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 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 air and space-borne observations, from intracellular to global systems, and from experimental to modeling.

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

$$\mu = dn / dt\ (1/n) \qquad (1)$$

In the field, the estimate of growth rates is limited by a number of factors since 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 sea water and has a spatial and size distribution that overlaps that of heterotrophic organisms. The plants in the plankton are microscopic (usually 2-200 μm) 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 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 carbon 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 taxa, primary production rates are then combined with cell size determinations or photosynthetic pigment complements (Gieskes *et al*. 1993).

Gross primary production (GPP) is the total amount of electron equivalents originating from the photolysis of water (Fogg, 1980; Falkowski & Raven 1997; see Ch. 9). 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; i.e., 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 defined as GPP minus CR (Williams 1993a). While the previous variables are based on carbon units, there exist parallel terms to express phytoplankton production in units of nitrogen (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}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 during the last 20 years. 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}C or ^{13}C (Goes and Handa 2002), but also ^{15}N (Le Bouteiller 1993) and ^{18}O (Bender *et al*. 1987). For field work these techniques require sampling of a parcel of water which is isolated from the environment and which is considered representative of the target population. Other methods involve direct, non-invasive 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 100's of km. Specific application of these methods is dependent upon their suitability to address a particular research question. Finally, the use of non-conservative tracers such as O_2, CO_2 and NO_3^- on ocean meso-scales (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 of widespread use 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; i.e., 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) and those 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, while 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 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.

Multi-platform sampling strategies (Steele 1978, Esaias 1981, Smith *et al*. 1987, Dickey 2003) utilizing buoy, ship, aircraft, and satellite 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 1 (Dickey 2003) 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 ship 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 helped to identify the physical and biological factors responsible for these variances.

Experimental Approaches to Primary Production: The Radiocarbon (^{14}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 a variety of experimental approaches with respect to the number of depths sampled and how these depths are selected. Also, the design and physical set up 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, where samples are returned to the depth and light conditions from where 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 that of 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}C method was introduced by Steeman Nielsen (1952) and measures the CO_2 incorporation by addition of trace amounts of ^{14}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}C data exist and it has become the standard method in marine research against which other methods are compared.

Samples for the ^{14}C method are obtained from the euphotic zone, defined as the layer where there is sufficient irradiance to support net primary production (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 review). Since the eupthotic depth is seldom directly measured, 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 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 the so called “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}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 set-up simulating *in situ* conditions for light and temperature (Lohrenz *et al*. 1992, Lohrenz 1993).

^{14}C incorporation in 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}C incorporated into the cells. Primary Production is calculated as

P_z = (DPM in the Light bottle - DPM in the Dark bottle) / Volume Sample Filtered * 24,000 * 1.05 * Hours of Incubation / (Specific Activity in the Sample/Volume Specific Activity) (2)

in units of [mg C m^{-3} h^{-1}], where P_z is production at depth z, total HCO_3^- in the water is ~24,000 [mg C kg^{-1}] (Carrillo and Karl 1999) and 1.05 is the discrimination factor between incorporation of ^{14}C and ^{12}C. P_z is the primary production expressed as carbon incorporated per unit volume of water per unit time (Fig. 2). Daily P_z is calculated by converting the hours into a 24-h day and it is considered as NPP where the balance of Photosynthesis – Respiration is > 0. Furthermore, P^B [mg C mg $chla^{-1}$ h^{-1}] is defined as Assimilation Number and calculated as P_z per unit of biomass in the sample, usually chlorophyll a, in units [mg chla m^{-3}]. The latter is used to standardize NPP when comparing different regions and it is a measure of photosynthetic efficiency.

The ^{14}C incorporation in the light bottle is considered to account both for biotic (i.e. photosynthesis and Ca CO_3 incorporation) as well as abiotic (i.e. adsorption) processes (Banse 1993). Thus, the ^{14}C incorporated is corrected by the dark bottle to account for biological ^{14}C uptake that can occur outside photosynthesis. The incorporation of ^{14}C into Ca CO_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 hours. 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-h 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 efficiency of carbon transfer to other trophic levels. Shorter time scales will be more dependent on physiological properties of phytoplankton and

would 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 based upon the distribution of solar radiation within the water column. Light decreases exponentially and sampling depths are defined as percentage of incident irradiance at the water surface, using the Lambert Beer Law for pre-determined light percentages:

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

Where E is PAR [(μEinst m^{-2} sec^{-1}] at depth z, E_o is incident PAR at the water-air interface, K_{PAR} is the attenuation coefficient in [m^{-1}] and z [m] is depth. K_{PAR} is estimated from measurement of PAR versus depth, where

$$K_{PAR} = - \ln (E_{z2} / E_{z1}) / (z_2 - z_1) \quad (4)$$

E_{Z1} and E_{Z2} 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_o,

$$z = - \ln (E_z / E_o) / K_{PAR} = - \ln (0.5) / K_{PAR} \quad (5)$$

Ideally, incubations should replicate the light field from which a sample has been obtained. If incubations are done *in situ* (IS), the light bottle is exposed to the irradiance and light quality at the depth sampled within the water column and the production value is thus representative of environmental condition at that depth. In *Simulated In Situ* experiments (SIS), the different irradiance levels are simulated by the use of neutral density filters placed over the incubation bottles that screen surface irradiance to simulate the percent PAR from the depth sampled. Simulating the change in light quality (i.e., spectral characteristics) with depth is not achieved by neutral density filters. In general there is no consistent and accepted method to simulate spectral characteristic with depth

but the difference in light exposure can be corrected by modeling (Barber *et al*. 1997). Depending on the body of water under study, blue or green filters have been recommended for the deep samples, green filters in coastal productive waters and blue filters for more oceanic or oligotrophic environments. The addition of color filters increases primary production estimates at depth by decreasing potential photoinhibition of cells suddenly exposed to white light (Tilzer *et al*. 1993).

^{14}C estimates of primary production usually lie somewhere between "true" GPP and NPP. The degree to which the ^{14}C incorporation approximates GPP or NPP is dependent on incubation time and photosynthetic rate (Williams 1993b). Models of the ^{14}C incorporation at varying photosynthetic and respiratory rates and time of incubation show that at low respiration rates and short incubation times ^{14}C derived production is a reasonable approximation to GPP. In phytoplankton cultures under controlled conditions, when comparing ^{14}C production and POC accumulation (as index of NPP), experiments show that at low growth rates ($<0.1\ d^{-1}$), ^{14}C production is about 5 times higher than POC accumulation (Peterson 1978) and thus more closely approximates GPP. Under conditions of high respiration (similar rates than production), ^{14}C production also approximates GPP (Calvario-Martinez 1989). On the other hand, at high growth rates ($>0.5\ d^{-1}$) ^{14}C production and POC accumulation agree, indicating that under these conditions the ^{14}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 photosynthesis in units of [mg C m^{-2} d^{-1}], individual sample depths are integrated by depth by polynomial interpolation. It is assumed that the production between two consecutive depths changes linearly and that any incubation less than 24 hours can be prorated to a full day. Second, time integration is carried out by interpolating between sampling dates, as is done when calculating seasonal primary production. This provides a seasonal or annual estimate in units of [mg C m^{-2} mo^{-1}] or [mg C m^{-2} 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 [mg C d^{-1}].

