




# Ocean Biology Studied from Space

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Received: 21 March 2023 / Accepted: 3 August 2023 / Published online: 11 September 2023  
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## Abstract

Visible spectral radiometric measurements from space, commonly referred to as ocean-colour measurements, provide a rich stream of information on ocean biota as well as on biological and ecosystem processes. The strength of the ocean-colour technology for observing marine life lies in its global reach, combined with its ability to sample the field at a variety of spatial and temporal scales that match the scales of the processes themselves. Another advantage lies in the growing length of the time series of ocean-colour-derived products, enabling investigations into any long-term changes, if present. This paper presents an overview of the principles and applications of ocean-colour data. The concentration of chlorophyll-a, the major pigment present in phytoplankton—single-celled, free-floating plants that are present in the sunlit layers of the ocean—was the first, and remains the most common, biological variable derived from ocean-colour data. Over the years, the list of ocean-colour products have grown to encompass many measures of the marine ecosystem and its functions, including primary production, phenology and ecosystem structure. Applications that exploit the data are many and varied, and include ecosystem-based fisheries management, biogeochemical cycles in the ocean, ecosystem health and climate change. An integrated approach, incorporating other modes of ocean observations and models with satellite observations, is needed to investigate the mysteries of the marine ecosystem.

**Keywords** Ocean colour · Remote sensing · Chlorophyll-a · Phytoplankton · Biological oceanography · Primary production

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## Article Highlights

- Ocean colour satellites are designed to investigate marine biota by their distinct optical signatures
- Some common ocean-colour products are concentration of chlorophyll-a and marine primary production along with many other indicators of marine ecosystem status
- Ocean colour has become a very useful tool in climate research and is recognized as an essential climate variable

## 1 Introduction

The global ocean covers two-thirds of the surface of our planet; it is about 3700 m deep on average; it is a highly dynamic fluid medium that experiences variability at multiple temporal and spatial scales. The ocean is the cradle of life as we know it and supports a complex network of species and ecosystems that have adapted to this fluid and at times hostile environment. There are many reasons why the ocean biota and their processes are essential for both humans and our green planet.

It is estimated that the oceans are home to some 2.2 million species, of which only 9% has been described (Mora et al. 2011). With such a small portion that has been observed and described, it is highly likely that we understand little about the diverse services that these organisms provide, to maintain the intricate and inter-connected properties that render the Earth a hospitable and pleasant environment for us humans; maintain the multitudes of life forms that make our planet beautiful and shape our landscape; and control the chemical composition of our atmosphere.

The ocean biota plays a significant role in the global biogeochemical cycles of this planet, notably the cycle of carbon, various nitrogen compounds (e.g., nitrate, nitrite, ammonia and nitrogen gas), phosphate, silica and iron. In fact, the role of marine phytoplankton (microscopic, free-floating, single-celled plants) as net primary producers of organic material in the ocean is estimated to be equivalent to that of terrestrial plants (Longhurst et al. 1995; Field et al. 1998). For this and other reasons, such as their role in absorbing sunlight and thereby modulating the depth distribution of solar heating of the upper ocean, phytoplankton are considered an important player in studies of the ocean carbon cycle.

Marine primary production, currently estimated to be about 50 Pg of carbon globally per annum (Kulk et al. 2020a, b, 2021), sustains all pelagic life in the oceans, including the fish and seafood that we rely on for nutritious, high-quality food (Budge et al. 2014). With aquaculture making an increasingly important contribution to the global supply of fish and seafood for human consumption, there are growing concerns on its potential adverse impact on the marine ecosystems and on water quality.

Whether it be from considerations of the impacts of human activities on water quality or the effect of climate change on marine ecosystems, or for understanding how to manage marine living resources in a sustainable manner, we have a need for observing the ocean biota globally, consistently, over long periods, and at various time scales commensurate with the intrinsic scales of biological processes and their variability.

Satellite-based observations have an important role to play in meeting this requirement. There are many factors that render remote sensing a suitable mode of observation. A particular advantage is the capability for observations at the global scale using a single instrument,

in a consistent manner. Another is the ability of satellites to observe the oceans at a variety of scales that are relevant for biological processes in the ocean—at temporal scales ranging from hours to decades, and spatial scales ranging from a few meters to the global scale.

Of all the various types of satellite-borne sensors that are available to us now, it is the visible spectral radiometric observations, commonly referred to as ocean-colour measurements, that have the proven capability to interrogate ocean biota directly. But many others are also relevant, particularly for placing the biota in their environmental context.

In this paper, we examine the principles that underlie the use of ocean-colour sensors, and the ancillary information from other satellite sensors that can be used to enhance the applications of ocean-colour data. We recognise that satellites cannot satisfy all our observational requirements relating to the biological system; and so, we examine the value and importance of what is amenable to remote sensing, how to make the most use of the observations, sometimes in conjunction with other types of observations. We examine the challenges and identify the need and advantages of combining satellite-derived information with other modes of observation, to enable a holistic view of ocean biota and ocean ecosystems.

In this paper, we have attempted to present the myriad of ways in which ocean-colour data have contributed to the study of ocean biota and marine ecology and biodiversity. To present the case, we have relied heavily on our own work, and the paper is not designed to be an exhaustive review of the field.

## 2 Principles of Ocean Biology from Ocean Colour

It is a matter of everyday observation that the colour of natural bodies of water changes with location and with time (Fig. 1). We know instinctively that the colour is an indicator of water quality: we associate limpid, blue, transparent waters with purity; brown and reddish waters that are more opaque are linked with high content of mud; and we know that green waters likely indicate high plant content. But to progress from this type of casual observation to quantitative assessment of life in the oceans, we need to invoke the principles of marine optics.

Marine optics is built on a bedrock of two subdisciplines (<https://www.oceanopticsbook.info/>). One of them is devoted to the study of inherent optical properties of various types of material, whether particulate or dissolved, that are present in seawater. Inherent optical properties include spectrally-resolved absorption and scattering coefficients, and the volume scattering function that describes the angular distribution

**Fig. 1** Examples of colour of natural aquatic bodies at different locations and times (images from CEOS Report 2018, courtesy CSIRO). In this paper, we examine the optical processes responsible for these changes; whether we can quantify the responsible agents; what biological information we can garner from colour; and the applications of the information



of scattered light. They represent the optical properties of the materials independent of the nature of the light field in which they are present. The second branch of marine optics deals with the study of radiative transfer in the oceans, and how the spectral and angular distribution of under-water light field (induced by sunlight or by artificial sources) is modified by the types and concentrations of material present in the water.

Ocean colour, as detected by a satellite, is defined by the spectral variations in remote-sensing reflectance, defined as the spectrally-resolved ratio of water-leaving radiance, normalised to the downward irradiance at the surface of the ocean:

$$R_{rs}(\lambda, \theta, \phi, 0) = \frac{L(\lambda, \theta, \phi, 0)}{E_d(\lambda, 0)} \quad (1)$$

In the equation above,  $R_{rs}(\lambda, \theta, \phi, 0)$  is the remote-sensing reflectance at wavelength  $\lambda$ , at depth zero (just above the surface), zenith angle  $\theta$  and azimuth angle  $\phi$ , with  $L(\lambda, \theta, \phi, 0)$  being the corresponding water-leaving radiance at the same wavelength, and  $E_d(\lambda, 0)$  being the downwelling irradiance, also at wavelength  $\lambda$  and depth zero. Note that radiance is defined as flux per unit surface area and per unit solid angle, whereas irradiance is flux per unit area. It is typical when processing remote-sensing data to normalise  $R_{rs}(\lambda)$  such that we deal with the special case of zenith angle of zero, to avoid any deviations in the signal arising from changes in the viewing angle. Intuitively, we can anticipate that reflectance will decrease as absorbing material increases in the water, and that it will increase with scattering, especially with back-scattering (or upward-scattering). In fact, various theoretical explorations have led to general solutions of the form (e.g., Morel and Prieur 1977; Sathyendranath and Platt 1997; 1998; Sathyendranath et al. 2001; Brewin et al. 2012):

$$R_{rs}(\lambda) = f \frac{b_b(\lambda)}{a(\lambda)}, \quad (2)$$

where  $f$  is a function of  $b_b(\lambda)$ , the back-scattering coefficient and  $a(\lambda)$ , the absorption coefficient. Note that here, and in the following, we have dropped the arguments  $\theta$ ,  $\phi$  and zero, for simplicity.

The optical properties of pure water itself (with low absorption in the blue and green parts of the visible spectrum, and high scattering in the blue) render pure, clean water its characteristic deep blue colour. Typically, four major groups of material are responsible for changes in ocean colour. These are:

- *Phytoplankton* that contain plant pigments—notably chlorophyll-a and its variants, and auxiliary pigments that have photosynthetic or photoprotective roles. Chlorophyll-a has an absorption maximum in the blue, a minimum in the green and a secondary maximum in the red, and a relatively flat backscattering spectrum that could be modulated in the vicinity of absorption bands.
- *Coloured dissolved organic matter (CDOM) or yellow substance*, which is characterised by an absorption coefficient with low values in the red part of the spectrum, increasing exponentially towards shorter wavelengths. Because these are dissolved substances, their contribution to scattering is considered negligible.
- *Detrital material*, which have absorption properties similar to those of CDOM; and

- *Suspended sediments*, whose optical properties vary, depending on the type of sediments present: whether they be mud or sand, for example. Suspended sediments become important in certain coastal areas and in areas of river outflow, but are largely absent in the surface waters of the open ocean.

