

Case Study 6

Monitoring Phytoplankton Productivity from Satellite: An Aid to Marine Resources Management

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6.1 Introduction

An important biogeochemical quantity monitored by satellites is the concentration of chlorophyll-*a*, an omnipresent pigment in all phytoplankton species and, for this reason, commonly used as an index of phytoplankton biomass. In marine waters, phytoplankton biomass is a key component of the ecosystem. Phytoplankton are responsible for the conversion of carbon dioxide to organic carbon through the process of photosynthesis, i.e. primary production. Marine photosynthesis represents approximately half of the total carbon fixation in the global biosphere, making it a critical element of the Earth's carbon budget and biogeochemical cycles. In addition, phytoplankton biomass and primary production are descriptors of the first trophic level in the marine food chain. Quantitative estimates of these variables from satellite could therefore provide important information on the structure and functioning of the rest of the food web, up to commercially exploited fish populations.

6.2 Materials and Methods

6.2.1 Modelling phytoplankton photosynthesis

The process of photosynthesis requires the energy from sunlight, and takes place essentially in the euphotic layer of the oceans. For ecosystem analysis, the meaningful quantity to retrieve is the daily water column primary production, in mg of carbon fixed per m² per day. Several numerical methods have been described to estimate primary production in marine waters (see Behrenfeld and Falkowski 1997), all differing to some extent according to their resolution in depth and irradiance. Friedrichs et al. (2008) distinguished four categories of models: depth-integrated,

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wavelength-integrated models; depth-resolved but wavelength integrated models; depth-integrated but wavelength-resolved models; and models resolving both the depth and the irradiance wavelength. For the purpose of this exercise, the model used fits within the fully resolved category, following the developments by Platt and Sathyendranath (1988) as implemented at global scale by Longhurst et al. (1995). A commonality in many of these models is the requirement for a suitable knowledge of the light field and phytoplankton biomass at any given location, depth and time. The instantaneous rate of photosynthesis or primary production is commonly formulated as:

$$PP(z, \lambda, t) = f[B(z), \phi(\lambda, z), E_{PAR}(\lambda, t)] \quad (6.1)$$

where B is the phytoplankton biomass commonly indexed by the concentration of chlorophyll- a , ϕ measures the physiological capacity of phytoplankton organisms to perform photosynthesis considering the surrounding conditions, and E_{PAR} is the total irradiance available for photosynthesis between 400 and 750 nm.

6.2.2 Estimation of surface irradiance

The estimation of surface irradiance and the modelling of its propagation through the water column are key aspects of oceanography. This is particularly true in the spectral range 350–700 nm that defines the photosynthetically available radiation, PAR. Assuming that this spectral interval represents roughly half of the total solar flux at the ocean surface, total PAR could be derived simply from a global database of solar fluxes, such as the International Satellite Cloud Climatology Project (ISCCP, Schiffer and Rossow 1983). Another method is to obtain PAR directly from ocean-colour satellites (Frouin et al. 2003). However, the selected model of primary production for this exercise requires a complete description of the spectral and angular characteristics of the incident light. Ignoring these properties could result in a significant bias in the light absorption by phytoplankton and subsequent errors in the final results (Kyewalyanga et al. 1992).

The formalism used here to calculate the incident light at the sea surface was originally described by Bird and Riordan (1986) and adapted by Platt and Sathyendranath (1988) for its implementation in marine primary production modelling. Gregg and Carder (1990) have completed this model for purely oceanographic applications with a spectral resolution for direct and diffuse irradiance of 1 nm over the interval 350–700 nm. In the case of clear sky, the direct [$E_{dd}(\lambda)$] and diffuse [$E_{ds}(\lambda)$] components of the irradiance are formulated separately as:

$$E_{dd}(\lambda) = \mu_0 E_0(\lambda) T_r(\lambda) T_a(\lambda) T_{03}(\lambda) T_{02}(\lambda) T_w(\lambda) \quad (6.2)$$

$$E_{ds}(\lambda) = E_{dsr}(\lambda) + E_{dsa}(\lambda) \quad (6.3)$$

where μ_0 is the cosine of the sun zenith angle, and E_0 the extra-terrestrial solar irradiance. The direct light path through the atmosphere is modified according to the transmittance properties of various compounds, including Rayleigh scattering (T_r), aerosol extinction (T_a), as well as ozone (T_{03}), water vapor (T_w), and oxygen (T_{02}) absorption. The diffuse component is the sum of the contributions from the molecules (Rayleigh scattering) E_{dsr} and the aerosols E_{dsa} .