The frequency of sampling is determined by the question to be addressed and the dominant process controlling primary production in the biome of interest. In long-term ecological studies in coastal Antarctica where the main question is to determine the seasonal evolution and the inter-annual variability, sampling is carried out twice weekly (Vernet, unpublished data). Thus, determining factors in scales less than one week is not possible. Mixing events that control the phytoplankton accumulation within surface waters are driven by large storms that pass the region once every three weeks. Each bloom is then characterized by an average of 5-7 data points, which provides detail on productivity increase, peak 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 ANPP 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 a temperature similar to those in the field. Two parameters are necessary to describe the P vs E relationships, alpha (α), or the initial slope of 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 et al (1975), Jassby and Platt (1975) and 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)$^{-1}$ h^{-1}], P_M^B is maximum rate of photosynthesis per unit chl a, α is the initial slope in units of [mg C (mg chl a)$^{-1}$ h^{-1} (μEinst m^{-2} sec^{-1})$^{-1}$] and E is irradiance in units of [μEinst m^{-1} sec^{-1}].

When photoinhibition is present, photosynthesis can be modeled as an extension of Eq. 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 (β) is the photoinhibition parameter with the same units as α, and where

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

Different from IS and SIS where one determination is taken at each depth, in P vs. E curves a whole 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 h, as the response curve is determined before photo-acclimation. Most recently, P vs. E curves have been determined with increased number of light treatments (i.e. 25) and decreased volume of incubation (i.e. 2 ml; Fig. 3). Sensitivity of the

determination is preserved by increasing the specific activity of the sample. Irradiance levels usually range from zero to 1000 [μEinst m^{-2} sec^{-1}] although adjustments in the light range are necessary in different geographic locations and depending on the time of the year. For example, Antarctic samples are usually exposed to 0-600 [μEinst m^{-2} s^{-1}] while open ocean samples in the North Pacific are exposed to between [0-2000 μEinst m^{-2} s^{-1}]. Relatively high irradiances are needed to determine the photoinhibition factor (β).

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 simulate in situ light quality in addition to obtain a range of illumination with the addition of neutral filters. Similar to SIS incubations, determination of the light quality can be achieved through colored filters. More accurate determination can be achieved with the use of solar simulators. Furthermore, the value of P_{max} is a function of ambient temperature (Geider and McIntyre 2002). Acclimation is sufficiently fast that P_{max} may differ for the same sample incubated at several temperatures (Fig. 4). It is recommended that incubations are carried out at in situ temperature. Alternatively, if both the temperature in the water and in the incubator is known, a pre-determined 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 α or P_{max} is not included in the primary production estimate. Changes in irradiance with depth determine the value of α in situ. The value of α 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, i.e. the euphotic zone is deeper than the mixed layer and the bottom of the euphotic zone is at different temperature, then P_{max} will change with depth in the water column thus influencing the estimated productivity and a further correction for temperature (see above) needs to be applied.

Experimental Approaches to Primary Production: Oxygen Methods

Oxygen Production. Oxygen evolution is a primary by-product of the splitting of the H_2O molecule during photon absorption (Falkowski and Raven 1997). Increased oxygen

concentration in a water sample is proportional to photosynthesis and thus production. Under light, oxygen production is measured as the difference between initial and final oxygen concentration in a light bottle. In the water column, bottles are incubated at different irradiances, as explained for the ^{14}C method, to estimate water column production. Oxygen evolution from photosynthesis can be masked by oxygen consumption by respiration, as 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 oxygen increase in the light bottle + consumption in the dark bottle. The proportion of O_2 produced to C uptake or O_2 evolved to 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 Ch. 11 of this volume.

Oxygen consumption by respiration in plankton samples has both autotrophic and heterotrophic components. Heterotrophic respiration by microzooplankton and bacteria can be higher than autotrophic oxygen production so that net community production is negative.

The ^{18}O method: Similar to the ^{14}C method, the ^{18}O tracer method was developed to measure gross production *in vitro* with light and dark bottles (Bender *et al*. 1987). This is an extension of O_2 production but in this case O_2 is not measured 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 μM) 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.

What is estimated using the ^{14}C method?

By comparing the method of ^{14}C incorporation with the oxygen-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, dependent upon conditions. In the North Atlantic, Marra (2002) observed that ^{14}C underestimated gross primary production (as measured by the ^{18}O method) (Fig. 5). ^{14}C agreed only with net primary production measured with O_2 production bottles over a 24h 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 carbon uptake and gross oxygen production cannot be equated as 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 re-assimilated in photosynthesis while O_2 released in photosynthesis is not re-assimilated by respiration. This conclusion agrees with modeled data where most, if not all CO_2 respired, is re-fixed as photosynthesis (Williams 1993b). Thus, as measured by ^{18}O, there is an imbalance between CO_2 and O_2 dynamics. If so, the cells use proportionally more H_2O (and $H_2{}^{18}O$) than external CO_2, as 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.

The action spectrum of photosynthesis, the solar spectrum and the underwater light field all vary with 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, phytoplankton particles via their photosynthetic pigments, dissolved organic matter (DOC) and 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 simulated *in situ* 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 α and P_{max} (Tilzer *et al*. 1993).

If the water column is uniformly mixed, it has been calculated that 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 non-uniform 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}C method. The onset of nutrient limitation or the production of 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 ^{14}C fixed if the $DO^{14}C$ returns to the dissolved pool (Jackson 1993). If the $DO^{14}C$ is taken up by heterotrophs, thus returning ^{14}C to the particulate pool, the analytical technique used to concentrate phytoplankton (i.e. the pore

size of the filters in use) will determine if this fraction is accounted or not as primary production.

Indirect, non-invasive methods of Primary Production

A new generation of instruments and methods, based on fluorescent properties of photosynthesis, has emerged during the past few decades in oceanography. These methods are non-invasive and do not depend on incubation of small water 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 at longer (or less energetic) wavelengths than the wavelength of absorption by specific molecules. 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, as 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 non-photochemical process. Furthermore, the dynamics of chlorophyll fluorescence shows a time-dependent response which can been 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 bandpass band 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 been 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 (Φ_f in [Einst emitted / Einst absorbed])

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

and

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

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

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

Where F_c is the rate of carbon incorporation in [g-at C m^{-3} s^{-1}] and Φ_c is the quantum yield of photosynthesis in [g-at C fixed / Einst absorbed]. Combing 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,

$$F_c = (\Phi_c / \Phi_f) * \Phi_f * a_c * E_{o,} \qquad (13)$$

for 24 h 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 order 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 since most of the chl a is associated with the Photosystem I. Modeling primary production based on fluorescence measurements is also subject to variability because Φ_f is a function not only of light but also 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 (Rabinowich and Govindjee 1969). Under weak flashes, pigment reaction centers remain open, i.e. they continuously receive photons as 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, or F_v, is defined as the difference between maximum and baseline fluorescence (F_m-F_o). The quantum yield of photochemistry (Φ_f), related to photosynthesis and thus 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 Ch. 11, this volume).

