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Primary Production in the Ocean

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1. Introduction

Primary productivity is the process by which inorganic forms of carbon are synthesized by living organisms into simple organic compounds. Most carbon on Earth is in inorganic oxidized forms such as carbon dioxide (CO_2), bicarbonate (HCO_3^-), and carbonate (CO_3^{2-}). Inorganic carbon must be chemically reduced to form the organic molecules which are the building blocks of life and the mechanism by which energy is stored in living organisms. The reduction of inorganic carbon requires an investment of energy and this can come from light or from energy stored in some reduced inorganic compounds. Autotrophs are organisms capable of fixing inorganic carbon. Photoautotrophs use light energy to fix carbon, whereas chemoautotrophs use the energy released through the oxidation of reduced inorganic substrates to fix carbon into organic compounds.

Both photosynthesis and chemosynthesis contribute to the primary production of the oceans, however oxygenic photosynthesis is by far the dominant process in terms of the amount of carbon fixed and energy stored in organic compounds. Photosynthesis occurs in all parts of the ocean where there is sufficient light, whereas chemosynthesis is limited to locations where there are sufficient concentrations of reduced chemical substrates. Although the vast majority of the ocean's volume is too dark to support photosynthesis, organic carbon and energy is transferred to the dark waters via processes such as particle sinking and the vertical migrations of organisms. Almost all ecosystems in the ocean are fueled by organic carbon and energy which was initially fixed by oxygenic photosynthesis. Anoxygenic photosynthesis does occur in the ocean, however it is confined to anaerobic environments in which there is sufficient light or associated with aerobic anoxygenic photosynthesis (Kolber et al., 2000), the global significance of which is yet to be determined. Consequently, in this overview of primary production in the ocean I will focus on oxygenic photosynthesis.

Blankenship (2002) defined photosynthesis as: 'a process in which light energy is captured and stored by an organism, and the stored energy is used to drive cellular processes.' Oxygenic photosynthesis may be expressed as an oxidation-reduction reaction in the form:

$$2H_2O + CO_2 + \text{light} \rightarrow (CH_2O) + H_2O + O_2 \text{ (Falkowski \& Raven, 2007)} \quad (1)$$

In this reaction carbohydrate is formed from carbon dioxide and water with light providing the energy for the reduction of carbon dioxide. Equation 1 is an empirical summary of the overall reaction, which in reality occurs in a number of steps. The light energy for the reaction is primarily absorbed by the green pigment chlorophyll.

2. Which organisms are important primary producers in the ocean?

In terms of number of species, phylogenetic diversity and contribution to total global primary production, the unicellular phytoplankton dominate primary production in the ocean (Falkowski et al., 2004). Almost all oxygenic photosynthetic primary producers in the ocean are either cyanobacteria (Cyanophyta) or eukarytotic algae. The eukaryotic algae are a diverse polyphyletic group, including both unicellular and multicellular organisms.

2.1 Multicellular primary producers

Most multicellular primary producers grow attached to substrates, therefore they are usually restricted to the coastal margins of the ocean in shallow waters where there are both attachment sites and sufficient light for photosynthesis. Important primary producers include seagrasses that form beds that are rooted in sediments in shallow water in tropical and temperate latitudes. Seagrasses (e.g *Zostera*) are flowering plants, unlike the macroalgae, which are not flowering plants and are phylogenetically diverse. Kelps, such as *Macrocystis* and *Laminaria* are locally significant macroalgae in shallow temperate and subpolar waters where there are suitable hard substrates for attachment. Geider et al. (2001) estimated that the net annual primary production by saltmarshes, estuaries and macrophytes was 1.2 Pg C, which is a relatively small proportion of total annual marine production (see section 6).

Some macroalgae are found in the open ocean; *Sargassum* is planktonic and forms rafts at the sea surface in tropical waters (Barnes & Hughes, 1988), mainly in the Gulf of Mexico and Sargasso Sea. The biomass of rafts rival phytoplankton biomass in the mixed layer in the Gulf of Mexico (on an areal basis) with a total standing stock of 2 - 11 million metric tons (Lapointe, 1995; Gower & King, 2008).

2.2 Phytoplankton

There are several groups of eukaryotic phytoplankton which make a significant contribution to global primary production. The most significant of these groups are the diatoms, dinoflagelletes and prymnesiophytes. Diatoms and dinoflagellates are usually found in the microphytoplankton (20 – 200 μm), whereas the prymnesiophytes are nanophytoplankton (2 – 20 μm). Photosynthetic bacteria contribute to the picophytoplankton and are < 2 μm in diameter. Oxygenic photosynthetic bacteria in the oceans belong to the division Cyanophyta, which contains the cyanobacteria (cyanophyceae) and the prochlorophytes (prochlorophyceae).

2.2.1 Photosynthetic bacteria

Arguably, the most important discovery of 20th century biological oceanography was the major role that prokaryotes have in nutrient cycling and production in the water column. As detection and enumeration methods improved it became apparent that photosynthetic bacteria are ubiquitous and make a significant contribution to biomass and primary productivity. The prochlorophytes possess the photosynthetic pigment divinyl chlorophyll *a*, but not chlorophyll *a* which is found in all other Cyanophyta and eukaryotic algae in the ocean. The prochlorophyte *Prochlorococcus marinus* is an abundant and significant primary producer in the open ocean (Chisolm et al., 1988; Karl, 2002) and can be found in concentrations in excess of 10^5 cells ml^{-1} (Chisolm et al., 1988). *Prochlorococcus* has been shown to contribute 9 % of gross primary production in the eastern equatorial Pacific, 39 %

in the western equatorial Pacific and up to 82 % in the subtropical north Pacific (Liu et al., 1997). *Prochlorococcus* is probably the most abundant photosynthetic organism on Earth.
Important cyanophyceae include the coccoid *Synechococcus*, which makes a significant contribution to biomass and photosynthesis of the open ocean. For example, Morán et al. (2004) found that picophytoplankton dominated primary production in the North Atlantic subtropical gyre in 2001. *Synechococus* spp. contributed 3 and 10 % of the picophytoplankton biomass, respectively, in the subtropical and tropical domains. However, although *Synechococcus* spp. was significant, *Prochlorococcus* spp. dominated, contributing 69 % of biomass to the subtropical and 52 % to the tropical domain.