All transmittance functions are calculated using meteorological variables either directly available from satellite data or from climatological databases. Under clear sky conditions, an accurate description of the aerosol optical properties and their distribution in time and space is a necessary requirement to estimate the irradiance at the surface. Satellite-based ocean colour radiometry has the capacity to provide aerosol characteristics (optical thickness and Ångström exponent), with an appropriate resolution in time and space to monitor their variability over the oceans.

The effect of clouds on the surface light field is three fold. They i) lower the irradiance intensity at the sea surface; ii) change the shape of the irradiance spectrum; and iii) reinforce the diffuse part of the irradiance with respect to the direct component. These effects can be modelled if appropriate information on clouds is available, such as the cloud optical thickness and structure derived by remote sensing, or the value of the albedo of the ocean-cloud system, for instance known with the distribution of reflectivity in the UV as provided by TOMS (McPeters 1998).

6.2.3 Underwater light field

Estimating primary production in the entire illuminated layer of the ocean requires some knowledge of the light field at any depth within the water column up to a level of minimum sunlight (i.e. euphotic depth). This is done through a bio-optical model which accounts for both the optical properties inherent to the water itself and material in suspension (absorption and scattering), and the distribution /geometry of the light field.

6.2.3.1 Water optical properties

As the sunlight penetrates in the water column, its magnitude and spectral quality is altered by water molecules (w) and optically significant constituents like phytoplankton (ph), non-algal particles (np) (detritus, minerals) and a coloured fraction of the total dissolved organic matter ($cdom$). The total absorption [$a(\lambda)$] and scattering [$b(\lambda)$] coefficients of the water are then:

$$a(\lambda) = a_w(\lambda) + a_{ph}(\lambda) + a_{np}(\lambda) + a_{cdom}(\lambda) \quad (6.4)$$

represented by the sum of the optical properties inherent to each of these constituents.

$$b(\lambda) = b_w(\lambda) + b_{ph}(\lambda) + b_{np}(\lambda) \quad (6.5)$$

In practice, the bio-optical model assumes Case 1 waters where the inherent optical properties of the constituents co-vary with phytoplankton concentration. The absorption spectrum of phytoplankton, $a_{ph}(\lambda)$, between 400 and 750 nm is characterized by a continuous envelope reflecting a strong coupling in the energy transfer between photosynthetic pigments to the photosystems. The spectral shape and magnitude of the absorption coefficient is parameterized as a function of the chlorophyll concentration according to Bricaud et al. (1995), statistically representative of various marine conditions. The formulation accounts for differences in the composition of pigments within the phytoplankton cells, as well as in cell size (package effect) which translates to a flattening effect of $a_{ph}(\lambda)$ for large-cell phytoplankton communities.

For non-algal particles and dissolved organic substances, the spectral absorption obeys a similar exponential curve defined by the absorption coefficient at a reference wavelength and its slope in the lower part of the spectrum (400–440 nm). The curve parameters for $a_{np}(\lambda)$ are parameterized as a function of the chlorophyll- a concentration according to Bricaud et al. (1998). In the case of $a_{cdom}(\lambda)$, the bio-optical model assumes a constant slope and an amplitude of the absorption coefficient at 440 nm equivalent to a fixed ratio of the total absorption by particles and pure sea water.

The absorption due to pure sea water, $a_w(\lambda)$, plays a large role in the photon budget calculation, particularly in the red part of the visible spectrum where it reaches maximal values. In the blue part of the spectrum, the absorption coefficient of water molecules is used to determine the level of the euphotic depth, hence the productive layer.

With respect to scattering properties, a clear identification of the particles responsible for the optical signal remains difficult. In the estimation of primary production, scattering properties are calculated for total particulate matter, i.e. phytoplankton and non-algal particles, based on a statistical regression between chlorophyll- a concentration and the scattering coefficient at 550 nm (Loisel and Morel 1998). Scattering by dissolved substances is assumed to be negligible.

6.2.3.2 Propagation of the light in the water column

The vertical propagation of the light field is modelled according to Sathyendranath and Platt (1988; 1989), taking into account the attenuation coefficients for direct and diffuse light. The geometry of the light field is expressed through the mean cosine of light propagation weighted by the direct and diffuse component of the

downwelling irradiance. The objective of this exercise is to estimate the light flux received by a unit volume of water from all directions, the so-called scalar irradiance, which is the quantity useful for photosynthesis.

6.2.4 Model implementation

Measuring the water column primary production from space also requires some knowledge of parameters that are not accessible from satellite, such as the vertical profile of phytoplankton biomass, as well as other optically-significant constituents, and the photosynthetic parameters reflecting the capacity of phytoplankton communities to assimilate dissolved inorganic carbon through photosynthesis. These parameters have to be retrieved from field observations and their interpolation to meet the spatial and temporal resolution of satellite data are a key step of the work.

