acclimation of the cells in the field. Thus, for each water column, several P vs. E determinations are needed. Furthermore, if temperature changes with depth (e.g., the euphotic zone is deeper than the mixed layer and the bottom of the euphotic zone is at different temperature), then  $P_{\text{max}}$  will change with depth in the water column, thus influencing the estimated productivity and requiring a further correction for temperature (see above).

## Experimental Approaches to Primary Production: Oxygen Methods

### *Oxygen Production*

Oxygen evolution is a primary by-product of the splitting of the  $\text{H}_2\text{O}$  molecule during photon absorption (Falkowski and Raven 1997). Increased  $\text{O}_2$  concentration in a water sample is proportional to photosynthesis, and thus to production. Under light,  $\text{O}_2$  production is measured as the difference between initial and final  $\text{O}_2$  concentration in a light bottle. In the water column, bottles are incubated at different irradiances, as explained for the  $^{14}\text{C}$  method, to estimate water column production. Oxygen evolution from photosynthesis can be masked by  $\text{O}_2$  consumption by respiration, since both happen simultaneously in the cells. To account for this process, dark bottles are incubated concurrently with light bottles. Assuming respiration is the same under dark and light conditions, gross production is calculated from  $\text{O}_2$  increase in the light bottle + consumption in the dark bottle. The proportion of  $\text{O}_2$  produced to C uptake or  $\text{O}_2$  evolved to  $\text{CO}_2$  assimilated is the photosynthetic quotient (PQ). For healthy, nutrient-replete cultures, PQ is 1.2 to 1.8, consistent with protein and lipids as the major products of photosynthesis (Laws 1991). (For further discussion of this method, see chapter 10 of this volume.)

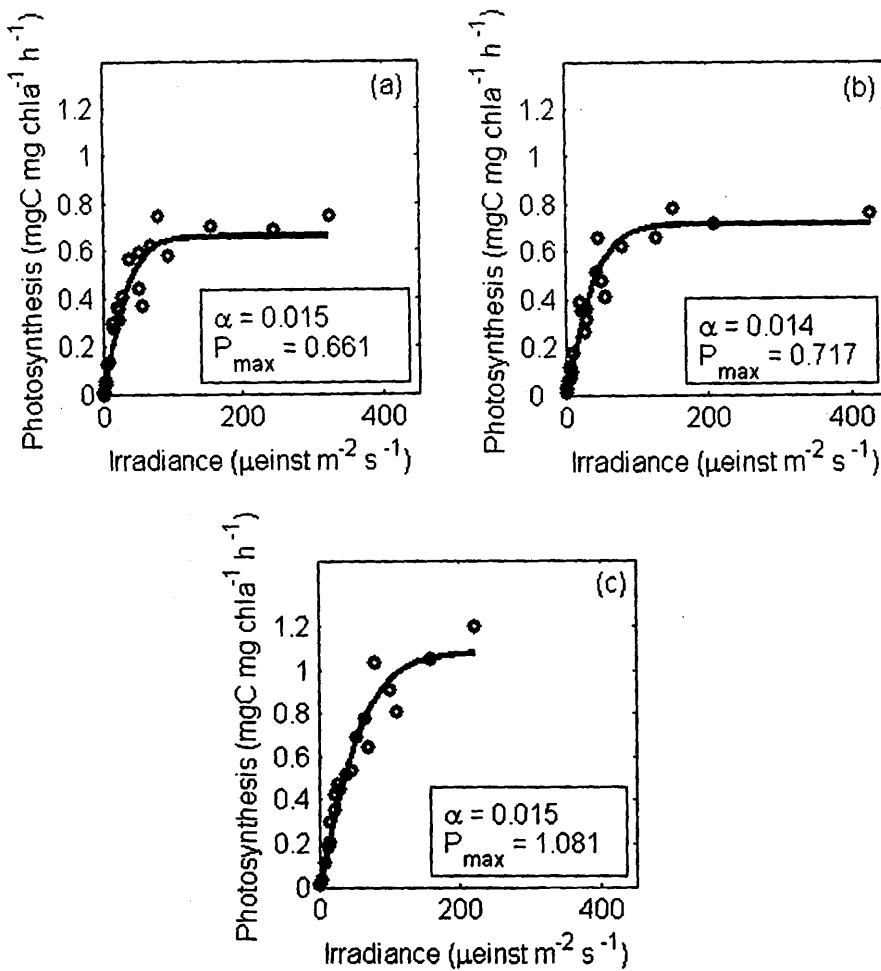


Figure 9.4. Photosynthesis [mg C chl a<sup>-1</sup> h<sup>-1</sup>] versus irradiance [μEinst m<sup>-2</sup> s<sup>-1</sup>] determined with <sup>14</sup>C incubations in the western Antarctic peninsula at different temperatures to show dependence of P<sub>max</sub> on temperature: (a) -1.5° C lower than ambient temperature, (b) incubation at ambient temperature, and (c) +1.5° C higher than ambient temperature.

Oxygen consumption by respiration in plankton samples has both autotrophic and heterotrophic components. Heterotrophic respiration by microzooplankton and bacteria can be higher than autotrophic O<sub>2</sub> production, so that net community production is negative.

#### The <sup>18</sup>O Method

Similar to the <sup>14</sup>C method, the <sup>18</sup>O tracer method was developed to measure gross production in vitro with light and dark bottles (Bender et al. 1987). This is an exten-

sion of  $O_2$  production, but in this case  $O_2$  is measured not by concentration but by using a radioactive tracer.  $^{18}O$  is an oxygen isotope with natural abundance of 0.204 atom%, while the major isotope  $^{16}O$  has an abundance of 99.758%. The  $^{18}O$  method involves spiking a water sample with  $H_2^{18}O$ , incubating in the light, and measuring the amount of  $^{18}O_2$  produced during photosynthesis. All  $O_2$  is in a dissolved phase and the ambient  $O_2$  is so large (150  $\mu M$ ) that only a negligible amount of  $O_2$  will be recycled by respiration during the incubation. Consumption has a very small effect on the  $^{18}O:^{16}O$  ratio, such that the ratio can be considered constant throughout the incubation. The only unknown source of error would be intracellular recycled  $O_2$ .