2.2.2 Diatoms

Diatoms (Heterokontophyta, Bacillariophyceae) are characterized by a cell wall composed of silica. Estimates of extant diatom species vary between 10,000 (Falkowski & Raven, 2007) and 100,000 (Falciatore & Bowler, 2002). They are found in a wide range of freshwater and marine environments, both in the water column and attached to surfaces. Diatoms make a significant contribution to global primary production on both a local and global scale. It is estimated that diatoms account for 40 to 45% of net oceanic productivity (approximately 20 Pg C yr^{-1}; 1 Pg = 10^{15} g) or almost a quarter of the carbon fixed annually on Earth by photosynthesis (Mann 1999; Falciatore & Bowler 2002; Sarthou et al. 2005), though in my opinion, this is probably an overestimate. Phytoplankton populations in relatively cool, well mixed waters are often dominated by diatoms in terms of productivity and biomass. In addition, diatoms often dominate the microphytobenthos (Thornton et al., 2002), which are populations of microalgae inhabiting the surface layers of sediments in shallow, coastal waters where there is sufficient light reaching the seabed to support photosynthesis. Diatoms may form monospecific blooms of rapidly growing populations; for example, *Skeletonema costatum* frequently forms blooms in coastal waters (Gallagher, 1980; Han et al., 1992; Thornton et al., 1999). Diatom blooms often terminate with aggregate formation, which in addition to the fecal pellets produced by grazers, can lead to the rapid flux of carbon and other nutrients from surface waters to deeper water and the seafloor (Thornton, 2002) (see section 7.1).

2.2.3 Prymnesiophytes

Prymnesiophytes (Prymnesiophyta) are motile, unicellular phytoplankton with two flagella. Most genera also have a filamentous appendage located between the flagella called a haptonema, the function of which is unknown. The cell surface of most prymnesiophytes is covered in elliptical organic scales, which are calcified in many genera. These scales of calcium carbonate are called coccoliths and the prymnesiophytes which possess them are coccolithophores. Coccolithophores are common in warm tropical waters characterized by a low partial pressure of carbon dioxide and saturated or supersaturated with calcium carbonate (Lee, 2008). The importance of the coccolithophores as primary producers during Earth's history is exemplified by the thick chalk deposits found in many parts of the world, such as the white cliffs along the coast of southern England. These deposits were formed from coccoliths that sank to the bottom of warm, shallow seas during the Cretaceous geological period. Moreover, calcium carbonate is the largest reservoir of carbon on Earth. Blooms of coccolithophores such as *Emiliania huxleyi* may be extensive and have been observed on satellite images as milky patches covering large areas of ocean (Balch et al.

1991). *Phaeocystis* is an important primary producer in coastal waters. This genus does not have coccoliths, it is characterized by a colonial life stage in which the cells are embedded in a hollow sphere of gelatinous polysaccharide. Colonies may be large enough to be seen by the naked eye. *Phaeocystis pouchetii* forms extensive blooms in the North Sea (Bätje & Michaelis, 1986) and *Phaeocystis antarctica* is an important primary producer in the Ross Sea (DiTullo et al., 2000).

2.2.4 Dinoflagellates

Dinoflagelletes (Dinophyta) are a largely planktonic division of motile unicellular microalgae that have two flagella. They can be found in both freshwater and marine environments. Generally, dinoflagellates are a more significant component of the phytoplankton in warmer waters. Some photosynthetic dinoflagellates form symbiotic relationships with other organisms, such as the zooxanthellae found in the tissues of tropical corals. Other dinoflagellates do not contribute to primary production as they are non-photosynthetic heterotrophs which are predatory, parasitic or saprophytic (Lee, 2008). Dinoflagellates often dominate surface stratified waters; in temperate zones there may be a succession from diatoms to dinoflagellates as the relatively nutrient rich, well mixed water column of spring stabilizes to form a stratified water column with relatively warm, nutrient poor surface waters. Dinoflagellates have a patchy distribution and may bloom to form 'red tides.' Some dinoflagellates are toxic and form harmful algal blooms; *Karenia brevis* blooms in the Gulf of Mexico and on the Atlantic coast of the USA, resulting in fish kills and human health problems (Magaña et al., 2003).

3. Measuring phytoplankton biomass

The best measure of biomass would be to determine the amount of organic carbon in the phytoplankton cells. However, such a measure is almost impossible in a natural seawater sample due to the presence of other organisms, detritus and dissolved organic matter. Consequently, photosynthetic pigments (usually chlorophyll *a*) are used as a proxy for the biomass of phytoplankton. There are a number of techniques for measuring the concentration of chlorophyll *a* and other photosynthetic pigments in water samples. These methods provide information that is relevant to that particular time and location, but these 'snapshots' have limited use at the regional or ocean basin scale. Over the last 30 years our understanding of the spatial and temporal distribution of phytoplankton biomass has been revolutionized by the measurement of ocean color from satellites orbiting the Earth. These instruments provide measurements over a short period of time of a large area, which is not possible from platforms such as ships.

3.1 Pigment analysis

Chlorophyll fluorescence has been used as tool to determine the distribution of phytoplankton biomass in the ocean since the development of flow-through flourometers (Lorenzen, 1966; Platt, 1972). Most oceanographic research vessels are fitted with flow-through chlorophyll fluorometers that provide continuous chlorophyll fluorescence data. However, there is not a truly linear relationship between *in vivo* flourescence and phytoplankton chlorophyll concentrations (Falkowski & Raven, 2007). The lack of linearity between *in vivo* fluorescence and chlorophyll is related to the fate of light energy absorbed

by chlorophyll; light energy is either lost through fluorescence, heat dissipation or used in photochemistry (Maxwell & Johnson, 2000) and the balance between these processes changes depending on the physiological status of the phytoplankton, including rate of photosynthesis and prior light history (Kromkamp & Forster, 2003).

A more accurate estimate of photosynthetic biomass than *in vivo* chlorophyll fluorescence may be obtained if the photosynthetic pigments are extracted from the organism. For water samples containing phytoplankton, a known volume is filtered onto a glass fiber filter and the photosynthetic pigments are extracted using a known volume of organic solvent such as acetone or methanol. The concentration of chlorophyll *a* is then measured in the extract by spectrophotometry or fluorescence (Parsons et al., 1984; Jeffrey et al., 1997). While still widely used, these relatively simple techniques have a number of drawbacks. Firstly, chlorophyll degradation products may absorb light at the same wavelengths as chlorophyll, leading to an overestimation of chlorophyll concentration (Wiltshire, 2009). Secondly, the emission spectra of chlorophyll *a* and *b* overlap, which will result in inaccurate measurement of chlorophyll *a* in water containing chlorophyll *b* containing organisms (Wiltshire, 2009). For the accurate measurement of chlorophyll *a*, other photosynthetic pigments, and their derivatives, high performance liquid chromatography (HPLC) methods should be used (see Wiltshire (2009) for description). HPLC enables the pigments to be separated by chromatography and therefore relatively pure pigments pass through a fluorescence or spectrophotometric detector. In addition to chlorophyll *a*, algae contain multiple pigments. These accessory pigments are often diagnostic for major taxonomic groups (see Table 10.1; Wiltshire, 2009). CHEMTAX (Mackay et al., 1996) is a method by which the total amount of chlorophyll *a* can be allocated to the major taxonomic groups of algae based on the concentrations and ratios of accessory pigments. Thus, HPLC can be used to estimate phytoplankton biomass in terms of chlorophyll *a* and potentially determine the dominant groups of phytoplankton in the sample.

