Remote Sensing of Primary Production in the Ocean: Promise and Fulfilment [and Discussion]

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Remote sensing of primary production in the ocean: promise and fulfilment

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SUMMARY

Remote sensing of ocean colour affords us our only window into the synoptic state of the pelagic ecosystem, and is likely to remain the only such option into the foreseeable future. Estimation of primary production from remotely sensed data on ocean colour is a research problem in two parts: (i) the construction of a local algorithm; and (ii) the development of a protocol for extrapolation. Good local algorithms exist but their proper implementation requires that certain parameters be specified. Protocols for extrapolation have to include procedures for the assignment of these parameters. One suitable approach is based on partition of the ocean into a suite of domains and provinces within which physical forcing, and the algal response to it, are distinct. This approach is still in its infancy, but is best developed for the North Atlantic. Using this method, and using the accumulated data from oceanographic expeditions, leads to an estimate for the annual primary production of the North Atlantic at the basin scale. Direct validation of the result is not possible in the absence of an independent calculation, but the potential errors involved may be assessed.

1. MOTIVATION FOR USE OF SATELLITE DATA ON OCEAN COLOUR

There are three principal reasons why remotely sensed data on ocean colour are used in global biogeochemical studies. One is to provide a synoptic field of chlorophyll concentration to compare with the calculated field derived from coupled, ocean-ecosystem models, or to use for initializing such models (Wroblewski *et al.* 1988; Ishizaka & Hofmann 1993; Yentsch 1993). Another is as a basis for the computation of regional- and basin-scale estimates of marine primary production (Platt & Sathyendranath 1988; Morel & André 1991; Platt *et al.* 1991*a*; Campbell & Aarup 1992; Sathyendranath *et al.* 1995). A third is as a generic vehicle for the extrapolation to large horizontal scale, of small numbers of discrete observations made from ships, of various ecophysiological rates and pools. Each of these applications requires that we emphasize particular aspects of the ocean-colour database, but at the same time there are features common to all applications. In this paper we focus mainly on the estimation of primary production at large scale as an example of how the ocean colour data can be used. But where one of the other two applications better illustrate a point, we discuss these also. Computation of primary production from remotely sensed data is an application of algal physiology. Not all the information required for this computation is accessible to remote sensing. We must combine the data from satellites with data collected by ship: but the incompatibility of scales in time and space between the two kinds of data is a major obstacle. We begin by outlining the salient properties of ocean-colour data.

2. THE OCEAN-COLOUR DATABASE

Currently, ocean-colour data taken by satellites exist only for the period 1978–1986. Within this window, the coverage of the global ocean is uneven in time and space: partly because the sensor was not always activated, and partly because useful data cannot be recorded through clouds (a limitation with both systematic and random components, and therefore a potential source of bias in some applications). Because the satellite flew in a polar orbit, the frequency of coverage varies with latitude. However, the large swath width of the sensor ensured that every point on the surface of the earth could be sampled at least once, cloud-free conditions permitting (Robinson 1985).

The sensor records ocean-leaving radiances in several wavebands and the ratio of two of these (the blue–green ratio) can be calibrated against concentration of phytoplankton concentration in the surface layer (Gordon & Morel 1983). The signal detected by the sensor emanates not just from the surface proper: it contains (progressively weaker) contributions from deeper horizons (Gordon & McCluney 1975). Contributions from horizons deeper than one optical depth (inverse of the diffuse attenuation coefficient) are generally agreed to be negligible (Gordon & Clark 1980). The data are collected at a spatial resolution of better than 1 km at the sea surface. Often, however, in the interest of making the files more compact, the data are reported at a 4 km resolution (Feldman *et al.* 1989). For the time resolution, one should distinguish between instantaneous images constructed for comparison with data collected by ship on a particular day, and 'averages' constructed from serial images. These are averages only in a special sense, and they are usually biassed. For example, in regions subject to frequent cloud cover, individual pixels in the average may be represented by only one or a small number of observations, or they may even be represented by no observations.

3. THE DATABASE COLLECTED FROM SHIPS

The relevant data accumulated by observations from ships consist of vertical profiles of pigment concentration, and measurements of the characteristics of the photosynthesis–light curve. Vertical profiles of *in situ* primary production can also be useful for checking and tuning the local algorithm. The spatial distribution of entries in these archives is very uneven. Of the quantities mentioned, the pigment profile has the richest archive, primary production the next richest, and the photosynthesis parameters the least rich of all. For example, in an archive we compiled for the North Atlantic (defined, for the present purpose, to be the area from 89° W to 1° E between 10° S and 70° N), we found some 6280 pigment profiles that met the required standards of quality, but only 1862 sets of photosynthesis parameters (Sathyendranath *et al.* 1995). The spatial distribution of the latter was heavily biassed towards the western side of the basin (mainly a consequence of their having all been measured by the same research group). Sporadic coverage, in both space and time, is the most salient characteristic of the ship archive. The existing coverage, or lack of it, is a useful guide to where future sea-sampling could be conducted.

4. THE LOCAL ALGORITHM

When the ocean-colour data are used to estimate primary production, the usual goal is to calculate the daily production of the ocean water column, $P_{Z,T}$. The problem has two principal parts: calculation of $P_{Z,T}$ at a particular time and place, where it is assumed that all the necessary information is given (the local algorithm); and the extrapolation of the results of the local algorithm to yield a figure representative of a larger region (Platt & Sathyendranath 1988). We deal first with the local algorithm.

Various procedures exist for calculation of primary production at a given location, all having broadly similar requirements for the information that must be supplied (Platt & Sathyendranath 1993). The first requirement is that the irradiance at the sea surface in the photosynthetically active waveband (400–700 nm), $I_0(t)$, a function of the time t, is known. This can be calculated by a standard astronomical method assuming that the sky is free of clouds. The effect of clouds can be allowed for using information collected by remote sensing (Bishop & Rossow 1991), or by using climatological data on clouds. The loss of irradiance by reflection at the sea surface depends on sea state, which is also accessible to remote sensing. In the strictly local context, the algorithm for primary production may be forced with irradiance measured 'on the spot'.

The next requirement is the vertical distribution of phytoplankton pigment, important as the principal determinant of the penetration of visible light through the sea and of the absorption of photons in the photosynthesis process. This profile cannot be derived directly by remote sensing; the most convenient way to supply the information is in the form of the parameters of a standardized vertical profile, such as the shifted Gaussian (Platt *et al.* 1988). Finally, we need to know the parameters of the photosynthesis–light curve, the initial slope, α^B, and the production at light saturation or assimilation number P_m^B (where the superscripts indicate normalization to pigment biomass B).

For the calculations of primary production presented below, we use the procedure of Platt and Sathyendranath (1988) in its most recent version, as presented in Sathyendranath *et al.* (1995). This method is usually applied with the photosynthesis parameters independent of depth, but because the integration over depth is done numerically, their possible variation with depth is easily accounted for, provided the necessary information is available.

5. EXTRAPOLATION TO LARGE HORIZONTAL SCALE

Calculations at large horizontal scale require that we implement the local algorithm at many field points (pixels) in the region of interest. The question immediately arises as to how the supplementary information (the parameters of the photosynthesis–light curve and of the pigment profile) should be supplied at each and every pixel. If these properties were invariant (constant and spatially uniform) over the region, this would be a trivial problem. Experience persuades us that things are not so simple.