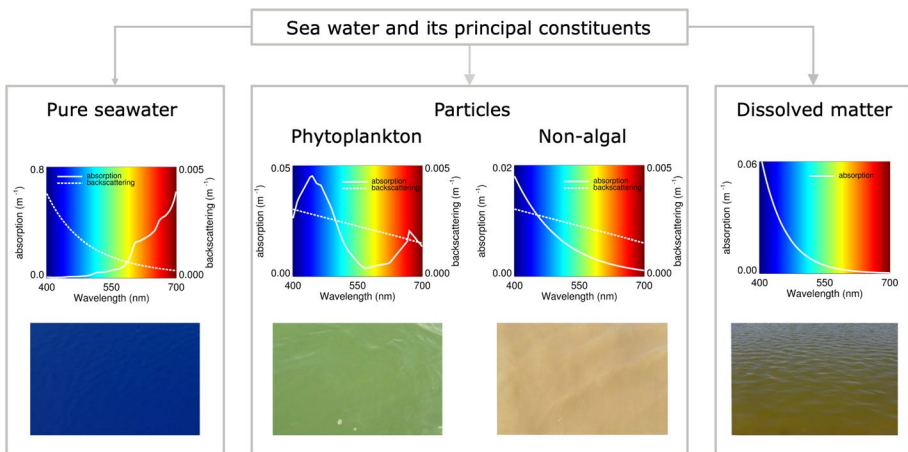
The optical properties of phytoplankton are such that the colour of water changes from blue to green with increasing concentrations of phytoplankton. CDOM and detrital material tend to impart colours to the water that range from a deep yellow to orange (often described as the colour of black tea), and suspended sediments yield muddy brown, blackish or turquoise coloured waters, depending on the type of sediment present. These transformations of the colour of water with the nature of substances present in it, is shown schematically in Fig. 2.

To extract quantitative information on these substances from ocean-colour data acquired by satellites, we express the absorption coefficient as the sum of absorptions by individual substances, as in:

$$a(\lambda) = a_W(\lambda) + Ba_B^*(\lambda) + Ya_Y^*(\lambda) + Da_D^*(\lambda) + Sa_S^*(\lambda) + \dots \tag{3}$$

where the notations *W*, *B*, *Y*, *D* and *S* stand respectively for water, phytoplankton biomass, yellow substances (CDOM), detritus and suspended material. Furthermore, for the latter four categories, the absorption is expressed as the product of their biomass-specific absorptions indicated by asterisks, and their concentrations *B*, *Y*, *D* and *S*. We recognise that, when other substances are present, it may be essential to include additional terms (as indicated by the trailing dots in the equation). The phytoplankton biomass is usually taken to be the concentration of the main phytoplankton pigment, chlorophyll-*a*.

Similarly, the back-scattering coefficient  $b_b(\lambda)$  can also be expressed as a sum of its components:



**Fig. 2** The optical properties of the principal constituents of seawater, and how they vary with wavelength in the visible portion of the electromagnetic spectrum. Photos of phytoplankton, non-algal and dissolved substances were adapted from Wernand et al. (2011). Photo of pure seawater taken in the centre of the oligotrophic North Atlantic subtropical gyre, during an Atlantic meridional transect

$$b_b(\lambda) = b_{bW}(\lambda) + Bb_{bB}^*(\lambda) + Db_{bD}^*(\lambda) + Sb_{bs}^*(\lambda) + \dots \quad (4)$$

where we have assumed there is no additional scattering from CDOM.

Once the theoretical framework is laid out, algorithm development in ocean-colour remote sensing becomes an inverse modelling problem of retrieving the concentrations of the constituents, given the remote-sensing reflectance  $R_{rs}(\lambda)$ . Alternatively, we can develop empirical algorithms relating  $R_{rs}(\lambda)$  to the concentrations of the constituents and ensure that the empirical approach is consistent with the theory.

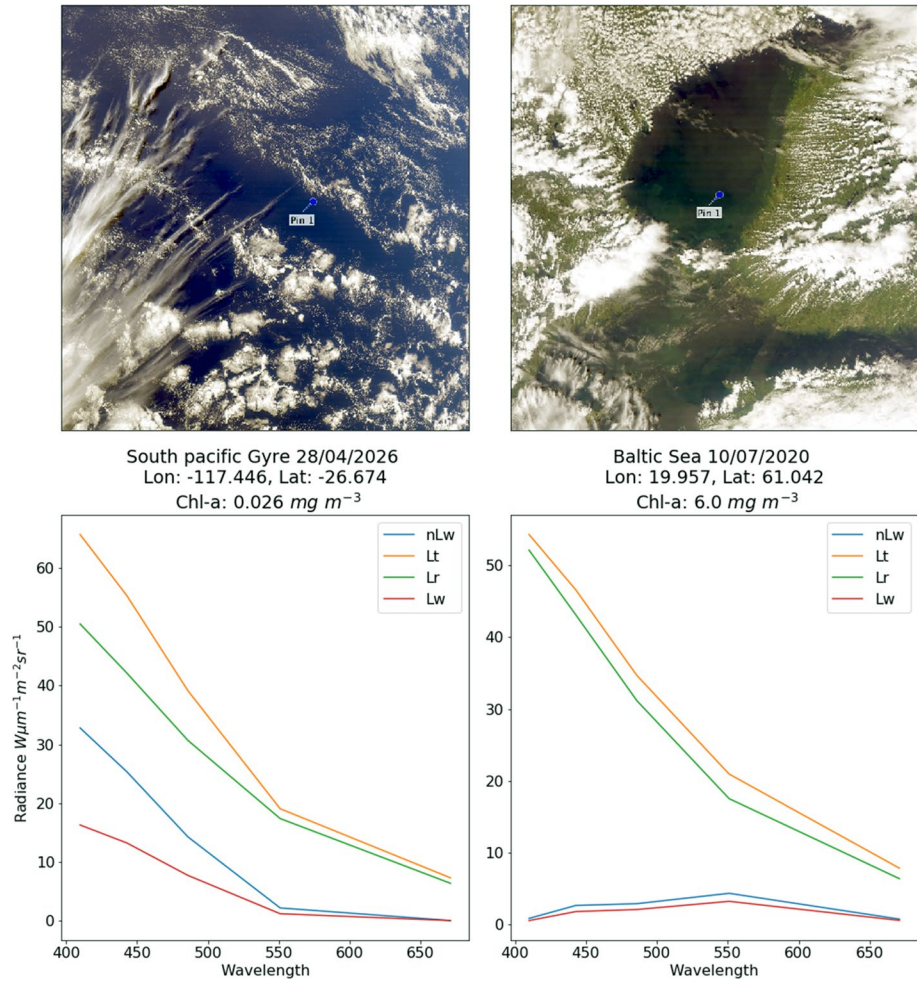
However, the remote-sensing reflectance at the sea surface is not what the satellites observe: they observe the radiance at the top of the atmosphere, which includes contributions to the signal from the atmosphere. The first step in the ocean-colour processing chain is therefore a procedure referred to as the atmospheric correction, designed to remove the atmospheric impact on the signal and to extract the water-leaving radiance. This is a critical step, since the atmospheric contribution to the signal at the top of the atmosphere is typically 80% or more of the overall signal (Fig. 3).

There are many sources of uncertainties in the retrieved remote-sensing products. These include uncertainties in the instrument calibration, errors introduced during the atmospheric correction procedure, uncertainties in pixel identification, and those in the algorithms used for retrieval of the in-water constituents. The overall uncertainties are established using formal error propagation analyses or through comparison of satellite products against field observations that are matched in time and location (Brewin et al. 2015a; Müller et al. 2015a; Jackson et al. 2017a; Sathyendranath et al. 2019; McKinna et al. 2019).

From this background, it becomes evident that the biological variable that is most readily retrieved from ocean-colour data is the concentration of the phytoplankton pigment, chlorophyll-a (see example in Fig. 4).