A second-generation fluorometer was designed to address some of the limitations of the PAM fluorometry (Kolber *et al*. 1998). The fast repetition rate fluorometery (FRRF) was developed to obtain specific parameters needed to model production (e.g., the cross section for absorption of irradiance (σ_{PSII}) and the parameter for photochemical quenching (q_p),$1/\tau$, which gives the rate of electron transport from initial donor (water) to final acceptor (CO_2). In FRRF, plankton cells are exposed to a series of flashes at sub-saturating 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 sub-saturating light is a measure of the time constant of re-oxidation of Qa-, which can be related to the turn-over 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 (Φ_{max}) is calculated from these variables.

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

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

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

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

Where P_C^B is the chlorophyll-specific rate of carbon fixation [moles of CO_2 $mole^{-1}$ Chl *a* t^{-1}], P_f is the fluorescence-based rate of photosynthetic electron flow [e- reaction $center^{-1}$ t^{-1}] and $\Delta\Phi_{max}$ is scaled to the maximal value of 0.65. Short-term photosynthetic rates calculated from F_v/F_m,as measured with a FRRF in the field (Fig. 6) correlate positively with hourly ^{14}C incubation in field samples (Fig. 7) suggesting this is a viable method for fast, incubation free and non-invasive 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 field work, as 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 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 carbon 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 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 are 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 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 Ch. 9.

Biomass Estimates. 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 up-welled 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). 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* (Chl_{sat}, [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 Chl_{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 Chl_{sat}. When limited to waters for 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 ±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 co-authors (1998, 2000) recently evaluated numerous pigment algorithms suitable 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* Chl_{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.ioccg.org).

Modeling Primary Production. Prior to the advent of satellite ocean color sensors, estimation 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 to remote observations and noted that this linkage requires mathematical models relating measurable optical properties to desired biological parameters. They also reviewed 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 photosynthetic available radiant (PAR) energy within the water column, and a variety of variables associated with the photo-physiological, quantum or assimilation efficiencies of

phytoplankton. Recently, Behrenfeld and Falkowski (1997b) reviewed the development of phytoplankton primary productivity models and showed a "fundamental synonymy" between nearly two dozen models developed over the past four decades. They noted that "all of these models can be related to a single formulation equating depth-integrated primary production (PP_{eu} [mgC m^{-2} d^{-1}]) to surface phytoplankton biomass (Chl_{sat} [mgChl m^{-3}]), a photoadaptive variable (P^b_{opt} [mgC(mgChl)$^{-1}$ h^{-1}]), euphotic depth (Z_{eu} [m]), an irradiance-dependent function ($f(E_{par})$), and daylength (DL [h d^{-1}])".

$$PP_{eu} = Chl_{sat} \cdot Z_{eu} \cdot f(E_{par}) \cdot DL \cdot P^b_{opt} , \qquad (16)$$

where PP_{eu} is the daily carbon fixation integrated from the surface to the euphotic depth (Z_{eu}) and P^b_{opt} is the maximum chlorophyll-specific carbon fixation rate observed within a water column measured under conditions of variable irradiance during incubations typically spanning several hours (equivalent to P_{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 dataset of 11,283 ^{14}C-based measurements of daily carbon fixation from 1,698 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 Eq. (1) they found that nearly all (~85%) could be attributed to changes in depth-integrated biomass (i.e., $Chl_{sat} \cdot Z_{eu}$) and the horizontal variability in the photoadaptive variable P^b_{opt}. Making use of their large data base, they developed a Vertically Generalized Production Model (VGMP, 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 (ε)

$$NPP = APAR \cdot \varepsilon \quad (17)$$

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 ε 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 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 these were the first single-sensor global observations of the photosynthetic biosphere. The CASA-VGPM model gave an NPP estimates 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 carbon (C) in these chlorophyll-based ocean NPP models is then made via a chlorophyll specific physiological variable (e.g., P^b_{opt} [$mgC \cdot (mgChl)^{-1} \cdot h^{-1}$]). For example, in the VGPM model all parameters could be estimated from ocean color-related satellite data save for the physiological variable. P^b_{opt} was then assumed 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 carbon-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 (μ [divisions d^{-1}]) and carbon-based NPP using,

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

Where C_{sat} is the estimate of surface carbon and h (Eo) describes how changes in is replaced by the phytoplankton growth rate μ (where C and μ are now directly estimated from remotely sensed data). Global estimates of μ and carbon-based NPP are comparable to earlier chlorophyll-based NPP estimates. Notably, the carbon-based estimates, when compared to the chlorophyll-based estimates, provide a different perspective of how ocean productivity is distributed over space and time. In particular, one expects that the physiological differences between carbon 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 1 (calculated from Longhurst 1998). Annual NPP is estimated for different 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 in variables retrieved from satellite data is an on going process. Some disagreement between modeled and *in situ* ^{14}C measured production is due to methodological differences and errors in the *in situ* data. However, Behrenfeld and Falkowski (1997a) also 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 recently 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 to 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 primary 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 flowcytometer (Li 1993), or biophysical approaches such as the Fast Repetition Rate Fluorometer have appeared in the last 15 years. 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 the reader to consider other methods as well.

The ^{14}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}C in one or more of its 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 primary production. As discussed above, different methods provide approximation to GPP or NPP depending on circumstances. Thus, the various methods offer different tools to better understand the system, the cycling of carbon within phytoplankton, and the transfer of carbon 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}C incorporation into particulate carbon is significantly affected by recycled intracellular CO_2, a large proportion of the new organic carbon can be exuded as dissolved organic carbon and active microzooplanton grazing is occurring during the length of the incubation, changing phytoplankton biomass and possibly composition. Experimentally, in these heterotrophic areas the ^{14}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 makes the ^{14}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}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}C method is ideal and the estimates provide a relatively accurate estimate 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 focus 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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FIGURE LEGENDS

Figure 1. Time-horizontal space scale diagram: (a) several physical and biological processes representative of ocean processes (ovals); (b) approximate sampling domain capabilities for several sensor platforms (rectangles). Reproduced From Dickey (2003) with permission from Elsevier.

Figure 2. Profiles of phytoplankton biomass as chlorophyll *a*, [mg chl*a* m^{-3}] Photosynthetically Active Radiation (PAR) measured with a 4π collector Model QSP-200L4S from Biospherical Instruments Inc. [μEinst m^{-2} s^{-1}], and Primary Production [mg C m^{-3} 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 denote the depth of sampling at 100%, 50%, 25%, 10%, 5% and 0.5% of incident radiation (E_o). Euphotic zone was calculated as 1% of incident radiation at 61 m with corresponding integrated primary production of 602 mg C m^{-2} d^{-1} and integrated chlorophyll a of 33 mg m^{-2}.

