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Scaling of coastal phytoplankton features by optical remote sensors: comparison with a regional ecosystem model

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Abstract:

Different scales of hydrological and biological patterns of the Bay of Biscay are assessed using space-borne and airborne optical remote sensing data, field measurements and a 3-dimensional biophysical model. If field measurements provide accurate values on the vertical dimension, ocean colour data offer frequent observations of surface biological patterns at various scales of major importance for the validation of ecosystem modelling. Although the hydrobiological model of the continental margin reproduces the main seasonal variability of surface biomass, the optical remote sensing data have helped to identify low grid resolution, input inaccuracies and neglect of swell-induced erosion mechanism as model limitations in shallow waters. Airborne remote sensing is used to show that satellite data and field measurements are unsuitable for comparison in the extreme case of phytoplankton blooms in patches of a few hundred metres. Vertically, the satellite observation is consistent with near surface in situ measurements as the sub-surface chlorophyll maximum usually encountered in summer is not detected by optical remote sensing. A mean error (60C) of 50.5% of the chlorophyll-a estimate in turbid waters using the SeaWiFS-OC5 algorithm allows the quantitative use of ocean colour data by the coastal oceanographic community.

Keywords: Phytoplankton / Satellite observation / Remote sensing / Scaling / Models / Bay of Biscay

Please find below the comments concerning the proofs correction of the manuscript

“Scaling of coastal phytoplankton features by optical remote sensors: comparison with a regional ecosystem model”

by J.-N. DRUON, S. LOYER and F. GOHIN

for publication in *International Journal of Remote Sensing*, reference TRES-PAP-2005-0190 (proofs reference 122767).

The queries are included and similarly quoted in the comments.

- Page 1, Authors section, line 3: replace “Inland and Marine Environment Unit” by “Inland and Marine **Waters** Unit”.
- Page 1, Authors section, line 4: replace “Atantide, Technopole” by “Atlantide, Technopôle”.
- Page 3, last line: replace “at short visible wavelengths added” by “at short visible wavelengths, added”.
- Page 4, first line: replace “and pigments leading to” by “ and pigments, **lead** to”.
- Page 4, line 4: replace “in OC4” by “**generated by** OC4”.
- Page 4, line 4 to 6: replace the sentence “The use of the 412 band is intended to detect an over extraction of signal in a coastal environment in the case of high concentration of suspended matter in the water and/or continental aerosols in the atmosphere” by “**The band at 412 nm is used to detect the over extraction of signal in a coastal environment characterized by a high content of suspended matter in water and/or continental aerosols in the atmosphere**”.
- Page 4, §2, line 10: replace “the time variability is lower” by “the time variability is lower, **i.e. open waters**”
- Page 4, §4, line 4: replace “The model helps to understand how the system responds to an increasing anthropogenic loading” by “The model helps to understand how the **Atlantic shelf ecosystems respond** to an increasing **discharge of nutrients from rivers**”.
- Page 4, §4, line 9: replace “the validation of the model” by “**the model validation**”.
- Page 6, §1, lines 9-10, query 1: replace “The latter is forced by the tide” by “**This larger scale model** is forced by the tide”.
- Page 6, §1, line 15: replace “the sun hour angle and the altitude and the fractional cloud cover” by “the sun hour angle **and altitude**, and the fractional cloud cover”.
- Page 6, §1, line 17: replace “The wind measurements of the Oléron Island (north of the Gironde estuary, see Figure 3 for location) are considered” by “The wind **measured at** the Oléron Island (north of the Gironde estuary, see Figure 3 for location) **is** considered”.
- Page 6, §2, line 7: replace “phosphorous” by “**phosphorus**”.
- Page 7, query 2: No, I do not have the agreement of Koutsikopoulos and Le Cann to modify their figure. In fact, the presented figure is similar to the original one; I just reproduced it to illustrate the general circulation patterns of the Bay of Biscay. “modified” should therefore be deleted in the figure legend.
- Page 8, last line, query 3: add this reference to the list “**Mazé, R., 1980, Formation d'ondes internes stationnaires sur un talus continental: application au Golfe de Gascogne. Annales Hydrographiques, 754, pp. 45-58.**”
- Page 9, lines 2-3, queries 4-5-6-7 : add the following references to the list.

Pingree, R.D., Griffiths, D.K., Mardell, G.T., 1984, The structure of the internal tide at the Celtic Sea shelf break. *Journal of the Marine Biological Association of the United Kingdom*, 64, pp. 99-113.

Mazé, R., Camus, Y., Le Tareau, J.Y., 1986, Formation de gradients thermiques à la surface de l'océan, au-dessus d'un talus, par interaction entre les ondes internes et le mélange dû au vent. *Journal du Conseil International pour l'Exploration de la Mer*, 42, pp. 221-240.

Mazé, R., 1987, Generation and propagation of non-linear internal waves induced by the tide over a continental slope. *Continental Shelf Research*, 7, pp. 1079-1104.

New, A.L., Pingree, R.D., 1990, Evidence for internal tidal mixing near the shelf break in the Bay of Biscay. *Deep-Sea Research*, 37, pp.1783-1803.

- Page 11, §2, line 7, query 8: The personal communication of P. Camus was in 2000.
- Page 17, §1, line 2, query 9: The personal communication of P. Le Hir was in 2000.
- Page 18, §1, line 4, query 10: Yes, replace “1l sample” by “1 litre sample”.
- Page 19, §1, line 13, query 11: add this reference to the list “Smith, R. C., 1981, Remote sensing and depth distribution of ocean chlorophyll. *Marine Ecology Progress Series*, 5, pp. 359-361.
- Page 20, §4, last line - §5, first line: Run on, no new paragraph “**in figure 9(b)). In this example**”.
- Page 21, §1, lines 6-7: replace “the swell-induced erosion process of bottom particulate matter” by “the swell-induced **re-suspension mechanism in the model regarding small size inorganic particles at sea bottom**”.
- Page 21, §1, line 7: replace “The model underestimates the turbidity and therefore over-estimates the light availability” by “The model **therefore** underestimates the turbidity and over-estimates the light availability”.
- Page 23, fifth reference, query 12: replace “Bull Fac Fish” by “Bulletin of the Faculty of Fisheries”.
- Page 24, third reference, query 13: replace “Int Rev Gesamt Hydrobiol” by “Internationale Revue der Gesamten Hydrobiologie”
- Page 24, fifth reference, query 14: replace “Ber Biol Anst Helgoland” by “Berichte der Biologischen Anstalt Helgoland”.
- Page 24, sixth reference, query 15: The publisher and location are “Ed. IFREMER, GREPMA-CNRS, Brest”.

Introduction

The major obstacle encountered in surveying the marine environment is the distance (and associated time) to sail to get sufficient number of samples. The two-dimensional instantaneous observation of the sea surface by remote sensing provides a complementary alternative to the *in situ* observations. Even if field measurements are more accurate than remote sensed estimations, the latter provide a synoptic description of physical and/or biological features of the sea surface. For the detection of physical features, the remote sensing of ocean colour is often complementary to thermal data, which may not detect salinity fronts linked to river plumes. These fronts are one of the main hydrological features of the French shelf of the Bay of Biscay (Lazure and Jégou 1998). Density gradients due to salinity are generally stronger than those due to temperature in coastal waters, as a usual salinity gradient of 2.5 PSU (between 35.5 and 33 PSU) leads to a density gradient equivalent to a temperature difference of 10°C. The larger penetration depth of ocean colour compared to thermal data (10 m typically on the continental shelf against 1 µm respectively) leads to detect more stable structures using optical sensors. The other physical features encountered in the Bay of Biscay such as upwelling, tidal and shelf break fronts and the intrusion of the warm Navidad current along the northern Spanish coasts display well marked signatures in the visible wavelengths. These mesoscale hydrological structures reveal the tight links between phytoplankton and its physical environment. While the occurrence and succession of the main hydrological features of the Bay of Biscay have been characterised (Koutsikopoulos and Le Cann 1996), their variability at different space and time scales, the linked biological productivity and food-webs are largely unknown. This knowledge is of major importance for the estimation of fishing quotas respecting a balance between economic activities and a sustainable marine environment. While the stock of the main exploited species can be roughly estimated (Biseau 1998), the role of the variability of the physical and biological environment on the recruitment of these living resources is largely unknown. After describing tools and data, this paper emphasizes the large range of scales of biophysical features encountered in the Bay of Biscay. The aim is to define the relevant sampling strategy in the different water types of this continental margin. For this purpose, the results from airborne and satellite remote sensing of ocean colour and a 3-D bio-physical model were compared with *in situ* measurements. A particular attention is given to the contribution of the visible remote sensing to the improvement of bio-physical modelling in coastal waters.