In this context, two approaches are possible. One is to derive the required parameters as functions of environmental variables, such as temperature, accessible to remote sensing (Method I). The other is to assign the parameters on the basis of a data archive, taking into account location and season (Method II). In principle, Method I would be the preferred method. It would: (i) be more objective; (ii) rely less on the skill and judgement of the user; (iii) give unambiguous parameter estimates at every field point, with some idea of the variance associated with those estimates. The difficulty with following this approach is that reliable estimator functions, as required by the method, do not exist; and they certainly do not exist as universal laws.

Lacking the necessary estimator functions, we can consider Method II, the assignment of parameters based on previous knowledge of their magnitudes at a given location in a particular season. This approach is based on the belief that the shape of the pigment profile and of the photosynthesis–light curve are, in general, more stable properties than the pigment biomass at the surface (the only biological property whose value can be updated continuously by remote sensing). The difficulties in following this approach are: (i) that the existing databases, especially that on photosynthesis parameters, are modest in size; (ii) that the existing observations are unevenly distributed in space and time; and (iii) that therefore some protocol has to be erected by which the archived data can be translated into the parameter field at a given time. Notice that, because we are unable to deduce the estimator functions directly from first principles, Method I would also rely on the use of a data archive: to the extent that the database is limited, both Methods will be compromised.

Inherent weaknesses in both methods (lack of universally valid estimator functions in Method I and sparse, unevenly distributed archives in Method II) impose a requirement for partition of the region of interest to facilitate the large-scale calculations. In the next section we consider how such a partition could be carried out.

6. DYNAMIC BIOGEOCHEMICAL PROVINCES

The conceptual basis for partitioning the ocean (Platt & Sathyendranath 1988; Mueller & Lange 1989; A.R. Longhurst, unpublished data) is as follows. We assume that in the pelagic ecosystem, the rates of important ecophysiological and biogeochemical processes (in particular the photosynthetic rate) are under physical control. Physical forcing regulates the environmental conditions that will determine: (i) the species assemblage flourishing at a given place and time; (ii) the magnitude of the nutrient flux into the photic zone and the manner in which it is supplied; (iii) the rate of vertical mixing and therefore the rate of photoadaptation; and (iv) the stratification in the water column and therefore the vertical distribution of photosynthetic pigments. We then partition the ocean by delineating those areas that share a common physical forcing, in as much as the forcing can be expected to control the rates of the processes just mentioned.

A complication is that the nature and intensity of physical forcing is known to vary seasonally and between years, in many parts of the ocean. Therefore it is essential that the partition scheme allow the partition boundaries to vary with time. This is one meaning of the qualifier 'dynamic' in the name of the method: dynamic biogeochemical provinces. The other connotation is that the parameters themselves may be allowed to vary from the default (constant) values in response to local forcing, provided that we know how to quantify their response. The tendency of the boundaries to move with time requires that we conceive of the provinces at two distinct levels: first in the Platonic or ideal sense (a pair of provinces with definable and dissimilar properties will exist adjacent to each other thus creating a boundary of a known, general character); and second in the particular sense (at a stated time, the said boundary is believed to follow a stated trajectory). The question then arises of how the realized boundaries may be delineated in routine applications. Because we intend to draw the boundaries at large geographical scale, the most useful criteria to use will be those that can be implemented from remotely sensed data: sea-surface temperature, sea-surface elevation, wind stress and ocean colour itself. This means that the characteristics by which we distinguish one province from another must be translatable into objective rules that can be applied to data on one or more of these properties, collected by satellites, such that any pixel in the ocean-colour field can be assigned unambiguously to a particular province. Such is the long-range goal of this approach. Until now, however, the appropriate rules have not been formulated.

Once the provinces are established, however, what roles are expected from them? They form a template upon which the parameters of the photosynthesis–light curve and of the vertical distribution of pigments can be assigned. In our view, some such template is essential no matter what protocol (archive; empirical function of environmental variables; rational function of environmental variables based on first principles) is used to assign parameters. This is because, at present, no universal rules exist to derive these parameters from environmental properties. At best we have rules that are useful only in a limited region, so that at large scale a series of such rules would have to be applied in a piecewise manner.

The provinces, then, depict the underlying oceanographic structure of an area, represented as an outline map on which the necessary parameters can be filled in as assigned according to one of several possible procedures. The simplest, or default, procedure is to assume that for a given season, whose extent may be defined to suit the particular requirements of the province, the parameters that we need are constant inside the boundaries of the province. The preferred way to assign them is on the basis of archived data for the same region and season (Method II). In the North Atlantic, as elsewhere, the weakness with this approach is the small size of the archive and its uneven coverage. Observe that Methods I and II are not mutually exclusive. It may be that for a given province and season, particular information is available about one or more of the parameters, such that the default procedure can be improved for this or these parameters. Thus, we are led to consider a Method III, in which the default procedure (Method II) would be used where no alternative was available but particular rules, province-specific or otherwise (Method I), would be applied wherever and whenever possible. Method III would be 'adaptive', in the sense of computational mathematics, selecting the algorithms to assign parameters according to circumstances.

A specific example of a rule that could be used in Method III is available for the North Atlantic. It is known both from observations and from theoretical work that for a broad swath of this ocean in the Summer, the depth of the chlorophyll maximum shallows to the North at a rate of 3.5 m per degree of