6.2.4.1 Biomass depth profile

The absorption and scattering coefficients, as well as the attenuation of light through the water column, are functions of the chlorophyll concentration. Two options can be considered for the vertical distribution of phytoplankton biomass: i) the vertical distribution of the phytoplankton biomass is uniform in a well-mixed surface layer, therefore the chlorophyll concentration at any depth is equivalent to that at the surface (possibly retrieved by satellite), and ii) in stratified conditions, a subsurface maximum usually occurs at depths ranging from close to the surface down to the bottom of the euphotic layer (i.e., 1% or 0.1% light level). The vertical distribution of the phytoplankton biomass in this case is represented by assuming a Gaussian distribution superimposed on a background chlorophyll concentration (Sathyendranath and Platt 1989). Its application in our primary production model requires *a priori* knowledge of three additional parameters defining the Gaussian curve.

6.2.4.2 Photosynthetic parameters

The relationship between the rate of carbon assimilation by phytoplankton and the submarine irradiance is described by a well-known photosynthesis-light model. More specifically, the primary production normalized to chlorophyll concentration is a function of scalar irradiance, described through a curve (P-E curve) defined by two parameters: the photosynthetic rate at light saturation (or assimilation number, P_m^B) and the initial slope of the curve (light-limited photosynthetic rate, α^B). A number of mathematical formalisms have been proposed to describe the P-E curve, starting with a 2-step linear function (Blackman 1906), to hyperbolic tangent (Jassby and Platt 1976), and exponential formulations with or without photo-inhibition (Platt et al. 1980). The photosynthetic parameters issued from statistical

regression on field measurements using one or another of these formalisms reflects the physiological characteristics of the phytoplankton community under specific environmental factors.

6.2.4.3 Biogeographical provinces

Applying satellite data to retrieve the water column daily primary production requires specification of the five parameters described above (three describing the vertical structure of the biomass profile and two for the photosynthetic efficiency) on a pixel-by-pixel basis. Different options can be considered when assigning the parameters: i) constant values of the parameters at all locations and time; ii) the parameters are continuously variable, responding in the same way to changes in the forcing factors or; iii) some regional differences in the relationship between the parameters and the forcing factors constrict the assignment of the parameters to some ecological provinces, well defined in time and space. Substantial variability has been observed in the parameters of the biomass profile (Morel and Berthon 1989; Uitz et al. 2006), as well as the photosynthetic parameters (Kyewalyenga et al. 1998; Forget et al. 2007). In light of these *in situ* measurements, assigning a constant value to the parameters is therefore not appropriate. The application of a global smooth function relating each, or a combination of these parameters, to physical variables would be ideal, especially if the physical variables can be retrieved from satellite. Morel and Berthon (1989) provided solutions to retrieve the Gaussian parameters of the biomass profile from surface chlorophyll, which was used as an indicator of the trophic state. These relationships were then confirmed by Uitz et al. (2006) using a different data set.

On the other hand, the relationships between phytoplankton physiology and physical variables are more complex. Spatial discontinuities in the photosynthetic parameters are perceptible, reflecting regional diversity in the phytoplankton community response to physical forcing (Bouman et al. 2005). One technique suggested by Platt and Sathyendranath (1988), consists of partitioning the studied area into several provinces, each having its own set of the required parameters. Within each province, the parameters are either assumed constant for a given time period, e.g. seasons (Longhurst et al. 1995; Sathyendranath et al. 1995) or vary continuously with the physical conditions (Platt et al. 2008).

6.3 Demonstration: Application to global primary production

The primary production budget is calculated for three different months in 2006 and given for the global ocean, as well as selected basins. The processing starts with the global estimation of the sun irradiance at the surface and satellite-derived

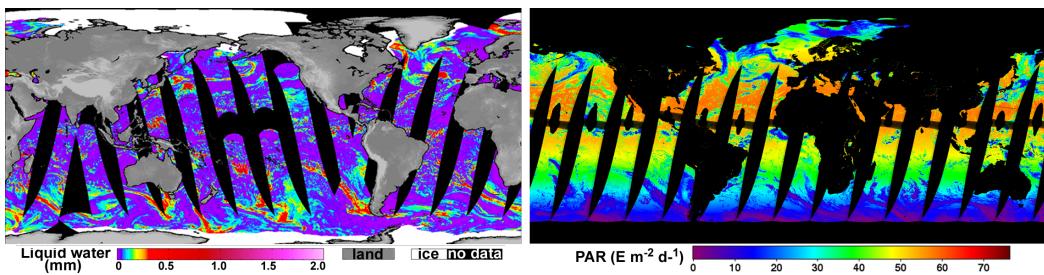


Figure 6.1 Daily maps of cloud liquid water path, LWP (left panel) and photo-synthetically available radiation, PAR (right panel) for May 8, 2006.

chlorophyll concentration. These are inputs to the local model of primary production which, after selection of the parameters, will then be integrated over time (first over a day), depth and wavelength to yield a monthly map of daily water-column primary production.