Tools and data

In situ measurements

Both methods used for the quantitative analysis of pigments, HPLC and spectrophotometry, are fully described in Gohin et al. (2002). HPLC analysis was used for the pigment analysis of the BioModycot-99 cruises. For the other cruises, chlorophyll-a seawater contents were measured using spectrophotometric analysis. The comparisons between HPLC and the acid spectrophotometric method of Lorenzen (1967) were satisfactory using pure pigment and the microalgal extract free of any degradation product ($r^2 = 0.85$). The phaeopigments were satisfactorily determined in pure pigment mixtures and field samples rich in phaeopigments using the Lorenzen (1967) method ($r^2 = 0.88$). However, in phaeopigment-free samples,

interference from chlorophyll-b produces high spectrophotometric concentrations (Mantoura et al. 1997).

A data set of *in situ* chlorophyll-a content was collected for the calibration of the Seaviewing Wide Field-of-view Sensor (SeaWiFS) algorithm specific of turbid waters (see below). The data base contains 156 near surface measurements of chlorophyll-a and total suspended matter in the Bay of Biscay and the English Channel during the whole seasonal cycle with the aim of covering a large range of coastal signatures (from January to September, with 48 % of samples in spring). Data in the English Channel are needed for the calibration of the algorithm as they are representative of high concentrations in chlorophyll-a and lithogenic suspended sediment. The calibration data include winter cruises when the optical signal mainly corresponds to lithogenic particulate matter (Biomet, Plagia 1, SRN and CadHiver). High concentrations of chlorophyll-a ($> 5 \text{ mg m}^{-3}$) were observed in May and June in coastal waters of the Atlantic shelf, and in spring and summer in waters of the English Channel under the influence of river plumes or near shore. Summer is the regular period of low freshwater input and small extension of plumes. High concentrations of lithogenic particulate matter occur in late autumn, in winter and sometimes in spring as in May 1998 (Loire and Gironde floods, see the Results section).

The airborne and space-borne ocean colour data

The airborne remote sensing data presented in this paper were obtained using a CASI (Compact Airborne Spectrographic Imager) instrument over coastal waters of south Brittany on June 10th 1999. The ground speed of the aircraft of 110 knots, the altitude of 4400 feet, and the integration time of the instrument of 35 ms generated a ground resolution of 2*2 m. The number of pixels per line in the spatial mode is 512 leading to a width of 1.024 km. The integration time of 35 ms allowed measurement over 16 spectral bands of approximately 20 nm wide. The maximum aperture of the instrument was used as the signal intensity over the ocean is low. The CASI data were roll-corrected. The RGB composites were obtained using the band centred on 705 nm or 620 nm (red, band 12 or 9), 555 nm (green, band 7) and 489 nm (blue, band 4). These three bands are used to emphasize the phytoplankton patterns observed this particular day, especially the red signal associated with *Noctiluca scintillans* bloom (705 nm). The RGB composites were obtained using an equalised contrast stretching to emphasize the patterns. Although this transect was oriented north-east south-west at 13h45 UT, the height of the sun at mid-June caused some specular reflection.

Level 1A SeaWiFS data were processed to level 2A data using SeaDAS version 3.3. This product was geo-corrected and the atmospheric correction was applied. The atmospheric correction leads to negative values of water-leaving radiance in low visible wavelengths in case of high turbidity or areas of heavy continental aerosol content. The empirical algorithm used to estimate the chlorophyll-a concentration in coastal waters from the level 2A product is a five channel algorithm, named hereafter OC5, which mitigates the effects of the lithogenic suspended matter, the coloured dissolved organic matter and aerosols. The five channel-three dimensional OC5 algorithm ($R_{\text{rsw}}(443>490>510)/R_{\text{rsw}}555 - L_{\text{nw}}412 - L_{\text{nw}}555$, where R_{rsw} is the remote sensing reflectance) used to estimate the surface chlorophyll-a content in turbid waters from SeaWiFS data is fully described in Gohin et al. (2002). The OC5 algorithm can be defined as a modified SeaWiFS Ocean Colour 4 band algorithm (OC4) making use of the channel at 412 nm in complement to the maximum ratio

amongst $R_{\text{rsw}443}/R_{\text{rsw}555}$, $R_{\text{rsw}490}/R_{\text{rsw}555}$ or $R_{\text{rsw}510}/R_{\text{rsw}555}$ proposed in the standard algorithm. The 412 band is used in the algorithm as an indicator of atmospheric over-correction. Negative values of water-leaving normalised radiance, frequently encountered in coastal waters, are the result of an over-estimation of the aerosol contribution that is extracted from the total signal. Different models were developed to extract the contribution of aerosols at low visible wavelengths from the signal measured at near infra-red wavelengths. This aerosol correction is based on the hypothesis of a zero oceanic contribution at near infra-red wavelengths due to the natural absorption of pure water. The over-estimation of the aerosol content can be attributed to whitish particles leading to a non-zero water-leaving radiance at near infra-red wavelengths and to the particular characteristics of the coastal atmosphere which are not included in the SeaWiFS reference set. This 'over extraction' of signal at short visible wavelengths added to the natural low values of radiance due to the absorption of yellow substance and pigments leads to frequent negative values in coastal waters. The consequence of an erroneously low radiance at short wavelength is a diminution of the reflectance ratios and an over-estimation of the chlorophyll concentration in OC4. The use of the 412 band is intended to detect an over extraction of signal in a coastal environment in the case of high concentration of suspended matter in the water and/or continental aerosols in the atmosphere.

A parameterisation of the observed relationship between the OC4 band ratio and the 412 and 555 water-leaving radiances, for chlorophyll isoconcentration classes, is proposed in the OC5 algorithm (Gohin et al., 2002). A look-up table relating SeaWiFS triplets (OC4 maximum band ratio, 412 and 555 bands) processed by SeaDAS to chlorophyll-a concentration has been calculated. Figure 1 presents the log-log comparison of OC5 chlorophyll-a estimate and field measurements for the various cruises. The stations represented on figure 1 are those used for the algorithm calibration and correspond to near surface measurements. The time shift between satellite and field measurements does not exceed 12 h for coastal (or in plumes) stations and 36 h for stations where the time variability is lower. When the coastal signal is largely dominated by the lithogenic suspended matter, *e.g.* during winter, the use of the channel at 555 nm in the empirical algorithm avoids a systematic over-estimation of the pigment content (Gohin et al., 2002). The chlorophyll-a content is slightly underestimated between 1 and 10 mg m⁻³ for all cruises except Plagia 3 and 4 where the reverse tendency is observed (figure 1d). No clear explanation can support this difference as the cruises Plagia 4 and BioModycot99.2 (figure 1c) partly cover each other in space and time. [Insert figures 1 and 2 about here]

A quality index of the pigment estimation defined as $100 \cdot (\text{chl}_{\text{sat}} - \text{chl}_{\text{in situ}}) / \text{chl}_{\text{in situ}}$ ($= \delta C/C$) was calculated for all the stations used for the calibration (figure 2). The algorithm yields an estimate of chlorophyll-a concentration with a mean $\delta C/C$ of 50.5 % over the range of 0.1-44 mg m⁻³ for chlorophyll-a and of 0.1-24 mg l⁻¹ for lithogenic suspended matter. For comparison, a mean error of 35 % over the range 0.05-50.0 mg Chl-a m⁻³ is the theoretic SeaWiFS objective. Using empirical algorithms based upon statistical regressions, chlorophyll-a estimates are within a mean error less than 50 % in oligotrophic coastal waters (Tassan 1994), and Habbane et al. (1998) obtained 23 % over the range 7-16 mg m⁻³ using an empirical algorithm based upon the spectral curve theory. The accuracy of the SeaWiFS-OC5 chlorophyll-a estimation is discussed below in relation with the high spatio-temporal variations in coastal waters and the limitation of the field sampling.

The model

The objective of the coupled bio-physical model is to determine how the forcing of meteorology, hydrodynamics and human activities influence the distribution and the abundance of phytoplankton in the continental margin. The model helps to understand how the system responds to an increasing anthropogenic loading. The environment management requires the knowledge of pathways through which the coastal zone accumulates and recycles the increasing fluxes of nutrients produced by the development of agriculture, industry and urbanisation. This model is the first physical-biological model of the whole French Atlantic shelf. A substantial part of the work is devoted to the validation of the model through *in situ* measurements and satellite data.