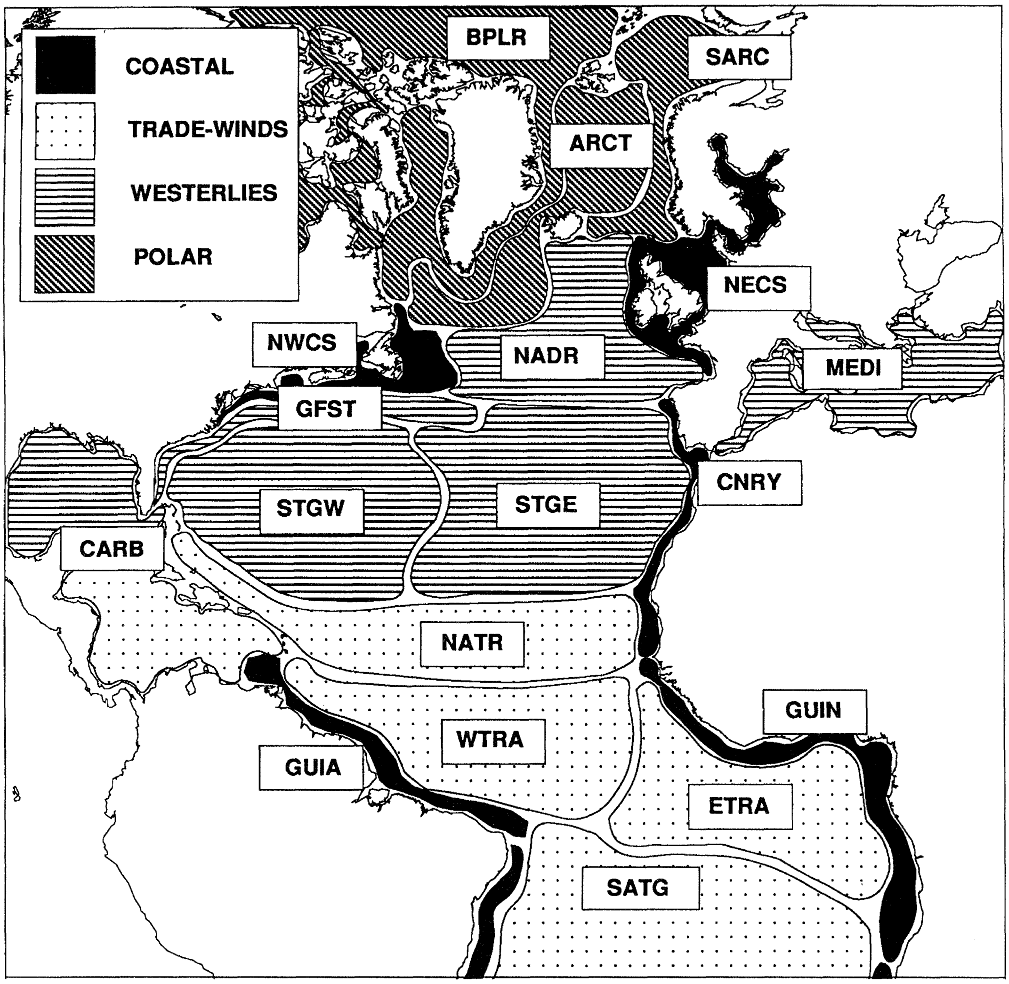

Figure 1. Schematic of the biogeochemical provinces of the North Atlantic, based on A.R. Longhurst, unpublished data and Sathyendranath *et al.* (1995).

latitude (Strass & Woods 1991). This is a robust result, it can be easily codified into an objective rule and it makes sense to use it, no matter what procedure is followed for the assignment of the rest of the parameters. In other words, it is in no way essential for all the parameters to be assigned by the default procedure, nor indeed by any single procedure: the preferred approach is to use the best information available for any parameter in the given circumstances. The example just given is region-specific: it would make little sense to use the same rule in the North Pacific.

Another example is the use of surface temperature data to estimate properties, such as surface nitrate concentration, useful for the calculation of new production (Dugdale *et al.* 1989; Sathyendranath *et al.* 1991). Although it has a basis that is easily understandable (upwelling water tends to be both colder and richer in nutrients than the water it replaces), and although it has been applied with success in a variety of oceanographic regimes, this approach lacks a detailed theoretical foundation. Its implementation in a particular region is based strictly on observation, but within this limitation it is easily codified into a rule: qualitatively, the rule would be the same everywhere – a regression of nitrate on temperature – but the coefficients in the regression would vary from province to province.

Ideally, we would prefer rules that were grounded in first principles and therefore free of region-specificity. At present no such rules exist, but this does not mean that we should not continue to seek them. Again, it is worth stressing that we are not required to assign all parameters by the same procedure, and a universal first-principle rule for even a single parameter would constitute a major advance. At this point it may be useful to summarize the concept of the biogeochemical provinces. They partition the ocean into a suite of regions having similar physical forcing with respect to the properties important for algal growth, and thus form a rational template (spatial and temporal) for the assignment of the parameters necessary for calculation of watercolumn primary production. Such a partition appears to be essential whether the parameters are assigned by empirical rules, by rules derived from theory or on the basis of a data archive. In practice, a combination of approaches may be used to assign parameters (Method III).

Against this background, what progress has been made in the partition of the North Atlantic? Longhurst's unpublished data recognizes four primary algal domains each with a distinctive coupling between physical forcing and algal ecology (Sathyendranath *et al.* 1995). The 'Polar Domain' is characterized by the presence in Spring and Summer of a stable, lowsalinity layer at the surface consequent upon ice-melt. In such conditions, development of phytoplankton blooms is under strict control of irradiance (intensity and daylength). The 'West-wind Domain' covers the mid-latitudes, where vertical mixing by storms competes with stabilization by solar heating to determine the structure of the upper water column. Here, the critical-depth model of Sverdrup is a useful basis for interpretation of phytoplankton dynamics as a response to local forcing. In contrast, the 'Trade-wind Domain' is seen as a domain where the principal forcing of algal dynamics may be remote, rather than local, a consequence of geostrophic adjustment to the large-scale wind field. Finally, the 'Coastal-boundary Domain' refers to the continental margins where coastal winds and local topography exert a strong influence on the local circulation. It includes the upwelling regions.

These four domains are sufficiently general as to be useful for any ocean. Indeed, they have already provided the basis for a calculation of global-scale primary production (Longhurst *et al.* 1995). If we want to consider the particular properties of the North Atlantic, however, a further partition is required: this is the partition that yields the biogeochemical provinces themselves. Thus, in the Polar Domain, we identify the Boreal-Polar, Arctic, and Subarctic Provinces; in the West-wind Domain we distinguish the Gulf Stream, North Atlantic Drift, Subtropical Gyre (East and West) and Mediterranean Provinces; in the Trade-wind Domain we recognize the Tropical Gyre, the West Tropical Atlantic, the East Tropical Atlantic, the South Subtropical Gyre, and the Caribbean and Gulf Provinces; and in the Coastal-boundary Domain we separate the Northwest Atlantic, Northeast Atlantic, the East Atlantic, the Guinea, and the Guiana Provinces. This gives a total of some 18 provinces (see figure 1).

7. IMPLEMENTATION IN THE NORTH ATLANTIC

We have used the suite of biogeochemical provinces outlined in the previous section, and the relevant database assembled from observations at sea, to calculate annual primary production in the North Atlantic, given the satellite archive of ocean colour (Sathyendranath *et al.* 1995). The steps involved in the implementation are as follows.

An archive of chlorophyll profiles was built, with data compiled from the work of a number of institutes over several decades. Each profile was checked for quality, and then fitted to a shifted Gaussian profile. After rejecting some 1665 profiles on the grounds of poor quality, we judged a further 6280 profiles to give acceptable fits. The fitted profiles were partitioned by province and by season, and average shapes of the chlorophyll profiles were established for each case (note that the archived chlorophyll profiles were used only to establish the shape of the profile, but not the magnitude). Similarly, an archive of some 1862 P–I parameters was used to establish mean parameters by season and by algal domain (the data set was insufficient for partition into provinces) i.e., the parameter assignment was made primarily according to Method II. A tentative step towards Method III was made for the Trade-wind Domain, where the photosynthesis parameters were assigned on the basis of surface light and nitrate availability.

Cloud-cover data were used with an atmospheric transmission model (Bird 1984) to compute the light available at sea level, on a monthly basis, for every 1° square in the North Atlantic. Monthly average values of satellite-derived chlorophyll data for 1979, also gridded by one degree, were combined with information on the shape of the chlorophyll profile for the season and the province (from archived data), to obtain the absolute profile at each grid point. A spectral, light-transmission model, which uses the chlorophyll profile as input, was then used to compute the light available at depth, and thus the primary production at that depth. The computations were carried out for some 12 time intervals over the day, and for every 0.5 m in the euphotic zone, and summed over depth and over time to obtain the daily, water-column production at that pixel.