### 3 Chlorophyll-a as an Index of Phytoplankton Biomass

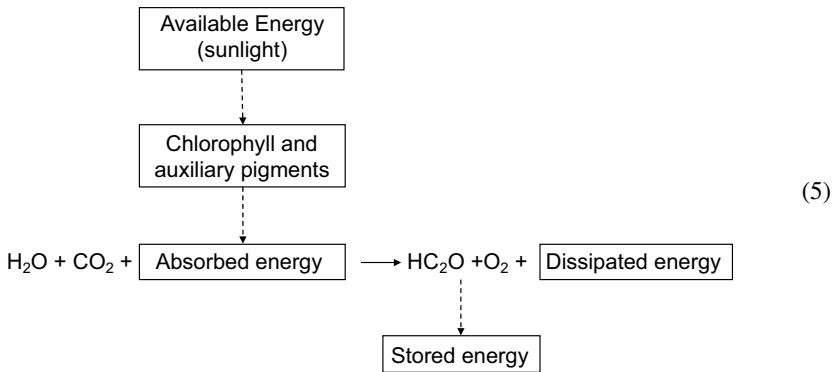
Phytoplankton are complex organisms, and no single measure of its biomass will constitute a complete description of the organism. So, when choosing an index of biomass for routine estimations of phytoplankton biomass, it would be worthwhile to consider the ideal characteristics of such an index and examine to what extent the selected index meets those requirements. Holm Hansen (1973) listed the desired properties of indicators of biomass of a community of living organisms and concluded that ATP (adenosine triphosphate) would be a suitable index. We could use a similar set of criteria for an ideal index of phytoplankton biomass rather than for the entire community (Table 1) and examine the extent to which chlorophyll-a meets those requirements, and carry out a similar evaluation for phytoplankton carbon, which is also often considered a desirable index of phytoplankton biomass. The table shows that chlorophyll-a meets most of the requirements of an ideal index of biomass for routine measurements, more so than carbon.



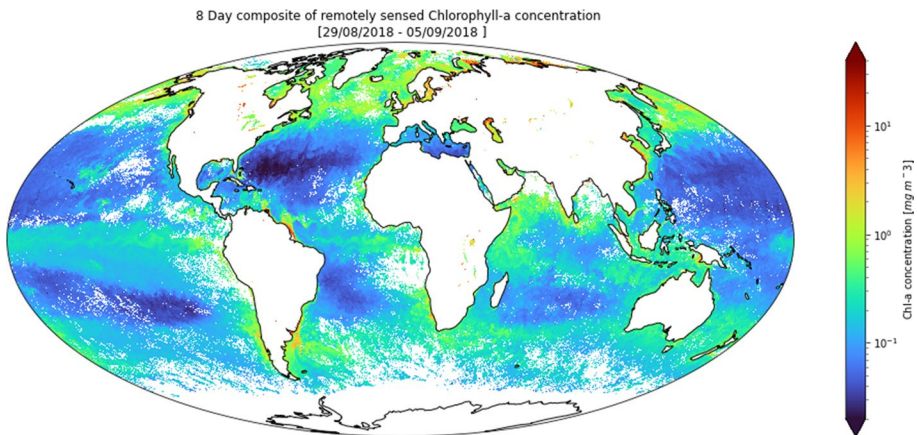
**Fig. 3** ‘True Colour’ images of a region in the South Pacific Gyre (top left) and the Baltic Sea (top right) derived from the VIIRS sensor aboard the Suomi NPP satellite. Lower panels show pixel extractions of radiances at pin locations. Lt, Lr, Lw and nLw are the top of atmosphere, Rayleigh, water leaving and normalised water leaving radiance respectively. Atmospheric correction was performed using the NASA 12gen processor (within SeaDAS version 7.5.3)

Chlorophyll-a is also an important biological molecule because of the central role it plays in photosynthesis, on land and in the oceans. In photosynthesis, light energy is absorbed by a photosynthesising organism, which is then used to convert carbon dioxide

and water into organic matter, and oxygen is released. In phytoplankton, as in all photosynthetic organisms, chlorophyll-a is at the heart of the photosynthetic unit and serves as the transducer that connects the supply of energy from the sun to the ecosystems of our planet. The photosynthesis equation can be written as follows:



Primary production is the rate of fixation of carbon dioxide in the presence of sunlight into organic matter, through photosynthesis. It is a rate, with dimensions  $[M(C)] [L]^{-3}[T]^{-1}$  (Mass of Carbon per unit volume and unit time), or  $[M(C)][M]^{-2}[T]^{-1}$  (Mass of Carbon per unit surface area, and per unit time). Any map of chlorophyll concentration (e.g., Fig. 4) shows how the strength of this energy–ecosystem coupling varies in the ocean: the higher the chlorophyll concentration, the stronger the coupling, and higher the potential for primary production. It is a most fundamental property of our ecosystem. Thus, in calculations of primary production, it is very useful to know the amount of chlorophyll-a that is available for the process. It is also possible to base primary production calculations using phytoplankton carbon as the state variable, rather than chlorophyll-a. But a comparison of the two indicators (Table 2) shows that chlorophyll-a has some advantages in this context, over carbon.



**Fig. 4** Example of an ocean-colour derived map of the chlorophyll concentration, from the ocean colour climate change initiative processing chain (version 5, dates 2018-08-29–2018-09-05)



**Table 1** Requirements of an ideal indicator for routine monitoring of phytoplankton, and the extent to which two candidate indicators, chlorophyll-a and carbon, meet those requirements

Requirement	Chlorophyll-a	Carbon
Indicator must be present in all living cells, but not in dead cells	✓	
Indicator must not be present in detrital material	✓	
Indicator must be absent from non-phytoplanktonic living cells (bacteria, zooplankton, virus...)	✓	
It must exist in fairly uniform concentrations in all living cells, regardless of environmental stresses		✓
Analytical techniques must be sufficiently sensitive	✓	
Quick, simple and inexpensive measurement techniques must be available	✓	
Easy to standardise across multiple investigators, globally	✓	
For operational applications, should not depend too heavily on expert intervention	✓	
The biomass of the indicator should form a significant part of the total biomass of phytoplankton		✓

All things considered, chlorophyll-a is an extremely useful variable for studies of marine ecosystems. It would be easy to make the argument that chlorophyll-a should be one of the top-most priorities for observations of the marine ecosystem, and it is fortunate that this property is accessible to remote sensing.

#### 4 Ecological Indicators from Remote Sensing

Phytoplankton chlorophyll concentration is not the only piece of information on ocean ecology and ecosystems that is accessible to remote sensing. Over the years, a formidable range of ecological indicators have been developed from ocean-colour data (Table 3). Chlorophyll concentration underlies many of these products, though not necessarily all of them. For example, combining chlorophyll data with light available at the sea surface and photosynthesis models, it has been possible to compute marine primary production.

The spectrally-resolved radiance data have been used to develop algorithms for detection of phytoplankton functional types and phytoplankton size structure (IOCCG 2014). Information on other environmental variables have been used to improve ocean-colour algorithms; for example, light and temperature have been used to refine models for detection of phytoplankton size classes from space (Brewin et al. 2015b, 2019). Recent years have seen considerable progress in our efforts to detect various biological pools of carbon in the ocean (Brewin et al. 2021). Availability of methods to detect phytoplankton carbon from space implies that it is no longer essential to choose between carbon or chlorophyll as the ideal index of phytoplankton biomass: we can choose one or the other according to the problem at hand or personal preferences.

The utility of ocean colour for mapping large-scale structures in the marine ecosystem is closely linked to our efforts to map marine diversity from space. Large-scale structures in the marine ecosystem include variance fields in chlorophyll concentration and primary production, as well as the organisation of the marine ecosystems into ecological provinces or optical classes. The ecological provinces have formed the foundation of recent efforts to map biotic biogeography, species distribution and diversity of the pelagic ocean

**Table 2** Comparison of chlorophyll-a and carbon as the state variable in computations of primary production

Chlorophyll-a	Carbon
Has distinctive optical and chemical signatures that cannot be mistaken for anything else (direct methods)	Phytoplankton carbon has no distinctive signal that allows separation from other types of particulate carbon at sea (indirect methods)
There is a wealth of data on chlorophyll from a variety of sources (both in situ and satellite)	Phytoplankton carbon is difficult to measure, not just from satellites, but also in situ
There is a large body of photosynthesis-rate parameters that are available from in situ observations that can underpin chlorophyll-based models	Carbon-based growth parameters from the field are difficult to measure, and hence hard to find in literature and data repositories
Chlorophyll-a is at the heart of the photosynthetic reaction (but note: not all chlorophyll-a is in the photosystems)	Not all carbon in the cell is linked to primary production
Chlorophyll-a is the transducer that acts to connect the supply of energy from the sun to the plant-based ecosystems on our planet	Phytoplankton carbon without chlorophyll-a in photosystems cannot produce organic material
There is perhaps less recognition of the central role played by chlorophyll-a and associated pigments in maintaining life as we know it on this planet	In the climate context, and in ecosystem models, the importance of biologically mediated carbon pools and fluxes is now well-recognised

(Reygondeau and Dunn 2019). Though most organisms other than phytoplankton are not directly observable using ocean colour, exceptions exist: for example, Basedow et al. (2019) have used ocean-colour data to map swarms of a particular species (*Calanus finmarchicus*) of copepods (a type of zooplankton). Indirect methods (e.g., exploiting the size structure in the marine biota) have also been employed to map zooplankton populations in general (e.g., Strömberg et al. 2009).