The three-dimensional physical model has been developed at IFREMER during the last decade (Lazure and Jegou 1998). The studied area extends from the coast to approximately the 200 m isobath in the west and from the English Channel entrance in the north (49°N) to the Gulf of Cap Breton in the south (43°50'N, see Figure 3 for location). The three main rivers are taken into account: the Loire, the Vilaine and the Gironde (figure 3). The model uses a rectangular Cartesian grid with a homogeneous mesh size (25 km²). Ten vertical layers are used with sigma co-ordinates with a grid step progressively increasing with depth. The numerical scheme uses a 3D finite difference scheme. The resolution of the turbulent kinetic energy equation and the use of an algebraic formula for the mixing length are used to calculate vertical eddy viscosity and diffusivity. The temperature and salinity distributions on the French Atlantic shelf are simulated taking into account the tidally and wind-induced advection and diffusion. A larger 2D model (vertically integrated) produces the boundary conditions. The latter is forced by tide at its open offshore boundaries and by wind fields at the surface. At the upper boundary, heat transfer at the ocean surface interface is calculated using climatological values for air temperature, cloudiness and specific humidity. The solar flux estimated primarily from a solar constant ($\text{J (m}^2 \text{ s)}^{-1}$) is corrected with respect to the orbital deviation (variation of the earth-sun distance), the sun declination, the sun hour angle and the altitude and the fractional cloud cover. The fractional cloud cover is a mean annual value modulated by a sinusoidal function to reproduce the seasonal cycle. The wind measurements of the Oléron Island (north of the Gironde estuary, see Figure 3 for location) are considered representative of the mean wind stress for the entire French Atlantic shelf. The Loire, Vilaine and Gironde discharges are measured with a frequency of 15 days to a month and linearly interpolated. [Insert figure 3 about here]

The physical model is linked to the biological model through the diffusion coefficient, the transport, the temperature and heat fluxes. The solar energy as well as the nutrient loading by rivers are used as inputs in the biological model. The biological scheme is a simplified representation of the pelagic ecosystem that includes three phytoplankton groups (diatoms, dinoflagellates and nanophytoplankton), two zooplankton groups (meso- and microzooplankton), a detritus compartment and one mineral compartment for phosphorous and silicon and two for nitrogen (nitrate and ammonium). This shallow water model includes the replenishment of the mixed layer with nutrients from the sediment. Three limiting elements of the phytoplankton growth are

modelled: nitrogen, phosphorus and silicon. The diatoms contribute to the silicon cycle and the dinoflagellates and the nanophytoplankton represent the other two groups of non-siliceous phytoplankton. The diatoms are the only sinking species. The small class of phytoplankton allows primarily taking into account the oligotrophic system of the oceanic waters and secondly to better simulating the ammonium consumption and regeneration after a microphytoplanktonic bloom. The inorganic matter is regenerated through the zooplankton excretion and the remineralization of dead cells and faeces. Only a small part of this detritus remains suspended in the water column and is rapidly regenerated as the major part reaches the bottom. The benthic compartment simulates the storage, regeneration and tidal-induced erosion processes. The detrital pool on the bottom was introduced to store the major fraction of detritus and to replenish the water column. All simulated phytoplankton biomass presented in the paper are the sum of the three phytoplankton compartments (diatoms, dinoflagellates and nanoflagellates).

The hydrological context of the Bay of Biscay

A general review of the hydrological characteristics of the Bay of Biscay was presented by Koutsikopoulos and Le Cann (1996). The hydrology of this large bay is particularly complex due to interactions between the general circulation, the topography (variable width of the continental margin), the tidal currents, the wind induced currents and the river inputs of freshwater mainly located on the French coast (the Vilaine, the Loire, the Gironde and the Adour rivers). Figure 3 presents the main circulation and currents in the Bay of Biscay. The general oceanic circulation on the west side of the bay is anticyclonic and can appear weak compared to the meso-scale dynamics such as sweddies (Slope Water Oceanic eDDIES, Pingree and Le Cann 1992). These eddies result from the interaction between current instabilities of the continental margin and bottom topography. Slope currents of the Bay of Biscay show a large seasonal variability (Pingree and Le Cann 1990), but a consistent pole-ward flow is apparent. Shelf currents are mainly controlled by the wind, tides and water density. The residual current over the shelf is a complex composite between the highly variable wind-induced current, the neap-spring tide current and density currents resulting from river outflows. Excepting the barotropic tidal current which is periodical (mainly the semi-diurnal component M2), the wind stress and river outflows are responsible for the high seasonal and inter-annual variability of the shelf waters which was classified as a high energy medium by Barthe and Castaing (1989). The tidal currents are maximal in the northern part of the Bay of Biscay where the width of the continental margin is the largest (Koutsikopoulos and Le Cann 1996). The wind action is dominant when the tide is weak, *i.e.* in the southern part or during neap tide, and is relatively weak in the Celtic Sea where tidal currents are strong (Pingree and Le Cann 1989). An eastern wind along the Spanish coast or a northern wind along the French coast generates an upwelling. Jegou and Lazure (1995) describe the upwelling along the Landes coast (see Figure 3 for location) with a south-westerly surface current and an easterly bottom current under a northerly wind stress. The strong vertical salinity gradient of river plumes (mainly the Loire and the Gironde) generates a northern current due to earth rotation. This surface freshwater current is very sensitive to the wind. Typically on shallow areas, the westerly winter winds lead to an accumulation of freshwater that slides over the oceanic waters of the

shelf in spring when the wind relaxes. Northerly winds can change the circulation patterns of river plumes towards the south-west (Jegou and Lazure 1995). As shown in the next section, the large range of variability of surface bio-physical features described above is observed by ocean colour sensors (from 1 m to several hundred kilometres).

Results

The bio-physical scaling of the sea surface by optical sensors

Figure 4 shows the SeaWiFS-OC5 result for May 26th 1999 illustrating a post bloom situation. The surface biomass is intermediate between the spring bloom and the summer situation characterised by nutrient depletion and low chlorophyll content. Low values of chlorophyll-a concentrations are located on the northern part of the outer shelf and over the abyssal plain. Oceanic waters off the slope are marked by meso-scale eddies. The shelf break front shows a well marked biological signature in the visible wavelengths resulting from the oscillation of internal waves (Druon, 1998). It was first proposed by Mazé (1980) that the interaction between bottom topography and the propagation of the barotropic tidal wave would generate an internal (baroclinic) tide over the shelf break. Further studies (Pingree et al. 1984, Mazé et al. 1986, Mazé 1987, New and Pingree 1990) confirmed this hypothesis. Druon (1998) showed that the upward flux of nutrients from below the euphotic zone linked to the local enhanced mixing together with the increased availability of light related to the internal wave oscillation are responsible for an increase of 25% in the annual primary production over the top of the shelf break. The Ushant front (north-west of Brittany, figure 4) is a thermal feature that is governed by the neap-spring tide cycle. This phenomenon was observed and described by visible remote sensing (LandSat) in Le Fèvre et al. (1983), and the importance of the temporal characteristics of physical phenomena on biological dynamics were shown by numerous authors (Videau 1985, Le Fèvre 1986, Le Fèvre and Frontier 1988, Videau 1987, Sournia 1988). The other large biological features observed on the shelf are the Loire and Gironde plumes. The phytoplankton biomass concentrates on the edge of the main turbid plume as nutrients and light are simultaneously available in the surface layer (Morin et al. 1991, Aminot et al. 1997, Cloern 1999, Lohrenz et al. 1999, Mallin et al. 1999). The low chlorophyll-a estimation in the highly turbid Gironde estuary illustrates the efficiency of the OC5 algorithm to identify low chlorophyll - high turbidity waters (see also a winter situation in Gohin et al., 2002). The horizontal surface gradient of chlorophyll-a from the estuary mouth to offshore water shows a maximum (figure 4) between a highly turbid area and a surface water nutrient-depleted where the phytoplankton growth is limited.

Figure 5 represents an airborne transect over the Bay of Vilaine on June 10th 1999 which confirms this aspect at a smaller scale. The bloom was identified as dominant *Noctiluca scintillans* by field sampling. The strong red signature (705 nm, band 12) reveals the development in patches at the edge of the turbid plume (number 5 on figure 5) with a horizontal variability on the order of 100 m. Four distinct turbid boundaries correspond to a decrease of the concentration in lithogenic suspended matter from the estuary mouth to offshore water (from number 1 to 4 on figure 5). An increase of the suspended sediment content leads to an increase of the reflectance

spectrum in the visible wavelengths as shown in figure 5. This qualitative airborne measurement agrees with the field measurement of Froidefond et al. (2002) who provided a quantitative approach relating field spectra with *in situ* measurements of suspended sediment and SeaWiFS radiance.

Figure 6 shows the results of a typical summer cruise with the corresponding satellite observation and model simulation. The Ecoloire campaign took place from July 28th to July 30th 1999 between the south of the Loire estuary and the Quiberon Bay (south of Brittany, Figure 3). The field measurements show low chlorophyll levels ($< 3 \text{ mg m}^{-3}$, see figure 6a) with particularly low concentrations in the Bay of Vilaine as a characteristic of a post-bloom situation (field observation, P. Camus, pers. comm.). The SeaWiFS scene of July 25th (figure 6c) shows conformingly the presence of high levels of surface chlorophyll-a (from 3 to 8 mg m^{-3}) three days earlier in the Loire and Vilaine plumes. The minimum vertical sampling strategy was set to measurements at surface, bottom and sub-surface maximum of chlorophyll.

