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REVIEW ARTICLE

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Studying marine microorganisms from space

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Abstract Microorganisms are but a few micrometers in diameter and are not visible to the naked eye. Yet, the large numbers of microorganisms present in the oceans and the global impact of their activities make it possible to observe them from space. Here a few examples of how microorganisms can be studied from satellites are presented. The first case is the best known: the main pigment used in photosynthesis (chlorophyll *a*) can be determined from satellites. These kinds of studies have contributed a tremendous amount of understanding about the distribution and dynamics of primary production in the oceans. Two other examples will concern analysis of heterotrophic prokaryotic production and estimates of dimethyl sulfide (DMS) concentration and flux to the atmosphere. These three processes are of fundamental importance for the functioning of the biosphere. Marine microbes carry out about half of the total primary production in the planet. A substantial fraction of the respiration in the oceans is due to the activity of heterotrophic prokaryotes. Finally, the flux of DMS to the atmosphere is believed to constitute one of the mechanisms by which the biota can regulate climate. The global implications of microbial processes in the oceans can only be addressed with the help of satellites.

Keywords Marine microorganisms · Chlorophylls · Dimethyl sulfide · Remote sensing · Primary production

Introduction

Microorganisms constitute a paradox. By definition they are so tiny that the microscope is needed to see them. Yet, due to their huge numbers, their activities have a global impact on Earth. This is particularly relevant when considering marine microorganisms. It is estimated that there are 10^{29} prokaryotes (both bacteria and archaea) in the world's oceans [23], and there should be about ten times more viruses. Although not as dramatically abundant, eukaryotic microorganisms are also extremely important in the oceans. Because of their larger size, the biomass of the latter is probably about the same order of magnitude as that of prokaryotes. Together, all these microorganisms are responsible for half of the CO_2 fixation in the planet and most of the respiration in the oceans. No wonder that their activities have a global impact. As a matter of fact, microorganisms were responsible for the most important global change in the history of the planet: the transformation of the atmosphere into an oxygen-rich environment about three billion years ago.

It seems appropriate, therefore, to seek tools to study marine microorganisms at the global scale. Remote sensing, from both satellites and airplanes, is an optimal way to analyze processes at a global scale [5, 18, 24]. Information of biological interest has resulted from the analysis of upwelling electromagnetic radiation. Using filters to analyze different wavelengths, and calibrations with simultaneous in situ determinations, several parameters can be estimated at a very large scale. The purpose of this review is to provide general microbiologists with an overview of the various approaches available to study marine microbes from space.

From the sun to the satellite sensor

Remote sensing can be either active or passive. In the first case, the satellite or airplane sends a beam of radiation towards the target and then collects the radiation sent back by the ocean or the organism. In the second case, the sun provides the stimulatory radiation and the sensor detects the radiation sent back by the target. In the present discussion only passive detection will be considered.

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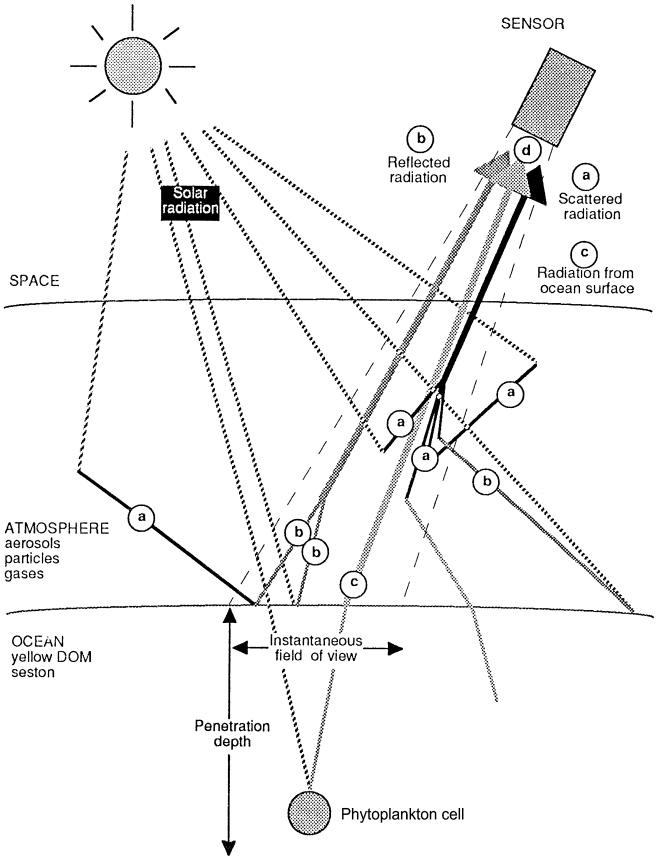