The computations were repeated for each pixel for each month of the year, and summed over the year and over the pixels assigned to each province, to obtain annual production per province. According to these calculations for the N. Atlantic Basin (10° S to 70° N; 89° W to 1° E; roughly 15% of the total area of the global ocean), the primary production in 1979 was 10.5 Gt C a^{-1}. The West-wind Domain contributed 2.3 Gt C a^{-1} to the total and the Polar Domain, 2.2 Gt C a^{-1}. The Trade-wind Domain was responsible for 3.1 Gt C a^{-1}, and the Coastal Domain for 2.9 Gt C a^{-1}. We do not insist that these figures are correct in any absolute sense; they merely represent the present state of our ability to combine the satellite and the ship archives to draw conclusions about the annual primary production in the North Atlantic.

Because the parameter assignment was based on seasonal averages, and because the calculations used monthly averaged fields of pigments and clouds, the resolution of the primary production estimates cannot be better than monthly. The estimated fields of primary production for each month are shown in figure 2.

8. PROBLEMS WITH VALIDATION OF RESULTS

Having made an estimate of basin-scale primary production for the North Atlantic, we can ask whether it is possible to validate the result, that is to test it against the result of a similar calculation made according to an independent method. Unfortunately, the answer is no: no such independent methods are available. There are two principal reasons for this. First, properly done, the remote sensing method for primary production uses all the available data from direct primary production measurements made by ships. It subsumes the ship database, and in addition uses the rich satellite archive as a vehicle for extrapolating to times and places where direct measurements are lacking. No data remain unused and therefore independent. Further, previous estimates of

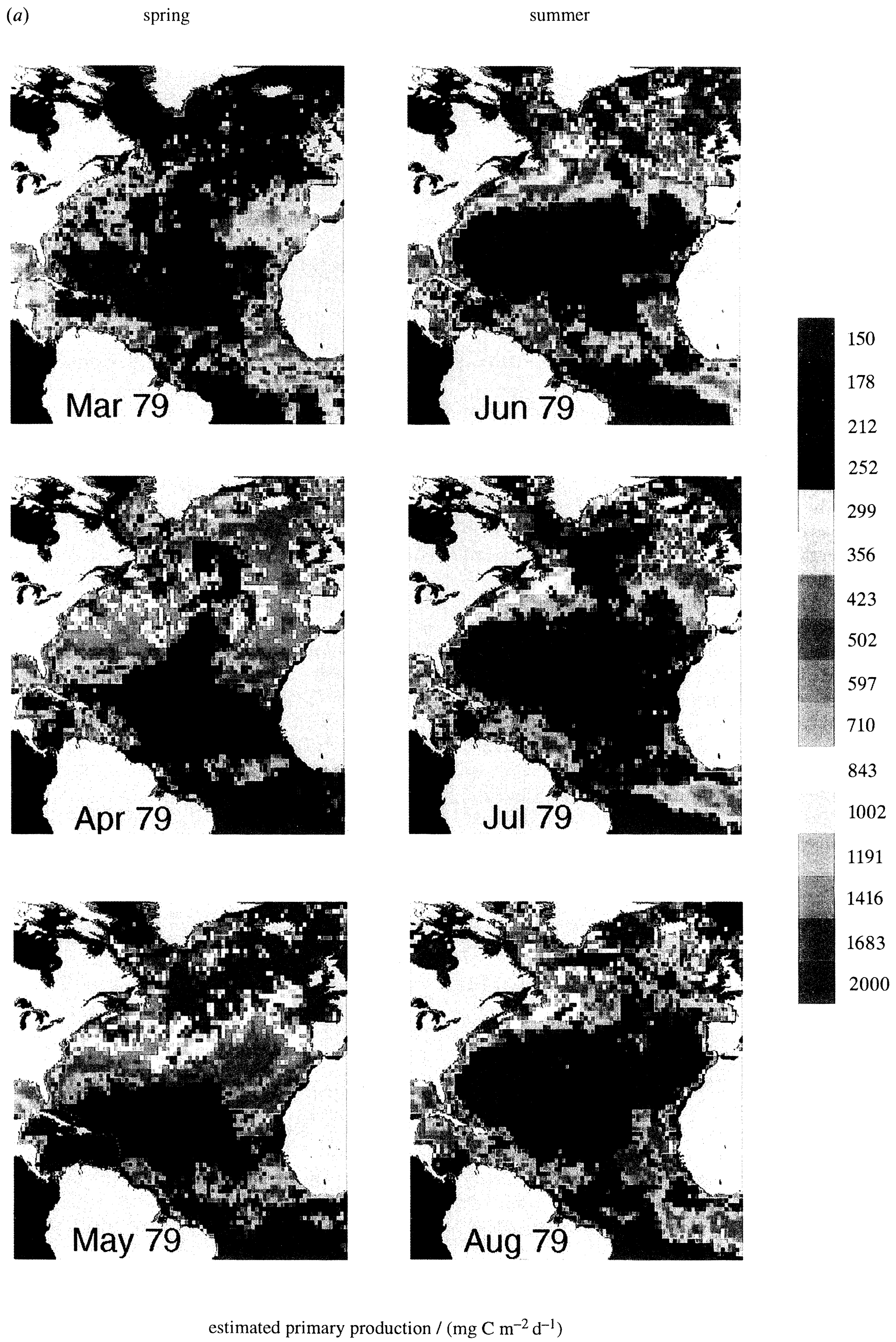

Figure 2. Monthly averages of daily primary production estimated from ocean-colour data for 1979. (*a*) Spring and summer; (*b*) autumn and winter. The grey areas represent land; the black areas indicate lack of ocean-colour data. By virtue of the spatial resolution in the satellite data, the images show considerable detail, but in using them it should be borne in mind that the parameters on which the computations are based are resolved only to the level of the algal domains (for the photosynthesis parameters) or the level of the biogeochemical provinces (in the case of the parameters describing the shape of the pigment profile). The resolution of the parameters will not improve until prescriptive functions become available for estimating their magnitudes at each pixel.