Figure 7 shows the vertical profile of fluorescence, the chlorophyll-a measurements and $\ln(\text{PAR})$ (Photosynthetic Available Radiation) for three stations from the estuary mouth (station 1) towards offshore (station 26). The fluorescence profiles represent a typical summer coastal situation with low surface values and a maximum from 3 to 10 m thick located at the maximum of the density gradient. At the end of July the pycnocline is dominated by the temperature gradient and is generally located between 15 to 25 m except in shallow stations ($< 15 \text{ m}$) near the estuaries where temperature decreases regularly with depth. These shallow stations show a maximum of chlorophyll concentration near the sea bed. Total suspended matter concentrations range from 0.3 to 7 mg l^{-1} , with high concentrations near the bottom and low values near the surface (from 0.3 to 1.3 mg l^{-1}). The satellite-derived chlorophyll-a map of July 30th (figure 6d) provides detailed biological features during the Ecoloire campaign. The Loire and Vilaine plumes have a slight signature in phytoplankton biomass at the surface, which is representative of the low river flow in summer. The highest horizontal pigment gradients are located on a transect starting at the estuary mouth towards offshore. An ‘island effect’ can also be observed around Belle Île-Houat-Hoëdic islands (north-west, see Figure 6c for location) and in the vicinity of the Noirmoutier peninsula (south-east). At these locations, local currents and associated mixing enhance the surface nutrient-depleted layer which stimulates phytoplankton growth. The model result (figure 6b) shows a noticeable over-estimation in the Loire plume compared to both the field measurements and the SeaWiFS-OC5 estimation, but the general gradient out of the Loire plume and the ‘island effect’ are well reproduced. A few days delay appears in the Loire plume when comparing the model result with the SeaWiFS scenes of July 25th and July 30th (figure 6c and 6d). This data sequence shows the transition in the river plumes from a bloom situation to low surface chlorophyll-a levels usually encountered in summer. The attenuation coefficient for downwelling irradiance (k) over the 26 stations has been calculated from PAR profiles using the relationship $I_z = I_{z=0} e^{-kz}$. The mean value is $k = 0.18 \text{ m}^{-1}$. The penetration depth of light above which 90 % of the diffusely reflected irradiance (excluding specular reflectance) originates, Z_{90} , is defined for an homogeneous ocean as $Z_{90} \approx k^{-1}$ (Gordon and McCluney 1975). This penetration depth thus corresponds to the depth at which light drops to $e^{-1} = 37 \%$ of its surface value. The satellite optical depth was estimated for each station (figure 6e). The value of Z_{90} ,

as reported in figure 7, is always smaller than the mixed layer depth. Consequently only small variations of fluorescence are observed in the top layer, except for the quenching effect which seems to influence the measurement in the first metre. Below the first metre, the quenching appears to be a second order error as shown by the good correlation between fluorescence profiles and chlorophyll-a measurements. The sub-surface chlorophyll-a maximum at station 16 corresponds to the attenuation of PAR, even in its logarithmic form. The mean value of Z_{90} for all stations is 5.46 m with a low standard deviation (1.57 m). These values are consistent with the results of Jerlov (1968) for various water types (types 3 and 1 [coastal] and III [oceanic]).

In this example off of south Brittany (Ecoloire cruise, figure 6), the comparison of *in situ* and satellite data is satisfactory as the summer surface biomass is low and relatively homogeneous compared to the field sampling (few kilometres) and the satellite resolution. The general horizontal gradients were therefore correctly represented by both field and satellite measurements. On the contrary during late spring in the Loire plume, high biomass levels ($> 20 \text{ mg m}^{-3}$, figure 8b) and phytoplankton features in patches of ca 100 m are observed (airborne data, figure 8a).

The two dominant species identified by field sampling are *Gymnodinium chlorophorum* (figure 8a, 'Gc') and *Noctiluca scintillans* (figure 8a, 'Ns'). The satellite algorithm over-estimates moderately the chlorophyll concentration under 0.8 mg m^{-3} and slightly underestimates it above this value (figure 2). The airborne (June 10th, 13h45 UT) and satellite (June 11th, 12h45 UT) data of the Loire plume (figure 8a and 8b) can be compared because during this time shift the wind is low (5.5 m.s^{-1} , N-NE) as well as the tide level in both cases (low tide at 13h00 UT on June 10th and at 13h45 UT on June 11th). The satellite-derived chlorophyll concentrations in the vicinity of the aircraft transect R1b show high values and high horizontal gradients (see the position of red pixels [$\sim 15 \text{ mg m}^{-3}$] next to green pixels [$\sim 3 \text{ mg m}^{-3}$], figure 8b). The complex environment of surface coastal waters where suspended sediment, yellow substance and pigments have their own optical signature is moreover marked by a high spatial variability (up to 100 m) and, depending on local conditions, by a high temporal variability (few hours with tides or floods or wind).

The seasonal variability of the Atlantic margin: comparison of model results with satellite data

[Insert figure 9 about here]

Optical remote sensing sensors measure the main surface physical and phytoplanktonic characteristics relevant for the calibration and validation of biophysical models. The seasonal chlorophyll variability is presented using three comparisons of satellite-derived and simulated products in 1998 (figure 9): a late winter case (March 23rd), a spring case (May 17th) and a summer case (August 14th). Conversely to other biomass maps, a linear colour scale between 0.01 and 10 mg m^{-3} was chosen to improve the comparison. The log-scale increases the importance of the low chlorophyll-a values where the model variations are not meaningful. A relatively good agreement in terms of horizontal extension of biomass on the shelf between SeaWiFS data and model results is observed for the three situations at the scale of the shelf. Locally however, a temporal or spatial shift of biological features appears. The better matching of chlorophyll structures and levels between the SeaWiFS data of March 23rd with the model results of March 18th compared to March 24th shows the

modelled phytoplankton growth starts one week too early. Both maps show maxima of surface biomass in south Brittany and north of the Gironde estuary in the vicinity of Oléron Island. In these locations pigment concentrations are between 2 and 4 mg m⁻³. In other areas of the northern part of the shelf a concentration on the order of 1 mg m⁻³ is commonly encountered and 0.5 mg m⁻³ in the southern part.

Both observed and simulated (figure 9b) spring situation of May 17th show a large contrast between the biomass of the Loire and Gironde plumes although a flood peak at up to 3000 m³ s⁻¹ occurred ten days earlier for both rivers (figure 10a and 10b). [Insert figure 10 and 11 about here] A difference in the surface concentration of lithogenic suspended matter estimated by the model between the Loire and Gironde plumes of ca 1.3 mg l⁻¹ (between ~0.8 and 2.1 mg l⁻¹, see figure 11) is sufficient to explain the contrast of biomass between both river plumes. The high load of lithogenic suspended matter encountered within the Gironde estuary is partly ejected by the flood (Le Hir, pers. comm.) and decreases the available light for phytoplankton growth in the top layer of the plume. The bloom observed by SeaWiFS on May 17th in south Brittany is more intense and northward compared to the model estimate (figure 9b, see discussion). A small upwelling event in the shallow water off the Landes coast (south of the Gironde plume, figures 9b and 9c) occurs due to northerly wind conditions (~5 m s⁻¹) during the first half of May and August (~day 137 and day 226, data not shown). The model overestimates the biomass off the Landes coast in both periods and along the coast of south Brittany in August. Although the model and SeaWiFS results have local disparities, the seasonal extension at the scale of the shelf of surface chlorophyll-a is reproduced.

Discussion

Remote observations versus variability of coastal waters

The capacity of optical remote sensors to observe the main spatio-temporal variability of phytoplankton and turbid features is used to assess the reliability of a sampling strategy. The error linked to the temporal difference between the field measurement and the remote sensing observation is limited in the Atlantic shelf where the tidal currents are relatively small. On the opposite in the English Channel the tidal effect can dramatically increase the error with a horizontal displacement of more than ten SeaWiFS pixels in few hours during spring tide (estimated with a maximum current velocity ~ 1 m s⁻¹, Le Hir and L'Yavanc 1986). Independently, a deviation due to the scale of measurements can be added in case the phytoplankton biomass is distributed in patches of few hundred metres wide. In this case, a 1 l sample for the field measurement is unsuitable for comparison with the 1.21 km² surface of the satellite pixel. The large grid sampling of the Modycot-99.2 cruise (> 50 km, figure 8c) is sufficient for the western part of the shelf off of the river plume influence. It is however largely inadequate to describe the biological features in plume areas where the satellite (figure 8b) and moreover the airborne data (figure 8a) show the full variability.