Figure 3. Photosynthesis [mg C $chla^{-1}$ h^{-1}] versus Irradiance [μEinst m^{-2} s^{-1}] determined with ^{14}C incubations in the Western Antarctic Peninsula. Curve fitting with (a) Equations 8 and 9 (Platt *et al*. 1980) and (b) Equation 7 (Platt and Jasby 1976).

Figure 4. Photosynthesis [mg C $chla^{-1}$ h^{-1}] versus Irradiance [μEinst m^{-2} s^{-1}] determined with ^{14}C incubations in the Western Antarctic Peninsula.at different temperatures to show dependence of P_{max} on Temperature: (a) -1.5^o C lower than ambient temperature, (b) incubation at ambient temperature and (c) +1.5^o C higher than ambient temperature.

Figure 5. Comparison between different approaches of measuring primary production in marine phytoplankton (a) Gross Primary Production measured with ^{18}O (Bender et al. 1987) and Daily Primary Production measured with 24-h In Situ ^{14}C incubations; (b)

Gross Primary Production measured with ^{18}O and Primary Production estimated with daytime In Situ ^{14}C incubations; and (c) Daily Net Primary Production measured with light-dark oxygen production compared to daily ^{14}C assimilation. Data obtained during several cruises in the North Atlantic and Equatorial Pacific. Reproduced from Marra (2002) with permission from Blackwell Publishing.

Figure 6. Fluorescence-based Primary Production calculated from the Fast Repetition Rate Fluorometer (FRRF) compared to short-term incubations with ^{14}C in [mg C mg chla^{-1} h^{-1}]. Reproduced from Falkowski and Kolber (1993) with permission from International Council for the Exploration of the Sea.

Figure 7. Profiles of Baseline Fluorescence (F_o) and F_v/Fm from the Fast Repetition Rate Fluorometer (FRRF) collected on the Western Antarctic Peninsula. Photosynthetically Active Radiation at each station is also shown. (a) Coastal station in Marguerite Bay, Western Antarctic Peninsula, and (b) slope waters of the continental shelf at similar latitude as (a).

Table 1. Annual Primary Production estimated from ocean color remote sensing of chlorophyll *a* during 1978-1986 on a 1^{o} grid (Longhurst 1998). A total of fifty-nine provinces were identified within nine biomes, based on monthly composites of surface chlorophyll *a* measured by the Coastal Zone Color Scanner. Primary production was modeled based on 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^{b}_{opt} by Behrenfeld and Falkowski 1997) and climatologies on surface solar irradiance (Longhurst *et al*. 1995; Platt and Sathyendranath 1988; Sathyendranath *et al*. 1995).

Fig. 1

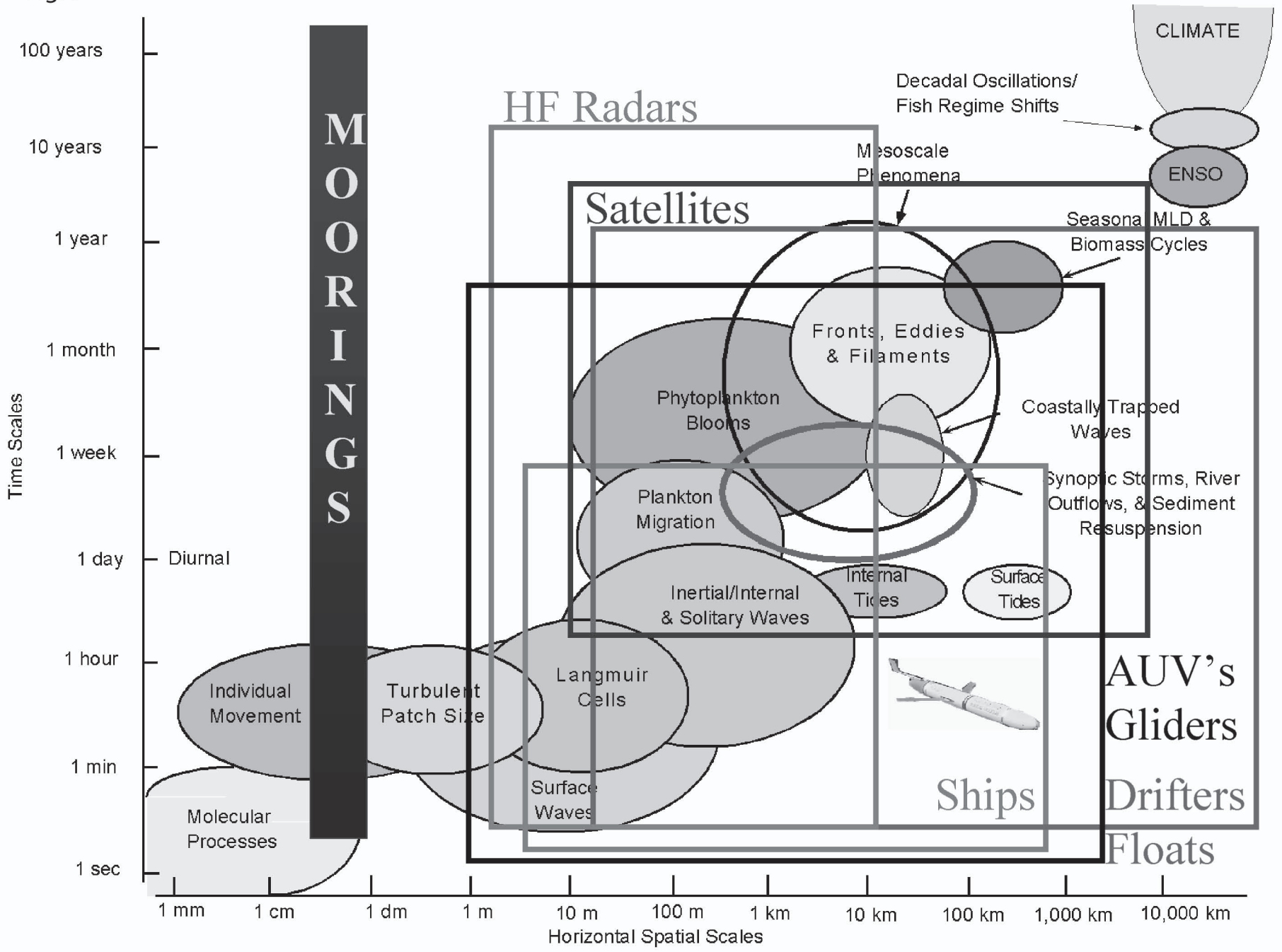

CLIMATE
Decadal Oscillations/
Fish Regime Shifts
ENSO
HF Radars
Mesoscale
Phenomena
Satellites
Seasonal MLD &
Biomass Cycles
Fronts, Eddies
& Filaments
Phytoplankton
Blooms
Coastally Trapped
Waves
Synoptic Storms, River
Outflows, & Sediment
Resuspension
Plankton
Migration
Internal
Tides
Surface
Tides
Inertial/Internal
& Solitary Waves
MOORINGS
Diurnal
Individual
Movement
Turbulent
Patch Size
Langmuir
Cells
Surface
Waves
Molecular
Processes
AUV's
Gliders
Ships
Drifters
Floats
100 years
10 years
1 year
1 month
1 week
1 day
1 hour
1 min
1 sec
Time Scales
1 mm
1 cm
1 dm
1 m
10 m
100 m
1 km
10 km
100 km
1,000 km
10,000 km
Horizontal Spatial Scales