Life under water is very much at the mercy of the underwater environment, with light and nutrients playing important parts in sustaining it. Ocean colour also enables the study of the underwater light environment, with algorithms to map various properties of the underwater light field, such as the diffuse attenuation coefficient (which determines the rate of penetration of solar light under water), the euphotic depth (at which light is reduced to 1% of its surface flux), turbidity, water colour and water clarity. Ocean colour data are also used to map concentrations of the suspended sediment load and coloured dissolved organic matter (IOCCG 2000; Sathyendranath et al. 2020b).

## 5 Ancillary Information from Satellites Needed to Probe Ocean Ecosystems

Whereas ocean-colour satellite sensors provide our only window into marine ecosystems at synoptic scales, we also rely on other satellite-derived physical variables as a complement to ocean-colour data. These include information on the optical thickness of aerosols in the atmosphere (essential for the atmospheric correction procedures), sea surface temperature, sea surface salinity and sea state (all of which influence phytoplankton community composition and dynamics).

**Table 3** Ecological indicators from remote sensing, adapted and updated from Platt and Sathyendranath (2008). Some key (and non-exhaustive) references are also given for further details

Indicator	Dimensions	Some key references
<i>Seasonal dynamics of phytoplankton biomass</i>		
Initiation of spring bloom	[T]	Platt et al. (2003); Platt and Sathyendranath (2008)
Amplitude of spring bloom	[ML <sup>-3</sup> ]	Platt et al. (2003); Platt and Sathyendranath (2008)
Timing of spring maximum	[T]	Platt et al. (2003); Platt and Sathyendranath (2008)
Duration of spring bloom	[T]	Platt et al. (2003); Platt and Sathyendranath (2008)
<i>Seasonal dynamics of phytoplankton production and loss</i>		
Total production in spring bloom	[ML <sup>-2</sup> ]	Platt and Sathyendranath (2008)
Annual phytoplankton production	[ML <sup>-2</sup> ]	Platt and Sathyendranath 1988; Longhurst et al. (1995); Kulk et al. (2020a, b, 2021)
Phytoplankton growth rate	[T <sup>-1</sup> ]	Sathyendranath et al. (2009); Jackson et al. (2017b); Sathyendranath et al. (2020a, b)
The F-ratio (ratio of new production to export production)	Dimensionless	Sathyendranath et al. (1991); Platt and Sathyendranath (2008)
Generalised phytoplankton loss rate	[ML <sup>-3</sup> T <sup>-1</sup> ]	Sathyendranath and Platt (2008); Zhai et al. (2008)
Integrated phytoplankton loss	[ML <sup>-3</sup> ]	Sathyendranath and Platt (2008)
<i>Biological pools of carbon</i>		
Particulate organic carbon	[ML <sup>-3</sup> ]	Evers-King et al. (2017)
Phytoplankton carbon	[ML <sup>-3</sup> ]	Martinez-Vicente et al. (2017); Jackson et al. (2017a, b); Roy et al. (2017); Sathyendranath et al. (2020a, b)
Carbon-to-chlorophyll ratio	Dimensionless	Kostadinov et al. (2016); Roy et al. (2017); Jackson et al. (2017a, b); Sathyendranath et al. (2020a, b)
<i>Large-scale ecosystem structure</i>		
Spatial variance in biomass field	[M <sup>2</sup> L <sup>-6</sup> ]	Platt and Sathyendranath (2008)
Spatial variance in production field	[M <sup>2</sup> L <sup>-4</sup> ]	Platt and Sathyendranath (2008)
Delineation of biogeochemical provinces	NA	Platt and Sathyendranath (2008); IOCCG (2009)
Distribution of optical water types	NA	Moore et al. (2009); Jackson et al. (2017a)
<i>Phytoplankton community composition</i>		
Phytoplankton functional types	NA	IOCCG (2014)
Phytoplankton size spectrum		Brewin et al. (2014); Kostadinov et al. (2016); Roy et al. (2017)

**Table 3** (continued)

Indicator	Dimensions	Some key references
<i>Biodiversity</i>		
Identification of niches occupied by phytoplankton types		Raitsoo et al. (2008); Palacz et al. (2013)
Mapping dominant algal blooms		Sathyendranath et al. (2004); IOCCG (2014)
Mapping copepods, zooplankton		Strömberg et al. (2009); Basedow et al. (2019) (2019)
Bacterial community, certain bacterial types		Gómez-Pereira et al. (2010); Sathyendranath et al. (2020a)
<i>Indicators of water quality</i>		
Diffuse attenuation coefficient	$[L^{-1}]$	Lee et al. (2005)
Turbidity		Nechad et al. (2009), Dogliotti et al. (2015)
Water colour (forel-ule scale)	NA	Woerd et al. (2015); Pitarch et al. (2021)
Water clarity (secchi depth)	[L]	Pitarch et al. (2021)
Suspended sediment load	$[M^{-3}]$	Volpe et al. (2011)
Euphotic zone	[L]	Lee et al. (2007)

*T* stands for time, *M* for mass, and *L* for volume

## 6 Applications

Chlorophyll concentration and the suite of ecological indicators listed above have been revolutionary in biological oceanographic studies, providing global coverage, with unprecedented detail at fine spatial and temporal resolution. Satellite-based observations are the only means available to us today to sample an entire area defined by the pixel size of the sensor, and that too, using a non-invasive method. With all other observational tools, the sampled volume or area is always a woefully small fraction of the area we wish to investigate, and much effort has to be invested into methods to fill the gaps in between spot observations. This high coverage from satellites bestows a distinct advantage for studies aimed at obtaining the large-scale view.

Studies of marine primary production have benefited hugely from ocean-colour observations. With phytoplankton biomass (indexed either as chlorophyll-a or as carbon) derived from satellites, photosynthesis models have been developed that incorporate photosynthetically active radiation (PAR), also from satellites, and photosynthetic models, to compute marine primary production at large scales. Phytoplankton are at the base of the marine food web, and understanding marine primary production is key to all studies of the maintenance of the various trophic levels of the ecosystem, including zooplankton and fish larvae at the second trophic levels, all the way to fish and shellfish at higher trophic levels that we harvest as high-protein, high-quality food from the sea.

It has been argued that fisheries management plans should incorporate considerations of bottom-up control on fish recruitment, in addition to considerations of top-down control through fishing, to enable long-term, sustainable, ecosystem-based management of fisheries. In this context, it has been demonstrated that metrics of phytoplankton phenology derived from satellites can shed light on survival rate of important commercial fish (Platt et al. 2003; Koeller et al. 2009; Kassi et al. 2018a, b; Menon et al. 2019).

In general, there is a link between ecosystem health and human health. Especially for the millions of people who make their home in coastal locations, the sea is an important source of food and of a sense of well-being. Degraded ecosystems threaten this food supply as well as the sense of well-being. Industries such as tourism and transport are affected. Water quality also implies the microbial quality of water. Bacteria and viruses are natural components of marine ecosystems; but some of these are pathogenic in nature and are associated with water-borne diseases such as cholera. The *Vibrio cholera* bacteria, responsible for cholera, are found in free-floating form in water, and also in association with phytoplankton and zooplankton, and other hosts. This link between the bacteria and plankton has been exploited in many studies to develop predictive models that rely on satellite-derived chlorophyll-a data as input (Sathyendranath et al. 2020a; Anas et al. 2021). Thus, satellite observations are being used increasingly, to elucidate the link between ecosystem and human health.

Issues related to climate are all-encompassing and all consuming, and the many applications listed above come to the fore as an ensemble, in studies of the impact of climate change on marine ecosystems and on the feedbacks between various elements of our climate system. The Global Climate Observing System (GCOS) has in fact recognised ocean colour and phytoplankton as essential climate variables, and there is currently a concerted effort to produce satellite-based climate-quality data records of spectrally-resolved remote-sensing reflectances and chlorophyll concentrations, for climate studies. One of such efforts is led by the European Space Agency within the umbrella of its Climate Change Initiative.