The attenuation coefficient of the top layer defines the optical depth of the ocean colour measurement. The optical depth is thus dependent on the absorption and scattering coefficient of phytoplankton, coloured dissolved organic matter and lithogenic suspended matter. The field measurements of the Ecoloire campaign (figures 6 and 7) provide information on the penetration depth of remote sensing,

notably as regards to the detection of the sub-surface chlorophyll maximum. Viollier et al. (1987) have shown that the remote sensing optical depth of measurements offshore of Brittany varied between 1.5 and 14 m. A higher correlation coefficient (0.88) between 57 chlorophyll profiles and satellite data (CZCS sensor) was found for a mean depth between 0 and 10 m. During the Ecoloire cruise, the optical depth value was found to vary between 2.5 and 13.5 m with a mean of 5.47 m. The fluorescence profiles described above showed a relatively constant value in the mixed layer. The satellite optical depth deepens from the estuary mouth to offshore waters together with the mixed layer depth and the chlorophyll maximum (from station 1 to 26, see figure 7). The remote sensor for this cruise therefore never detected the sub-surface chlorophyll maximum. For chlorophyll-a concentrations above 0.5 mg m^{-3} , which is a basic value in coastal waters, Smith (1981) showed that the optical depth, derived from an optical classification model (Smith and Baker, 1978), is always shallower than 10 m. A small wavelength dependency of Z_{90} ($\sim 2 \text{ m}$ maximum deviation between $Z_{90}^{443 \text{ nm}}$ and $Z_{90}^{550 \text{ nm}}$) is observed when the chlorophyll-a concentration is above 0.5 mg m^{-3} . This dependency appears to be inversely linked to the chlorophyll-a concentration (for instance for 0.1 mg m^{-3} : $Z_{90}^{443 \text{ nm}} - Z_{90}^{550 \text{ nm}} = 23 \text{ m}$). In other words and on a first approximation in coastal waters, the optical depth is not dependent on the wavelength in the visible spectrum and the near surface *in situ* measurement is representative of the first optical depth. Because chlorophyll content in the mixed layer is relatively constant and because the mixed layer is generally greater than the first optical depth in coastal waters, the near surface chlorophyll measurement (from 2 to 5 m depending on the local attenuation coefficient) is suitable for comparison with the satellite-derived value. The top layer value of the model which integrates a depth from 0.3 to 2.4 m for the Ecoloire stations was also chosen as the simulated biomass profile is homogeneous in the mixed layer.

When a high spectral resolution is available, optical remote sensing can also characterize phytoplankton groups through the pigment signature. The pattern in patches and the particular spectral signature of *Noctiluca scintillans* provide information on the dynamics of this species. A true colour picture of the phytoplankton patches as observed from the aircraft is also presented (figure 8a). *Noctiluca scintillans* is a large non-photosynthetic (no chloroplasts) heterophageous dinoflagellate, but its optical signature shows the same peak of reflectance in the NIR (around 705 nm) as *Alexandrium minutum* for example (data not shown) which contains a set of pigments responsible for the red colour. The diffraction of incident light through several layers of large cells of *Noctiluca scintillans* (from 200 to 2000 μm) near the ocean surface appears to be responsible of the red colour (for concentrations above $10^9 \text{ cells l}^{-1}$). This large phagotrophic phytoplankton is euryhaline, occurring at salinities of about 10 to 37 PSU (Elbrächter and Qi 1998), but its optimal growth occurs at 22 PSU (Lee and Hirayama, 1992). The river plumes are therefore favourable areas of growth as they are also areas of high food concentration (phytoplankton, copepod, fish eggs and bacteria). As shown in figure 8a, the species *Gymnodinium chlorophorum* is feeding *Noctiluca scintillans*. The red tide created by the accumulation near the sea surface of *Noctiluca scintillans* only occurs in low vertical turbulence situations (low currents, tides and wind; Elbrächter and Qi 1998) or in the vicinity of fronts (Le Fèvre and Grall 1970, Holligan 1979) at the end of its life cycle when positive buoyancy occurs. In our experiment, a neap tide occurred three days earlier and the wind was low. Conversely to European waters, an increase of *Noctiluca scintillans* blooms was reported in south-Asian waters. In these waters

there is no evidence for an increase neither in population densities nor in bloom occurrence over a period of 25 years (Uhlig and Sahling 1995), whereas there was evidence of considerable increase of nutrient inputs in all coastal waters. There is thus no evidence that *Noctiluca* blooms are stimulated by eutrophication. Large bloom events in south-Asian seas were reported to be responsible for fish kills resulting from the consumption of oxygen through their heterotrophic behaviour and the accumulation and release of ammonia when lysing (Schaumann et al. 1988). Such indirect toxic effects of *Noctiluca* blooms were not reported in European waters. However red tides are generally associated with the alteration of the structure and functioning of ecosystems. The last generation of optical sensors MODIS and MERIS has a specific red channel devoted to the detection of red tides.

Phytoplankton patterns in patches of the order of one hundred metres observed by a 1.1 km x 1.1 km satellite cell as shown in figure 8 show the difficulty to compare field and satellite measurements. Moreover, it should help to define the proper horizontal field sampling to characterise bloom events.

Contribution of ocean colours sensors to improve the modelling

The high spatial variability of physical and biological patterns in coastal areas particularly along river plumes or in shallow waters requires a refined sampling strategy. The comparison of remote sensed and modelled chlorophyll-a is difficult because both estimations have uncertainties and the estimation integrates a surface of 1.21 km² and 25 km² respectively. Although the accuracy of the satellite-derived chlorophyll-a is relatively low, these data provide a unique observation of spatial features. For this reason, ocean colour data are used to calibrate the model and to estimate its capacity to reproduce physical and biological structures. Comparing the modelled surface results with remote sensing data avoids neglecting important physical or biological processes in the conceptual model. Although the model presents some limits, such as the large grid preventing the reproduction of small scale structures near the coast, it is adapted to study the French Atlantic shelf in its whole extent.

The current model version takes into account a single geographic point for the wind stress at the Ré Island (between the Loire and Gironde estuaries: 46.2N, 1.25W, see Figure 3 for location). The wind decrease southward in the Bay of Biscay and its rotating orientation associated to low-pressure systems may affect respectively the simulated circulation and river plume position (cf the spatial shift of the south Brittany spring bloom in figure 9b).

In this example, the northerly wind (~ day 137, data not shown) oriented both simulated plumes towards south. Such orientation is well observed by SeaWiFS for the Gironde plume but not for the Loire plume. A refined wind field input constitutes therefore a significant improvement of the modelling.

The use of fractional cloud cover based on climatology may even be more limiting the accuracy of the biomass estimate. If the seasonal biological cycle is correctly reproduced, inter-annual variations including high solar radiation periods are responsible of time shifts for simulated bloom starts and duration. Another source of spatio-temporal shift is the delay in estimating the halocline establishment on the margin due to the near-shore accumulation of fresh water during winter followed by the relaxation of strong westerly winds. The chlorophyll over-estimation by the model in March 24th (figure 9a) is mainly due to an establishment of the halocline ahead of

time together with solar radiation inaccuracies. More realistic wind field and solar radiation are therefore required to better simulate the biomass.

The chlorophyll over-estimation in shallow waters off the Landes coast (figure 9b and 9c) is due to the lack of the swell-induced erosion process of bottom particulate matter. The model underestimates the turbidity and therefore over-estimates the light availability. The remote sensing revealed the swell-induced erosion process as a major mechanism neglected by the model in shallow waters. The erosion process will be taken into account in the biological model as a function of bottom friction.

The accuracy of the simulated biomass is affected in shallow waters by the low horizontal model resolution (5 km) relatively to the variability of local topography. The simulation presented in figure 8d shows a reasonably good agreement with the satellite and field data even if small scale chlorophyll gradients cannot be reproduced by the 25 km² model grid. The general tendency of the model is to smooth the gradients, over-estimating low concentrations and underestimating high concentrations.

Conclusion

The large variability of water quality parameters in coastal areas requires the definition of specific sampling strategies. In opposition to traditional means, a large range of surface phytoplankton and meso-scale hydrological variability is detectable by optical remote sensing. Such observations help to identify bio-physical features and understand the mechanisms involved. Coastal waters are complex in terms of hydrology, dissolved or particulate constituents and ecosystem structure; a single satellite optical view of the Bay of Biscay is able to show the tight links between meso-scale physical features and phytoplankton dynamics. Multispectral airborne remote sensing in the visible wavelengths provides a qualitative (spatial) and quantitative (spectral) description of the various water constituents at smaller scales (1 m to few kilometres). An empirical five-channel algorithm was developed to estimate the surface chlorophyll-a content in turbid waters (OC5, Gohin et al., 2002) using a field database covering the seasonal variability. The mean error ($\delta C/C$) for coastal waters of the English Channel and the French Atlantic shelf is 50.5 %. The SeaWiFS-OC5 data and the simulated phytoplankton biomass of a 3D biophysical model show large seasonal variability depending mainly on meteorological conditions. Wind stress and precipitation, which defines the extension of the river plume, together with solar radiation control the major phytoplankton dynamics of the French Atlantic shelf. The model reasonably reproduces the main seasonal biological features. However the low resolution (5 km x 5 km), inaccuracies of inputs (single point of measurement for wind stress, climatological solar radiation) and the absence of the erosion process limits the accuracy of the simulated biomass in shallow waters. The sub-surface chlorophyll maximum generally encountered during summer and located at the maximum of density gradient is not detected by optical sensors as the mixed layer in coastal waters is deeper than the penetration depth of remote sensing. The remote sensing observation therefore integrates a relatively homogeneous water depth (top part of the mixed layer) and the near surface *in situ* measurements is consistent with the ocean colour data. Horizontally, the traditional sampling of coastal areas is largely limited by the time of displacement between two stations as regards to the advection and by the sampling grid as regards to the scale of phytoplankton

patterns (ca. 100 m for patches). Regional algorithms applied to SeaWiFS data quantify water constituents with a sufficient accuracy for coastal studies.