Fig. 2

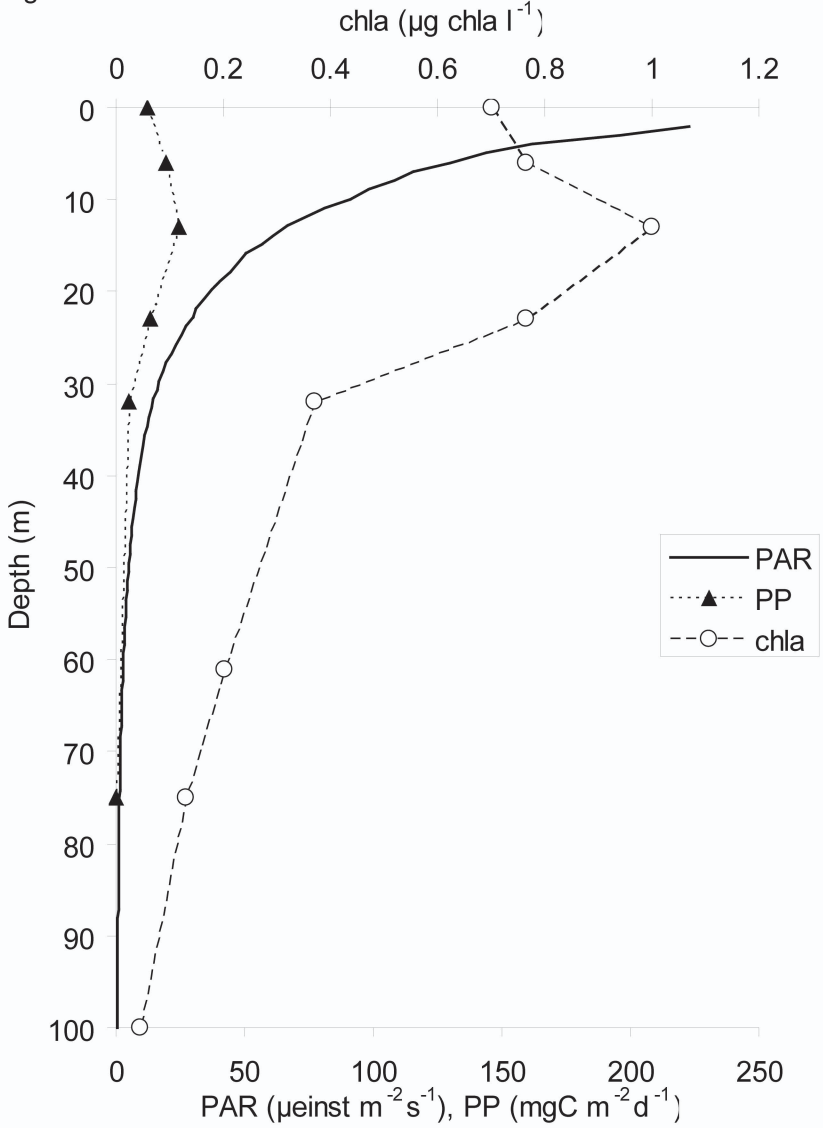
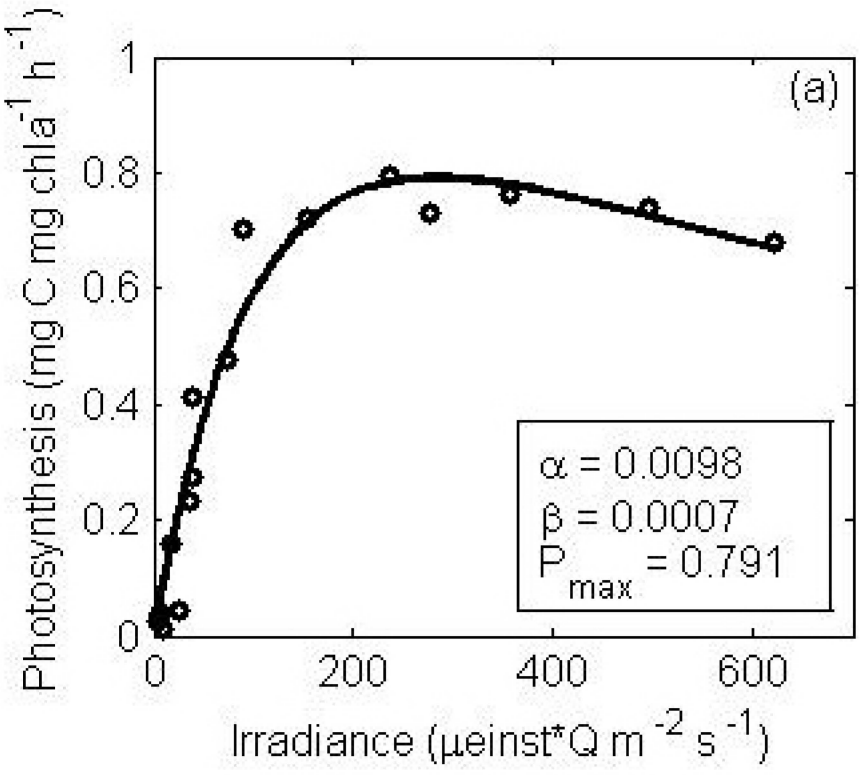

chla (µg chla l -1)
0
0.2
0.4
0.6
0.8
1
1.2
Depth (m)
0
10
20
30
40
50
60
70
80
90
100
PAR
PP
chla
0
50
100
150
200
250
PAR (µeinst m -2 s -1), PP (mgC m -2 d -1)

Fig. 3


(a)
Photosynthesis (mg C mg chla^{-1} h^{-1})
Irradiance (μeinst*Q m^{-2} s^{-1})
α = 0.0098
β = 0.0007
P_{max} = 0.791
0
0.2
0.4
0.6
0.8
1
0
200
400
600