## Further Considerations on Experimental Methods

### *What Is Estimated Using the $^{14}C$ Method?*

By comparing the method of  $^{14}C$  incorporation with the  $O_2$ -based methods, we can evaluate what is estimated by using the  $^{14}C$  method in field measurements. As mentioned above,  $^{14}C$  estimates approximate gross or net primary production or something in between, depending upon conditions. In the North Atlantic, Marra (2002) observed that  $^{14}C$  underestimated gross primary production (as measured by the  $^{18}O$  method) (fig. 9.5).  $^{14}C$  agreed only with net primary production measured with  $O_2$  production bottles over a 24 hr period. According to these comparisons, the  $^{14}C$  method seemed to best approximate net community production. This result might be due to the fact that gross C uptake and gross  $O_2$  production cannot be equated because they are associated with different biochemical pathways within the cell. Ryther (1956) encountered similar discrepancies in culture experiments. He concluded that respired  $CO_2$  is reassimilated in photosynthesis, whereas  $O_2$  released in photosynthesis is not reassimilated by respiration. This conclusion agrees with modeled data where most, if not all, respired  $CO_2$  is refixed as photosynthesis (Williams 1993b). Thus, as measured by  $^{18}O$ , there is an imbalance between  $CO_2$  and  $O_2$  dynamics. If that is so, the cells use proportionally more  $H_2O$  (and  $H_2^{18}O$ ) than external  $CO_2$ , because internal  $CO_2$  from respiration is a source. This would mean higher  $^{18}O$  uptake than  $^{14}C$  uptake for the same production rate. Thus, it would appear that  $^{18}O$  more closely approximates gross photosynthesis and  $^{14}C$  more closely approximates net photosynthesis. If respiration is low (i.e., low  $CO_2$  from respiration is available for photosynthesis), the  $^{14}C$  method would approximate gross production. Under all other conditions the  $^{14}C$  uptake approximates net production (Marra 2002; Williams 1993a).

### *Errors and Limitations*

Accurate estimation of daily water-column primary production is challenging by its very definition: the extrapolation of results from short incubations to daily rates; from results obtained in small containers scaled to ecologically relevant spatial scales; and the influence of respiration and heterotrophic activity on gross vs. net estimations.

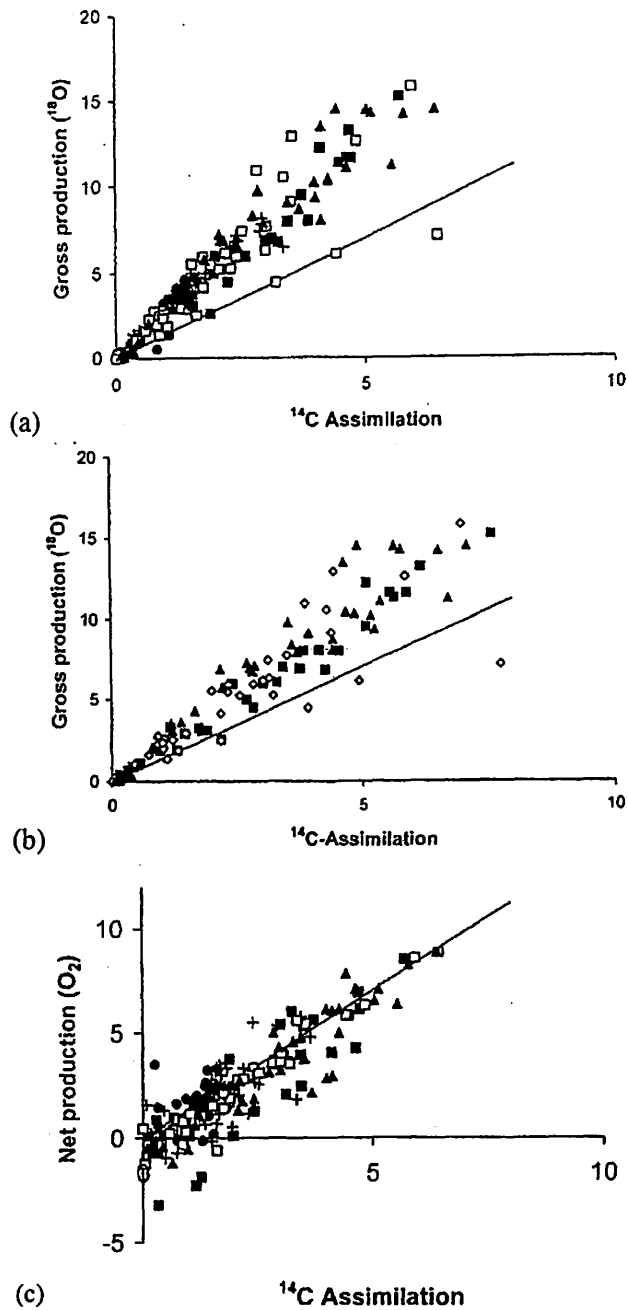


Figure 9.5. Comparison of different approaches to measuring primary production in marine phytoplankton. (a) Gross primary production measured with  $^{18}\text{O}$  (Bender et al. 1987) and daily primary production measured with 24-hr in situ  $^{14}\text{C}$  incubations. (b) Gross primary production measured with  $^{18}\text{O}$  and primary production estimated with daytime in situ  $^{14}\text{C}$  incubations. (c) Daily net primary production measured with light-dark  $\text{O}_2$  production compared to daily  $^{14}\text{C}$  assimilation. Data obtained during several cruises in the North Atlantic and equatorial Pacific. Reproduced from Marra (2002) with permission from Blackwell Publishing.

The action spectrum of photosynthesis, the solar spectrum, and the underwater light field all vary as a function of wavelength. The spectral characteristics of underwater irradiance change as the irradiance is transmitted downward through the water column. Maximum penetration occurs in the green (530 nm) in coastal waters and in the blue (485 nm) in open ocean (Tyler and Smith 1970). The differential absorption through the water column is due to absorption by water per se, to phytoplankton particles (via their photosynthetic pigments), to dissolved organic matter (DOC), and to any suspended inorganic material. If the measurements are done in situ, this potential problem is minimized (Dandonneau 1993). If the profile of primary production with depth within the euphotic zone is measured with SIS incubations on ship deck, then the matching of the vertical variability in the water column requires a more rigorous treatment. The addition of either blue or green filters to better simulate natural light conditions at low irradiances has been found necessary for accurate estimates of both  $\alpha$  and  $P_{\max}$  (Tilzer et al. 1993).

It has been calculated that if the water column is uniformly mixed, ignoring spectral effects can lead to an error as high as 30% of the integrated primary production (Platt and Sathyendranath 1991). When biomass distribution is nonuniform with depth, error can reach 60%. The key factor to consider is the depth dependence of the attenuation coefficient of light. These errors may be further minimized with information and modeling of the spectral attenuation coefficient (Tilzer et al. 1993).

Heterotrophic activity and phytoplankton physiological state can adversely affect estimates using the  $^{14}\text{C}$  method. The onset of nutrient limitation or the production of  $\text{NH}_4$  by microzooplankton during the incubation period can either depress or stimulate production estimates, but experimental evidence to date indicates this influence is typically insignificant (Harrison 1993). DOC released by the cells during incubation can lead to underestimation of the amount of  $^{14}\text{C}$  fixed if the  $\text{DO}^{14}\text{C}$  returns to the dissolved pool (Jackson 1993). If the  $\text{DO}^{14}\text{C}$  is taken up by heterotrophs, thus returning  $^{14}\text{C}$  to the particulate pool, the analytical technique used to concentrate phytoplankton (i.e., the pore size of the filters used) will determine if this fraction is or is not accounted as primary production.