## 7 The Challenges to Producing Climate Quality Time Series from Ocean-Colour Data

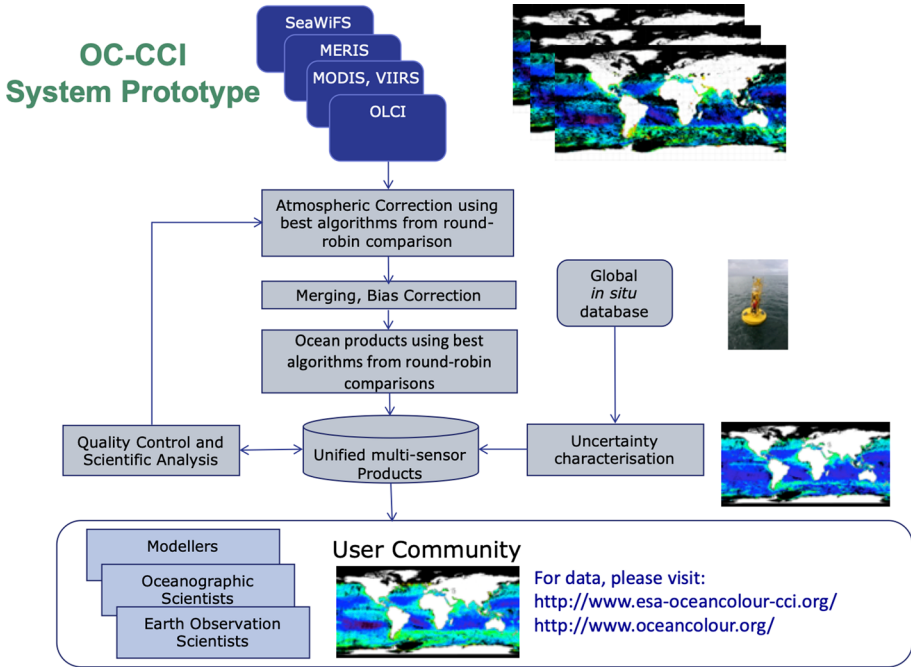
Preparing climate-quality data records brings stringent requirements over and above those that are required for most other applications. These additional requirements arise from the need to detect not just the state of the marine ecosystem or short-term changes and variability, but also long-term trends in the ecosystem status and processes. Since any putative climate-change related signal could be a small one embedded within a noisy environment that experiences high natural variability at multiple time scales, it becomes particularly important to ensure that the data are of the highest precision possible. Since the standard error in the mean decreases with increasing number of observations, high coverage and high number of repetitive measurements become important. Because we have to discount natural variability at all shorter scales to extract the climate signal, it also becomes of importance to avoid gaps in data. Another key requirement for climate data streams is that for a long time series, in which the data are acquired and processed in a consistent manner. For example, one has to avoid artefacts introduced into the time series because of systematic biases between sensors. Since satellite sensors have a finite life span, one could introduce spurious trends in the data when multiple sensors are merged to extend the time series, if inter-sensor bias is not corrected for. One also has to consider whether the in-water algorithms employed are appropriate for detection of changes in the marine ecosystem, whether they be in the biomass of phytoplankton present, as indexed by chlorophyll concentration, or in the community composition or in the phytoplankton phenology (Sathyendranath et al. 2017, 2019).

These considerations have led, within the ocean colour component of the Climate Change Initiative (CCI), to put in place dedicated, specialised processing chains (Fig. 5) for generation of multi-sensor, consistent, error-characterised, inter-sensor bias-corrected time series of remote-sensing reflectance and chlorophyll concentration (Sathyendranath et al. 2019). The philosophy that underpins the approach is explored in Sathyendranath et al. (2017). Some samples of ocean colour CCI chlorophyll products are shown in Fig. 6.

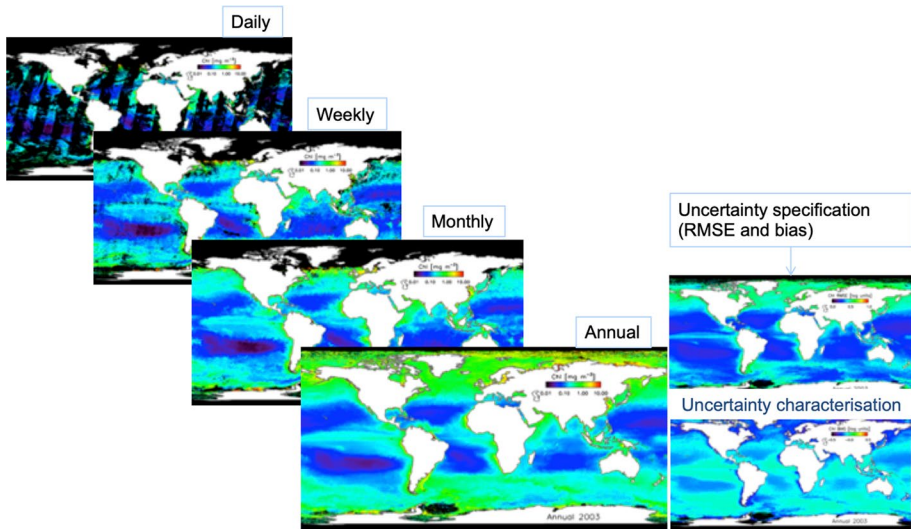
The Ocean Colour Climate Change Initiative chlorophyll products and marine primary production derived from these products (Kulk et al. 2020a, b, 2021) can be used to map the 23-year climatology and linear trends (Fig. 7a, b).

## 8 Synergy with Ecosystem Models

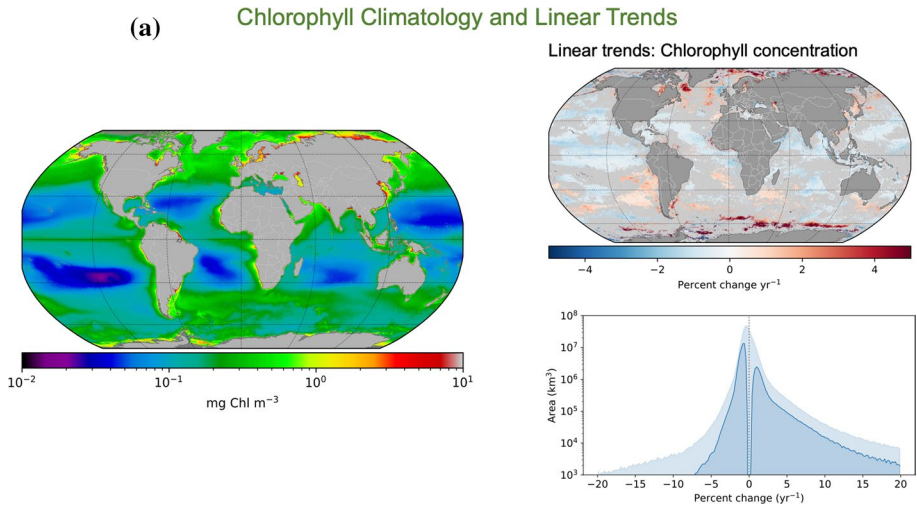
There has always been a close association between ecosystem models and ocean-colour data. Over the years, chlorophyll concentration derived from ocean-colour data has served to test outputs from ecosystem models. Conversely, models have helped fill the spatial and temporal gaps of the ocean-colour observations, as well as explain the mechanism that underlie their patterns. With the advent of data assimilation in ecosystem models, ocean-colour products became the primary source of biological and bio-optical data that are assimilated into those models. The incorporation of phytoplankton functional types into ecosystem models has paralleled development of algorithms for detection of phytoplankton types and size classes from space (IOCCG 2014). State-of-the-art models are now capable



**Fig. 5** Processing chain used in the ocean colour climate change initiative to generate long-term time series of climate-quality ocean-colour products



**Fig. 6** Some examples of chlorophyll products from ocean colour climate change initiative (OC-CCI) showing daily, weekly, monthly and annual products, from an early version of OC-CCI. For further details about OC-CCI products, see Sathyendranath et al. 2019



**Fig. 7** Climatology and linear trends in a) chlorophyll-a and b) primary production for 1998–2020, derived from the ocean-colour climate change initiative data, version 4.2. The linear trends in chlorophyll and primary production (as a rate of change over time) are provided as maps, with non-significant trends in grey, and as histograms after area weighing, with all trends in light blue and significant trends ( $p < 0.05$ ) in darker blue. Figures are adapted and updated (extended by 2 more years) from Kulk et al. (2020a, b, 2021), also see the IPCC AR6 working group I report, chapter 2

of assimilating ocean colour phytoplankton types for both ecosystems functioning studies and operational biogeochemistry predictions (Ciavatta et al. 2018; Skákala et al. 2018).

In the climate context, in the absence of long time series of ocean-colour products, one relied heavily on models for understanding threats to the marine ecosystems from climate change, and to predict future changes. But as the time series of ocean-colour data grows—for example, the ocean-colour time series from the Climate Change Initiative is now 24 years long—the satellite data are being used increasingly to test model outputs and to examine whether model structures are appropriate for detection of climate impacts on the ocean biota.