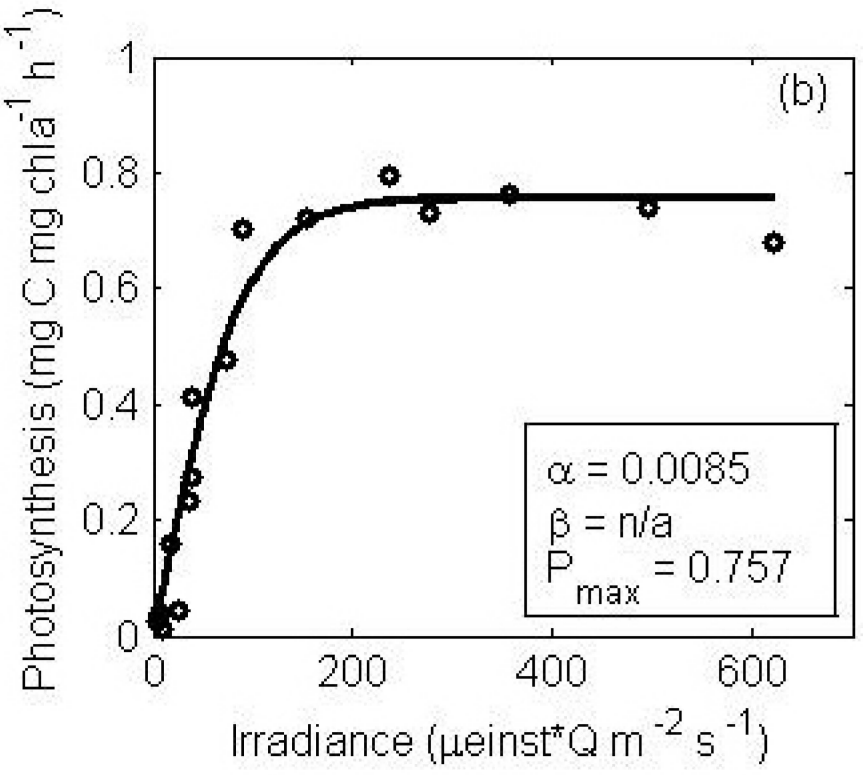

(b)
Photosynthesis (mg C mg chla^{-1} h^{-1})
Irradiance (μeinst*Q m^{-2} s^{-1})
α = 0.0085
β = n/a
P_{max} = 0.757
0
0.2
0.4
0.6
0.8
1
0
200
400
600

Fig. 4

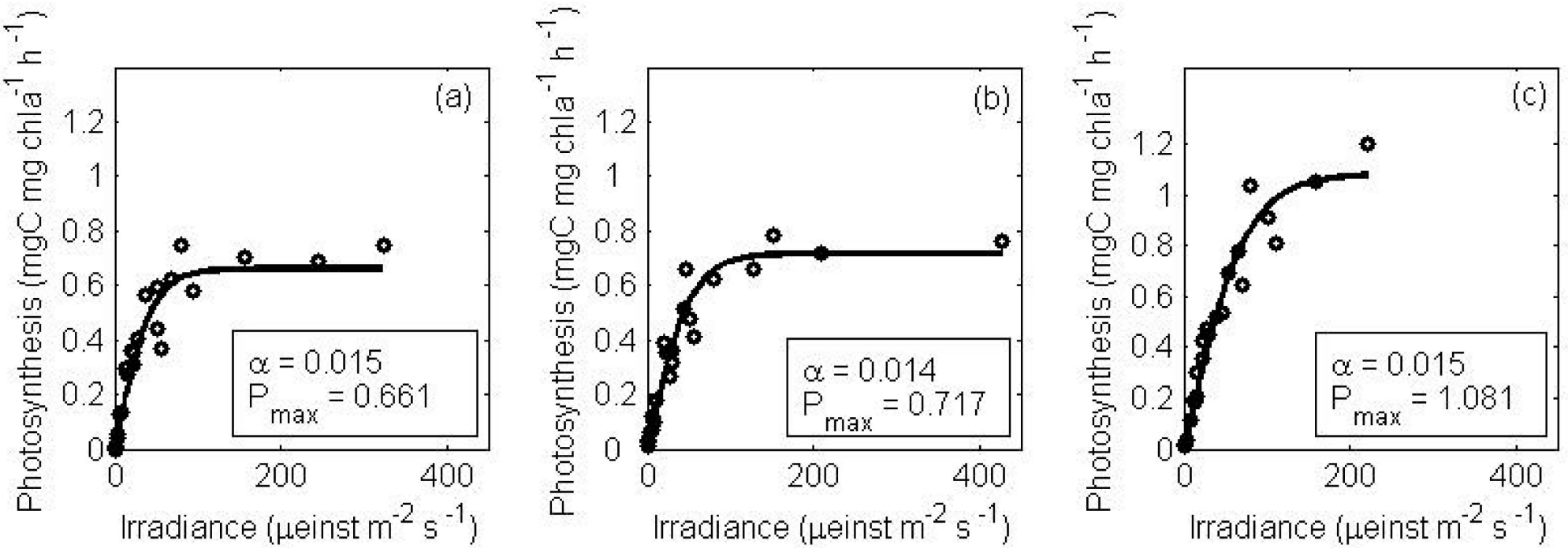
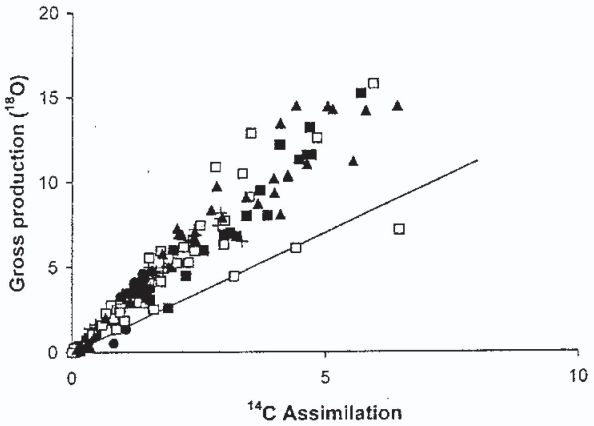
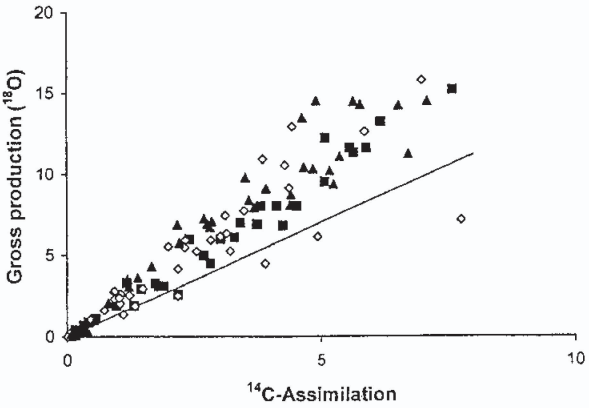

(a)
Photosynthesis (mgC mg chla^{-1} h^{-1})
Irradiance (μeinst m^{-2} s^{-1})
α = 0.015
P$_{max}$ = 0.661
(b)
α = 0.014
P$_{max}$ = 0.717
(c)
α = 0.015
P$_{max}$ = 1.081