### Indirect, Noninvasive Methods of Measuring Primary Production

A new generation of instruments and methods, based on fluorescent properties of photosynthesis, has emerged in oceanography during the past few decades. These methods are noninvasive, and do not depend on incubation of small samples captured from the water column. An important advantage of these measurements is that they permit higher temporal sampling rates that are more closely matched to sampling rates for physical variables (e.g., temperature, salinity, oxygen, etc.), which allows for a better coupling between environmental and production measurements.

Fluorescence is the production of visible light emitted by specific molecules at longer (or less energetic) wavelengths than the wavelengths absorbed. In the case of photosynthesis, chlorophyll *a* absorbs energy in the blue region of the spectrum (430–440 nm) and emits in the red region (680–685 nm), corresponding to the Sorel



maxima of absorption for chlorophyll *a* (Jeffrey et al. 1997). After photon absorption by chlorophyll *a*, the energy can be used for photochemistry, lost as heat, or emitted as light through fluorescence. As a first approximation, it would seem that fluorescence would be inversely proportional to photosynthesis. The relationship is not strong, however, because fluorescence is highly dependent on intensity and quality of the incident light. Low irradiance levels of incident light induce fluorescence that has a positive correlation with chlorophyll *a* concentration in the cell. High irradiance levels of incident light quench chlorophyll fluorescence in a nonphotochemical process. Furthermore, the dynamics of chlorophyll fluorescence shows a time-dependent response which can be used to infer several biophysical variables related to photosynthesis (Falkowski and Kolber 1993).

### *Passive Fluorescence Methods*

Fluorescence can be induced by both solar radiation and artificial illumination. In vivo solar-induced fluorescence can be measured passively and detected at 683 nm in near-surface waters (Kiefer et al. 1989; Chamberlin et al. 1990). Measurement of solar-induced fluorescence is accomplished by lowering a photometer with appropriate band-pass filter into the water to obtain a continuous vertical profile of fluorescence. Photometers to detect in vivo fluorescence can be deployed on buoys to obtain data over diel cycles. In vivo fluorescence can also be measured as a component of water-leaving radiance at 683 nm by new satellite sensors with multi-spectral resolution (Topliss and Platt 1986; Doerffer 1993).

Natural fluorescence emitted mostly from Photosystem II by the cells ( $F_f$  in [Einst  $m^{-3} s^{-1}$ ]) is a product of the flux of absorbed light ( $F_a$  in [Einst  $m^{-3} s^{-1}$ ]) and the quantum yield of fluorescence ( $\Phi_f$  in [Einst emitted/Einst absorbed]).

$$F_f = \Phi_f * F_a \quad (10)$$

and

$$F_a = a_c * E_o \quad (11)$$

where  $a_c$  is the absorption coefficient for phytoplankton [ $m^{-1}$ ] and  $E_o$  is irradiance in [Einst  $m^{-2} s^{-1}$ ]. Similarly,

$$F_c = \Phi_c * F_a \quad (12)$$

where  $F_c$  is the rate of carbon incorporation in [g-at C  $m^{-3} s^{-1}$ ] and  $\Phi_c$  is the quantum yield of photosynthesis in [g-at C fixed/Einst absorbed]. Combining the last three equations, primary production can be estimated (where the relevant parameters are determined at each depth  $z$  in the water column) from the model,

$$F_c = (\Phi_c / \Phi_f) * \Phi_f * a_c * E_o \quad (13)$$

for 24 hr and at depth  $z$ . Field tests using  $^{14}C$  incubations have shown that  $F_c$  can be modeled from natural fluorescence over a range of three orders of magnitude in production. This method approximates GPP as it relates to photon absorption. Fluorescence measured in the field can be overestimated because of fluorescence from detrital chlorophyll or phaeopigments, and can be underestimated by the

presence of planktonic cyanobacteria because most of the chl *a* is associated with the Photosystem I. Modeling primary production based on fluorescence measurements is also subject to variability because  $\Phi_f$  is a function not only of light but also of nutrient status (Chamberlin et al. 1990).

### Active Fluorescence Methods

Lamp-induced fluorescence measurements are based on the dynamics of fluorescence decay in the first few milliseconds after a light flash (Rabinowitch and Govindjee 1969). Under weak flashes, pigment reaction centers remain open (i.e., they continuously receive photons because some molecules within the antenna pigment always remain in the ground state). Under strong flashes, all the chlorophyll molecules in the antenna pigment saturate, the reaction centers close (i.e., no more photons are absorbed). By using an appropriate combination of weak and strong flashes, several parameters of the fluorescence decay can be determined ( $F_o$ , or baseline fluorescence, and  $F_m$ , maximum fluorescence). A third term, variable fluorescence ( $F_v$ ), is defined as the difference between maximum and baseline fluorescence ( $F_m - F_o$ ). The quantum yield of photochemistry ( $\Phi_f$ ), related to photosynthesis and thus to productivity, is defined as  $F_v/F_m$  or  $(F_m - F_o)/F_m$ . The pulse-amplitude-modulated (PAM) fluorometer uses repeating strong flashes of light against a continuous background of weak light in order to determine  $F_m$  and  $F_o$ . This technique may be used to model productivity (Neale and Priscu 1998; Hartig et al. 1998; see also chapter 10, this volume).

A second-generation fluorometer was designed to address some of the limitations of PAM fluorometry (Kolber et al. 1998). The fast repetition rate fluorometry (FRRF) was developed to obtain specific parameters needed to model production (e.g., the cross section for absorption of irradiance ( $\sigma_{PSII}$ ) and the parameter for photochemical quenching ( $q_p$ ),  $1/\tau$ , which gives the rate of electron transport from initial donor ( $H_2O$ ) to final acceptor ( $CO_2$ ). In FRRF, plankton cells are exposed to a series of flashes at subsaturating intensities. The rapid series of flashes produces an increase in fluorescence as the antenna pigment reaches saturation. The rate of fluorescence increase is related to the functional cross section of Photosystem II, while the subsequent rate of fluorescence decay at subsaturating light is a measure of the time constant of reoxidation of  $Qa^-$ , which can be related to the turnover time of photosynthesis at irradiance levels that completely reduce the PQ pool. Turnover time of photosynthesis is  $1/I_k \sigma_{PSII}$ . Quantum yield for fluorescence ( $\Phi_{max}$ ) is calculated from these variables.

By measuring  $\sigma_{PSII}$ ,  $\Delta\Phi_{max}$  of fluorescence,  $q_p$ , and incident PAR ( $E_o$ ), we can calculate the noncyclic electron transport rate of each PSII reaction center as

$$P_f = [\Delta\Phi_{max}/0.65] q_p * E_o * \sigma_{PSII} \quad (14)$$

It is assumed that there is a constant ratio of PSII reaction centers to chl *a* (~1500, in moles). Furthermore, to derive photosynthetic rates it is assumed that 4 electrons are required to reduce a molecule of  $CO_2$  to the level of carbohydrate, and that the only terminal electron acceptor is  $CO_2$ —this is the upper limit approximation.