Fig. 1 Scheme of the paths of solar radiation to a sensor in a satellite. Radiation is scattered (*a*) and reflected (*b*). Upwelling radiation from the ocean surface (*c*) reaches the sensor modified by the atmosphere. Radiation received by the sensor (*d*) includes the latter plus reflected and scattered radiation. *DOM* Dissolved organic matter

Figure 1 shows the typical situation. Gases, aerosols and particles in the atmosphere scatter downwelling solar radiation before reaching the surface of the oceans (Fig. 1, a). Part of this radiation is reflected at the surface (Fig. 1, b) and part penetrates into the water, where dispersion and absorption by different components further modify it. Water itself absorbs and scatters different wavelengths. Dissolved substances (in the ocean, yellow dissolved organic carbon is most important) and sestonic particles also scatter, reflect or absorb light. Finally, some of the substances absorb radiation and emit fluorescence in response (for example chlorophyll and other pigments of phytoplankton). All these processes modify the spectrum of radiation and determine both the intensity and the spectral composition of the upwelling radiation that leaves the water surface towards the atmosphere (Fig. 1, c). The upwelling radiation has to travel through the atmosphere again, and thus it is subjected once more to the previously discussed scattering and absorption processes before reaching a sensor on a satellite (Fig. 1, d). Even though the sequence of interaction is complex, the physics of all the processes is relatively well understood, and it is possible to use the radiation received by the satellite (Fig. 1, d) to estimate several properties of the water masses several kilometers below. Only about 1% of the radiation received by the sensor is useful (Fig. 1, c), most radiation being either reflected or scattered solar radiation. Thus, an angle with respect to the sun must be chosen that minimizes these sources of undesirable radiation.

Calculation of relevant data

Values of the variables of interest in the ocean have to be calculated from the radiation received at the sensor. This process has several steps: (1) Raw data, which are the electronic signals for each pixel at the sensor. (2) Level 0; the position and time at which the signal was received are added to the electronic value for each pixel. (3) Level 1; the electronic signal received at the satellite is converted into radiation. The latter is a critical step that needs careful calibration of the sensor. Measurements taken today must be comparable to those taken yesterday or several years ago. Measurements taken from different satellites must also be comparable. Since sensors necessarily suffer decay in space, they must be recalibrated periodically. One way to do this is to point the sensor at the full moon. Since the radiation reflected from the moon's surface does not change at relevant scales, the sensor can be recalibrated. Then, the necessary corrections are applied to the electronic signal in order to convert it into a radiation level. (4) Level 2; the next step is to calculate the radiation leaving the water surface (c in Fig. 1) from the radiation received at the satellite (d in Fig. 1). To do this, an atmospheric correction must be applied to eliminate all the interferences from the processes described above. At this step, other corrections are also applied; for example, areas of land, ice or clouds are masked. Also, flags are added to pixels whose information is suspect for some reason. Further steps can be taken to calculate biogeophysical data from level 2 data by applying algorithms. These steps will be discussed below. (5) Level 3, finally, all the data corresponding to a given pixel of the earth's surface are filed together into a "bin" for future reference.

The rest of this review shows three examples of conversion of level-2 data into biological data. These three examples are at very different stages of development, from the preliminary to the well-established, and they offer an overview of the available possibilities.

Chlorophyll *a*

Chlorophyll *a* (Chl *a*) is the main pigment involved in photosynthesis, both on land and in the ocean. Alternative forms of trapping the sun's energy in the sea involve the use of bacteriochlorophyll *a* by α-Proteobacteria related to *Roseobacter* and *Erythrobacter* and of proteorhodopsin by bacteria belonging to the uncultivated SAR 86 cluster of the γ-Proteobacteria. Recently,

these light-dependent metabolisms have been shown to be relevant in the sea [4, 13]. The reactions do not seem to be necessarily linked to CO_2 fixation; rather, they probably constitute an additional source of energy for the organisms involved. At any rate, most photosynthesis is clearly linked to Chl-*a*-containing microorganisms: eukaryotic algae and cyanobacteria. Since CO_2 fixation is the starting point of all marine food chains, it is obvious that estimates of Chl *a* at a global scale are essential for any serious attempt to model the carbon cycle.