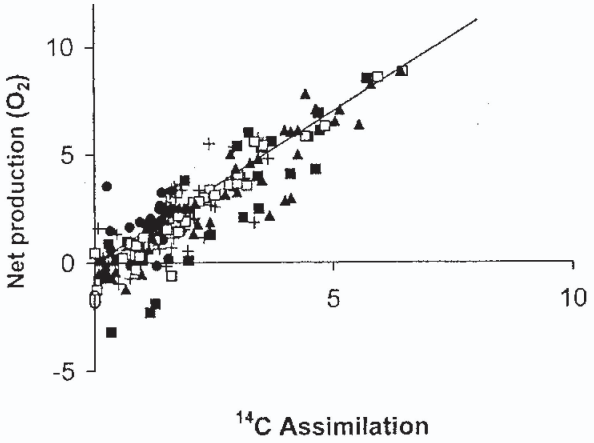
Fig. 5


Gross production (^{18}O)
20
15
10
5
0
0
5
10
^{14}C Assimilation

(a)


Gross production (^{18}O)
20
15
10
5
0
0
5
10
^{14}C-Assimilation

(b)


Net production (O_2)
10
5
0
-5
0
5
10
^{14}C Assimilation

(c)

Fig. 6

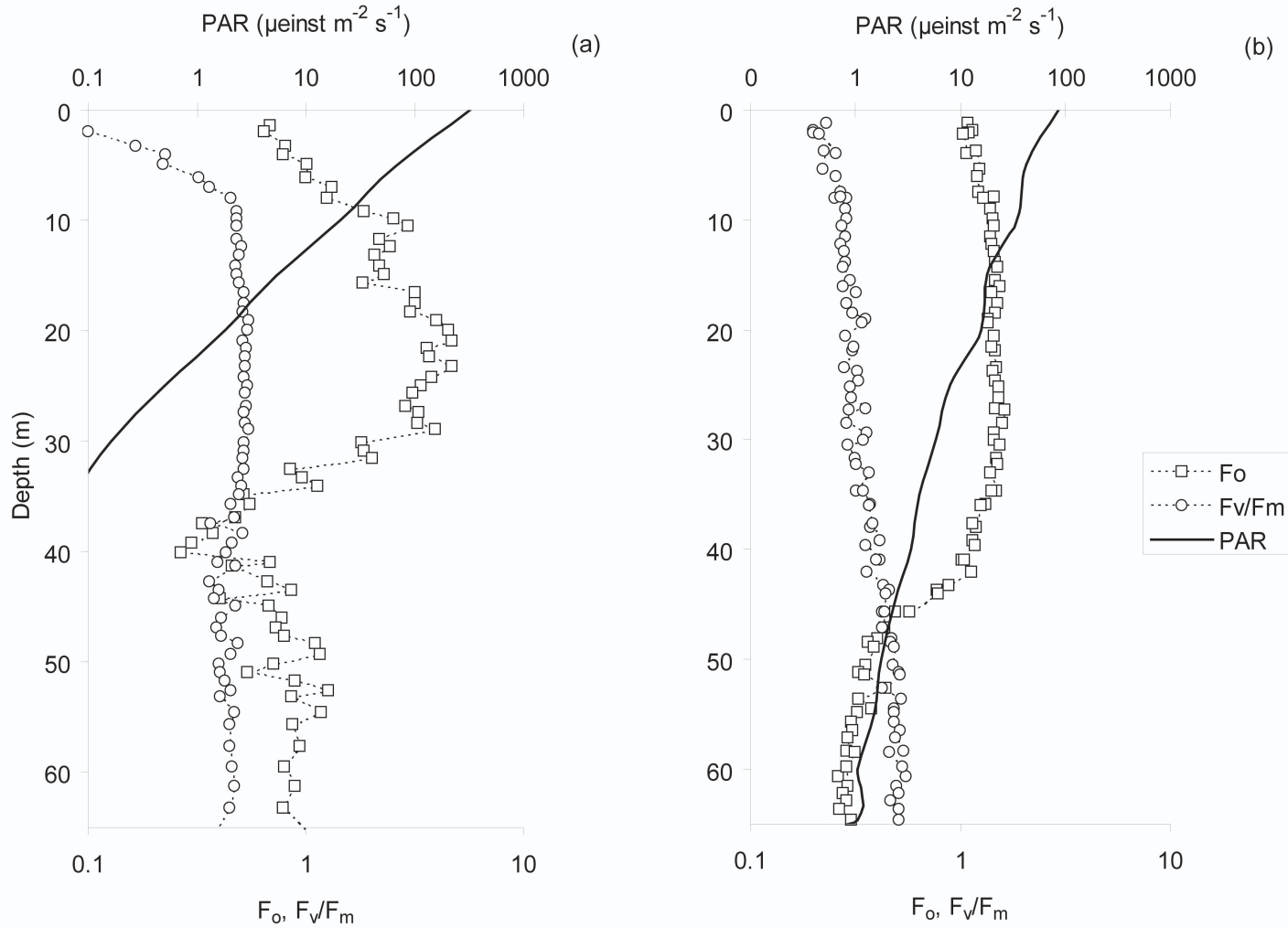

PAR (µeinst m-2 s-1)
(a)
0.1
1
10
100
1000
0
10
20
30
40
50
60
Depth (m)
0.1
1
10
Fo, Fv/Fm
PAR (µeinst m-2 s-1)
(b)
0
1
10
100
1000
0.1
1
10
Fo, Fv/Fm
Fo
Fv/Fm
PAR