Then

$$P_C^B = P_f * b/4, \quad (15)$$

where  $P_C^B$  is the chlorophyll-specific rate of C fixation [moles of  $\text{CO}_2$  mole<sup>-1</sup> chl  $\text{a}^{-1}$   $\text{t}^{-1}$ ],  $P_f$  is the fluorescence-based rate of photosynthetic electron flow [e- reaction center<sup>-1</sup>  $\text{t}^{-1}$ ], and  $\Delta\Phi_{\text{max}}$  is scaled to the maximal value of 0.65. Short-term photosynthetic rates calculated from  $F_v/F_m$ , as measured with an FRRF in the field (fig. 9.6) correlate positively with hourly <sup>14</sup>C incubation in field samples (fig. 9.7), suggesting this is a viable method for fast, incubation-free, and noninvasive determination of photosynthetic electron transport (Kolber and Falkowski 1993).

### Errors and Limitations

Estimating primary production from passive solar-induced fluorescence requires the assumption of a constant quantum yield of fluorescence. The FRRF technique has shown that this is not a valid assumption for fieldwork, since nutrient conditions as well as irradiance levels affect this yield (Falkowski and Kolber 1993). In addition, there is no estimate of fluorescence quenching at high irradiance. This effect cannot be corrected without active measurements of fluorescence. Finally, the

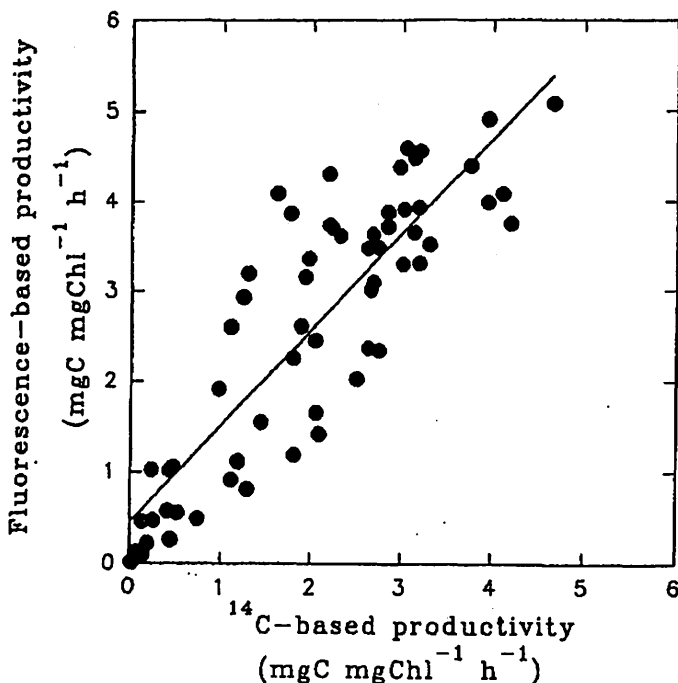


Figure 9.6. Fluorescence-based primary production calculated from the fast repetition rate fluorometer (FRRF), compared to short-term incubations with <sup>14</sup>C in [ $\text{mg C mg chl}^{-1} \text{ h}^{-1}$ ]. Reproduced from Falkowski and Kolber (1993) with permission from International Council for the Exploration of the Sea.

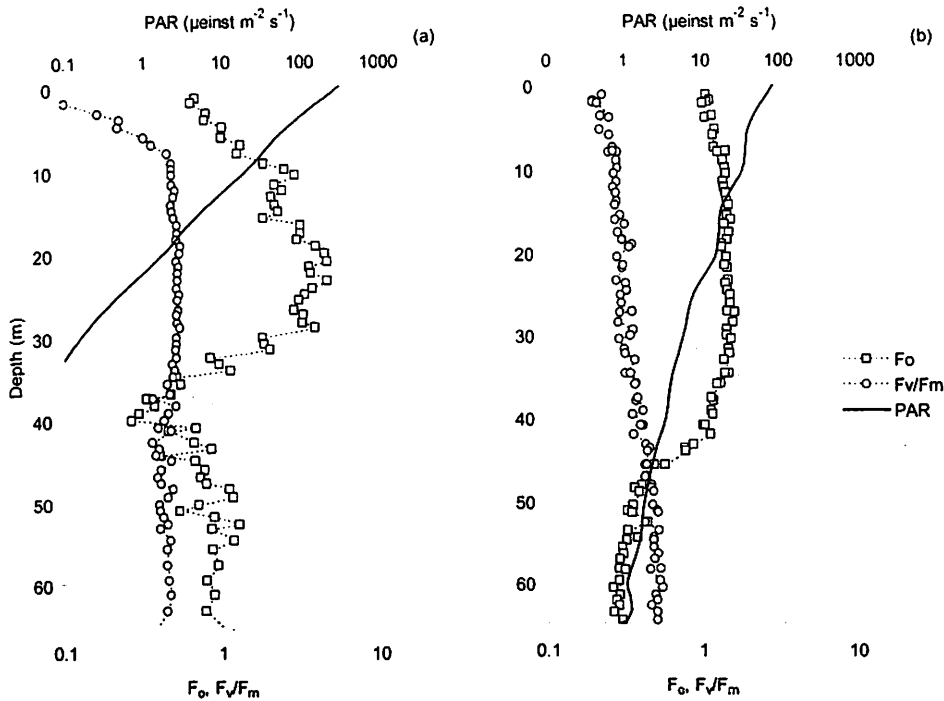


Figure 9.7. Profiles of baseline fluorescence ( $F_0$ ) (squares) and  $F_v/F_m$  (rounded squares) from the fast repetition rate fluorometer (FRRF), collected on the western Antarctic peninsula. PAR (solid line) at each station is also shown. (a) Coastal station in Marguerite Bay, western Antarctic peninsula. (b) Slope waters of the continental shelf at similar latitude as (a).

method assumes that the quantum yield of fluorescence changes similarly to the quantum yield of carbon (Kiefer et al. 1989). Laboratory studies show that the two quantum yields vary as passive fluorescence signal increases almost linearly over the whole range of irradiances, while C fixation saturates at irradiance levels above  $E_k$ . The consensus is that fluorescence methods are very promising and that we need more studies to interpret the fluorescent signal in the field as it relates to NPP estimates (Laney 1997). As the method becomes more widely used, a better characterization of its results and limitations is becoming available (Laney 2003).

All fluorescence methods make use of short time intervals, from milliseconds to minutes, and necessitate a knowledge of their response to environmental variability and an estimate of that variability in order to scale up to daily rates. The challenge is to integrate biophysics with ecological scales of interest.