Chl *a* absorbs certain wavelengths and emits certain other wavelengths and that is why it appears green. Therefore, it should be possible to measure the ocean color due to Chl *a*. The process is relatively simple for "case 1" waters. These are water masses in which changes in the spectrum of emitted light are due essentially to phytoplankton and associated debris. Most of the open ocean belongs in this category. Coastal waters, however, are considerably more complicated to analyze, since terrigenous influence adds resuspended sediments, land drainage and anthropogenic inputs. Usually, "case 2" waters, as these are called, require involved empirical calibration with samples taken locally.

The Coastal Zone Color Scanner (CZCS) launched in the Nimbus-7 satellite in 1978, was the first sensor specifically designed to monitor ocean color. It consisted of a scanning radiometer able to determine absorbance at five visible and one rear-infrared wavelengths (443, 520, 550, 670, and 750 nm) and at one thermal infrared wavelength band (10.5–12.5 μm). Since it was a passive detector, it relied on sunlight for its data gathering. The system was calibrated by simultaneous determination of chlorophyll a concentration from ships ("ground truth"). The log-transformed data were then fitted by regression to the equation:

$$C = Ar_{ij}^{-B}$$

where C is the pigment concentration, r_{ij} is the ratio between absorbances at wavelengths i and j, and A and B are coefficients estimated by the regression. The wavelengths chosen were 443 nm (absorption maximum of Chl *a* and thus a minimum in the upwelling radiation) and 550 nm (a minimum in the absorption spectrum of Chl *a*). Therefore, when the ratio is high, the Chl *a* concentration is low and vice versa. The relationship was quite good for case 1 waters but it needed to be locally tuned for case 2 waters [19].

This empirical approach is necessary because many different factors complicate a calculation from theoretical grounds. For example, the absorption and/or emission spectrum of Chl *a* may be shifted by accessory pigments. Because of this, CZCS was unable to detect phycoerythrin-containing cyanobacteria despite their abundance in the sea. In addition, attempts are underway to use these shifts in the spectrum precisely to identify the major accessory pigments and to try to quantify them. This would allow quantitative determination of the abundance of different groups of phytoplankton. The size of the phytoplankton cells also alters the spectrum. Finally, the pigment content changes with the identity of the phytoplankton and with their physiological state. Thus, conversion of pigment abundance to phytoplankton biomass is not straightforward.

The CZCS stopped gathering data in 1985, after an extremely successful period of 7 years that yielded a first glimpse at the distribution and modes of variability of global oceanic phytoplankton [11, 15, 17]. Some of the "classic images" obtained by the CZCS can be seen at the Web page http://daac.gsfc.nasa.gov/CAMPAIGN_DOCS/OCDST/classic_scenes, where they are used to illustrate how remote sensing works. In September 1997, the SeaStar satellite was launched with the much improved Sea-Viewing Wide Field-of-View Sensor (SeaWiFS). This satellite remains in operation, and the SeaWiFS Web page is an excellent source of information on the characteristics and data obtained by the sensor http://seawifs.gsfc.nasa.gov/SEAWIFS.html. Since December 1999, the NASA satellite Terra, equipped with the Moderate-Resolution Imaging Spectroradiometer (MODIS), has been recording ocean color from space in parallel with SeaWiFS [25].

Color is not the only property that can be determined from above. Chl *a* and other pigments are fluorescent, and determination of fluorescence may be extremely sensitive and informative. Chl *a* fluoresces when the absorbed radiation has not been used for photosynthesis. Therefore, for the same level of solar radiation received, fluorescence will be low when photosynthesis is high and vice versa. This provides a way to quantify photosynthesis from fluorescence. The first global estimates of marine photosynthesis from satellite data can be seen in the reports of Platt and Sathyendranath [17] and Longhurst et al. [15].

Unfortunately, only surface events can be followed from satellites. Anything occurring below a depth of approximately 25 m (penetration depth in Fig. 1) is invisible. Despite this limitation, our understanding of the distribution of phytoplankton, especially in the oceans, has improved dramatically since the advent of remote sensing. With satellite images one can immediately gain a synoptic picture of the spatial distribution of phytoplankton (see, for example, the SeaWiFS image on the cover of this issue). Comparing a sequence of such pictures, the kinetics of phytoplankton can be followed. Even though ground truth is essential to calibrate the data, the combination of satellite images and field data is an extremely powerful tool to estimate global phytoplankton distribution and production [26].