3.2 Ocean color

The Coastal Zone Color Scanner (1978-1986) was the first satellite mission that measured chlorophyll *a* concentrations using top of the atmosphere radiances (McClain, 2009). The success of this mission led to a number of missions to measure ocean color at either global or regional spatial scales by Japanese, European and United States space agencies. As a result of these missions, we now have over 30 years of ocean color measurements. The color of the ocean is affected by particulates and dissolved substances in the water and the absorption of light by water itself. Water is transparent at blue and green wavelengths, but strongly absorbs light at longer wavelengths (McLain, 2009). Chlorophyll *a* has a primary absorption peak near 440 nm and chromophoric dissolved organic matter (CDOM) absorbs in the UV (McLain, 2009). Thus, there is a shift from blue to brown water as pigment and particulate concentrations increase (McLain, 2009).

Measurements of ocean color enabled oceanographers to infer the spatial and temporal distribution of phytoplankton on ocean basin and global scales for the first time. The Sea-viewing Wide Field-of-view Sensor (SeaWIFS) and Moderate Resolution Imaging Spectroradiometers (MODIS) are currently active and have been collecting data since 1997 and 2002 (Aqua MODIS), respectively. MODIS collects data from 36 spectral bands from the entire Earth's surface very 1 to 2 days (http://modis.gsfc.nasa.gov). SeaWIFS also produces complete global coverage every two days (Miller, 2004). Goals for accuracy of satellite

products are ± 5% for water-leaving radiances and ± 35 % for open-ocean chlorophyll *a* (McLain, 2009). In addition to rapid regional or global estimates of chlorophyll *a*, algorithms have been developed to estimate net primary productivity (NPP) based on ocean color (Behrenfield & Falkowski, 1997. See section 6 of this chapter).

4. Measuring marine photosynthesis

Photosynthesis results in primary productivity. The terms production and productivity are often used interchangeably and there no generally accepted definition of primary production (Underwood & Kromkamp, 1999). Falkowski & Raven (2007) define primary productivity as a time dependent process which is a rate with dimensions of mass per unit time; whereas primary production is defined as a quantity with dimensions of mass. In contrast, Underwood & Kromkamp (1999) define primary production as a *rate* of assimilation of inorganic carbon into organic matter by autotrophs. For the purposes of this review, I will use the definitions of Falkowski & Raven (2007).

There are a number of methods that are regularly used to measure rates of primary productivity. Techniques are based around gas exchange, the use of isotope tracers, or chlorophyll fluorescence. Primary productivity is usually expressed as the production of oxygen or the assimilation of inorganic carbon into organic carbon over time (equation 1). Carbon assimilation is a more useful measure as it can be directly converted into biomass and used to calculate growth. Common units for primary productivity in marine environment are mg C m^{-2} day^{-1} or g C m^{-2} $year^{-1}$. Primary productivity is often normalized to biomass, as it is useful to know how much biomass is responsible for the observed rates of productivity.

Different techniques will produce slightly different rates of productivity (Bender et al., 1987) as a result of the biases associated with each method. No single technique provides a 'true' measurement of primary productivity. Consequently, researchers should select their methodology based on what factors they want to relate their measurements to, time available to make the measurements, and which assumptions and sources of error are tolerable to answer their particular research questions. Most methods for measuring primary productivity in the ocean require that a sample of water is enclosed in a container, this in itself effects the primary producers. Phytoplankton may be killed on contact with the container or there may be an exchange of solutes between the walls of the container and the sample (Fogg & Thake, 1987). When working in oligotrophic waters contamination of the samples onboard ship is a serious problem. Williams & Robertson (1989) found that the rubber tubing associated with a Niskin sampling bottle severely inhibited primary productivity in samples taken in the oligotrophic Indian Ocean. Moreover, large areas of the ocean are iron limited (Boyd et al., 2000) and it is a challenge to prevent iron contamination in these areas given that oceanographers generally work from ships fabricated from steel.

4.1 Gas exchange methods

Changes in oxygen concentration over time in water samples can be used to calculate rates of photosynthesis and therefore primary productivity. This method involves enclosing water samples and incubating them in the dark and light either onboard ship or *in situ*. Bottles incubated in the dark are used to measure dark respiration rates. To ensure that the rates of photosynthesis are representative, the bottles should be incubated at *in situ* temperature and under ambient light. One way of doing this is to deploy the bottles on a

line *in situ*; bottles deployed at different depths will be exposed to the ambient light and temperature at that depth. Changes in oxygen concentration can be monitored with oxygen electrodes or by taking water samples that are fixed and oxygen concentration is subsequently measured by Winkler titration (Parsons et al., 1984). In laboratory studies using pure cultures of phytoplankton oxygen electrode chambers have been used extensively in photosynthesis research (e.g. Colman & Rotatore, 1995; Johnston & Raven, 1996). These systems comprise of a small, optically clear, chamber (usually a few ml) which has a Clark-type oxygen electrode set in the base (see Allen and Holmes (1986) for a full description). Carbon assimilation rates based on oxygen production often assume a ratio of moles of O_2 produced for every mole of CO_2 assimilated, called the photosynthetic quotient, which usually deviates from the 1:1 ratio indicated by equation 1.

In sediments, profiles and changes in oxygen concentration over time may be made using oxygen microelectrodes (Revsbech & Jørgensen, 1983). The microphytobenthos is usually limited to the surface 2 or 3 mm of sediment, therefore high resolution measurements are required; photosynthesis is measured to a resolution of 100 μm and the sensing tips of the microelectrode have diameters of only 2 – 10 μm (Revsbech et al., 1989). While oxygen microelectrodes just measure oxygen concentration, it is possible to measure gross photosynthesis rates using the light-dark shift method (Revsbech & Jørgensen, 1983; Glud et al., 1992; Lassen et al., 1998; Hancke & Glud, 2004). Moreover, oxygen concentration profiles can be used to calculate respiration and net photosynthesis rates according to Kühl et al. (1996) and Hancke & Glud (2004) based on Fick's first law of diffusion. Estimates of benthic primary productivity are also made using oxygen exchange across the sediment-water interface using benthic chambers or sediment cores (Thornton et al., 2002).