## Remote Sensing

The most effective (and perhaps the only practical) way to adequately sample the space/time variability of the 75% of the earth's surface covered by oceans is by

means of remote sensing. Phytoplankton is mechanistically linked with optical properties of the ocean, so the determination of in-water optical properties offers the possibility of both synoptic (e.g., via satellite) and continuous (e.g., via moorings) estimation of pigment biomass parameters over a range of space and time scales. As a consequence, there has been considerable progress in the development and use of optical proxy measures of pigment biomass and phytoplankton production, and in the use of bio-optical models that can accommodate data from satellites and aircraft as well as a range of in-water platforms such as ships, moorings, autonomous underwater vehicles, drifters, and gliders (Dickey 2003). These approaches are in many ways analogous to those for terrestrial ecosystems described in chapter 11 of this volume.

### *Biomass Estimates by Remote Sensing*

It has long been recognized (Kalle 1938; Jerlov 1951; Yentsch 1960; Morel and Smith 1974; Morel and Prieur 1977) that the color of ocean waters varies with the concentration of dissolved and suspended material (i.e., that the spectrum of backscattered sunlight shifts from deep blue to green as the concentration of phytoplankton increases). That ocean color could be detected by remote optical sensors led to the desire to relate ocean optical properties, in particular upwelled spectral radiance from the sea surface, to the various constituents of the medium (Duntley et al. 1974). These early studies led to the development and launch of the coastal zone color scanner on the Nimbus-7 satellite in October 1978 (Hovis et al. 1980; Gordon et al. 1980) and to subsequent advances in ocean color satellite systems. A more recent (May 2004) accounting by the International Ocean-Color Coordinating Group (IOCCG) lists ocean color satellite missions deployed by various international space agencies: eight historical sensors, nine current sensors, and five scheduled sensors ([http://www.ioccg.org/semsprs\\_ioccg.html](http://www.ioccg.org/semsprs_ioccg.html)). This advancement in satellite technology has been accompanied by significant advances in bio-optical field instruments and methods, and improved theoretical analyses, both of which are enhancing our understanding of marine ecosystems.

Early workers using ocean color satellite observations focused on the retrieval of regional and global near-surface chlorophyll *a* ( $\text{Chl}_{\text{sat}}$ , [ $\text{mgChl m}^{-2}$ ]) concentrations and the quantitative comparison with ship-based observations (Gordon et al. 1980; Smith and Baker 1982; Gordon and Morel 1983). Early algorithms for estimating  $\text{Chl}_{\text{sat}}$  were empirically derived by statistical regression of radiance ratios at different wavelengths versus chlorophyll *a*. In spite of their simplicity, these algorithms captured roughly two-thirds of the variation in radiance band ratios and the three orders of magnitude variation in  $\text{Chl}_{\text{sat}}$ . When limited to waters in which phytoplankton and their derivative products play a dominant role in determining their optical properties (so-called Case 1 waters; Morel and Prieur 1977), these pigment algorithms enabled the retrieval of chlorophyll *a* from satellite observations with an accuracy of roughly  $\pm 35\%$  (Smith and Baker 1982; Gordon and Morel 1983). This estimated accuracy is a baseline against which more recent and improved algorithms can be compared.

Ocean color pigment algorithm development is an ongoing process. O'Reilly and a host of coauthors (1998, 2000) evaluated numerous pigment algorithms suit-

able for operational use by the SeaWiFS (Sea-viewing Wide Field-of-view Sensor) Project Office (Firestone and Hooker 1998; McClain et al. 2004). Their goal was to permit estimation of in situ  $\text{Chl}_{\text{sat}}$  concentrations with the highest possible accuracy and precision over a wide range of bio-optical conditions and with due consideration to the atmospheric correction algorithms necessary for accurate retrievals. There has also been advancement in so-called semi-analytic algorithms that seek improvements in understanding the theoretical linkages between biological constituents and their corresponding optical properties (Gordon et al. 1988; Morel and Berthon 1989; Morel 1991; Platt et al. 1992; Garver and Siegel 1997; Carder et al. 1991). To date, empirical algorithms generally perform better than semi-analytic algorithms when considering both statistical and graphical criteria (O'Reilly et al. 1998, 2000). Also, it is recognized that algorithms designed for global scales may be less accurate than algorithms tuned for local and regional scales, and considerable current research is devoted to improving both regional and global algorithms. Because algorithm development progresses rapidly, interested readers should consult Web sites for specific satellite sensors to obtain the most recent developments (e.g., <http://www.iocccg.org>).

### Modeling Primary Production

Prior to the advent of satellite ocean color sensors, estimations of regional and global ocean production were biased by the errors associated with the inability to sample on the appropriate time and space scales (Harris 1986). Bidigare et al. (1992) discuss the scaling of discrete measurements to remote observations and note that this linkage requires mathematical models relating measurable optical properties to desired biological parameters. They also review the evolution of bio-optical production models which can accommodate ship, mooring, and satellite data. Early workers (Talling 1957; Rodhe 1966; Ryther and Yentsch 1957) related NPP to the product of chlorophyll biomass, daily integrated surface solar radiation, a parameter to estimate attenuation of photosynthetically available radiation (PAR) within the water column, and a variety of variables associated with the photophysiological, quantum or assimilation efficiencies of phytoplankton. Behrenfeld and Falkowski (1997b) reviewed the development of phytoplankton primary productivity models and showed a "fundamental synonymy" between nearly two dozen models developed since the 1960s. These authors noted that "all of these models can be related to a single formulation equating depth-integrated primary production ( $\text{PP}_{\text{eu}}$  [ $\text{mgC m}^{-2} \text{d}^{-1}$ ]) to surface phytoplankton biomass ( $\text{Chl}_{\text{sat}}$  [ $\text{mgChl m}^{-3}$ ]), a photoadaptive variable ( $\text{P}^{\text{b}}_{\text{opt}}$  [ $\text{mgC}(\text{mgChl})^{-1} \text{h}^{-1}$ ]), euphotic depth ( $Z_{\text{eu}}$  [m]), an irradiance-dependent function ( $f(E_{\text{par}})$ ), and day length (DL [ $\text{h d}^{-1}$ ])":

$$\text{PP}_{\text{eu}} = \text{Chl}_{\text{sat}} Z_{\text{eu}} f(E_{\text{par}}) \text{DL P}^{\text{b}}_{\text{opt}}, \quad (16)$$

where  $\text{PP}_{\text{eu}}$  is the daily C fixation integrated from the surface to the euphotic depth ( $Z_{\text{eu}}$ ) and  $\text{P}^{\text{b}}_{\text{opt}}$  is the maximum chlorophyll-specific C fixation rate observed within a water column measured under conditions of variable irradiance during incubations typically spanning several hours (equivalent to  $\text{P}_{\text{max}}$  as determined by P vs. E

curves).  $PP_{eu}$  may be considered a measure of net primary production (NPP) because this equation is based on  $^{14}C$  incubations.