Prokaryotic heterotrophic production

The activities of heterotrophic prokaryotes have a major impact on the metabolism of the global ocean, for example, by catalyzing transformations between dissolved and particulate organic matter [3]. In particular,

prokaryotic respiration is a key factor in determining the outcome of the balance between production and respiration in the oligotrophic ocean, pushing it towards net heterotrophy [9, 10]. This has obvious implications for global change. Furthermore, prokaryotes are the most important biological components in the transformation and mineralization of organic matter and thus become the main regulators of the dynamics of the biosphere [12].

Since the study of Cole et al. [8], it has been well-known that prokaryotic heterotrophic production (PHP) is approximately 30% of primary production in aquatic environments. The actual values, however, change considerably in space and time. The magnitude of this proportion has major consequences for the routes of carbon flow in the plankton: the more carbon that circulates through the microorganisms, the less carbon sediments and the more CO_2 is produced and potentially liberated to the atmosphere. It would clearly be very useful to be able to predict prokaryotic heterotrophic production on a global scale. By comparing these predictions with the equivalent ones for primary production, areas and times of the year in which it is more probable that the surface ocean acts as a sink or as a source of CO_2 could be identified. The problem, however, is that, unlike phototrophic microbes, heterotrophic prokaryotes are colorless and do not emit fluorescence. How can we observe these colorless microorganisms from space? The answer is that we cannot observe them directly. Instead, indirect ways are needed to estimate their abundance and activities from parameters that can be estimated by remote sensing. Let us consider the case of heterotrophic prokaryotes.

The model shown in Fig. 2 summarizes the factors that are believed to affect the abundance and activity of heterotrophic prokaryotes. If temperature increases, one would expect PHP to increase in a proportional way. The same would be true for the other factors. Some of these factors, such as sea surface temperature or Chl *a*, can be determined from satellites. Thus, if we could find a relationship between these variables and prokaryotic abundance or production, we could indirectly estimate the values of the latter from the satellite-obtained values of the former. We have developed a multiple regression model to predict PHP from water temperature and Chl *a* concentration [16]. The determination coefficient of the regression was 0.82, which is extremely good for field data. Since both independent variables can be estimated from satellite data, if the regression were applicable anywhere in the global ocean, it should be possible to predict marine PHP from satellites. Unlike the example of Chl *a*, this prediction is still at an early stage of development. Hopefully, we will be able to improve the algorithm and obtain maps of PHP similar to those for Chl *a*.

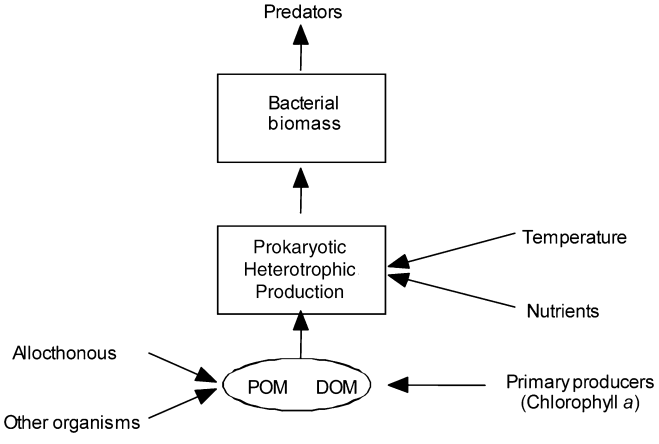

Fig. 2 Conceptual model for the analysis of the factors determining the abundance and production of heterotrophic prokaryotic plankton. *POM* Particulate organic matter. (Full details in [16])

Microbial production of dimethyl sulfide

Emission of reduced sulfur compounds from the oceans to the atmosphere plays a central role in the global sulfur cycle [1]. The main volatile compound is the biologically originated dimethyl sulfide (DMS). In the atmosphere, DMS is oxidized, generating acidic particles that disperse radiation and act as the main water-condensation nuclei in the troposphere over the open oceans. The size and abundance of these nuclei determine the optical density of clouds and, therefore, the amount of solar radiation reflected back to space (the albedo). In 1987, Charlson et al. [6] proposed that this effect of biologically derived substances on cloud albedo could form the basis for a feedback mechanism between the biota and climate. An increase in DMS production by the plankton would result in a decrease in the solar radiation received at the surface of the ocean. This, in turn, would reduce biological activity, eventually decreasing the DMS emission to the atmosphere and the cloud albedo. This hypothesis has generated a tremendous amount of discussions and research [20]. Nowadays, the first steps of the mechanism, from DMS production to cloud albedo, are well established [2,7]. Recently, a relationship between the efficiency of DMS production and the dynamics of the surface mixed-layer has been proposed [22]. This relationship would work in favor of the feedback mechanism proposed by Charlson et al. [6]. Given this situation, it is apparent that a way to determine DMS concentration and flux on a global scale is fundamental for any models of global change.