Optodes have recently been used to measure changes in oxygen concentrations associated with photosynthesis. Optodes work by using fluorescence quenching by oxygen of a luminophore. The intensity of fluorescence is inversely proportional to the O_2 partial pressure at the luminophore (Glud et al., 1999). For example, Glud et al. (1999) used the luminophore ruthenium (III)-Tris-4,7-diphenyl-1,10-phena-throline, which absorbs blue light (450 nm), with the intensity of the emitted red light (650 nm) decreasing with increasing O_2 partial pressure. Unlike Clark-type oxygen electrodes, optodes do not consume oxygen. Two designs of optodes are used in photosynthesis measurements: optodes that are used in a similar way to oxygen microelectrodes (Miller & Dunton 2007), and planer optodes that produce a two-dimensional image of oxygen concentrations (Glud et al., 1999, 2001). Miller & Dunton (2007) used a micro-optode to measure photosynthesis-irradiance curves for the kelp *Laminaria hyperborea*. Planar optodes have been used to produce images of oxygen concentrations across the sediment-water interface in sediments colonized by photosynthetic biofilms (Glud et al., 1999, 2001). As planar optodes produce a two dimensional image, multiple oxygen profiles can be extracted from a single measurement (Glud et al., 2001). Moreover, the light-dark shift method can be used to measure gross photosynthesis rates (Glud et al., 1999).

4.2 Isotopes as tracers of aquatic photosynthesis

Carbon exists in three isotopes in nature. The most common isotope is ^{12}C, which makes up 98.9% of the natural carbon on Earth. Carbon also exists in another stable form as ^{13}C (1.1 %) and an insignificant amount of the radioactive isotope ^{14}C (< 0.0001 %) (Falkowski & Raven, 2007). The relatively low abundance of ^{14}C and ^{13}C means that these isotopes can potentially

be used to measure photosynthesis rates and follow the passage of carbon through photosynthetic organisms when added as tracers. Uptake and assimilation of inorganic carbon into acid-stable organic carbon (Falkowski & Raven, 2007) is the most commonly employed method for measuring photosynthesis using the radioactive tracer ^{14}C (Steeman-Nielson, 1952). The rationale for the ^{14}C method is that the incorporation of radioactively labeled carbon is quantitatively proportional to the rate of incorporation of non-labeled inorganic carbon. Over relatively short incubations the results are a good approximation of gross photosynthesis and an approximation of net photosynthesis over longer time periods (Falkowski & Raven, 2007). This technique (described in Parsons et al., 1984) has been the primary method for measuring the primary productivity of phytoplankton for over fifty years. The method has the advantage of being relatively simple and sensitive. Although widely used, the technique is not without drawbacks and ambiguities. For example, there is an isotopic discrimination between ^{14}C and the natural isotope ^{12}C; less ^{14}C is fixed as it is heavier than ^{12}C, and a discrimination factor of 5 % is usually incorporated into the calculation of inorganic carbon fixation rates (Falkowski & Raven, 2007). Furthermore, the organic carbon, including the ^{14}C which has been fixed during the incubation, is usually separated from the sample by filtration. This can lead to a loss of ^{14}C labeled organic carbon due to rupture of cells on contact with the filter (Sharp, 1977) or exudation of photosynthetic products. There is also a continuing debate as to whether primary productivity measured with the ^{14}C method represents gross or net rates, or something in between the two (Underwood & Kromkamp, 1999).

The advantage of using ^{13}C as a tracer for photosynthesis is that it is not radioactive. This means that it is logistically simpler to use if one has access to an isotope ratio mass spectrometer. Moreover, unlike ^{14}C, ^{13}C can be added as tracer to natural ecosystems and used to trace the assimilation of carbon and transfer to higher trophic levels. Miller & Dunton (2007) used ^{13}C to measure the photosynthesis of the macroalga *Laminaria hyperborea*. Middelburg et al. (2000) and Bellinger et al. (2009) used ^{13}C as a tracer to trace carbon flow through intertidal benthic biofilms dominated by diatoms and cyanobacteria. The tracer was added to the sediment at low tide and followed through the ecosystem over a period of hours to days. Middelburg et al. (2000) showed that carbon fixed through photosynthesis was transferred to bacteria and nematodes within hours. Bellinger et al. (2009) examined the incorporation of the tracer into important biomolecules, including exopolymers (EPS) and phospholipid fatty acids (PLFAs).

Photosynthesis rates have also been measured with the stable isotope ^{18}O by adding labeled water as a tracer and measuring the production of ^{18}O labeled oxygen with a mass spectrometer (Bender et al., 1987; Suggett et al., 2003). The method produces a relatively precise measurement of gross photosynthesis (Falkowski & Raven, 2007). However, this technique has not been used extensively.

Oxygen exists in nature in the form of three isotopes; ^{16}O (99.76 % of the oxygen on Earth), ^{18}O (0.20 %), and ^{17}O (0.04 %) (Falkowski & Raven, 2007). Luz & Barken (2000) developed the triple isotope method using natural abundances of oxygen isotopes to estimate the production of photosynthetic oxygen using the isotopic composition of dissolved oxygen in seawater. The method was based on the ^{17}O anomaly ($^{17}\Delta$), which is calculated from $^{17}O/^{16}O$ and $^{18}O/^{16}O$ (Luz & Barkin, 2000, 2009). This innovative technique does not require water to be enclosed in bottles and therefore avoids bottle effects. The method is used to determine gross photosynthesis rates, enabling integrated productivity to be estimated on a time scale

of weeks (Luz & Barkin, 2000). Luz & Barkin (2009) showed that combining $^{17}\Delta$ with O_2/Ar ratios enables gross and net oxygen production to be estimated.

4.3 Chlorophyll fluorescence

Chlorophyll *a* fluorescence can be used for more than estimating phytoplankton biomass (see 3.1) and there has been a wealth of research over the last 20 years on the application of variable chlorophyll *a* fluorescence to the measurement of photosynthesis and the physiological status of photosynthetic organisms. Energy absorbed by chlorophyll *a* may be used in photochemistry and stored in photosynthetic products, dissipated as heat, or lost as fluorescence. Chlorophyll *a* fluorescence is largely derived from the chlorophyll *a* associated with photosystem II (PSII); changes in the quantum yield of fluorescence directly relate to O_2 evolving capability as PSII is the oxygen evolving complex within the photosynthetic apparatus (Suggett, 2011). There are two main types of fluorometers that are used to measure variable chlorophyll *a* fluorescence; Pulse Amplitude Modulation (PAM) fluorometers (Schreiber et al., 1986) and Fast Repetition Rate (FRR) fluorometers (Kolber et al., 1998). These instruments use a modulated light source that allows measurements to be made in the presence of background light or under field light conditions (Maxwell & Johnson, 2000). The PAM approach is not sensitive enough to use in open ocean conditions (Suggett et al., 2003), although it is increasingly being used to measure photosynthetic parameters associated with the microphytobenthos (Underwood, 2002; Perkins et al., 2002; 2011; Serôdio, 2004), macrophytes (Enríquez & Borowitzka, 2011), and has been used with cultures of phytoplankton (Suggett et al., 2003; Thornton, 2009). FRR has been used in the open ocean (Babin et al., 1996; Suggett et al., 2001). The difference between PAM and FRR is beyond the scope of this review; for an overview see Huot & Babin (2011).