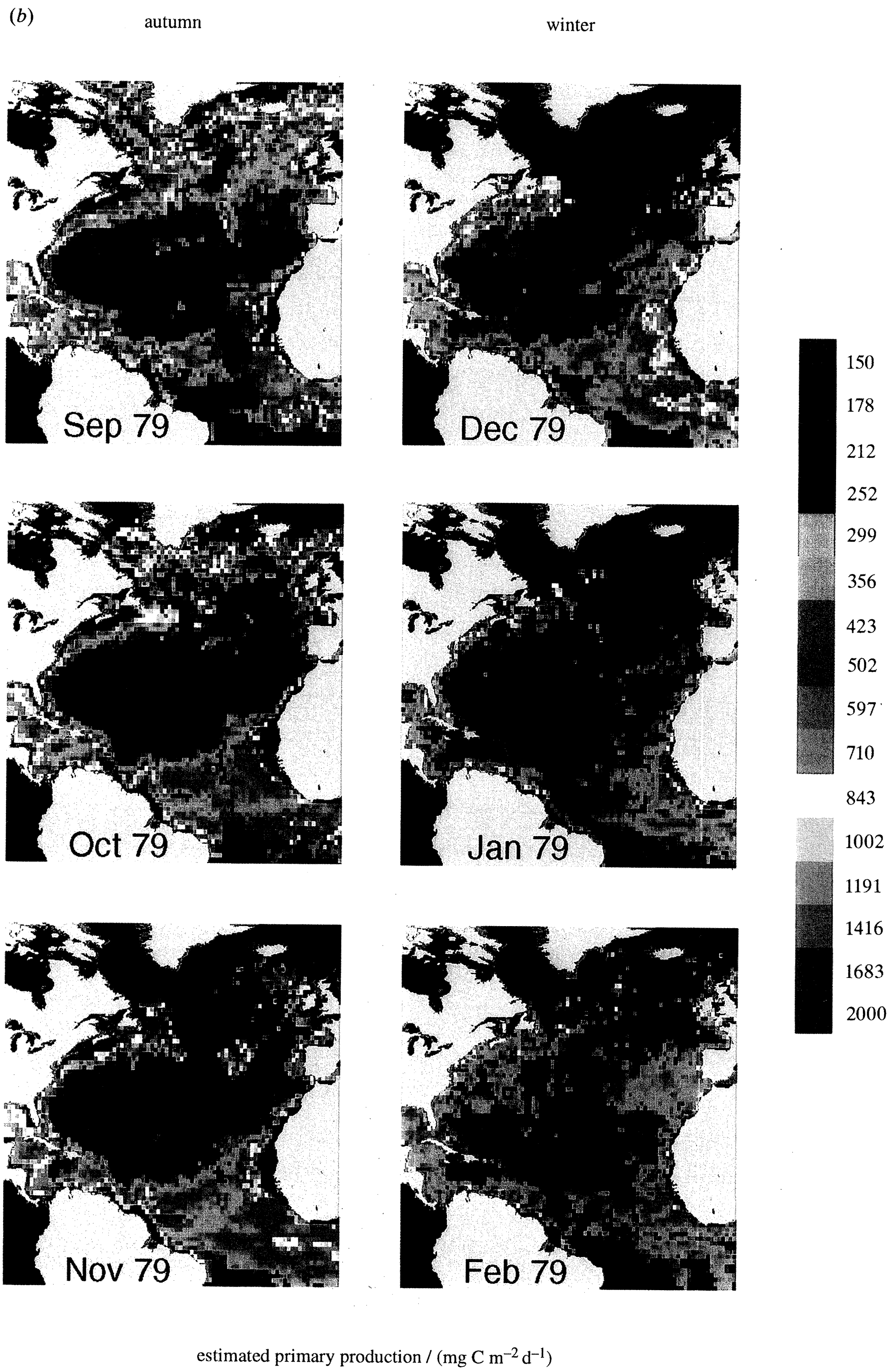

Figure 2. (*cont.*)

basin-, or global-, scale primary production have, necessarily, combined data from many different years as a device to offset, partially, the incompleteness of the database. Remote sensing is the only method that affords (albeit in the medium to long term) a realistic chance of estimating annual primary production for a particular year, and therefore of detecting interannual variations.

One method that might be thought of for validation is the use of results in the prediction of pigment fields at some future time. The difficulty with applying this approach is that we would need information on the loss terms for phytoplankton, which are not accessible to remote sensing, and for which the data archive is considerably more sparse than that for the growth terms. The flow field would also be required but this is a more feasible objective than the loss terms, whether approached by modelling or remote sensing.

Another major obstacle to validation of estimates of primary production by remote sensing relates to comparisons with results from indirect or bulk-property methods. An example of these methods is that based on apparent oxygen utilization rate. Such methods usually have a long intrinsic timescale as well as large spatial-scales. One of the characteristics of primary production measurements is that long timescale methods do not estimate the same component of primary production as those with short temporal scales (Platt *et al.* 1989 1992; Platt & Sathyendranath 1993). Specfically, bulk-property methods estimate new production, whereas the ship database of short-term incubations refer to gross production. The fundamental incompatibilty of scales between these two classes of method implies a limitation on our ability to compare their results. At the very least, the results of the one class of method would have to be extrapolated before they could be compared with the results of the other, and the robustness or otherwise of the extrapolation procedure itself would interfere with the attempt to validate.

A basin-scale estimate of primary production using remotely sensed data is unusual in that it refers to large spatial scales, but is based on physiological parameters that are valid at short temporal scales, being derived from short-term incubations using a radioactive tracer for the inorganic carbon assimilated. The same would be true of basin-scale estimates made using the ship database alone, but any such calculation that overlooks the potential of the ocean-colour data as a tool to aid interpolation of sparse observations should be regarded as of only limited value.

9. NEW PRODUCTION

One way to circumvent the incompatibility between scales and components of primary production is to attempt to estimate new production directly by remote sensing. The basic procedure is first to estimate total primary production, as before, and then to multiply the result by the ratio of new production to total production, as estimated by remote sensing or by any other method (the calculation should be a weighted integration over time and space). To date, this has not been done at the basin scale in the Atlantic or in any other ocean. However, localized calculations have been made, for example on Georges Bank (Sathyendranath *et al.* 1991) and off North Africa (Dugdale *et al.* 1989). The pigment fields derived from satellite have been used as a guide to the calculation of new production in the North Atlantic, from information on nitrate distribution (Campbell & Aarup 1992).

A crude way to establish a lower bound for new production at the basin scale might be based on the observation that any primary production below the mixed layer is very likely to be new production. Stating this another way, any production in the deep chlorophyll maximum is probably new production. The difference between daily production calculated for a uniform water column (surface value of pigment maintained throughout) and that for a non-uniform column is one way to estimate primary production in the chlorophyll maximum, and therefore the lower limit of new production. The result of such an admittedly approximate calculation for the North Atlantic is 1.0 Gt C m^{-2} a^{-1}, implying an *f*-ratio (equal to the ratio of new production to total production) of at least 0.1. Any losses of organic material from the mixed layer would augment the estimate of new production and of the implied *f*-ratio.

Approximate though it may be, this calculation emphasises the value of including information on the shape of the pigment profile in the estimation of primary production. It might be argued that because the estimate increases by only about 10% when the chlorophyll maximum is accounted for, the effort involved in assembling the database on pigment profiles and controlling it for quality is not worthwhile. However, we maintain that the database on pigment profiles, and the estimates of primary production made from them contain useful information whose value should not be overlooked. Moreover, the error is systematic rather than random, and will not disappear through mutual cancellation when the estimates of primary production are averaged over many pixels.

10. ERROR ANALYSIS

Although it is not possible to validate the basin-scale estimates in the normal sense, it is possible to make some assessment of the errors inherent in the calculation. To do this, we consider each element of the calculation separately.

Following Platt *et al.* (1988), we suppose the precision of the surface irradiance is within 10% (Gautier & Katsaros 1984), and that of the pigment concentration derived from ocean colour is within 35% (Gordon *et al.* 1983). The error on the photosynthesis parameters will contain a component arising from the measurement itself, and one arising from the aggregation of data within domains. The first component is well established (5% for P^B_m, 20% for α^B, Platt *et al.* 1980). The second can be estimated from the parameter archives (Sathyendranath *et al.* 1995) as the standard error relative to the mean: it is about 7% for both α^B and P^B_m. Platt *et al.* (1988) found the compounded error on the local algorithm, as used in the context of remote sensing, to be approximately 42%, with the error in biomass retrieval dominating. If we now include the further 7% error associated with aggregating the photosynthesis parameters into domains, we can estimate the resultant error to be approximately 50%.