Until recently, quantitative comparisons of model outputs and satellite products have been hampered by the differences in the currencies used in the two approaches: ecosystem models use biogeochemically-important variables, such as carbon or nitrogen, as their main currency. On the other hand, the principal output from satellites is the chlorophyll concentration. This required a conversion between carbon and chlorophyll to enable comparisons between model outputs and satellite products. However, the recent developments in satellite oceanography, which have enabled computation of phytoplankton carbon from space using photo-acclimation models (Sathyendranath et al. 2020b and references therein) have facilitated model-data comparisons at a more fundamental level. More recent ecosystem models include chlorophyll as a state variable that depends on light availability, with the assimilation of ocean-colour chlorophyll leading to an impact on the simulation of the physiological status of phytoplankton (Ciavatta et al. 2011). One of the challenges of ecosystem modelling is in the assignment of suitable values for the many physiological and ecological rate parameters that are used in the models. Ocean-colour data assimilation into ecosystem models can also serve to improve our understanding of model parameters (Roy et al. 2012). Sathyendranath et al. (2020b) have argued that the focus of future research



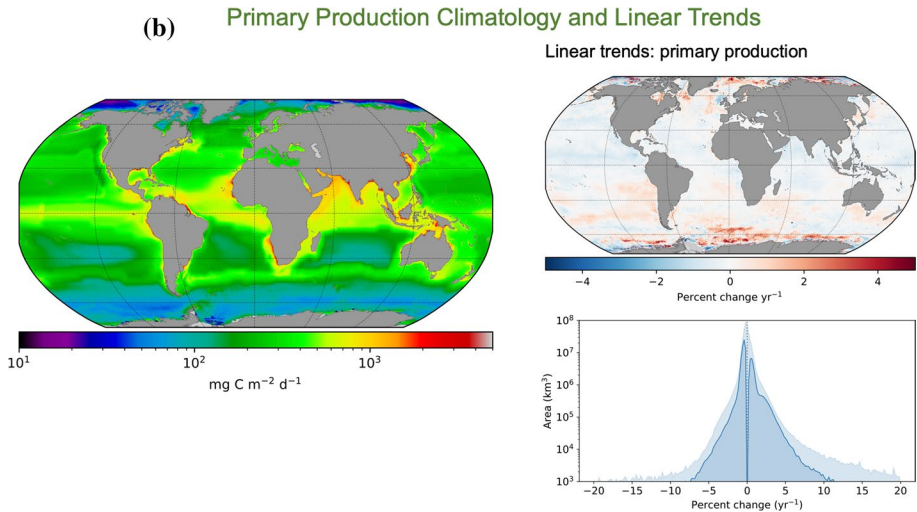


Fig. 7 (continued)

should be on understanding variability in model parameters that define rates of physiological processes, even more than on variability in the biological pools themselves.

Some of the recent ecosystem models include bio-optical modules, which expand the use of ocean colour to assimilate diffuse light attenuation products (Ciavatta et al. 2014), remote sensing reflectance (Jones et al. 2016), and light absorption of phytoplankton functional types (Skákala et al. 2020), in combination with water column observations from gliders in shelf-seas (Skákala et al. 2021) and biogeochemical-Argo floats in the ocean (Teruzzi et al., 2021).

A recent IOCCG report (IOCCG 2020) is devoted to the synergy between ocean colour and ecosystem models, which constitutes an excellent reference material on this topic.

## 9 The Need to Integrate Ocean Colour with Other Essential Variables

The strengths of satellite observations lie in their capability to provide synoptic views of the marine ecosystem; to provide global coverage using a single, or a handful of, sensors, ensuring consistency across all observations; in their capability to sample the entire area within each pixel of a satellite image; and to do this in a non-invasive manner, repeatedly and over long time-scales.

These strengths have to be balanced against their limitations: satellites only observe a finite layer of the surface ocean; ocean-colour sensors are unable to penetrate clouds; the need for stringent atmospheric correction further limits coverage under other adverse conditions (clouds, cloud shadow, high aerosol concentrations, low solar elevation, to name a few); the interpretation of the signal is complex, and may be associated with varying optical properties of phytoplankton (with changes in community structure and pigment composition) or with the presence of other substances in the water, obscuring the phytoplankton signal; and above all, by the limited number of

ecosystem properties that are amenable to satellite observation. The list of observable properties can be extended by the use of proxies that include chlorophyll concentration and relevant environmental properties also amenable to remote sensing, such as photosynthetically active radiation, sea surface temperature, sea state and salinity. Yet, it would be hard to argue that satellites tell us everything we need to know about biology and ecosystems of the oceans.

Typically, one relies on meticulous process studies, in the laboratory or at sea, for new insights into the structure and function of marine ecosystems. Other modes of observations are essential to extrapolate surface observations from satellites through the water column, and to cover those properties and processes that are not observable through satellites. Furthermore, we rely on models of various sorts—conceptual, theoretical, and simulation models—to interpret and synthesise observations and understanding, and for predictions. Thus, it is only through an integrated approach that we can delve deeper into the mysteries of the ocean ecosystems.

Our understanding that biological systems on land and in the oceans are integral parts of our climate system is a relatively new one and was perhaps first revealed through paleontological studies that highlighted the links between biological processes, notably primary production, and changes in our planetary climate over geological time scales. But subsequent explorations of climate using Earth system approaches have led to new revelations on the inter-connectedness between various elements of the climate system. This leads to one of the grand challenges of the day: to explore the links between ocean biota and biogeochemical processes in relation to various components of the climate system, not only in the oceans, but also on land, atmosphere and cryosphere.

## 10 Concluding Remarks

Ocean colour from space has become the mainstay of biological oceanographic and marine biological research, making significant contributions to various subdisciplines of the fields. The achievements in ocean-colour research in the last few decades have been remarkable. However, it is by no means a closed chapter now: one anticipates further improvements in products and development of new products in the near future, keeping pace with technological developments, notably with the advent of hyperspectral optical sensors.

**Acknowledgements** This work is a contribution to the Simons Foundation Project Computational Biogeochemical Modeling of Marine Ecosystems (CBIOMES, number 549947, S.S.). This paper is also a contribution to the ESA projects Ocean Colour Climate Change Initiative (OC-CCI); Biological Pump and Carbon Exchange Processes (BICEP); Biodiversity of the Coastal Ocean: Monitoring with Earth Observation (BiCOME); and Biodiversity in the Open Ocean: Mapping, Monitoring and Modelling (BOOMS). Additional support from the National Centre for Earth Observations (UK) is also gratefully acknowledged.

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## References

- Anas A, Krishna K, Vijayakumar S, George G, Menon NN, Gemma Kulk G, Jasmin C, Ciambelli A, Hridya KV, Tharakan B, Jaleel Abdul KU, Goult E, Vengalil J, Platt T, Sathyendranath S (2021) Dynamics of *Vibrio cholerae* in a typical tropical lake and estuarine system: potential of remote sensing for risk mapping. *Remote Sens* 13(5):1034
- Basedow SL, McKee D, Lefering I, Gislason A, Daase M, Trudnowska E, Egeland ES, Choquet M, Falk-Petersen S (2019) Remote sensing of zooplankton Swarms. *Sci Rep* 9:686. <https://doi.org/10.1038/s41598-018-37129-x>
- Brewin RJW, Dall'Olmo, G, Sathyendranath, S, Hardman-Mountford, NJ, (2012) Particle backscattering as a function of chlorophyll and phytoplankton size structure in the open-ocean. *Opt Express* 20(16):17632–17652. <https://doi.org/10.1364/oe.20.017632>
- Brewin RJW, Sathyendranath S, Tilstone G, Lange PK, Platt T (2014) A multicomponent model of phytoplankton size structure. *J. Res. Oceans, Geophys.* <https://doi.org/10.1002/2014JC009859>
- Brewin RJW, Sathyendranath S, Müller D, Brockmann C, Deschamps P-Y, Devred E, Doerffer R, Fomferra N, Franz B, Grant M, Groom S, Horseman A, Hu C, Krasemann H, Lee ZP, Maritorea S, Mélin F, Peters M, Platt T, Regner P, Smyth T, Steinmetz F, Swinton JW, J, White, GN, III, (2015a) The ocean colour climate change initiative: III. a round-robin comparison on in-water bio-optical algorithms. *Remote Sens Environ* 162:271–294. <https://doi.org/10.1016/j.rse.2013.09.016>
- Brewin RJW, Sathyendranath S, Jackson T, Barlow R, Brotas V, Airs R, Lamont T (2015b) Influence of light in the mixed-layer on the parameters of a three-component model of phytoplankton size class. *Remote Sens Environ* 168:437–450. <https://doi.org/10.1016/j.rse.2015.07.004>
- Brewin RJW, Stefano Ciavatta S, Sathyendranath S, Skákala J, Bruggeman J, Ford D, Platt T (2019) The influence of temperature and community structure on light absorption by phytoplankton in the north atlantic. *Sensors* 19:4182. <https://doi.org/10.3390/s19194182>
- Brewin RJW, Sathyendranath S, Platt T, Bouman H, Ciavatta S, Dall'Olmo G, Dingle J, Groom S, Jönsson B, Kostadinov TS, Kulk G, Laine M, Martínez-Vicente V, Psarra S, Raitsos DE, Richardson K, Rio M-H, Rousseaux CS, Salisbury J, Shutler JD, Walker P (2021) Sensing the ocean biological carbon pump from space: a review of capabilities, concepts, research gaps and future developments. *Earth-Sci Rev* 217:103604. <https://doi.org/10.1016/j.earscirev.2021.103604>
- Budge SM, Devred E, Forget MH, Stuart V, Trzcinski MK, Sathyendranath S, Platt T (2014) Estimating concentrations of essential omega-3 fatty acids in the ocean: supply and demand. *ICES J Mar Sci* 71(7):1885–1893. <https://doi.org/10.1093/icesjms/fsu003>
- Ciavatta S, Torres R, Saux-Picart S, Allen JI (2011) Can ocean color assimilation improve biogeochemical hindcasts in shelf seas? *J Geophys Res* 116:C12043. <https://doi.org/10.1029/2011JC007219>
- Ciavatta S, Torres R, Martínez-Vicente V, Smyth T, Dall'Olmo G, Polimene L, Allen JI (2014) Assimilation of remotely-sensed optical properties to improve marine biogeochemistry modelling. *Prog Oceanogr* 127:74–95. <https://doi.org/10.1016/j.pocean.2014.06.002>
- Ciavatta S, Brewin RJW, Skákala J, Polimene L, de Mora L, Artioli Y, Allen JI (2018) Assimilation of ocean-color plankton functional types to improve marine ecosystem simulations. *J Geophys Res Oceans* 123:834–854. <https://doi.org/10.1002/2017JC013490>
- Dogliotti AI, Ruddick KG, Nechad B, Doxaran D, Knaeps E (2015) A single algorithm to retrieve turbidity from remotely-sensed data in all coastal and estuarine waters. *Remote Sens Environ* 156:157–168. <https://doi.org/10.1016/j.rse.2014.09.020>
- Evers-King H, Martínez-Vicente V, Brewin RJW, Dall'Olmo G, Hickman A, Jackson T, Kostadinov T, Krasemann H, Loisel H, Röttgers R, Roy S, Stramski D, Thomalla S, Platt T, Sathyendranath S (2017) Validation and intercomparison of ocean-colour algorithms for estimating particulate organic carbon in the oceans. *Front Marine Sci* 4:251. <https://doi.org/10.3389/fmars.2017.00251>
- Field CB, Behrenfeld MJ, Randerson JT, Falkowski P (1998) Primary production of the biosphere: integrating terrestrial and oceanic components. *Science* 281:237–240. <https://doi.org/10.1126/science.281.5374.237>
- Gómez-Pereira PR, Fuchs BM, Alonso C, Oliver MJ, van Beusekom JEE (2010) Distinct flavobacterial communities in contrasting water masses of the North Atlantic Ocean. *ISME J* 4:472–487. <https://doi.org/10.1038/ismej.2009.142>
- Holm-Hansen, O (1973) The use of ATP determinations in ecological studies. *Bulletins from the Ecological Research Committee/NFR, No. 17, Modern Methods in the Study of Microbial Ecology* pp 215–222. <https://www.jstor.org/stable/20111565>
- IOCCG (2000) Remote sensing of ocean colour in coastal, and other optically-complex, waters. Sathyendranath S (ed), Reports of the International Ocean-Colour Coordinating Group, No. 3, IOCCG, Dartmouth, Canada