Modulated chlorophyll *a* fluorometers cannot be used to measure photosynthesis directly. One of the primary measurements made with modulated chlorophyll *a* fluorometers is the quantum yield of PSII photochemistry (Φ_{PSII}). Genty et al. (1989) demonstrated that Φ_{PSII} correlated with CO_2 assimilation in maize and barley, raising the possibility that variable chlorophyll *a* fluorescence could be used to estimate photosynthesis rates. Φ_{PSII} multiplied by the rate of light absorption by PSII is used to calculate electron transfer rate (ETR_{PSII}) through PSII (Enríquez & Borowitzka, 2011; Suggett et al., 2011; White & Critchley, 1999). ETR_{PSII} has been used as a proxy for photosynthesis. However, there are several reasons why the relationship between Φ_{PSII} (and therefore ETR_{PSII}) and CO_2 assimilation or O_2 production may not be constant (see Suggett, 2011). This effect may be compounded in the algae due to their taxonomic and resultant physiological diversity (Suggett, 2011). Suggett et al., (2009) used an FRR fluorometer to measure ETR_{PSII} and examined the relationship between ETR_{PSII} and photosynthesis measured by either gross O_2 production or $^{14}CO_2$ fixation. Measurements were made using six species of eukaryotic phytoplankton, representing a diversity of taxonomic groups. ETR_{PSII} was linearly related to the rate of gross O_2 production in all species; however, the slope of the relationship was significantly different for different species. ETR_{PSII} was also linearly related to $^{14}CO_2$ fixation; however, both the slope and intercept of the relationship was different for different species. These results highlight some of the challenges involved in using ETR_{PSII} to estimate photosynthesis rates, especially in natural populations of phytoplankton which are likely to be diverse both in terms of taxonomic composition and physiological status.

There are several advantages to variable fluorescence techniques; the techniques are not intrusive and do not harm the organisms, measurements can be made at high spatial and temporal resolution (Suggett et al., 2003), measurements do not require any wet chemistry, and the water sample does not have to be enclosed in a bottle (Kolber et al., 1998). Consequently, variable fluorescence instruments are suited to ocean observing programs; Yoshikawa & Furuya (2004) used a fluorometer moored *in situ* to monitor photosynthesis in coastal waters. Some of the disadvantages to variable fluorescence stem from the fact that this is a relatively young and rapidly evolving field. In the 1970s and 1980s technology was the limiting factor to the development of the field. Since the 1990s there has been a rapid evolution of the technology leading to a large number of commercially available instruments. However, an understanding of the physiology and development of theory associated with variable chlorophyll *a* fluorescence has arguably lagged behind instrument development in recent years. For new users, the large number of fluorescence parameters and their definitions can be confusing (Cosgrove & Borowitza, 2011). This is compounded by the fact that there is no standardized terminology and many fluorescence parameters have several synonyms in the literature. Attempts have been made to standardize terminology (Kromkamp & Forster, 2003).

Photoacoustics has also been used to study phytoplankton photosynthesis (Grinblat & Dubinsky, 2011). This is not a fluorescence technique, however it is based on the same principle that only a small and variable fraction of the energy absorbed by photosynthetic pigment is stored in photosynthetic products. While the preceding discussion has focused on fluorescence, only a few percent of the absorbed light energy is actually lost as fluorescence. The major loss of energy is through heat, which may account for over 60 % of the energy absorbed (Grinblat & Dubinsky, 2011). The photoacoustic method is based on the conversion of light energy to heat energy that results in a rise in temperature and an increase in pressure (photothermal effect) (Grinblat & Dubinsky, 2011). In practice, a suspension of phytoplankton is exposed to a laser pulse, some of the energy from the laser pulse is stored in the photochemical products of photosynthesis and the remainder is dissipated as heat, resulting in an acoustic wave which is measured by a detector (Grinblat & Dubinsky, 2011). This technique has not been used extensively; for further details see Grinblat & Dubinsky (2011).

5. Temporal and spatial variation in oceanic primary production

The mean chlorophyll *a* concentration in the global ocean is 0.32 mg m^{-3} (Falkowski & Raven, 2007). However, this is not evenly distributed throughout the ocean. Primary production at any one location will vary in space and time in response to factors limiting or stimulating photosynthesis and phytoplankton growth. Photosynthesis and growth in the sea are limited by nutrients, light or temperature. In the dynamic environment of a water column resources are patchy both in time and space. Consequently, phytoplankton may receive nutrients and light in pulses rather than a continuous supply. Generally, it is the interplay between nutrient and light availability that affects phytoplankton photosynthesis and primary production.

The traditional paradigm of biological oceanography was that bioavailable nitrogen is the nutrient limiting primary production in the ocean (Ryther & Dunstan, 1971; Howarth, 1988). This is an over simplification and is increasingly being challenged. For example, the Mediterranean Sea appears to be phosphorus limited (Thingstad & Rassoulzadegan, 1995)

and there is evidence of phosphorus limitation in coastal ecosystems (Sundareshwar et al., 2003). In over 20 % of the ocean there are excess nutrients (nitrate, phosphate, silicate) and light, but the biomass of phytoplankton is relatively low (Martin et al., 1994). These areas are known as the high-nitrate, low-chlorophyll (HNLC) areas. They are located in the equatorial Pacific, the subarctic Pacific, and the Southern Ocean (Falkowski & Raven, 2007). Iron is an essential component of the nitrogenase enzyme, consequently iron limitation limits nitrogen fixation by cyanobacteria over large areas of the ocean (Falkowski et al., 1998) (see 7.3). Iron is supplied to the open ocean via wind blown dust from arid areas of the continents (Duce & Tindale, 1991). The upwelling of deep waters containing nitrate and phosphate produced from the remineralization of organic matter is important in maintaining high primary productivity in many areas of the ocean, such as along the western margins of Africa and South America. Conversely, thermal stratification and downwelling will limits primary production in the subtropical gyres as the sunlit surface waters are largely isolated from nutrient rich waters below the thermocline.