Acknowledgements

The authors would like to thank the SeaWiFS Project (Code 970.2) and the Distributed Active Archive Center (Code 902) at the Goddard Space Flight Center, Greenbelt, MD 20771, for the production and distribution of these data, respectively. These activities are sponsored by NASA's Mission to Planet Earth Program. The authors are indebted to NASA and GSFC for SeaWiFS data and SeaDAS software. We are extremely grateful to all who provided the field measurements allowing the calibration of the ocean colour algorithm: J.F. Chiffoleau (BloomSeine, Marina 8, CadHiver), the Ifremer's group of Port-en-Bessin (SeineSat), V. Duquesne (SRN), J.M. Froidefond (Biomet), S. L'Helguen and N. Savoye (Bloom/QuickSeine), A. Herbland and C. Labry (Plagia), L. Lampert and T. Labasque (Modycot.99), P. Cann (Ecoloire). This work was supported by Ifremer. The authors thank Olivier Archer for providing useful tools to visualise SeaWiFS scenes and field data.

References

AMINOT, A., GUILLAUD, J.-F., and KEROUEL, R., 1997, La baie de Seine: hydrologie, nutriments et chlorophylle (1978-1994). Editions IFREMER, Repères Océan, 14.

BARTHE, X., and CASTAING, P., 1989, Etude théorique de l'action des courants de marée et des houles sur les sédiments du plateau continental du Golfe de Gascogne. *Oceanologica Acta*, 12, 325-334.

BISEAU, A., 1998, Definition of a directed fishing effort in a mixed species trawl fishery, and its impact on stock assessments. *Aquatic Living Resources*, 11, 119-136.

CLOERN, J. E., 1999, The relative importance of light and nutrient limitation of phytoplankton growth: a simple index of coastal ecosystem sensitivity to nutrient enrichment. *Aquatic Ecology*, 33, 3-16.

DRUON, J.-N., 1998, Modélisation d'écosystèmes pélagiques dans le proche Atlantique : interactions entre les phénomènes physiques et biologiques. Thèse de doctorat de l'Université Paris 6, Océanographie Biologique.

ELBRÄCHTER, M., and QI, Y. Z., 1998, Aspects of *Noctiluca* (Dinophyceae) population dynamics. In *Physiological Ecology of Harmful Algal Blooms*, edited by D. M. Anderson et al. (Berlin: Springer-Verlag), NATO ASI Series, Vol. G 41, pp. 315-335.

FROIDEFOND, J.-M., LAVENDER, S., LABORDE, P., HERBLAND, A., and LAFON, V., 2002, SeaWiFS data interpretation in a coastal area in the Bay of Biscay. *International Journal of Remote Sensing*, 23, 881-904.

GOHIN, F., DRUON, J.-N., and LAMPERT, L., 2002, A five channel chlorophyll algorithm applied to SeaWiFS data processed by SeaDAS in coastal waters. *International Journal of Remote Sensing*, 23, 1639-1661.

GORDON, H. R., and MCCLUNEY, W. R., 1975, Estimation of the depth of sunlight penetration in the sea for remote sensing. *Applied Optics*, 14, 413-416.

HABBANE, M., DUBOIS, J. M., EL-SABH, M. I., and LAROUCHE, P., 1998, Empirical algorithm using SeaWiFS hyperspectral bands: a simple test. *International Journal of Remote Sensing*, 19, 2161-2169.

HOLLIGAN, P. M., 1979, Dinoflagellate blooms associated with tidal fronts around the British Isles. In *Toxic Dinoflagellate Blooms*, edited by D. L. Taylor and H. H. Seliger (North Holland: Elsevier), pp. 249-256.

JEGOU, A.-M., and LAZURE, P., 1995, Quelques aspects de la circulation sur le plateau Atlantique. *Actas del IV Coloquio Internacional sobre Oceanografia del Golfo de Viscaya*, pp. 99-106.

JERLOV, N. G., 1968, *Optical Oceanography* (Amsterdam: Elsevier).

KOUTSIKOPOULOS, C., and LE CANN, B., 1996, Physical processes and hydrological features related to the Bay of Biscay anchovy. *Scientia Marina*, 60, 9-19.

LAZURE, P., and JEGOU, A.-M., 1998, 3D modelling of seasonal evolution of Loire and Gironde plumes on Biscay Bay continental shelf. *Oceanologica Acta*, 21, 165-177.

LEE, J. K., and HIRAYAMA, K., 1992, Effects of salinity, food level and temperature on the population growth of *Noctiluca scintillans* (Macartney). *Bull Fac Fish, Nagasaki University*, 71, 163-168.

LE FÈVRE, J., and GRALL, J., 1970, On the relationships of *Noctiluca* swarming off the western coast of Brittany with hydrobiological features and plankton characteristics of the environment. *Journal of Experimental Marine Biology and Ecology*, 4, 287-306.

LE FÈVRE, J., VIOLLIER, M., LE CORRE, P., DUPOUY, C., and GRALL, J. R., 1983, Remote sensing observations of biological material by LANDSAT along a tidal thermal front and their relevancy to the available field data. *Estuarine and Coastal Shelf Sciences*, 16, 37-50.

LE FÈVRE, J., 1986, Aspects of the biology of frontal systems. *Advanced Marine Biology*, 23, 163-299.

LE FÈVRE, J., and FRONTIER S., 1988, Influence of temporal characteristics of physical phenomena on plankton dynamics, as shown by north-west European marine ecosystems. In *Toward a theory of biological-physical interactions in the world*

ocean, edited by B. J. Rothschild (Dordrecht: Kluwer Academic Publishers), pp. 245-272.

LE HIR, P., and L'YAVANC, J., 1986, Observations de courant en Baie de Seine. La Baie de Seine (GRECO-MANCHE), Université de Caen, 24-26 avril 1985 (Brest: IFREMER, Actes de colloques), 4, pp. 25-34.

LOHRENZ, S. E., FAHNENSTIEL, G. L., REDALJE, D. G., LANG, G. A., DAGG, M. J., WHITLEDGE, T. E., and DORTCH, Q., 1999, Nutrients, irradiance, and mixing as factors regulating primary production in coastal waters impacted by the Mississippi River plume. *Continental Shelf Research*, 19, 1113-1141.

LORENZEN, C.J., 1967, Determination of chlorophyll and phaeopigments: spectrophotometric equations. *Limnology and Oceanography*, 12, 343-346.

MALLIN, M. A., CAHOON, L. B., MCIVER, M. R., PARSONS, D. C., and SHANK, G. C., 1999, Alternation of factors limiting phytoplankton production in the Cape Fear River estuary. *Estuaries*, 22, 825-836.

MANTOURA, R. F. C., JEFFREY, S. W., LLEWELLYN, C. A., CLAUTRE, H., and MORALES, C. E., 1997, Comparison between spectrophotometric, fluorometric and HPLC methods for chlorophyll analysis. In *Phytoplankton pigments in oceanography: Guidelines to Modern Methods*, edited by S. W. Jeffrey, R. F. C. Mantoura and S. W. Wright (Paris: SCOR-UNESCO), pp. 361-380.

MORIN, P., LE CORRE, P., MARTY, Y., and L'HELGUEN, S., 1991, Evolution printannière des éléments nutritifs et du phytoplancton sur le plateau continental armoricain (Europe du Nord-Ouest). *Oceanologica Acta*, 14, 263-279.

PINGREE, R. D., and LE CANN, B., 1989, Celtic and Armorican slope and shelf residual currents. *Progress in Oceanography*, 23, 303-338.

PINGREE, R. D., and LE CANN, B., 1990, Feature, strength and seasonality of the slope currents in the Bay of Biscay region. *Journal of the Marine Biological Association, UK*, 70, 857-885.

PINGREE, R. D., and LE CANN, B., 1992, Three anticyclonic Slope Water Oceanic eddies (SWODDIES) in the southern Bay of Biscay in 1990. *Deep-Sea Research*, 39, 1147-1175.

SCHAUMANN, K., GERDES, D., and HESSE, K. J., 1998, Hydrographic and biological characteristics of a *Noctiluca scintillans* red tide in the German Bight, 1984. *Meeresforsch*, 32, 77-91.

SMITH, R. C., and BAKER, K. S., 1978, Optical classification of natural waters. *Limnology and Oceanography*, 23, 260-267.

SOURNIA, A., 1988, A physical, chemical and biological characterization of the Ushant tidal front. *Int Rev Gesamt Hydrobiol*, 73, 511-536.

TASSAN, S., 1994, Local algorithms using SeaWiFS data for the retrieval of phytoplankton pigments, suspended sediment, and yellow substance in coastal waters. *Applied Optics*, 33, 2369-2378.

UHLIG, G., and SAHLING, G., 1995, *Noctiluca scintillans* : Zeitliche Verteilung bei Helgoland und räumliche Verbreitung in der Deutschen Bucht (Langzeitreihen 1970-1993). *Ber Biol Anst Helgoland*, 9, 1-127.