Simó and Dachs [21] developed an algorithm that predicts DMS concentration from Chl *a* concentration and mixed-layer depth. As explained above, Chl *a* can be determined with certain degree of confidence from ocean color data. The mixed-layer depth, however, cannot be determined from a satellite. In part, this is because the depth of the mixed layer in the ocean is often larger than the penetration depth of remote sensing. This parameter must be determined from climatologies. Climatologies are data sets generated by averaging, for every pixel of

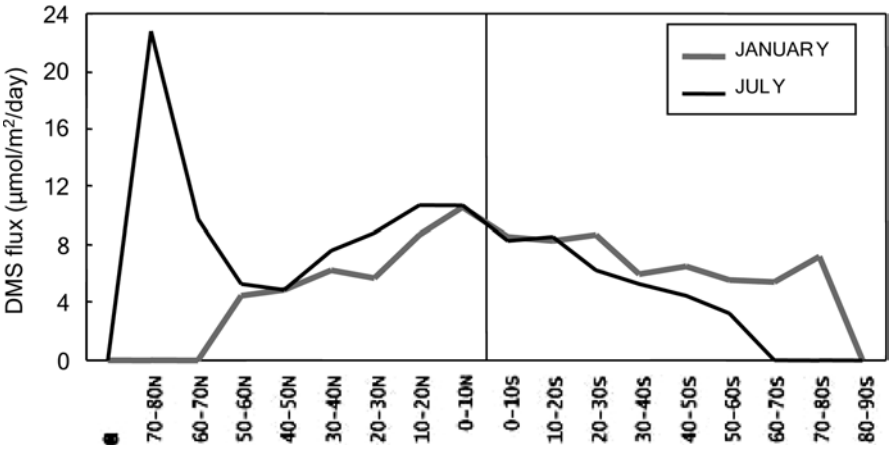

Fig. 3 Ocean-to-atmosphere emission flux of dimethyl sulfide predicted from monthly global climatologies of field-observed mixed-layer depths (NOAA) and remotely sensed chlorophyll *a* (SeaWiFS), sea surface temperature (AVHRR) and wind speed (QuickScat). (Full details in [21])

coordinates, the instantaneous data obtained over several-to-many years. Mixed-layer depth climatologies are constructed from concurrent climatologies of in situ temperature and salinity.

In the case of DMS, Simó and Dachs [21] were able to produce monthly global maps for DMS concentration. The interesting thing is that, once the concentration in the surface of the ocean of a volatile compound such as DMS is known, its flux to the atmosphere can be calculated as the product of the concentration by the exchange coefficient of the substance between air and water (also known as *piston velocity*). The gas-exchange coefficient is parameterized as a function of wind speed and sea surface temperature (e.g. [14]). Again, both wind speed and sea surface temperature can be obtained by remote sensing from satellites. Thus, global maps of the DMS ocean-to-atmosphere emission flux could also be obtained from the initial estimates of DMS concentration (Fig. 3) [21]. The combination of these two sources of data – remote sensing and climatologies of field observations – has become a very useful tool to predict parameters on a global scale. This example shows a further turn of the screw in our ability to use remote sensing to study marine microorganisms and their activities.

Conclusions

Remote sensing has allowed estimation of several important variables in a quasi-synoptical way and at a global scale. Conversion of remote sensing data into biologically and biogeochemically meaningful parameters, however, is far from trivial. Several international research programs within the International Geophysical and Biological Programme (IGBP) have pointed out the need to develop algorithms and models to make such conversions reliable. Climatologies and global integration of historical records of field data are extremely useful for this purpose, since they fill the gaps left by remote sensing, either because the right sensor does not exist or because of the intrinsic limitation of remote sensing to only the uppermost layer of the ocean. Simultaneous use of remote sensing data and climatologies is an extremely powerful tool to build algorithms. These data will provide, in turn, the predictive capabilities necessary to answer questions about global change. In conclusion, not only can marine microbes be observed from space, but some of their activities can be – or will be in the near future– monitored at a scale unthinkable only a decade ago.

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