Light (solar radiation) provides the energy that drives photosynthesis. Light is variable on a number of spatial and temporal scales. Low latitudes receive more solar radiation than high latitudes and have less variation in solar radiation over the course of one year. At high latitudes there are pronounced seasons and variations in day length. Imposed on these month to month or season to season variations in solar radiation are short term fluctuations. The angle of the sun above the horizon affects how much light is reflected off the surface of the ocean. At midday, when the sun is at an angle of 90^{o} to the sea surface, 2 % of the incoming solar radiation is reflected; this value increases to 40 % during the evening and early morning when the sun is at an angle of 5 ^{o} (Trujillo & Thurman, 2005). Reflection off cloud cover also significantly reduces the input of solar radiation into the ocean. Conversely, net primary productivity may be inhibited by too much light, which can lead to photoinhibition or conditions conducive to photorespiration (Fig. 1).

The depth of the euphotic zone (surface layer in which there is enough light to support photosynthesis) is often less than 10 m and rarely greater than 100 m (Fogg & Thake, 1987), whereas the mean depth of the ocean is approximately 3,700 m. Therefore, photosynthesis and primary production is limited to a thin layer at the ocean surface and whether phytoplankton cells are mixed into the dark waters below will effect primary productivity. As the mixed layer of a water column increases the average photon flux density (i.e. light) to which the cells are exposed will decrease as the circulating cell will spend longer in darkness. Therefore the total gross productivity of the phytoplankton population will decrease (Fig. 1). However, the respiration rate of the population will be relatively constant, whatever the depth of mixing. This results in a *critical depth* in a mixed water column; if the cells are mixed below the critical depth then there will be no net productivity as the respiratory loss of carbon will exceed photosynthetic carbon gain. Net photosynthesis and the resulting net primary productivity will only occur in mixed water where the mixing is less than the critical depth (Sverdrup, 1953; Kirk, 1983).

Grazing also effects production; in a heavily grazed population of phytoplankton individual cells may show high rates of productivity, but there may be a low biomass of primary producers as a large proportion of the primary production is transferred to other trophic levels. In recent years there has been a realization that phytoplankton are subject to lytic viral infection (Suttle et al., 1990; Nagasaki et al., 2004), which will have an effect similar as grazing by reducing the biomass of primary producers in the water column.

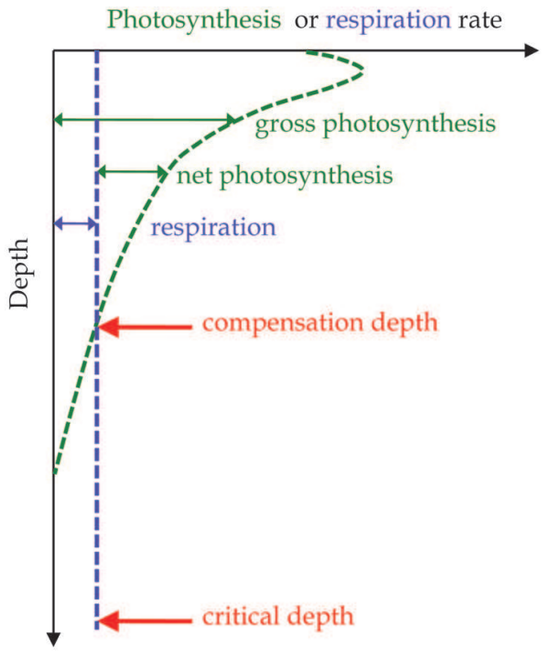

Fig. 1. Schematic of photosynthesis and respiration rates with depth in the ocean. The green line shows gross photosynthesis rate, which declines from a maximum just below the surface to zero in response to the availability of light. Phytoplankton respiration rate is constant with depth and is shown in blue; net photosynthesis is gross photosynthesis minus respiration. The compensation depth occurs where the net photosynthesis rate is zero as the respiration rate is equal to the gross photosynthesis rate. The critical depth occurs deeper in the water column and it is where depth integrated gross photosynthesis equals depth integrated respiration.

6. Global estimates of primary productivity

Estimates of net primary productivity in the oceans are on the order of 40 -55 Pg C yr^{-1} (1 Pg = 1 gigaton = 10^{15} g), which is approaching half of global annual net primary productivity. Falkowski et al. (1998), citing data from a number of papers, estimated that marine phytoplankton fix approximately 45 Pg C yr^{-1}. Falkowski et al. (1998) estimated that 16 of the 45 Pg C yr^{-1} are exported from the surface to the ocean interior (see 7.2).

A key goal of satellite observations of ocean color has been to convert ocean color data to net primary productivity (NPP) and a variety of NPP algorithms exist (McCLain, 2009). Longhurst et al. (1995) estimated global net primary productivity of the oceans to be 45 – 50 Pg C yr^{-1} and Field et al. (1998) estimated a value of 48.5 Pg C yr^{-1}. Since this initial work, many different algorithms have been developed to estimate NPP from ocean color data. Carr et al. (2006) compared 24 algorithms and found that the mean NPP estimate for the ocean was 51 Pg C yr^{-1}, with the range of the estimates spanning 32 Pg C yr^{-1}. Most of these algorithms have an empirical physiological parameter to account for phytoplankton physiological status (McClain, 2009), which is difficult to determine from space based observations (Behrenfeld et al., 2005).

Behrenfeld et al., (2005) developed a carbon-based model that does not require a physiological parameter. The logic of their approach was that laboratory experiments have

shown that phytoplankton respond to changes in light, nutrients and temperature by adjusting cellular pigment content to meet requirements for photosynthesis. This physiological response can be seen in changes in the carbon: chlorophyll *a* ratio of the phytoplankton and therefore a remote sensing measure of the carbon: chlorophyll *a* ratio may provide an index of the physiological status of the phytoplankton. Westberry et al., (2008) recently refined this model and estimated a global ocean NPP of approximately 52 Pg C yr^{-1}.

Geider et al. (2001), based on the data of Longhurst et al. (1995) and Field et al. (1998), estimated NPP for different ocean environments, with values of: 1.2 Pg C yr^{-1} for salt marshes, macrophytes and estuaries; 0.7 Pg C yr^{-1} for coral reefs; 10.7 Pg C yr^{-1} for the coastal domain; 6.4 Pg C yr^{-1} for the polar regions; 29.3 Pg C yr^{-1} for the remaining ocean. The average NPP of the land (excluding areas permanently covered in ice) is 426 g C m^{-2} yr^{-1}, compared to 140 g C m^{-2} yr^{-1} for the ocean (Field et al., 1998). NPP per unit area of the land is three times greater than that of the ocean; however, the ocean contributes almost half of net global primary production as it covers approximately three quarters (70.8 %) of the surface area of Earth.