VIDEAU, C., 1985, Analyse écophysiological du phytoplancton du front thermique d'Ouessant en août et septembre 1982. In *Le front thermique d'Ouessant en août et septembre 1982 : campagne Satir-Dynatlant*, edited by P. Le Corre and V. Mariette, pp. 215-226.

VIDEAU, C., 1987, Primary production and physiological state of phytoplankton at the Ushant tidal front (west coast of Brittany, France). *Marine Ecology Progress Series*, 35, 141-151.

VIOLLIER, M., SOURNIA, A., BIRRIEN, J. L., and MORIN P., 1987, Observations satellitaires du phytoplancton dans les zones de discontinuité hydrologique au large de la Bretagne. *Oceanologica Acta*, SP, Actes du Colloque d'Océanographie Spatiale, Brest, 19-20 novembre 1985, pp. 51-56.

Figure legends

Figure 1: Comparison of chlorophyll-a estimation from SeaWiFS-OC5 algorithm with *in situ* data (near surface measurements). The four upper graphs corresponds to Atlantic shelf cruises (a, b, c and d) and the two lower graphs to Channel cruises (e and f).

Figure 2: Mean error of satellite-derived chlorophyll-a content: the mean of $\delta C/C$ is 50.5 %, with a mean value for the Atlantic shelf stations of 48.6 % and of 55.5 % for the Channel stations.

Figure 3: Main circulation and currents in the Bay of Biscay: (1) general oceanic circulation, (2) eddies, (3) slope currents, (4) shelf residual circulation, (5) tidal currents, (6) wind induced currents, (7) density currents (modified from Koutsikopoulos and Le Cann 1996). Location of areas cited in the text: (α) Ushant Front, (β) Bay of Quiberon, (χ) Bay of Vilaine, (δ) Belle Île island, (ε) Houat-Hoëdic islands, (ϕ) Noirmoutier Peninsula, (γ) Ré island, (η) Oléron island, (φ) Landes coast, (λ) Cap Breton.

Figure 4: Chlorophyll-a estimation (mg m^{-3}) of the Bay of Biscay on May 26th 1999 using SeaWiFS-OC5 algorithm. See text for a detailed description of the meso-scale bio-physical features emphasized.

Figure 5: A multispectral observation of the Vilaine plume (south Brittany) on June 10th 1999. Note the turbid fronts with a phytoplankton bloom at the outer part and the specific optical signatures.

Figure 6: Surface chlorophyll-a contents during the Ecoloire cruise (south Brittany) in July 1999: (a) *in situ* measurements, July 28-30th; (b) model result (sum of diatoms, dinoflagellates and nanoflagellates), July 29th (three days mean); (c) SeaWiFS-OC5 chlorophyll estimation, July 25th and (d) July 30th; (e) SeaWiFS optical depth estimated from PAR profiles (linear scale).

Figure 7: Measurements of fluorescence, chlorophyll-a, $\ln(\text{PAR})$ and temperature profiles for three stations during Ecoloire: station 1 – shallower station in the Loire river mouth (July 28th, 7h20 UTC+2), station 16 – mean depth (July 29th, 13h25 UTC+2), station 26 – deeper station (July 30th, 15h20 UTC+2): see figure 6e for the localisation. The optical depth ($Z_{90} \approx k^{-1}$) has been estimated using the linear interpolation of PAR: $\ln(\text{PAR}_z) = k * z + \ln(\text{PAR}_{z=0})$.

Figure 8: Comparison of (a) airborne and (b) satellite remote sensed phytoplankton patterns with (c) field measurements and (d) modelled chlorophyll-a content of the Atlantic shelf in June 1999: (a) airborne data (CASI), June 10th, 13h45 UT, RGB composite (705-555-489 nm), 'S' is specular reflection; (b) SeaWiFS-OC5 chlorophyll-a estimation, June 11th, 12h45 UT ; (c) *in situ* measurements,

BioModycot-99.2 cruise, June 8-14th (zoom: June 9-12th) ; (d) model result (sum of diatoms, dinoflagellates and nanoflagellates), June 11th.

Figure 9: Comparison of SeaWiFS-OC5 (left column) and modelled (right column) chlorophyll-a content of the Bay of Biscay in 1998: a- March 23rd (March 18th and March 24th for the model), b- May 17th and c- August 14th (August 12th for the model). The simulated chlorophyll-a content is a surface, three days mean value representing the sum of diatoms, dinoflagellates and nanoflagellates. The colour scale is linear between 0.01 and 10 mg m⁻³.

Figure 10: The Loire (a) and the Gironde (b) flow (m³ s⁻¹) in 1998.

Figure 11: Vertical transects of the lithogenic suspended matter provided by the model on May 18th 1998: (a) Loire plume and (b) Gironde plume.