- IOCCG (2009) Partition of the ocean into ecological provinces: role of ocean-colour radiometry. Dowell M and Platt T (eds), Reports of the International Ocean-Colour Coordinating Group, No. 9, IOCCG, Dartmouth, Canada
- IOCCG (2014) Phytoplankton functional types from space. Sathyendranath S (ed), Reports of the International Ocean-Colour Coordinating Group, No. 15, IOCCG, Dartmouth, Canada.
- IOCCG (2020) Synergy between ocean colour and biogeochemical/ecosystem models. Dutkiewicz S (ed), IOCCG Report Series, No. 19, International Ocean Colour Coordinating Group, Dartmouth, Canada. <https://doi.org/10.25607/OBP-711>
- Jackson T, Sathyendranath SP (2017b) An exact solution for modelling photoacclimation of the carbon-to-chlorophyll ratio in Phytoplankton. *Front Mar Sci* 4:283. <https://doi.org/10.3389/fmars.2017.00283>
- Jackson T, Sathyendranath S, Mélin F (2017a) An improved optical classification scheme applied to ocean colour ECV. *Remote Sens Environ* 203:152–161. <https://doi.org/10.1016/j.rse.2017.03.036>
- Jones EM, Baird ME, Mongin M, Parslow J, Skerratt J, Lovell J, Margvelashvili N, Matear RJ, Wild-Allen K, Robson B, Rizwi F, Oke P, King E, Schroeder T, Steven A, Taylor J (2016) Use of remote-sensing reflectance to constrain a data assimilating marine biogeochemical model of the great barrier reef. *Biogeosciences* 13:6441–6469. <https://doi.org/10.5194/bg-13-6441-2016>
- Kassi J-B, Racault M-F, Mobio BA, Platt T, Sathyendranath S, Raitsos DE, Affian K (2018a) Remotely sensing the biophysical drivers of *Sardinella aurita* Variability in Ivorian waters. *Remote Sens* 10:785. <https://doi.org/10.3390/rs10050785>
- Kassi J-B, Racault M-F, ID, Mobio, BA, Platt, T, Sathyendranath, S, Dionysios E. Raitsos, DE, Affian, K, (2018b) Remotely sensing the biophysical drivers of *Sardinella aurita* variability in Ivorian waters. *Remote Sens* 10:785. <https://doi.org/10.3390/rs10050785>
- Koeller P, Fuentes-Yaco C, Platt T, Sathyendranath S, Richards A, Ouellet P, Orr D, Skúladóttir U, Wieland K, Savard L, Aschan M (2009) Basin-scale coherence in phenology of shrimps and phytoplankton in the North Atlantic Ocean. *Science* 324:791–793. <https://doi.org/10.1126/science.1170987>
- Kostadinov T, Milutinovic S, Marinov I, Cabré A, (2016) Carbon-based phytoplankton size classes retrieved via ocean color estimates of the particle size distribution. *Ocean Sci* 12: 561–575 [www.ocean-sci.net/12/561/2016/10.5194/os-12-561-2016](http://www.ocean-sci.net/12/561/2016/10.5194/os-12-561-2016)
- Kulk G, Platt T, Dingle J, Jackson T, Jönsson BF, Bouman HA, Babin M, Brewin RJW, Doblin M, Estrada M, Figueiras FG, Furuya K, González-Benítez N, Gudfinnsson HG, Gudmundsson K, Huang B, Isada T, Kovač Ž, Lutz VA, Marañón E, Raman M, Richardson K, Rozema PD, Poll WH, Segura V, Tilstone GH, Uitz J, Dongen-Vogels V, Yoshikawa T, Sathyendranath S (2020a) Primary production, an index of climate change in the ocean: satellite-based estimates over two decades. *Remote Sens* 12:826. <https://doi.org/10.3390/rs12050826>
- Kulk G, Platt T, Dingle J, Jackson T, Jönsson B, Bouman HA, Babin M, Doblin M, Estrada M, Figueiras FG, Furuya K, González N, Gudfinnsson HG, Gudmundsson K, Huang B, Isada T, Kovac Z, Lutz VA, Marañón E, Raman M, Richardson K, Rozema PD, Van de Poll WH, Segura V, Tilstone GH, Uitz J, van Dongen-Vogels V, Yoshikawa T, Sathyendranath S (2021) Correction: Kulk et al. Primary production, an index of climate change in the ocean: Satellite-based estimates over two decades (*Remote Sensing* 2020b, 12, 826). *Remote Sens* 13: 3462 <https://doi.org/10.3390/rs13173462>
- Lee ZP, Du KP, Arnone R (2005) A model for the diffuse attenuation coefficient of downwelling irradiance. *J Geophys Res* 110:C0201. <https://doi.org/10.1029/2004JC002275>
- Lee Z, Weidemann A, Kindle J, Arnone R, Carder KL, Davis C (2007) Euphotic zone depth: Its derivation and implication to ocean-color remote sensing. *J Geophys Res* 112:C03009. <https://doi.org/10.1029/2006JC003802>
- Longhurst A, Sathyendranath S, Platt T, Caverhill C (1995) An estimate of global primary production in the ocean from satellite radiometer data. *J Plankton Res* 17:1245–1271. <https://doi.org/10.1093/plankt/17.6.1245>
- Martinez-Vicente V, Evers-King H, Roy S, Kostadinov T, Tarran G, Graff J, Brewin RJW, Dall’Olmo G, Jackson T, Hickman A, Röttgers R, Krasemann H, Marañón E, Platt T, Sathyendranath S (2017) Pico-phytoplankton carbon from ocean colour algorithms. *Front Marine Sci* 4:378. <https://doi.org/10.3389/fmars.2017.00378>
- McKinna LIW, Cetinić I, Chase AP, Werdell PJ (2019) Approach for propagating radiometric data uncertainties through NASA ocean color algorithms. *Front Earth Sci* 7:176. <https://doi.org/10.3389/feart.2019.00176>
- Menon NN, Sankar S, Smitha A, George, G, Shalin, S, Sathyendranath, S, Platt, T, (2019) Satellite chlorophyll concentration as an aid to understanding the dynamics of Indian oil sardine in the southeastern Arabian Sea. *Mar Ecol Prog Ser* 617–618:137–147. <https://doi.org/10.3354/meps12806>