Behrenfeld and Falkowski (1997a) assembled a data set of 11,283  $^{14}C$ -based measurements of daily C fixation from 1698 oceanographic stations in both ocean and coastal waters. When they partitioned the variability in  $PP_{eu}$  into the variability associated with each of the variables in equation (16), they found that nearly all (~85%) could be attributed to changes in depth-integrated biomass (i.e.,  $Chl_{sat} Z_{eu}$ ) and the horizontal variability in the photoadaptive variable  $P^b_{opt}$ . Making use of their large database, they developed a vertically generalized production model (VGPM; eq. [16]), discussed the limitations of productivity models, estimated total global annual productivity, and compared their results with those of earlier ship-based global estimates (Eppley and Peterson 1979; Longhurst et al. 1995; Antoine et al. 1996).

Integrated estimates of primary production based on satellite measurements for both oceanic and terrestrial ecosystems have been presented by Field et al. (1998) and Behrenfeld et al. (2001). For both land (Monteith 1972) and oceans (Morel 1991), NPP can be computed as the product of the absorbed photosynthetically active (400–700 nm) solar radiation (APAR) and an average light utilization efficiency ( $\epsilon$ ):

$$NPP = APAR \epsilon. \quad (17)$$

These authors note that while models based on this approach are “diverse in terms of mechanistic detail, they are all strongly connected to global-scale observations.” The uncertainty in  $\epsilon$  is a primary source of error for both land and ocean NPP estimates. Both the Carnegie-Ames-Stanford for land (CASA; Potter et al. 1993) and the VGPM (eq. [16]) models are conceptually similar (eq. [17]), and can be used to estimate primary production for the whole biosphere. The SeaWiFS sensor was the first satellite instrument with both the spectral coverage and the dynamic range necessary to derive both  $Chl_{sat}$  and NDVI (the Normalized Difference Vegetation Index used in the CASA and other terrestrial models) (Behrenfeld et al. 2001). Their observations allowed the comparison of simultaneous ocean and land NPP responses to a major El Niño-to-La Niña transition, and were the first single-sensor global observations of the photosynthetic biosphere. The CASA-VGPM model gave an NPP estimate for the total biosphere of 104.9 [ $Pg\ C\ yr^{-1}$ ] (annual mean for the period September 1997 to August 2000) with a contribution of 56.4 [ $Pg\ C\ yr^{-1}$ ] for the terrestrial component and 48.5 [ $Pg\ C\ yr^{-1}$ ] for the oceanic component ( $P = 10^{15}$ ).

Ocean color satellite data now routinely provide estimates of chlorophyll biomass ( $Chl_{sat}$ ) and incident PAR. The conversion to C in these chlorophyll-based ocean NPP models is then made via a chlorophyll-specific physiological variable (e.g.,  $P^b_{opt}$  [ $mgC\ (mgChl)^{-1} \cdot h^{-1}$ ]). For example, in the VGPM model all parameters, save for the physiological variable, could be estimated from ocean color-related satellite data.  $P^b_{opt}$  was then assumed to be known from laboratory data or estimated from satellite sea surface temperature (SST) via empirical models previously determined (Antoine et al. 1996; Behrenfeld and Falkowski 1997b; Balch et al. 1992). In contrast to these chlorophyll-based models, Behrenfeld et al. (2005) have proposed a C-based model. They show that derived Chl:C ratios are consistent with expected physiological dependencies on light, nutrients, and temperature. With this

information, they make global estimates of phytoplankton growth rates ( $\mu$  [divisions  $d^{-1}$ ]) and carbon-based NPP, using

$$NPP [mgC m^{-2} d^{-1}] = C_{sar} [mgC m^{-3}] \cdot \mu [divisions d^{-1}] Z_{eu} [m] \cdot h(E_o), \quad (18)$$

where  $C_{sar}$  is the estimate of surface C and  $h(E_o)$  describes how changes in surface light influence the depth-dependent profile of carbon fixation. Equation 18 is the same form as eq. [16] except that Chl is replaced by C and the empirical estimate of  $P_{opt}^b$  is replaced by the phytoplankton growth rate  $\mu$  (where C and  $\mu$  are now directly estimated from remotely sensed data). Global estimates of  $\mu$  and C-based NPP are comparable with earlier chlorophyll-based NPP estimates. Notably, the C-based estimates, when compared with the chlorophyll-based estimates, provide a different perspective on how ocean productivity is distributed over space and time. In particular, one expects the physiological differences between C and chlorophyll biomass models to differ in response to changing light, nutrient, and temperature conditions.

Remote sensing provides the most consistent method of estimating NPP at regional and global scales. An example is given in table 9.1. Annual NPP is estimated for different marine biomes, such as the polar, west wind drift, trade winds, and coastal biomes in the Pacific, Atlantic, Indian, and Antarctic oceans.

### Errors and Limitations

Quantitative estimates of the accuracy of variables retrieved from satellite data are an ongoing process. Some disagreement between modeled and in situ  $^{14}C$  measured production is due to methodological differences and errors in the in situ data.

Table 9.1. Annual primary production estimated from ocean color remote sensing of chlorophyll *a* (1978–1986) on a  $1^\circ$  grid

Ocean	Biome	ANPP( $gC m^{-2} yr^{-1}$ )		Province (n)
		Average	Std. Dev.	
Atlantic Ocean	Atlantic Polar	350.83	48.61	3
	Atlantic Westerly Winds	183.30	64.03	4
	Atlantic Trade Winds	130.66	44.05	5
	Atlantic Coastal	525.38	161.91	8
Indian Ocean	Indian Ocean Trade Winds	88.40	24.32	2
	Indian Ocean Coastal	360.72	157.76	6
Pacific Ocean	Pacific Polar	359.00	—	1
	Pacific Westerly Winds	177.00	25.78	4
	Pacific Trade Winds	89.33	19.78	6
	Pacific Coastal	382.31	141.75	8
Southern Ocean	Antarctic Westerly Winds	126.50	9.90	2
	Antarctic Polar	170.75	66.11	2

Notes: A total of 51 provinces were identified within 12 biomes, based on monthly composites of surface chlorophyll *a* measured by the coastal zone color scanner. Primary production was modeled on the basis of monthly averages of surface chlorophyll *a*, 21,872 sets of oceanographic profiles determining vertical distribution of chlorophyll *a* ( $Z_{eu}$ ), a photosynthesis-irradiance relationship (similar to  $P_{opt}^b$  by Behrenfeld and Falkowski (1997b), and climatologies on surface solar irradiance.

Sources: Longhurst (1998); Longhurst et al. (1995); Platt and Sathyendranath (1988); Sathyendranath et al. (1995).