The geophysical products necessary for the calculation of irradiance in the case of a clear sky can be identified as: i) atmospheric pressure, relative humidity, precipitable water vapor, and wind at the water surface; ii) ozone concentration; iii) aerosol characteristics. The values for the first group are provided as meteorological products by NCEP (National Center for Environmental Prediction, <http://www.ncep.noaa.gov/>), with a spatial resolution of $1^\circ \times 1^\circ$ (only the NCEP map given at noon is used). The ozone concentration is available through TOMS (Total Ozone Mapping Spectrometer, <http://toms.gsfc.nasa.gov/>) with a spatial resolution of 1.25° in longitude and 1° in latitude, which is extrapolated onto a grid of $1^\circ \times 1^\circ$. The aerosol characteristics are provided on a monthly basis by the SeaWiFS products (~ 9 km resolution, as provided by the GSFC- DAAC, Goddard Space Flight Center, Distributed Active Archive Center, <http://oceancolor.gsfc.nasa.gov>). Since this temporal frequency does not guarantee a complete coverage, the SeaWiFS aerosol maps are re-gridded onto maps of reduced spatial resolution (1°).

For cloudy sky, it is assumed that the value of the albedo of the ocean-cloud system is known with the distribution of reflectivity (at 360 nm) provided by TOMS (McPeters 1998). The value of reflectivity provided by TOMS is then compared to the content of a look-up table of solutions of the radiative transfer problem for the cloud layer, pre-computed for various values of cloud liquid water path (LWP, Figure 6.1). The associated value of LWP immediately provides the value of transmittance for direct light from the same look-up table of pre-computed solutions of the radiative transfer problem with the cloud layer. Total direct irradiance is finally calculated as the direct irradiance for clear sky weighted by the direct transmittance under cloud conditions (Figure 6.2).

The surface chlorophyll concentration or phytoplankton biomass can be obtained directly from various ocean colour sensors and data archives, at the appropriate space agencies (e.g., <http://oceancolor.gsfc.nasa.gov>). In the case of SeaWiFS

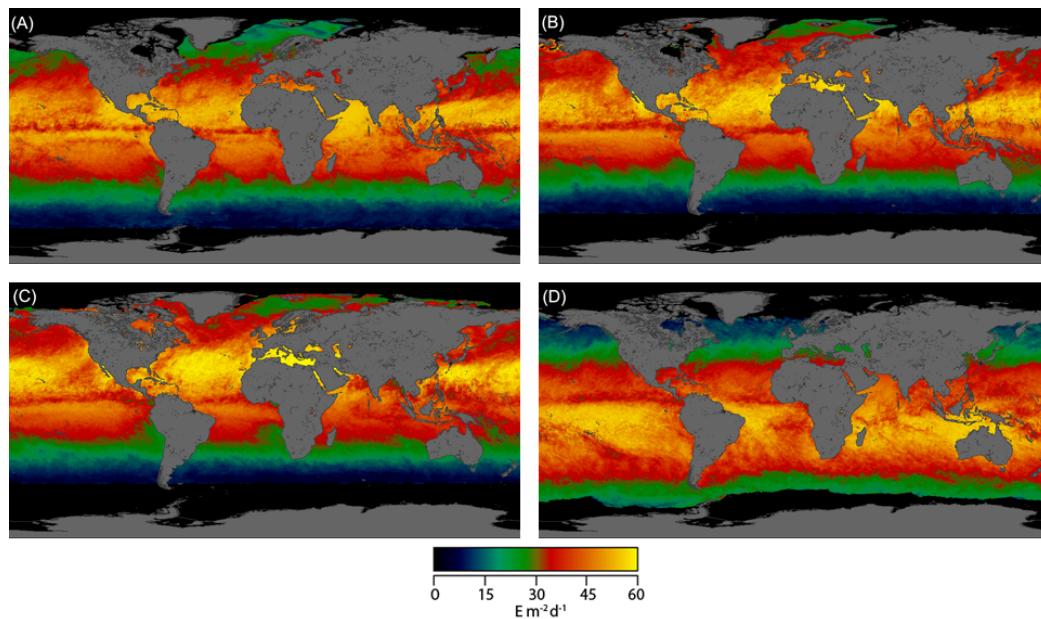


Figure 6.2 Monthly composites of daily photosynthetically active radiation (PAR) as computed directly from SeaWiFS data for April (A), May (B), July (C) and October (D), using top-of-atmosphere radiance to infer the attenuation of solar irradiance through the atmosphere (Frouin et al. 2003). Units are Einstein m^{-2} day $^{-1}$ with a scale typically ranging from 0 to 60. One "Einstein" is equivalent to one mole of photons.