With respect to the errors associated with defining the shape of the pigment profile, a set of data from three provinces of the Westerlies Domain is available. These data were collected using an undulating body equipped with a profiling fluorometer calibrated for chlorophyll retrieval. The data were averaged over segments 5 km long of transects up to approximately 1000 km long run during September/October 1992, and fitted to the standard, shifted-Gaussian shape. Of interest is the stability of the profile parameters within a province. In the notation of Platt *et al.* (1988), the appropriate properties to consider are z_m and σ, respectively the depth and thickness of the chlorophyll maximum, and ρ, the ratio of the Gaussian amplitude at z_m to the total pigment at z_m. Using the standard error divided by the mean for an estimate of relative error as before, the results for rho were 0.8% in the Eastern Subtropical Gyre province (244 profiles); 0.7% in the Western Subtropical Gyre province (187 profiles); and 0.7% in the Gulf Stream province (47 profiles). For z_m, the error averaged 1.7%, and could be reduced by roughly one third if the data were normalized to photic depth. For σ, the variation was 2.8% in the Gyre and 3.4% in the Gulf Stream: normalizing to photic depth did not reduce these figures in either case.

The observed stability in ρ supports our basic approach to specification of the pigment profile, where the shape is fixed by the profile parameters but the magnitude is scaled to the satellite signal. Further, we have seen that, at the basin scale, the maximum systematic error that could be associated with vertical structure in the pigment field (if it were ignored) is about 10%. In this context, the variability observed in z_m and σ must be considered insignificant at this scale.

11. OCEAN COLOUR DATA AS A GENERALIZED EXTRAPOLATION TOOL

In addressing the use of remotely sensed data on ocean colour as a vehicle for the extrapolation of sparse observations on primary production, we should not forget the broader use as a tool for the extrapolation of ecophysiological rates in general. The basis for this more universal application is the widespread use in modern theoretical work on biological oceanography of biomass-specific variables. For example, in summing the effects of the various loss processes to balance against phytoplankton growth in accounting for the incidence of algal blooms, it is expedient to normalize all the terms, including those representing the effect of zooplankton, to phytoplankton biomass (Platt *et al.* 1991*b*). This is certainly a mathematical convenience. If biomass-normalized rates are measured at a few stations, they can be extrapolated more easily if the synoptic field of biomass is given. Of course, the limitations imposed by the colour scanner's inability to collect an unweighted image of the vertical distribution of pigment biomass remain: the requirement to have independent data on the vertical profile of biomass still exists.

Another sense in which the ocean colour data serve as a general vehicle for the extrapolation and synthesis function is that they provide a yardstick of comparison for that other method capable of delivering synoptic fields: three-dimensional modelling. One long-term goal of both remote sensing and modelling must be to make comparisons in real time between the fields generated by the two methods. An important intermediate step, and one that will continue to be useful in the future, is to apply the ocean colour results as data to be assimilated, intermittently or continuously, into the three-dimensional models, as a device to prevent the models diverging indefinitely from reality.

A final example of the use of remotely sensed data in the extrapolation and synthesis function of marine biogeochemistry is that it can provide the oceanographic context for detailed ship studies carried out in a limited area. The importance of this application would be difficult to overestimate.

12. DISCUSSION

It is no exaggeration to state that the ocean-colour data provided by the Coastal Zone Colour Scanner has revolutionized biological oceanography. The ability to see a synoptic image of the pelagic ecosystem, even if only a two-dimensional one, is of the highest value. But for biogeochemical applications, the greatest reward will come when the biomass fields can be turned, in a routine and reliable way, into fields of primary production.

As an ancilliary to the estimation of basin-scale primary production in the ocean, the remote-sensing method has been developed furthest in the North Atlantic. The reason is that in this ocean, the archive of collateral data, especially data on the photosynthesis parameters, is larger than that for any other ocean. If the remote-sensing method is judged and found wanting in the North Atlantic, it must be found wanting in every other ocean, highly localized applications always excepted.

Even though the archive of complementary data is richest in the North Atlantic, one should not conclude that it is adequate for the job. The historical information on vertical profiles of pigments is the most complete: one would like to see a more even distribution over regions and seasons. But the archive of photosynthesis parameters should certainly be improved, whether we intend to assign parameters by Method I, II, or III. Development of empirical algorithms for prescription of photosynthesis parameters is as strongly dependent on the existence of a good database as is the direct assignment by region and season. The construction of prescriptive algorithms from first principles merits further study, but robust results are unlikely to appear overnight.

Whatever method is used for the assignment of parameters, it seems inevitable that it will be applied within the context of some scheme of algal domains and biogeochemical provinces. Considerable progress has been made to this end in the North Atlantic. However, the paucity of the data on photosynthesis parameters precludes exploitation of this work to the full: it was judged feasible to assign them only at the level of the algal domain, rather than at the finer level of the biogeochemical provinces.

We believe that the theory available for calculation of primary production given information on the irradiance, the pigment profile and the photosynthesis parameters, is adequate for the job. It is certainly not the major obstacle to progress. Where effort needs to be invested is in the translation of knowledge about the provinces into rules that can then be incorporated into an adaptive computational scheme. The algorithms to assign parameters should respond to the input fields in an 'intelligent' (in the sense that the word is used in cybernetics) way, rather than a passive one. To date, the protocols are only rudimentary in this respect.

Ocean-colour data have many weaknesses. But they remain our only window into the synoptic state of the pelagic ecosystem. Learning to extract from them the information they contain about the ocean carbon cycle, an exercise in applied plant physiology, must remain a high priority activity within biological oceanography. Increasing reliance on remotely sensed data will not displace the requirement for oceanographic vessels, but it will provide strong indicators of where, when and how they should be deployed to best advantage. Our ability to interpret remotely sensed data on ocean colour will improve as more relevant sampling is carried out from ships, and thus more generalizations uncovered that can be coded into rules for inclusion in the adaptive algorithms on which interpretation will be based.

Compared with the data that can be collected by ship, the data collected by remote sensing are of lower precision and lack information on vertical structure. However, they make up in sample size what they lack in precision. For example, a ship might be able to sample 50 points on the perimeter of a 100 km box in one day. At a local resolution of 1 km, the satellite will provide 10^4 simultaneous observations inside the box. (Generally speaking, sampling variance is inversely proportional to the number of observations.) Furthermore, remote sensing will show how conditions inside the box relate to those outside, even as far as the edges of the ocean. Also, the observations can be repeated on the next and subsequent days, for as long as required. Finally, sea-surface temperature, and other physical properties, can be collected by remote sensing on the same time and space scales, opening the possibility of a multidisciplinary, synoptic approach to marine ecosystem. Remote sensing gives us the possibility to examine the spatial gradients of primary production, their seasonal variation, and their fluctuations between years. It is the best option we have to establish the long-term history of the pelagic ecosystem in any region.

We thank those scientists whose painstaking measurements of chlorophyll profiles were made available to us. The sources of all the data used are listed in table 1 of Sathyendranath *et al.* (1995) and we sincerely thank those responsible. We also thank those scientists at NASA, especially Gene Feldman and Norman Kuring, who processed and made available the satellite data. The work presented in this paper was supported by the European Space Agency, with additional support from the Office of Naval Research; the National Aeronautics and Space Administration; the Department of Fisheries and Oceans, Canada; the Natural Sciences and Engineering Research Council; and the Department of National Defence, Canada. This research was carried out as part of the Canadian contribution to the Joint Global Ocean Flux Study. We thank Carla Caverhill, Cathy Porter and George White for their help with the data analysis.