However, Behrenfeld and Falkowski (1997a) suggest that much of the discrepancy must also result from limitations of the models. For example, the differences observed between the C-based and Chl-based models depend upon differences in the conceptual framing and parameterization of physiological variables. How the models handle the physiological complexity of phytoplankton productivity remains a continuing research effort. Maritorena and Siegel (2005) have addressed the issue of retrieval accuracy within the context of how data from different and/or sequential ocean color satellites can be used together. They use the normalized water-leaving radiances ( $L_{wN}(\lambda)$ ) from SeaWiFS and MODIS in a semi-analytical merging model to produce global retrievals of chlorophyll *a*, dissolved plus detrital absorption coefficient, and particulate backscattering coefficient. These authors show that, compared with the individual data sources, the merged products provide enhanced global daily coverage and lower uncertainties in the retrieved variables. Ultimately, the overall accuracy of multiplatform sampling strategies will hinge on the space/time integration of diverse data sets by means of increasingly robust mathematical models. Success will also be measured by a more complete view of the space/time abundance and distribution of ocean primary producers and by increased understanding of fundamental processes governing marine ecosystems.

### Summary and Recommended Methods

Methods to improve our ability to estimate primary production are constantly being developed. Molecular methods (LaRoche et al. 1993), single-cell determinations as in the use of the flow cytometer (Li 1993), or biophysical approaches such as the fast repetition rate fluorometer have appeared since the 1990s. The use of new radioactive isotopes as tracers, the introduction of stable isotopes, and the extensive development of analytical as well as experimental models, spurred in part by remote sensing of ocean color, indicate that a careful evaluation of the method of estimating primary production is important to better answer the question posed. We have presented in this chapter the more widespread approaches to the estimate of NPP in marine ecology, but we recommend that the reader consider other methods as well.

$^{14}\text{C}$  is still the most commonly used method to estimate photosynthesis and primary production in marine pelagic systems. Long studied in detail, it is the standard against which most other methods are compared and/or are calibrated. Thus, most marine ecological projects include  $^{14}\text{C}$  in one or more of their approaches (IS, SIS, P vs. E, etc.), and a careful evaluation of its performance for any particular study is of the utmost importance. The limitations of the method, if not always corrected, are usually well understood, and that broadens its usefulness for comparative studies.

### *The Nature of the Biome*

The diversity of phytoplankton communities in the ocean makes it difficult to recommend any single method for the measurement of primary production. As discussed above, different methods provide approximations to GPP or NPP,

depending on circumstances. Thus, the various methods offer different tools to better understand the system, the cycling of C within phytoplankton, and the transfer of C among trophic levels. Furthermore, the range of response of any given method under different environmental conditions argues that the method of choice should be based on the scientific question at hand and the space/time scales under investigation.

For example, in the tropical gyres of the oceans, the system is highly heterotrophic, and on average  $R > P$ , so that the NCP is negative. These systems are dominated by small phytoplankton cells and the microbial loop. Thus,  $^{14}\text{C}$  incorporation into particulate C is significantly affected by recycled intracellular  $\text{CO}_2$ , a large proportion of the new organic C can be exuded as dissolved organic C, and active microzooplankton grazing is occurring during the length of the incubation, changing phytoplankton biomass and possibly composition. Experimentally, in these heterotrophic areas the  $^{14}\text{C}$  uptake in dark bottles can be as high as the uptake in light bottles, and it is not usual to subtract one from the other. All these characteristics make the  $^{14}\text{C}$  method less than ideal in heterotrophic dominated areas of the oceans, and complementary approaches are sometimes needed to better understand the results obtained with the  $^{14}\text{C}$  method (Laws et al. 1984; Grande et al. 1989). In contrast, ice-edge blooms in polar areas can be highly autotrophic, dominated by large cells, with low microzooplankton grazing and low DOC and bacterial activity. Under these conditions the  $^{14}\text{C}$  method is ideal, and the estimates provide relatively accurate data for the estimation of NPP. In general this is true for most of the eutrophic areas of the world's ocean, where relatively high levels of primary productivity lead to high levels of upper trophic level biomass.

### *Scale Considerations*

With observations covering spatial scales from molecular to global, the consideration of scale is critical when selecting a method. As noted above, multiplatform sampling strategies are necessary in order to effectively sample the wide range of space/time variability in the oceans. High accuracy in estimating productivity in a single incubation bottle can provide valuable physiological insight for the system. However, the value of a point measurement for scaling to larger scales and longer times is dependent upon how representative the sample is within the context of greater scale. This context can be provided by various sensors on multiple platforms, and the overall accuracy of the combined data can largely be a function of the robustness of the integrative models used to merge disparate data.

Small-scale (shipboard) methods provide a level of detail that various remote sensing methods do not currently offer. For example, remote sensing (both in-water and satellite sensors) of pigment biomass currently focuses on chlorophyll *a*, whereas shipboard observations permit detailed analysis of pigment composition. Consequently, studies aimed at a greater understanding of community composition must currently rely on shipboard methods of analysis. Possible future advancement beyond this stage would require more complete models of phytoplankton growth that include community (and pigment) composition, and another generation of sensors aimed at more detailed physiological information. In short, the accurate estimation

of phytoplankton production requires observations across a range of space/time scales and robust integrative phytoplankton models.

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# PRINCIPLES AND STANDARDS FOR MEASURING PRIMARY PRODUCTION

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*Edited by*

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## Foreword

A common and enthusiastically viewed exhibit at many museums is a cross section of a large tree on which annual rings recording the growth of the tree are labeled so that they can be correlated with events in human history. The cross section is the visualization of a long ecological record that reflects both changing environmental conditions and changes in the tree itself. Perhaps the tree was struck by lightning, which affected its growth rate. A drought, flood, or insect infestation may have affected growth. All of these interacting factors are integrated and summarized in a single variable: the width of the annual rings. However, the complexities of comparison of things such as growth rate or primary productivity are not really reflected in the simple visualization of the tree's cross section. In particular, the growth represented by the rings in the tree is only one element of primary productivity even though it may correlate strongly with overall productivity. This book attempts to address the complexity that is inherent in collecting, interpreting, and presenting long-term data sets on primary productivity. It focuses on the principles underlying the specific details of collecting data and emphasizes the need for standardized methods. Standardization is key because the overall goal of any kind of ecological study or environmental monitoring is an improved understanding of the processes that are ongoing in the ecosystem. In order to fully appreciate these processes, we need to examine their dynamics over time and space. But to compare various measurements along these temporal or spatial dimensions, we need to collect measurements that are comparable as well as accurate and precise. While there are many ways to manipulate data to allow comparison, certainly the most productive approach is to start data collection with a preconceived idea of the methodology and intent of the study. By standardizing methodology among studies endeavoring to measure the same parameter, we ensure the maximum comparability in our data sets.