Fig. 7

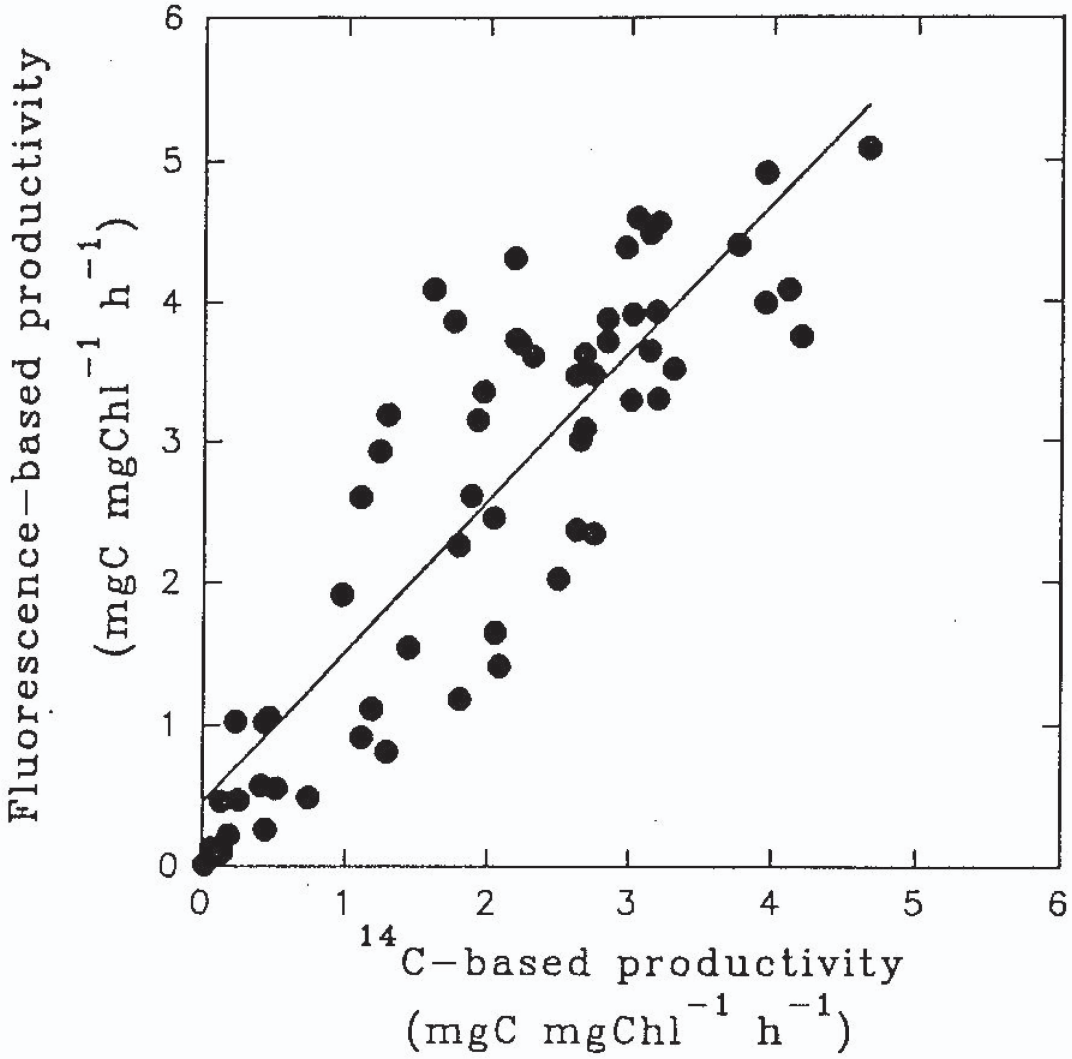

Fluorescence-based productivity
(mgC mgChl^{-1} h^{-1})
^{14}C-based productivity
(mgC mgChl^{-1} h^{-1})
0
1
2
3
4
5
6

Fig. 8

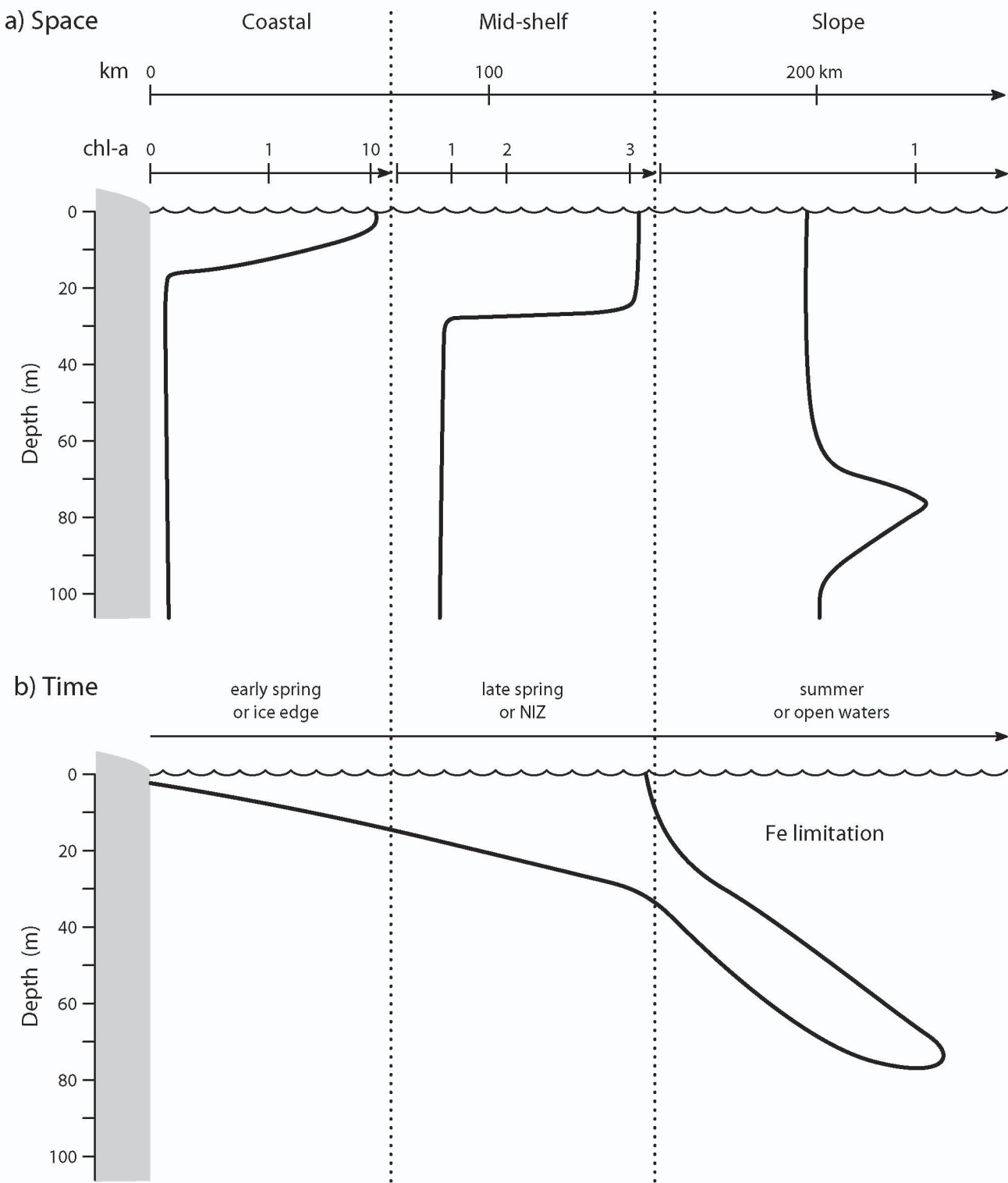

a) Space
Coastal
Mid-shelf
Slope
km
0
100
200 km
chl-a
0
1
10
1
2
3
1
Depth (m)
0
20
40
60
80
100
b) Time
early spring
or ice edge
late spring
or NIZ
summer
or open waters
Fe limitation
Depth (m)
0
20
40
60
80
100

Table 1

Ocean	Biome	ANPP ($gC\ m^{-2}\ a^{-1}$)		Provinces
		Average	*St.Dev.*	(n)
Atlantic Ocean	Atlantic Polar	350.83	48.61	3
	Atlantic Westerly	183.30	64.03	4
	Atlantic Trade Wind	130.66	44.05	5
	Atlantic Coastal	525.38	161.91	8
Indian Ocean	Indian Ocean Trade Wind	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