7. Oceanic primary production and the biogeochemical cycling of elements

Biogeochemical cycles occur as a result of the interplay between physical, geological, chemical and biological processes, which affect the distribution of elements between living and non-living reservoirs on Earth. Living organisms both react to changes in the environment and affect environmental change. This concept has led to 'Earth system science' in which the biosphere, chemosphere and geosphere are not regarded in isolation, but as an integrated whole. Phytoplankton play a crucial role in biogeochemical processes on the Earth. Phytoplankton and other marine primary producers are composed of elements in addition to carbon, oxygen, and hydrogen (equation 1). A 'typical' phytoplankton cell is composed of 25 to 50 % protein, 5 to 50 % polysaccharide, 5 to 20 % lipids, 3 to 20 % pigments, and 20 % nucleic acids (Emerson & Hedges, 2008). Therefore, the elements nitrogen, phosphorus and sulphur are required in relatively large quantities to build a functioning phytoplankton cell. Other elements are required in trace amounts, such as many metals. Consequently, phytoplankton photosynthesis and subsequent phytoplankton growth directly affect the cycling of biologically important elements on Earth. For example, cyanobacteria have been extant on Earth for at least 2.7 billion years (Knoll, 2003) and have been the dominant oxygenic photosynthetic organisms on Earth for most of that time. Photosynthesis by cyanobacteria led to an accumulation of oxygen in the atmosphere, replacing an anoxic atmosphere with something approaching the contemporary atmosphere by 2.2 billion years ago (Falkowski et al., 1998; Knoll, 2003).

7.1 Ecological stoichiometry of phytoplankton

Stoichiometric variation in the elemental composition of photosynthetic organisms profoundly affects biological productivity, food web dynamics and the biogeochemical cycling of elements across all spatial and temporal scales (Sterner & Elser, 2002). One of the earliest ecological stoichiometry paradigms was the Redfield ratio. Redfield showed that the ratio of C:N:P in organic material collected with a plankton net (i.e. mainly phytoplankton and zooplankton) was conservative and 106:16:1 (Redfield, 1958). Redfield proposed that the ratio of nitrate: phosphate in the ocean was determined by the requirements of

phytoplankton, which release nitrogen and phosphorus into the environment as they are remineralized (Arrigo, 2005).

In the last few years there has been a resurgence of interest in measuring the elemental stoichiometry of marine phytoplankton (Quigg et al., 2003; Ho et al., 2003; Leonardos & Geider 2004; Bertilsson et al., 2003; Klausmeier et al., 2004), as determining the degree to which C:N:P stoichiometry can deviate from the Redfield ratio of 106:16:1 is seen as critical in the understanding of the role of phytoplankton in biogeochemistry (Falkowski, 2000; Geider & La Roche, 2002). For example, as we have seen, the Redfield ration of C:N:P of 106:16:1 represents a mean value for marine phytoplankton; there are actually significant differences in C:N, C:P and N:P ratios in different phyla of phytoplankton (Quigg et al., 2003). Klausmeier et al. (2004) used a modeling approach to show that N:P ratios depend on ecological conditions and that optimum N:P ratios vary between 8.2 and 45.0. Stoichiometric variation may occur between taxa or even within one species depending on growth conditions. A source of variation comes from the fact that different components of the cell's structure have different stoichiometric ratios (Arrigo, 2005). Cell machinery for acquiring resources (light and nutrients), such as chlorophyll and protein, are rich in N and contain low P. On the other hand, growth machinery such as ribosomal RNA are rich in both N and P. Consequently, changes in the relative proportions of key cell components will affect the stoichiometry of an individual phytoplankton (Arrigo, 2005). Different growth strategies will result in different cell stoichiometries; exponentially growing bloom-forming phytoplankton have an optimal N:P ratio of 8 as they are optimized for growth. Whereas the N:P ratio of phytoplankton in a resource scarce environmental is optimal at 36 to 45 as they contain more machinery for resource acquisition (Klausmeier et al., 2004; Arrigo, 2005).

7.2 Primary production and carbon cycling

As we have seen, marine photosynthesis supports approximately half of global primary production and therefore marine primary producers have a profound effect on the global carbon cycle. While there are some non-photosynthetic primary producers in the ocean, their contribution to carbon fixation in the ocean is negligible. Therefore, ultimately all the organic matter was originally fixed by oxygenic photosynthetic organisms. The pool of organic carbon associated with living organisms in the ocean is relatively small. Falkowski and Raven (2007) estimate that the amount of carbon in phytoplankton in the global ocean is between 0.25 and 0.65 Pg. To support an annual primary production of 50 Pg C yr^{-1}, the biomass of phytoplankton must turn over between 60 and 150 times per year, or every 2 to 6 days. This is very different from terrestrial primary productivity, which is dominated by multicellular woody organisms and has a mean turnover time of 12 to 16 years (Falkowski & Raven, 2007). The pool of non-living organic carbon in the ocean is much larger than the carbon associated with living organisms, with an estimate of 1000 Pg C (Falkowski et al. 2000). Most of the non-living carbon in the ocean is in the form of dissolved organic carbon (DOC) rather than particulate organic carbon (POC). Hansell et al. (2009) estimated that the oceans contain 662 Pg C as dissolved organic carbon (DOC). To put this into context, the atmosphere contained 612 Pg C in 1850 and 784 Pg C in 2000 (Emerson & Hedges 2008). However, the largest pool of carbon in the ocean is dissolved inorganic carbon, which contains 38,000 Pg C (Emerson & Hedges, 2008).

Given that the annual rate of marine primary productivity is around 50 Pg C $year^{-1}$, it can be seen that primary productivity in the ocean has the potential to affect the atmospheric

content of carbon dioxide. For example, if there is a significant change in either marine photosynthesis or respiration, or the balance between the two processes, then the mixing ratio of carbon dioxide in the atmosphere will change. Consequently, determining the fate of primary production in the ocean is important in understanding the global carbon cycle and global climate change. An important question is how much organic carbon is exported from surface waters and into the deep ocean. Most of the carbon fixed through photosynthesis is remineralized back to carbon dioxide in surface waters. However, some organic carbon sinks into deeper water and a very small fraction of organic carbon will make it all the way to the seafloor. Even if the organic matter is remineralized at depth, it may take thousands of years for it to be returned to the atmosphere as CO_2 and carbon buried in the seafloor may be potentially sequestered for millions of years. The carbon pump refers to processes that affect a vertical gradient in dissolved inorganic carbon concentration in the ocean (Emerson & Hedges, 2008). These processes collectively remove carbon from the surface ocean and atmosphere and into the deep ocean. The carbon pump has two components, the solubility pump and biological carbon pump. The biological carbon pump is the biologically mediated processes that transport carbon from the surface ocean into the deep ocean, such as the sinking of phytoplankton aggregates (Thornton, 2002), fecal pellets, dead organisms, and DOC.