Humans are fascinated by change in the world. Environmental change is a constant topic of conversation, although much discussion is speculative and uninformed by data. We constantly compare conditions as we see them now with those in the past, and anticipate how things might look in the future. However, most of our mental comparisons suffer from the imprecision of faulty memory or the kind of exaggeration that the passage of time introduces. This is why we are powerfully drawn to tree rings, which enable us to check our own memories and recollections against unbiased information from the past. We are inveterate collectors of bits of information that help us remember and record a historical event. Innumerable measurements made by amateurs have been aimed at comparing the present with the past and forecasting the future. In most cases, measurements of this type are simple enough that we need not worry about standardized methods or changes in technique over time. For example, many places in the northern hemisphere have long records of the duration of ice cover on lakes during the winter. Some of these data sets are municipal records, and others are used to anticipate such important events as the start of the fishing season or the optimal time for agricultural activities. These kinds of information put our lives in the context of an environment that constantly changes, sometimes too subtly for us to appreciate within our usual time frame of reference. Long-term data provide an unbiased record at a temporal scale appropriate for understanding the nature and pace of environmental change.

Productivity is among the most fundamental characteristics of ecosystems, and the measurement of productivity is usually a central element of research programs focused on ecosystems. For example, the Long Term Ecological Research Network, a group of twenty-six sites funded by the U.S. National Science Foundation, has primary productivity as one of its five core research areas. This interest in productivity stems both from its crucial role in ecosystem dynamics as well as from its importance to human enterprise. Productivity is intimately related to the services that humans receive from natural ecosystems. In many systems, the entire productive output is harvested by human societies and used for their support and maintenance. The level of productivity often determines whether humans can exist in a particular location, as well as the structure and the dynamics of their social systems and cultures. Productivity is closely related to the governance of nations and the relationships between nations. The importance of productivity is acknowledged in the development of religious systems around the world and is a fundamental measure of the health of ecosystems for indigenous peoples. The desire to improve productivity has engendered complicated scientific enterprises focusing on mechanisms to increase food and fiber output of communities and has resulted in multibillion-dollar industries with the sole goal of maximizing production. Most recently, the role of productivity in the global carbon cycle has elicited particular interest because of the developing crisis of greenhouse-gas-driven climate change.

Measurement of primary productivity is a complex task. The elements that go into determining productivity are varied, and measurement schemes for each of these elements are diverse.

Because of the way our scientific enterprise is structured, measurements at different times or at different places are often conducted by different investigative teams. They may be funded by a variety of agencies, employ diverse methods that

capture different time scales, and have unique goals. In most cases, the immediate need or objective of study is the one that drives the methodology used. However, for science to make efficient use of resources and to provide information that can be compared across ecosystems and across scales, we need to go beyond local planning as we collect data. In fact, each study should have a developed plan for integrating with other scales in addition to the focal scale of the investigation. Only in this way can we be sure that the questions we ask in our own backyards are relevant to broader regional and national issues. Moreover, as we change our focus from local to regional to landscape to national and global scales, we need to be aware that our measures may also change both in the details of methodology and in underlying principles. Clearly, studies with methodologies that are robust over a wide range of temporal and spatial intervals will be the most valuable.

Understanding the interactions of ecological processes acting at different temporal and spatial scales is one of the key challenges facing ecologists. Most ecological data are collected at small spatial and short temporal scales, generally less than one year on approximately 1–10,000 m<sup>2</sup> plots. However, environmental changes act at scales larger than those at which field data are generally collected, and result in a mismatch or decoupling of important parameters that contribute to our understanding. Mechanisms for converting locally collected data into information that applies to larger landscape or regional scales are lacking, as is the firm theoretical basis for scaling up in most of ecology. Nonetheless, the need to understand ecosystem processes at multiple scales is real, and results in the use of an amalgam of different tools and methods. For example, measures of primary productivity at the plot or stand scale are often collected by field workers measuring individual organisms or extrapolating from stand-level simulation models. At larger scales, primary productivity may be estimated through remotely sensed data, aerial photography, land-use change analysis, or a variety of other large-scale techniques. The conversion or the homogenization of data collected by one technique with those collected by another technique is a serious problem for ecological science. The fine-scale spatial and temporal heterogeneity that leads to stand-level productivity is not measured by aircraft or satellite instruments. At the same time, the expense and time required for ground-based measurements do not permit widespread sampling, which results in the aforementioned problem with scaling up. Because of these issues, it is even more important that the utility of ground observations be maximized through a methodology which is comparable and scalable over large spatial extents. We cannot afford to lose data because of idiosyncratic methodology or mismatched methods.

Various obstacles confront research synthesis by acting as barriers to the standardization of ecological data. The training that ecologists undergo often involves considerable emphasis on individual effort and self-reliance. Research projects undertaken by undergraduates, dissertation studies, and postdoctoral research often involve single individuals who make a significant investment of their lives in these efforts. As a result, we are encouraged to think for ourselves through our academic development, and this training carries over into our later professional lives. However, the decisions on methodology made during this formative stage are often taken without regard to possible future expansion of the research horizon. Methodology

is often chosen to address specific small-scale, relatively self-contained projects. Moreover, once we are locked into a particular method, we may find it difficult to change our approach because we have invested too much time and energy to risk a new method.

This problem affects more than just individuals. Although the U.S. LTER Network has focused on common core research areas (including primary production) since its inception, the lack of an initial emphasis on standardization of measurements has resulted in the development of varying methods at different sites even with the same biome type. Efforts to address this problem by adopting standard methods are hindered by the high cost of calibrating old and new methods over the long time frames of ongoing experiments and measurements. Hence, our reaction to new approaches tends to be conservative—unless, of course, our own chosen method is the basis for standardization.

If technology stood still, we would be more likely to reach common ground eventually. However, new technologies and approaches arise constantly, and may provide faster, cheaper, or more accurate measurements than our tried-and-true favorites. For example, the current revolution in wireless sensor networks holds enormous promise for ecology. However, early adopters of this new technology may find themselves out of step with practitioners of more traditional methods, and as a result their ability to compare results may suffer. Moreover, increased technology requires increased understanding of the processes and assumptions underlying the technology, adding an additional burden to our capability to conduct robust comparisons using different methods. One solution to this problem is to maintain a clear focus on common methodological principles and insist that new technology incorporate these principles. Finally, heterogeneity of sampling approaches is introduced by funding limitations and cost restrictions. Because the availability of resources varies among research sites, and the proportional allocation of funds to measurements of productivity differs across studies, there is inevitable heterogeneity in the precision and accuracy of our data sets. No simple solution exists that will resolve each and every issue that challenges us when we attempt to compare our results across sites, studies, or sampling periods. However, the establishment and adoption of underlying principles and standards to guide the selection of field methods will improve our ability to make these kinds of comparisons. With that in mind, the contributors to this book have endeavored to lay out a series of principles and standards for the measurement of primary productivity that, hopefully, will guide future investigators in choosing methods that are both effective and efficient, and at the same time lead to meaningful comparisons of data across studies, ecosystems, and times.

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