and MODIS chlorophyll products, daily standard mapped image (SMI) Level 3 (Figure 6.3) are distributed in a global equidistant cylindrical projection (or sinusoidal equal area grid for MERIS data) with a spatial resolution of 4320 pixels in longitude and 2160 pixels in latitude. The resolution is approximately 0.0833, equivalent to 9.28 km at the equator. For global and regional analysis, higher resolution data can be obtained by processing Level 1-A data with dedicated software packages freely available from space agencies (e.g., SeaDAS, <http://oceancolor.gsfc.nasa.gov/seadas/>; and BEAM, <http://www.brockmann-consult.de/cms/web/beam/software>).

Having defined the surface photosynthetically active radiation and phytoplankton biomass, we now need to specify the five parameters required to obtain the water-column integrated daily primary production i.e. three parameters to describe the vertical structure of the phytoplankton biomass, and two parameters to describe the photosynthetic efficiency of the organisms.

In this exercise, the primary production model uses a partition of the global ocean into biomes and provinces (Longhurst 1998; Figure 6.4), based on factors such as light conditions, circulation patterns, nutrient inputs, the bathymetry and other elements linking our current knowledge on regional oceanography to the response of phytoplankton to physical forcing. Statistical analyses are performed on the available *in situ* databases to retrieve the most representative set of parameters for

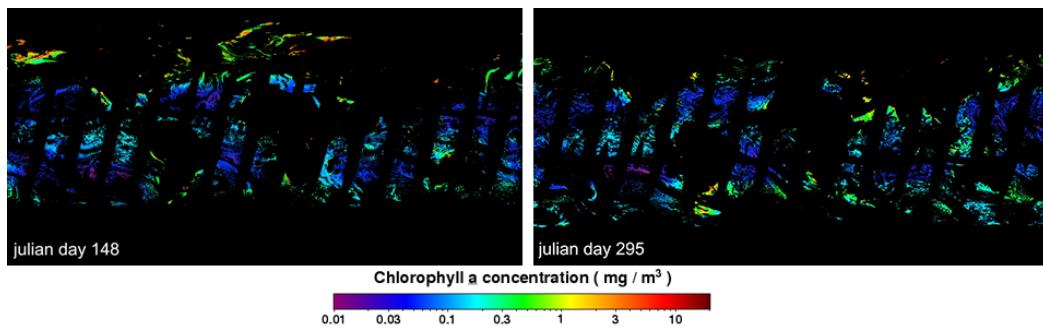


Figure 6.3 Daily scenes of Level 3 chlorophyll product as processed from SeaWiFS for day 148 (May 28, 2006) and day 295 (Oct. 22, 2006).

each of the provinces and/or biomes that will be assumed to remain constant for an appropriate time period (e.g. seasons).

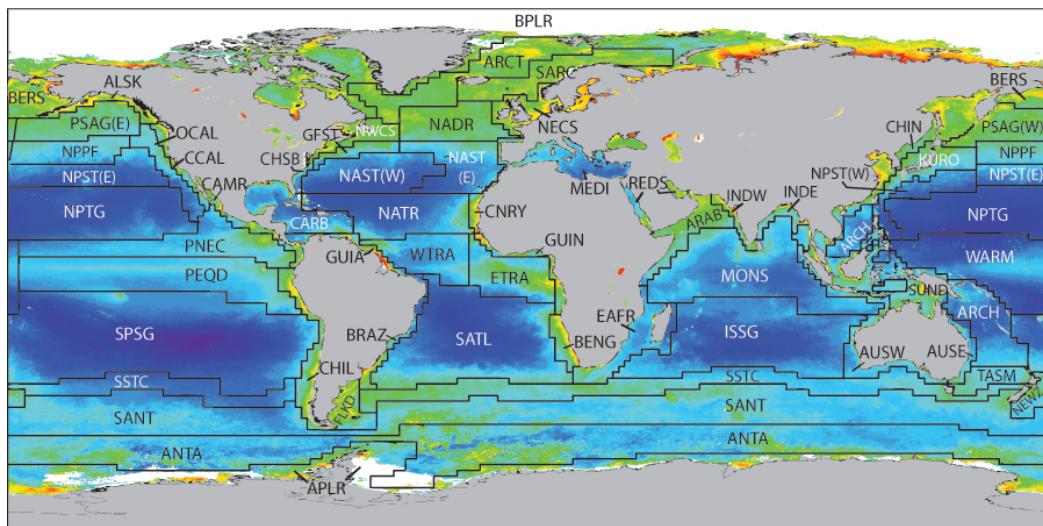


Figure 6.4 Distribution of the Longhurst oceanographic provinces adopted for the global ocean. Definition and acronyms of the provinces are detailed in Longhurst (1998; 2006).