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Discussion

T. R. S. Wilson (*Department of Earth Sciences, University of Liverpool, U.K.*). If I could tempt Dr Platt to further speculation. Suppose he were asked to estimate the ocean $p\mathrm{CO}_2$ field using remote sensing (and given the resources required). Would he accept the job?

T. Platt. The surface field of $p\mathrm{CO}_2$ is controlled mainly by temperature, which is accessible to remote sensing. Primary production imposes further control on the carbon system: it is accessible to remote sensing according to the methods we have described. If the application for the primary production estimates is merely to calculate $p\mathrm{CO}_2$, the first order requirement is to estimate only mixed-layer primary production, a simpler task than the total production for the water column. However, a more refined estimate of the impact of biological processes on the carbon system would take into account the respiratory losses due to community metabolism, which result in a partial restoration of the carbon dioxide consumed by photosynthesis. Although these loss terms are difficult to estimate, they have the advantage that they can all be normalised to pigment biomass, and to this extent access to synoptic fields of pigment biomass simplifies estimation of the loss terms at large geographical scale. In summary, remote sensing has much to offer as a tool for the prescription of the surface $p\mathrm{CO}_2$ field in the ocean.

J. Woods (*NERC, Swindon, U.K.*) My question is concerned with the contribution of production at the deep chlorophyll maximum. My Sea Rover observations between the Azores and Greenland indicate annual production at the deep chlorophyll maximum (during the seasonally oligotrophic regime) to equal the annual new production in the mixed layer. This conclusion has recently been extended to the permanently oligotrophic regime by multiyear integration of models based on the Lagrangian-Ensemble method (J. D. Woods & W. Barkmann, unpublished results). A feature of the model simulations is synoptic decoupling between production in the mixed layer and in the deep chlorophyll maximum, in both the seasonally and permanently oligotrophic regimes. Given the evidence of the Sea Rover observations and model simulations, it seems that ocean colour measurements contain little information about oligotrophic production. How does Dr Platt address this problem?

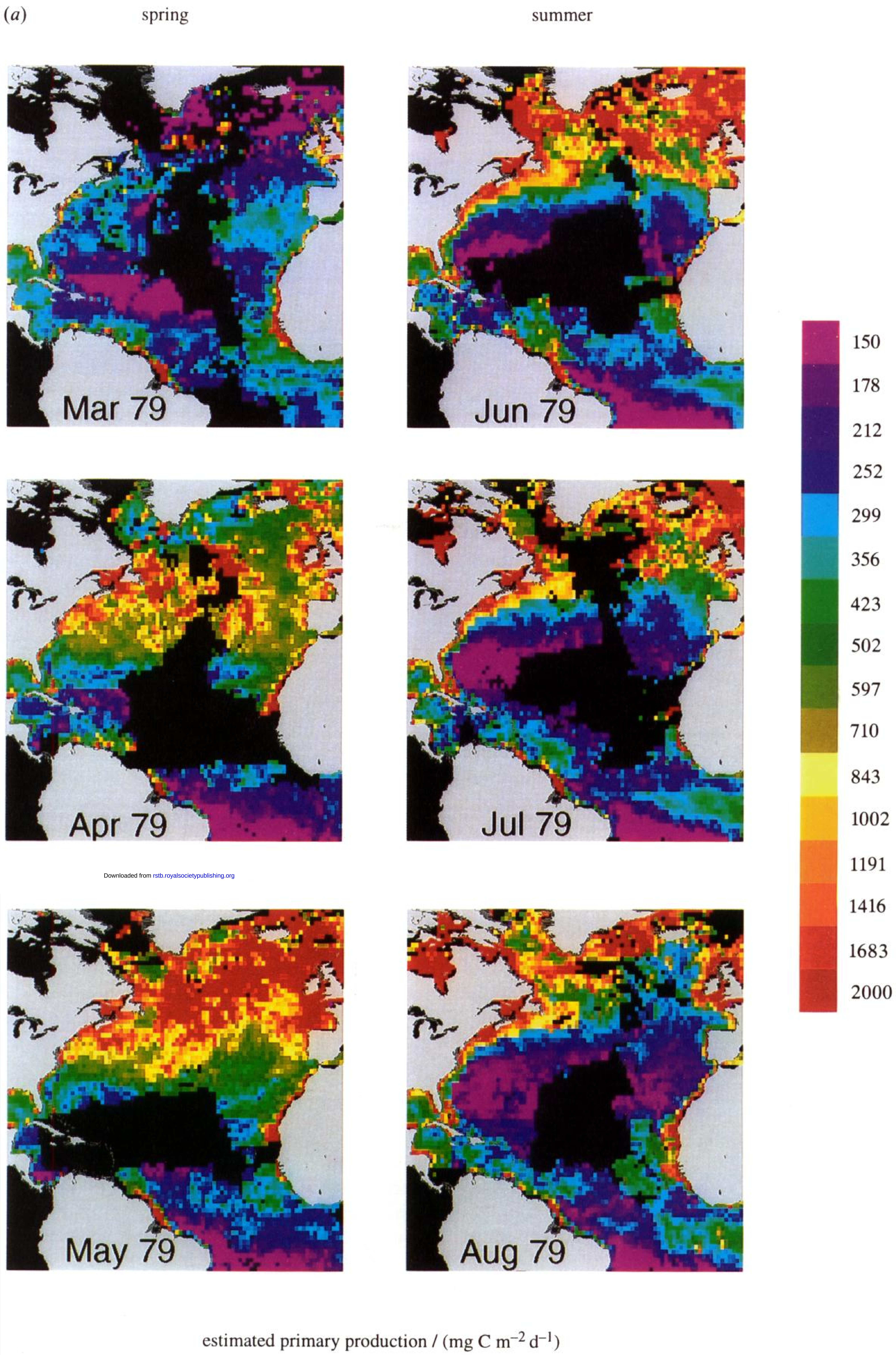
T. Platt. By themselves, ocean colour measurements contain no information on pigment concentrations in the deep chlorophyll maximum when this horizon lies, as it generally does, more than two optical depths below the surface. It is for this reason we recommend that the ocean colour data be supplemented by information, independently obtained, on the shape of the pigment profile at given space–time points. Such information could be prescribed either from archival oceanographic data, or from empirical, statistical relations between surface pigment and pigment profile, or from robust rules, derived from observation and/or theory, relating properties of the pigment profile, such as the depth of its maximum, to objective factors, such as latitude. Once the pigment profile is prescribed, calculation of the primary production below the mixed layer is simple.

The apparent decoupling between primary production in the mixed layer and that in the deep chlorophyll maximum may be explained as follows. The production in any layer is forced by the irradiance incident at the top of the layer. When the biomass in the mixed layer is high, the production there will tend to be high. However, the light transmitted by the layer will be reduced as the biomass in it is increased, such that the layer below will be forced with a diminished irradiance. Hence the production per unit biomass below the mixed layer will be depressed when the mixed layer biomass (and production) is high. One could then draw the conclusion that production levels in the two layers were decoupled from each other, whereas in fact they are necessarily related by virtue of their sharing the same energy source, albeit attenuated in the case of one of the layers.