- Moore TS, Campbell JW, Dowell MD (2009) A class-based approach to characterizing and mapping the uncertainty of the MODIS ocean chlorophyll product. *Remote Sens Environ* 113:2424–2430. <https://doi.org/10.1016/j.rse.2009.07.016>
- Mora C, Tittensor DP, Adl S, Alastair GB, Simpson AGB, Worm B (2011) How many species are there on earth and in the ocean? *PLoS Biol* 9(8):e1001127. <https://doi.org/10.1371/journal.pbio.1001127>
- Morel A, Prieur L (1977) Analysis of variations in ocean color. *Limnol Oceanogr* 22:709–722. <https://doi.org/10.4319/lo.1977.22.4.0709>
- Müller D, Krasemann H, Brewin RJW, Brockmann C, Deschamps P-Y, Doerffer R, Fomferra N, Franz B, Grant M, Groom S, Mélin F, Platt T, Regner P, Sathyendranath S, Steinmetz F, Swinton J (2015) The Ocean colour climate change initiative: I. a methodology for assessing atmospheric correction processors based on in-situ measurements. *Remote Sens Environ* 162:242–256. <https://doi.org/10.1016/j.rse.2013.11.026>
- Nechad, B, Ruddick, KG, Neukermans, G (2009) Calibration and validation of a generic multisensor algorithm for mapping of turbidity in coastal waters. In: *Remote Sensing of the Ocean, Sea Ice, and Large Water Regions 2009*; Proc. Of SPIE: Bellingham, WA, USA, 7473, p 74730H, <https://doi.org/10.1117/12.830700>.
- Palacz AP, StJohn MA, Brewin RJW, Hirata T, Gregg WW (2013) Distribution of phytoplankton functional types in high-nitrate, low-chlorophyll waters in a new diagnostic ecological indicator model. *Biogeosciences* 10:7553–7574. <https://doi.org/10.5194/bg-10-7553-2013>
- Pitarch, J, Bellacicco, M, and Marullo, S, and van der Woerd, HJ (2021) Global maps of Forel-Ule index, hue angle and Secchi disk depth derived from 21 years of monthly ESA Ocean Colour Climate Change Initiative data, *Earth System Science Data*, 13(2):481–490 <https://essd.copernicus.org/articles/13/481/2021/>, 10.5194/essd-13-481-2021
- Platt T, Sathyendranath S (1988) Oceanic primary production: estimation by remote sensing at local and regional scales. *Science* 241:1613–1620. <https://doi.org/10.1126/science.241.4873.1613>
- Platt T, Sathyendranath S (2008) Ecological indicators for the pelagic zone of the ocean. *Remote Sens Environ* 112:3426–3436. <https://doi.org/10.1016/j.rse.2007.10.016>
- Platt T, Fuentes-Yaco C, Frank KT (2003) Spring algal bloom and larval fish survival. *Nature* 423:398–399
- Raitsos DE, Lavender SJ, Maravelias CD, Haralabous J, Richardson AJ (2008) Identifying four phytoplankton functional types from space: an ecological approach. *Limnol Oceanogr* 53(2):605–613. <https://doi.org/10.1016/j.jmarsys.2011.10.001>
- Reygondeau G, Dunn D (2019) Pelagic biogeography. In: *Encyclopedia of Ocean Sciences* (3rd ed), pp 588–598 <https://doi.org/10.1016/B978-0-12-409548-9.11633-1>
- Roy S, Broomhead DS, Platt T, Sathyendranath S, Ciavatta S (2012) Sequential variations of phytoplankton growth and mortality in an NPZ model: a remote-sensing-based assessment. *J Mar Sys* 92:16–29
- Roy S, Sathyendranath S, Platt T (2017) Size-partitioned phytoplankton carbon and carbon-to-chlorophyll ratio from ocean-colour by an absorption-based bio-optical algorithm. *Remote Sens Environ* 193:177–189. <https://doi.org/10.1016/j.rse.2017.02.015>
- Sathyendranath S, Platt T (1997) Analytic model of ocean color. *Appl Optics* 36:2620–2629. <https://doi.org/10.1364/AO.36.002620>
- Sathyendranath S, Platt T (1998) Ocean-colour model incorporating transspectral processes. *Appl Optics* 37:2216–2227. <https://doi.org/10.1364/ao.37.002216>
- Sathyendranath S, Platt T, Horne EPW, Harrison WG, Ulloa O, Outerbridge R, Hoepffner N (1991) Estimation of new production in the ocean by compound remote sensing. *Nature* 353:129–133. <https://doi.org/10.1038/353129a0>
- Sathyendranath S, Cota G, Stuart V, Maass H, Platt T (2001) Remote sensing of phytoplankton pigments: a comparison of empirical and theoretical approaches. *Int J Remote Sens* 22:249–273. <https://doi.org/10.1080/014311601449925>
- Sathyendranath S, Watts L, Devred E, Platt T, Caverhill C, Maass H (2004) Discrimination of diatoms from other phytoplankton using ocean-colour data. *Mar Ecol Prog Ser* 272:59–68. <https://doi.org/10.3354/meps272059>
- Sathyendranath S, Brewin RJW, Jackson T, Mélin F, Platt T (2017) Ocean-colour products for climate-change studies: what are their ideal characteristics? *Remote Sens Environ* 203:125–138. <https://doi.org/10.1016/j.rse.2017.04.017>
- Sathyendranath S, Brewin RJW, Brockmann C, Brotas V, Calton B, Chuprin A, Cipollini P, Couto AB, Dingle J, Doerffer R, Donlon C, Dowell M, Farman A, Grant M, Groom S, Horseman A, Jackson T, Krasemann H, Lavender S, Martinez-Vicente V, Mazeran C, Mélin F, Moore TS, Müller D, Regner P, Roy S, Steele CJ, Steinmetz F, Swinton J, Taberner M, Thompson A, Valente A, Zühlke M, Brando VE, Feng H, Feldman G, Franz BA, Frouin R, Gould RW Jr, Hooker SB, Kahru M, Kratzer S, Mitchell BG, Muller-Karger F, Sosik HM, Voss KJ, Werdell J, Platt T (2019) An ocean-colour time series for

- use in climate studies: the experience of the ocean-colour climate change initiative (OC-CCI). *Sensors* 19:4285. <https://doi.org/10.3390/s19194285>
- Sathyendranath S, Platt T, Kovač Ž, Dingle J, Jackson T, Brewin RJW, Franks P, Marañón E, Kulk G, Bouman HA (2020b) Reconciling models of primary production and photoacclimation [Invited]. *Appl Opt* 59:C100–C114. <https://doi.org/10.1364/AO.386252>
- Sathyendranath S, Abdulaziz A, Menon N, George G, Evers-King H, Kulk G, Colwell R, Jutla A, Platt T (2020a) Building capacity and resilience against diseases transmitted via water under climate perturbations and extreme weather stress. In: *Space Capacity Building in the XXI Century*, Ferretti S (ed.), Publisher: Springer Nature Switzerland AG, [https://doi.org/10.1007/978-3-030-21938-3\\_24](https://doi.org/10.1007/978-3-030-21938-3_24).
- Skákala J, Ford DA, Brewin RJW, McEwan R, Kay S, Taylor BH et al (2018) The assimilation of phytoplankton functional types for operational forecasting in the northwest European Shelf. *J Geophys Res Oceans* 123:5230–5247. <https://doi.org/10.1029/2018JC014153>
- Skákala J, Bruggeman J, Brewin RJW, Ford DA, Ciavatta S (2020) Improved representation of underwater light field and its impact on ecosystem dynamics: a study in the North Sea. *J Geophys Res Oceans*. <https://doi.org/10.1029/2020JC016122>
- Skákala J, Ford D, Bruggeman J, Hull T, Kaiser J, King RR et al (2021) Towards a multi-platform assimilative system for North Sea biogeochemistry. *J Geophys Res Oceans*. <https://doi.org/10.1029/2020JC016649>
- Strömberg KHP, Smyth TJ, Allen JI, Pitois S, O'Brien TD (2009) Estimation of global zooplankton biomass from satellite ocean colour. *J Mar Syst* 78(2009):18–27. <https://doi.org/10.1016/j.jmarsys.2009.02.004>
- Teruzzi A, Bolzon G, Feudale L, Cossarini G (2021) Deep chlorophyll maximum and nutricline in the Mediterranean Sea: emerging properties from a multi-platform assimilated biogeochemical model experiment. *Biogeosciences* 18:6147–6166. <https://doi.org/10.5194/bg-18-6147-2021>
- Volpe V, Silvestri S, Marani M (2011) Remote sensing retrieval of suspended sediment concentration in shallow waters. *Remote Sens Environ* 115(1):44–54. <https://doi.org/10.1016/j.rse.2010.07.013>
- Wernand M (2011) Poseidon's paintbox: historical archives of ocean colour in global-change perspective. PhD thesis, Utrecht University. <https://dspace.library.uu.nl/handle/1874/212589>
- Woerd HJvd, Wernand MR (2015) True colour classification of natural waters with medium-spectral resolution satellites: SeaWiFS, MODIS, MERIS and OLCI. *Sensors* 15:25663–25680. <https://doi.org/10.3390/s151025663>
- Zhai L, Platt T, Tang C, Dowd M, Sathyendranath S, Forget M-H (2008) Estimation of phytoplankton loss rates by remote sensing. *Geophys Res Lett*. <https://doi.org/10.1029/2008GL035666>

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