Equation 17.1 can now be used to calculate primary production from daily scenes of surface chlorophyll concentrations, applying a spectral model to estimate the underwater light field at a given time and depth interval within the euphotic zone. The final output is the water-column integrated daily rate of primary production given in $\text{g C m}^{-2} \text{ d}^{-1}$.

6.4 Questions

Q1: Based on Figure 6.2 and the section on estimation of surface irradiance (Section 6.2.2), what would be the primary and secondary drivers of PAR (photosynthetically active radiation) on a global scale?

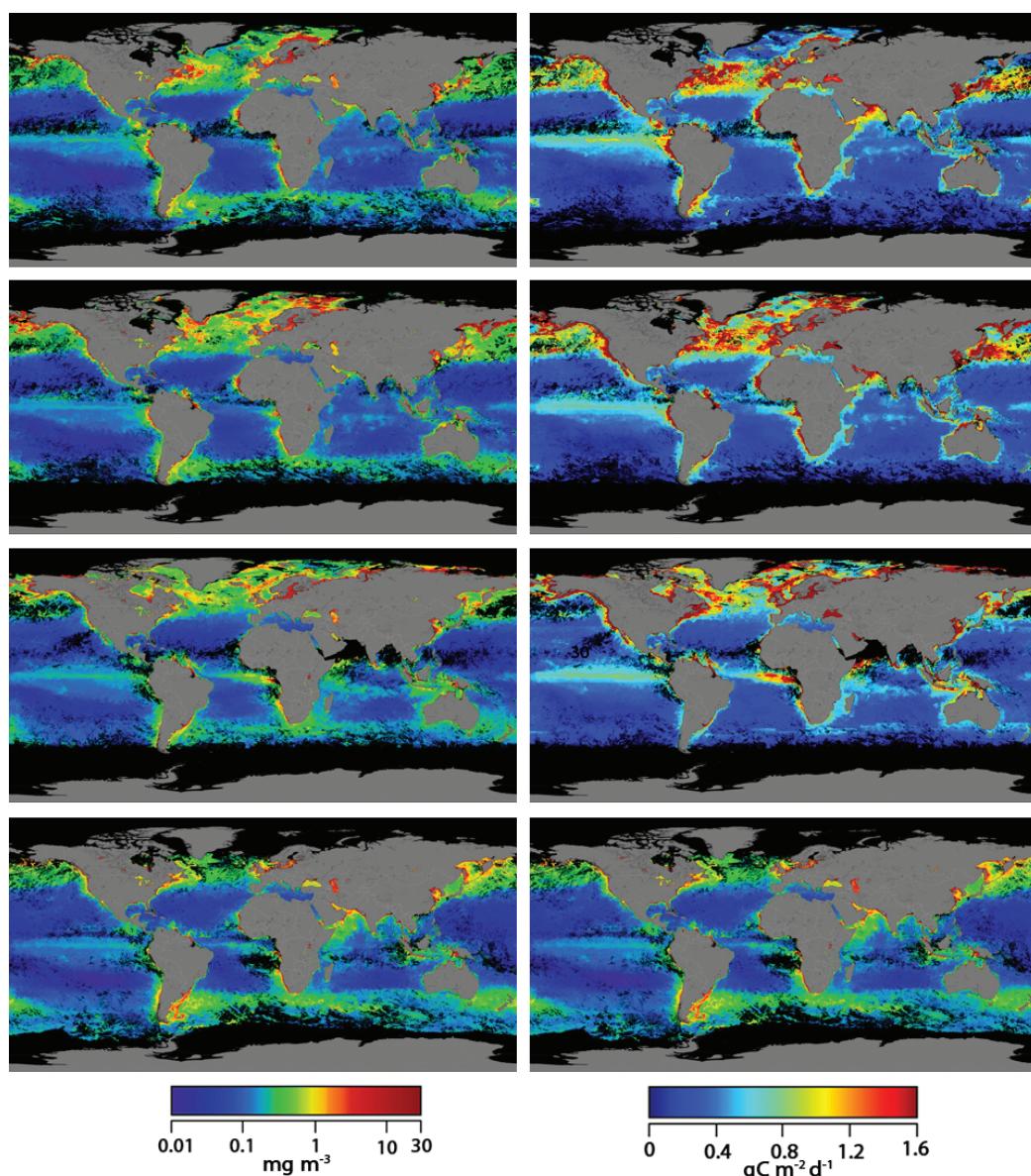


Figure 6.5 Global monthly composites of surface chlorophyll concentration (left panel) and primary production (right panel) as derived from SeaWiFS data for April, May, July and October 2006. Areas in black have no data.