T. Takahashi (*Lamont-Doherty Geological Earth, Columbia University, Palisades, U.S.A.*). Dr Roger Wilson asked Dr Platt an important question about an implication of primary productivity estimates on obtaining $p\mathrm{CO}_2$ and uptake of CO_2 by the global oceans. I would like to rephrase his question more quantitatively and ask Dr Platt if such a goal may be attainable in the near future. The mean air–sea $p\mathrm{CO}_2$ difference over the global ocean is about 10 μatm. This means that the $p\mathrm{CO}_2$ values in seawater must be known with a precision of better than 10 μatm. Since the mean Revelle factor, $(\mathrm{d}p\mathrm{CO}_2/p\mathrm{CO}_2)/(\mathrm{d}T\mathrm{CO}_2/T\mathrm{CO}_2)$, for the global surface ocean water is about 10, the total CO_2 concentration dissolved in sea water $T\mathrm{CO}_2$, should be known with a precision of about 0.3 % (= [10 μatm/350 μatm]/10). There are about 900 Gt C of CO_2 dissolved in the surface mixed layer of the global ocean, and this quantity is modulated seasonally by the net primary production of carbon. For us to be able to compensate $p\mathrm{CO}_2$ with a precision of better than 10 µatm, we should know the carbon inventory in surface ocean waters with a precision better than 2.7 Gt C (= 0.3% × 900 Gt C).

Dr Platt gave an estimate of 55 Gt C a^{-1} for the gross primary production of the global ocean with an error estimate of 35%. Let us assume that the net primary production is a similar order of magnitude as this estimate. In order to compute the effect of primary production on $p\mathrm{CO}_2$ values with a precision of better than 10 µatm, the primary productivity must be known with a precision better than about (2.7 Gt C/55 Gt C =) 5%. This suggests that a sevenfold improvement of Dr Platt's primary productivity is required. Would it be possible to attain this level of improvements in the remote-sensed measurements of primary production?

T. Platt. The error analysis in our paper deals mainly with the error associated with the estimate of primary production for a particular pixel. The dominating source of error is that associated with biomass retrieval. Fortunately, it is an error that can be expected to be reduced as ocean-colour sensors improve. Another source of reduction in random error derives from spatial and temporal averaging. The calculations described here are based on one-degree squares for each month. Given raw data at 1 km resolution and daily coverage (admittedly optimal circumstances), the biomass used for each one degree square for a calculation in a given month would be based on 3×10^5 estimates. Although it is clear that these estimates are not all independent, some statistical advantage must accrue from the multiplicity of estimates. However, it will be difficult to quantify. Although it would be speculative, at this stage, to say whether the error in global annual production could be brought down to ~ 3 Gt C, we can say at least that the errors in global annual production would be much less than those at the pixel level. It is also worth emphasizing that, despite its limitations, remote sensing still affords the best estimate of global production available to us. Note also that when interannual differences in global production are calculated, the systematic component of the associated error will disappear.



gure 2. Monthly averages of daily primary production estimated from ocean-colour data for 1979. (*a*) Spring and mmer; (*b*) autumn and winter. The grey areas represent land; the black areas indicate lack of ocean-colour data. virtue of the spatial resolution in the satellite data, the images show considerable detail, but in using them it should borne in mind that the parameters on which the computations are based are resolved only to the level of the algal omains (for the photosynthesis parameters) or the level of the biogeochemical provinces (in the case of the arameters describing the shape of the pigment profile). The resolution of the parameters will not improve until escriptive functions become available for estimating their magnitudes at each pixel.

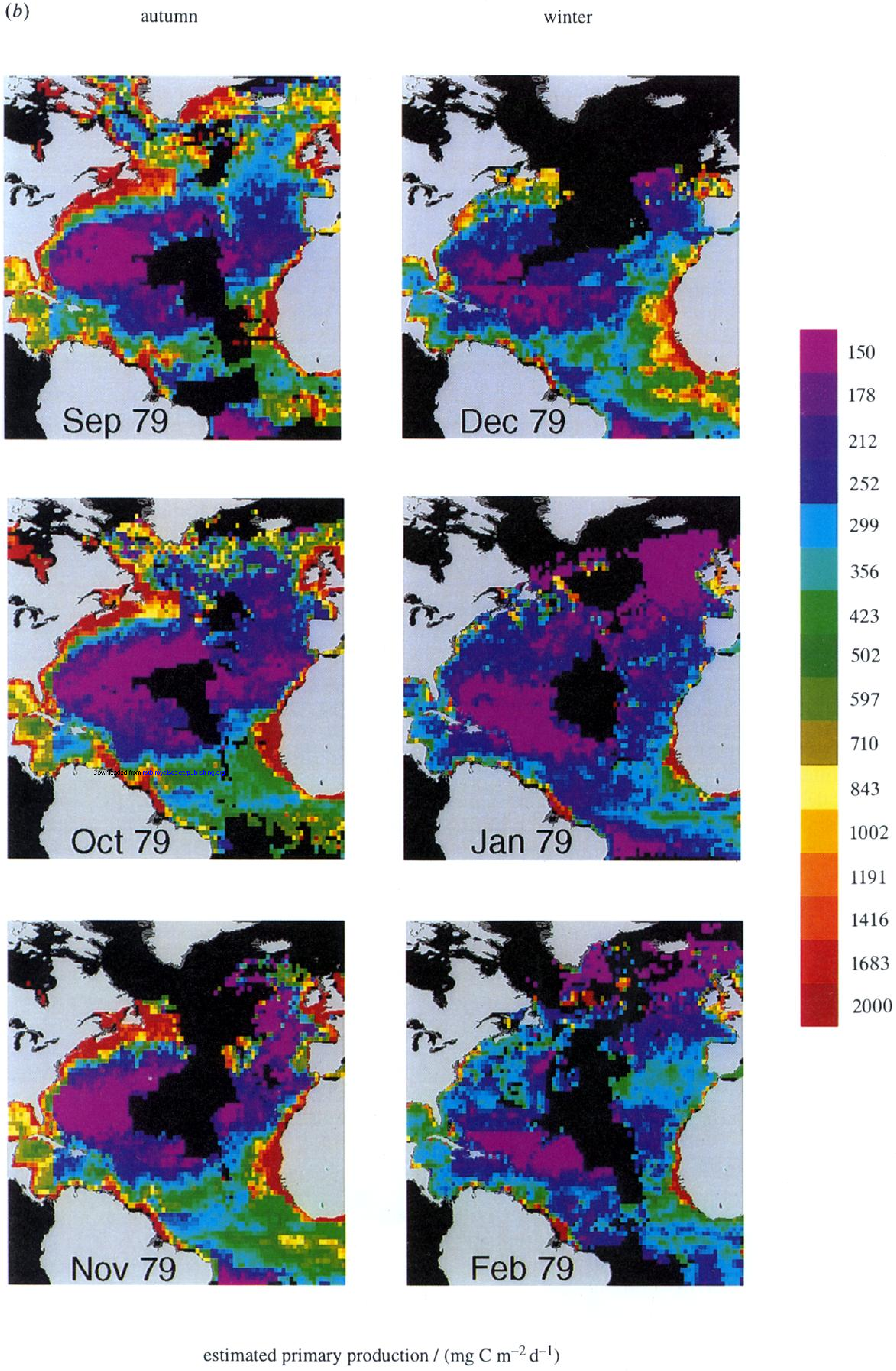


Figure 2. (*cont.*)