7.3 Primary production and nitrogen cycling

Cyanobacteria have an important role in the nitrogen cycle as many species are nitrogen fixing and consequently sustain primary productivity in nitrogen-limited areas of the ocean (Capone, 2000). The availability of nitrogen generally limits phytoplankton photosynthesis and growth in the ocean (Ryther & Dunstan, 1971; Howarth, 1988; Tyrell 1999). Although 78 % of the atmosphere is in the form of N_2, this can only be used by organisms possessing nitrogense enzymes to reduce N_2 to biologically available NH_4^+; this nitrogen fixing ability is limited to certain groups of prokaryotes, including many cyanophyceae. In the vast oligotrophic tropical and subtropical areas of ocean the colonial, filamentous cyanobacteria of the genus *Trichodesmium* are important primary producers as they can overcome nitrogen limitation by fixation (Capone et al., 1997). *Trichodesmium* may form extensive surface blooms (it is buoyant due to gas vesicles) in stable, clear, low nutrient water columns. It has a cosmopolitan distribution and is probably a significant contributor to global primary productivity (Capone et al., 1997). The remineralization of carbon associated with the cyanobacteria will release bioavailable nitrogen into the water column which may support the growth of other groups of primary producers. See Zehr & Paerl (2008) for a recent review of nitrogen fixation in the ocean.

The discussion above implies that cyanobacteria are constantly fixing nitrogen from the atmosphere and enriching the ocean with bioavailable nitrogen, which would accumulate in the ocean over time. This is not the case as there are processes that remove bioavailable nitrogen from ecosystems. A description of the marine nitrogen cycle is beyond the scope of this review (see Capone 2000; Thamdrup & Dalsgaard, 2008). However, nitrogen exists in a number of oxidation states in the ocean with the transformation between oxidation states largely conducted by prokaryotes. There are two major microbial processes that remove bioavailable nitrogen from the ocean and return it to the sink of the atmosphere: denitrification and anaerobic ammonium oxidation (anammox) (Thamdrup & Dalsgaard, 2008).

7.4 Primary production and phosphorus cycling

Concentrations of phosphorus in the ocean are controlled by geological processes; phosphorus is added to the ocean from the weathering of rocks and removed by burial in marine sediments. Unlike nitrogen, phosphorus has no atmospheric source. On geological time scales phosphorus is the *ultimate limiting nutrient* for primary production in the ocean (Tyrell, 1999). However, on shorter timescales bioavailable nitrogen is the *proximate limiting nutrient* in the sense of Liebig's law (Tyrell, 1999). The addition of just nitrogen (i.e. nitrate or ammonium) to surface waters from most of the ocean would result in an enhancement of phytoplankton production. Moreover, there is a slight excess of phosphate in the ocean compared to nitrate in surface waters as nitrate is depleted before phosphate (Tyrell, 1999).

7.5 Primary production and iron cycling

There was a vigorous debate as to what limited primary production in the HNLC areas of the global ocean (see section 5). John Martin (1992) proposed the hypothesis that iron availability limits the growth of phytoplankton in the HNLC ocean. The implications of this hypothesis are that the uptake of other nutrients is limited by iron availability and that the amount of carbon dioxide in the atmosphere varies as a function of iron transport to the surface of the ocean (Millero, 2006). This has implications for the global carbon cycle as it implies that iron supply to iron limited phytoplankton plays a role in determining how much carbon is sequestered in the deep ocean and underlying sediments. The iron hypothesis was tested in the laboratory and during ship board experiments. While these experiments showed iron limitation, the results do not necessary reflect the *in situ* response to iron fertilization as small samples enclosed in bottles are subject to bottle effects and do not capture the complexity of natural systems. Consequently, a number of experiments have been conducted in which large areas of ocean have been fertilized with iron (Martin et al., 1994; Coale et al., 1996; 2004; Boyd et al., 2000; Tsuda et al., 2003). These experiments have shown that HNLC are iron limited. There was a significant increase in phytoplankton biomass over the course of a few days in the iron fertilized patches resulting in a significant draw down of carbon dioxide due to photosynthetic carbon fixation. Moreover, the alleviation of iron limitation affected the efficiency of photosynthesis as there was an increase in Φ_{PSII} (Kolber et al., 1994; Coale et al., 2004). The addition of iron to HNLC areas has been proposed as a geoengineering approach to sequester atmospheric carbon dioxide in the deep ocean and thereby partially offset anthropogenic inputs of carbon dioxide from fossil fuel burning and land use change. This is controversial, as although the addition of iron to HNLC areas stimulates primary production and the drawdown of carbon dioxide, there is relatively little evidence that a significant proportion of the resulting organic carbon sinks into the deep ocean and is sequestered (Buesseler et al., 2004; Boyd et al., 2004).

8. Conclusion

Photosynthesis and primary production in the ocean is dominated by a phylogenetically diverse group of microalgae that make up the phytoplankton. A number of techniques are used to measure phytoplankton photosynthesis. These techniques are based on gas exchange, the use of radioactive or stable isotopes as tracers, and variable chlorophyll *a* fluorescence. The techniques are not equivalent, and different techniques will produce different rates of photosynthesis dependent on the biases and assumptions intrinsic in the methodology. Phytoplankton photosynthesis is a globally significant process. Using satellite

data of ocean color, NPP in the global ocean is estimated to be around 50 Pg C year^{-1}, which is similar to terrestrial NPP. Primary production in the ocean affects the cycling of biologically significant elements, such as carbon, nitrogen, and phosphorus. A key question is how phytoplankton production affects the biogeochemical cycling of elements (e.g. carbon, nitrogen, phosphorus, and iron) and climate change.

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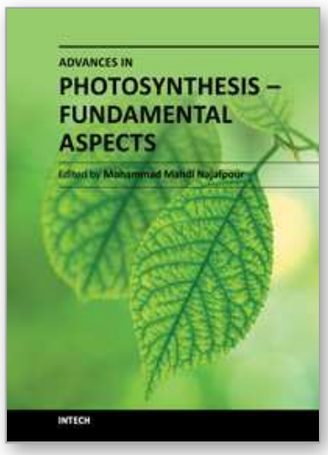

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Photosynthesis is one of the most important reactions on Earth. It is a scientific field that is the topic of many research groups. This book is aimed at providing the fundamental aspects of photosynthesis, and the results collected from different research groups. There are three sections in this book: light and photosynthesis, the path of carbon in photosynthesis, and special topics in photosynthesis. In each section important topics in the subject are discussed and (or) reviewed by experts in each book chapter.

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