Q2: What are the main drivers of primary production on a global scale? Discuss this by comparing the maps for primary production (Figure 6.5 right panel) with those of PAR (Figure 6.2) and chlorophyll concentrations (Figure 6.5 left panel).

Q3: What are the reasons for lack of data for Chla and primary production on Figure 6.5?

Q4: Looking at the maps in Figure 6.5, what are the main features you can observe in terms of temporal and spatial variability?

Q5: High primary production can be seen in coastal zones and marginal seas. Why is it consistent with expectations? Given the models presented above, why is the uncertainty on the derived primary production likely to be higher?

Q6: Looking at the global maps of primary production and zooming in on some regions, e.g. southeastern Africa and the Agulhas Current (Figure 6.6), what can you say about some of the surface features?

Q7: At what level of accuracy can primary production be retrieved using satellite data?

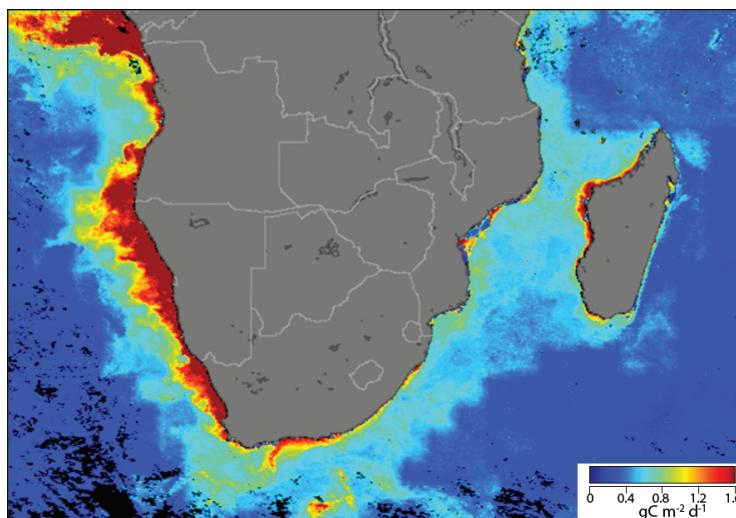


Figure 6.6 Primary production along South Africa-Madagascar region (extracted from the global map in Figure 6.5)

6.5 Answers

A1: On a theoretical basis, the solar irradiance at the top-of-atmosphere is proportional to the cosine of the solar zenith angle. The irradiance value at the sea surface is therefore directly affected by the solar angle. In turn, the solar zenith angle is a

function of latitude and day of the year (or season). PAR intensity and day length thus vary with location and season, which can be seen when comparing Figures 6.2c and d: the zone of maximum PAR shifts in latitude with season.

The other main driver of PAR is cloud cover. It changes the PAR amplitude, spectral shape at the surface, and geometry (diffuse-to-direct ratio). Aerosols have a similar effect, even though it is less pronounced, except in cases of strong aerosol events linked with desert dust or biomass burning. In general, these secondary effects are seen in the figures by zonal variations of PAR at a given latitude (Figure 6.2). A persistent feature is the relative minimum in PAR found slightly north of the Equator. This should be a region of maximum PAR, but it is characterized by a recurrent cloud cover associated with the Inter-Tropical Convergence Zone, where convection generates clouds.

A2: Phytoplankton biomass or chlorophyll concentration is the main driver of primary production. This is further modulated by PAR. If PAR was the dominant controlling factor, areas at subtropical latitudes with high PAR would show high productivity, which is generally not the case. At these latitudes, heat energy from the more intense sunlight is absorbed in the upper layers of the ocean, leading to a quasi-persistent stratification of the water column. This structure would prevent any supply of new nutrients from the deep oceans to the productive illuminated surface layer, thus keeping the productivity at low levels based on locally regenerated nutrients.

At higher latitudes, stratification of the water column occurs in spring as temperature increases, subsequently trapping large amount of nutrients from winter mixing in the euphotic layer. Favourable conditions of nutrients and light trigger phytoplankton blooms and productivity as seen in Figure 6.5 in the April and May composites.

A3: Lack of data in monthly composites of phytoplankton biomass and primary production could result from:

1. Very low sun zenith angle in local winter: for example, the northern seas between Scandinavia and Greenland have significantly more coverage in April and May than in October (Figure 6.5). Processing of chlorophyll images, and hence the estimation of primary production, is restricted to sun zenith angles lower than 70°. The sun zenith angle is a function of time, day number and latitude.
2. Persistent cloud cover: ocean colour sensors only perform in clear sky conditions. Time-composite mapping enables a better coverage of the area of interest, to some extent, increasing the probability of obtaining cloud free scenes over each pixel. Nevertheless, areas with no data are still visible in monthly maps (Figure 6.5), especially along the equator. This area corresponds to a zone of persistent cloud cover previously described (see Answer 1) as the

Inter-Tropical Convergence Zone.

3. Persistent thick aerosol plumes: as for clouds, important aerosol emission events such as desert dust plumes or biomass burning can prevent any signal from the water surface from reaching the satellite sensor. These events are recurrent along the west coast of Africa as wind blows over the Sahara and Sahel regions.

A4: On a global scale, the variability in primary production is driven by the seasonal cycle. Comparing productivity values in the North Atlantic in April-May with that in October clearly shows an intensification of phytoplankton production in spring. On the contrary, in the southern hemisphere, productivity at higher latitudes tends to be higher in the October map than in April-May. The mechanism associated with that seasonal cycle is partly explained in Answer 2. Another noticeable feature in Figure 6.5 is a narrow band of higher productivity along the equator. The prevailing currents, combined with the Earth's rotation generates an upwelling process, and nutrient-rich deep waters are lifted to the surface layers.

A5: Relative to open ocean waters, coastal and shelf areas receive large fluxes of nutrients from rivers, and from upwelling processes at the coast. Higher productivity in these waters is thus expected. The four major eastern boundary upwelling systems along the coast of north- and southwest Africa, California, and Peru are well identified in the primary production maps (Figure 6.5) as permanent features, although the strength of the upwelling process varies seasonally. Note that these upwelling systems account for only 5% of the global ocean, but support major world fisheries.

Caution should be taken in the interpretation of primary production values in coastal areas: the bio-optical model presented above follows the Case-1 water assumption, where optical properties co-vary with Chlorophyll-*a*. At the coast, the water can be optically more complex than the open ocean waters because of the large influence by the land system and catchment basins delivering significant amounts of dissolved and particulate material to the coast. These additional substances, evolving independently from phytoplankton, impact on the derivation of chlorophyll concentration from satellite using standard "case 1 water" algorithms, but also on the propagation of light through the water column, as they compete with phytoplankton for light absorption.

A6: Caution should be taken in the interpretation of some surface features observed in the primary production maps (e.g. staircase-like features, straight and squared angle fronts). These are methodological artefacts associated with the partition of the global ocean into specific biogeographical provinces, each of them having their own set of model parameters reflecting their ecological characteristics (Longhurst, 1998). To tackle regional issues, it may be necessary to re-examine in more detail, the interactions between physics and biology in the region and the annual variability

of the forcing fields, such that more realistic provinces can be established for the studied area. The number of provinces will depend on the knowledge of the regional oceanography and the availability of the data required for primary production calculation.

In Longhurst's original work, the provinces have geometrical shapes (Figure 6.4) with fixed boundaries in space and time, although some adjustment could be applied from year to year according to the variability of inter-annual forcings. As a result, sharp squared-like discontinuities occur between provinces. This artefact does not alter in any way the estimated value of the primary production for each province, which relies on careful selection of parameters. Various protocols have been developed for a more dynamic partitioning of the oceans, using remotely-sensed data to locate the province boundaries and enable their adjustment in real-time. Readers are referred to Report # 9 of the International Ocean Colour Coordinating Group (IOCCG, 2009) for the various approaches in addressing oceanic ecosystem classification.

A7: As mentioned in the introduction, several models to retrieve primary production from remotely-sensed data have been developed during the last two decades. The performance of these models, including the one described in this exercise, were analysed in a series of round-robin experiments aiming at an extensive comparative assessment of the models (Carr et al., 2006), and their validation against *in situ* measurements (Friedrichs et al., 2009; Saba et al., 2011). The mean RMSD (root mean square deviation) of 21 ocean colour models was 0.29 relative to *in situ* primary production values collected in the tropical Pacific, with the model described here being amongst the best performing (Friedrichs et al., 2009). However, the model's success varies substantially from region to region (Saba et al., 2011), and in general the performance is still limited by the accuracy of the input variables, particularly uncertainties in satellite-derived chlorophyll values.

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