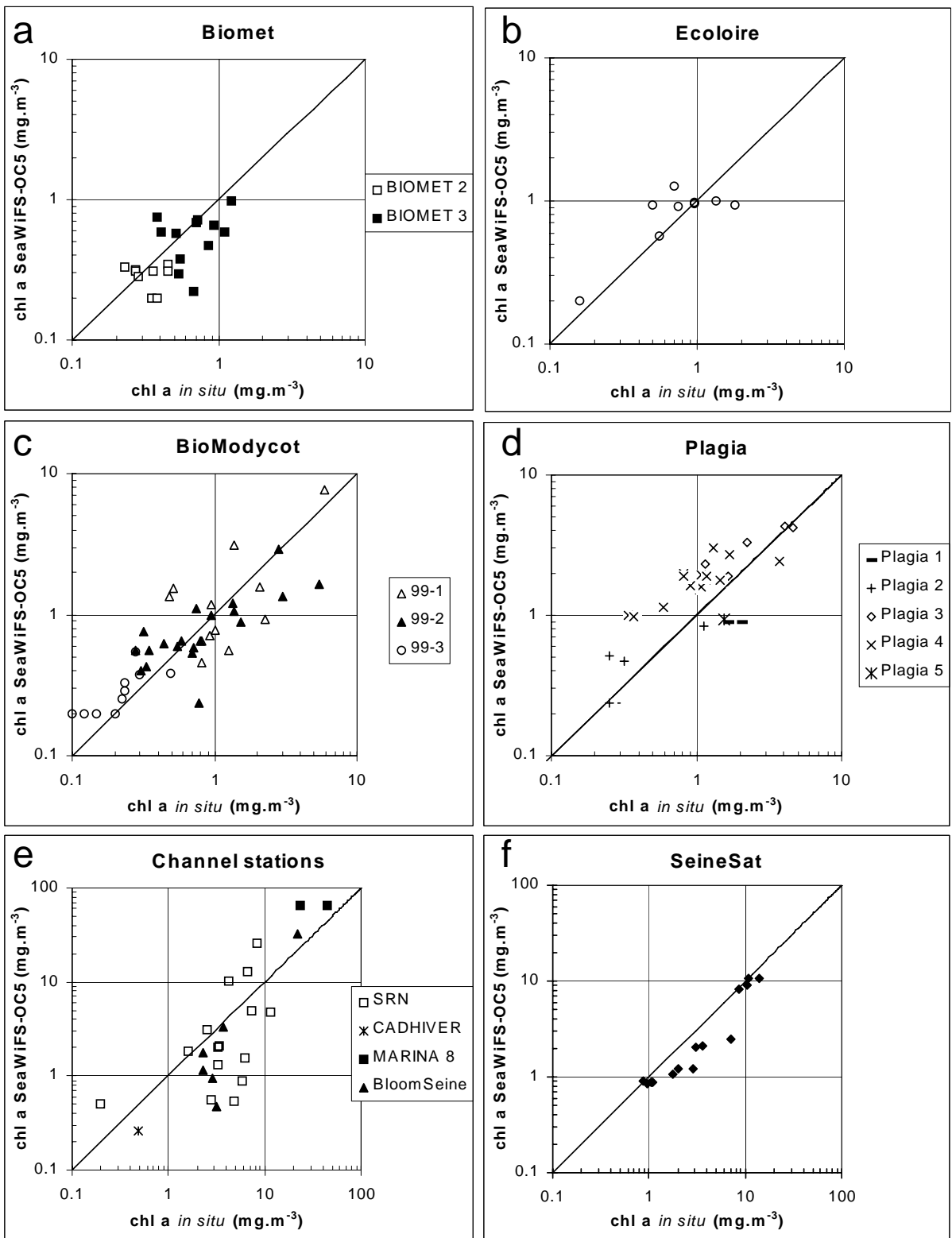


Figure 1

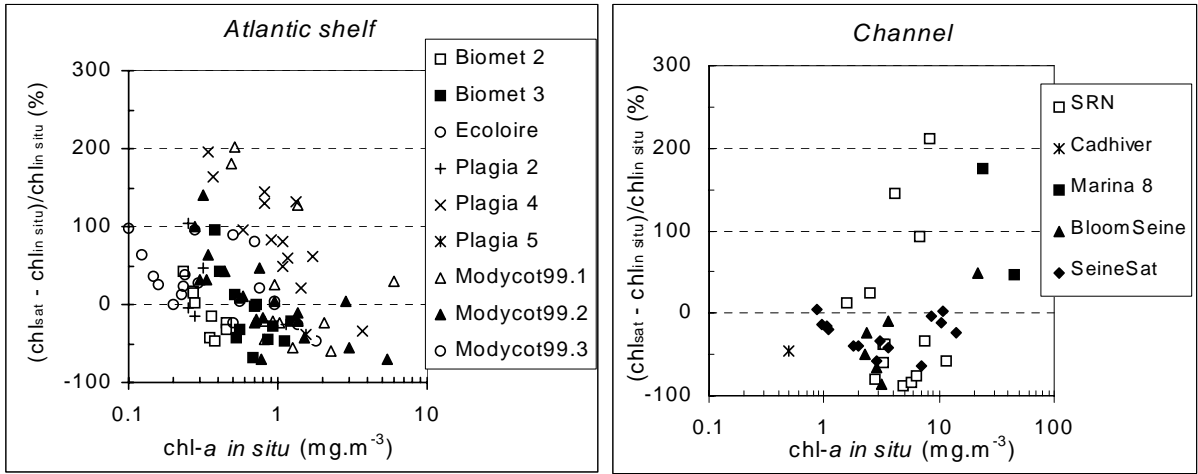


Figure 2

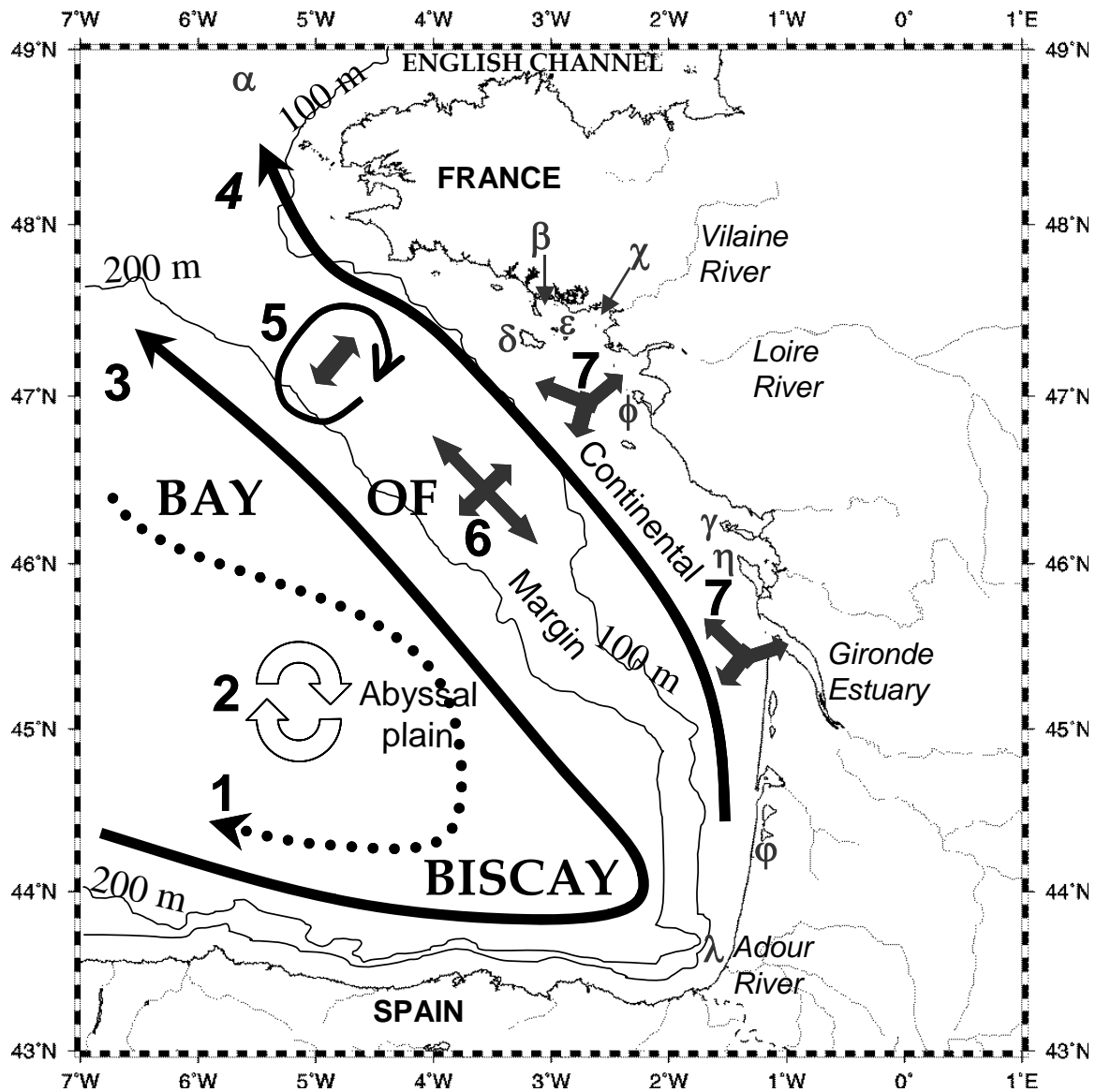


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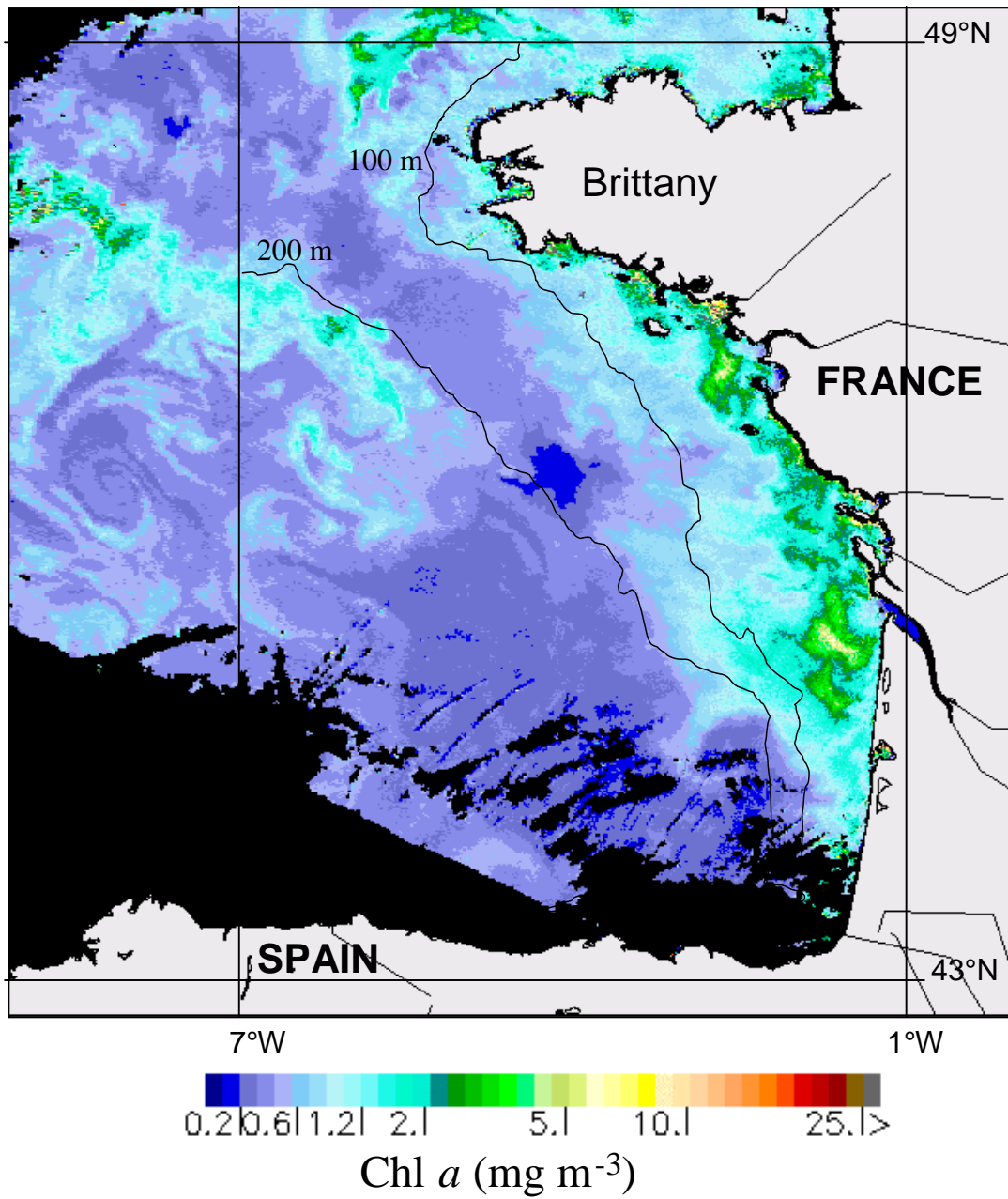


Figure 4

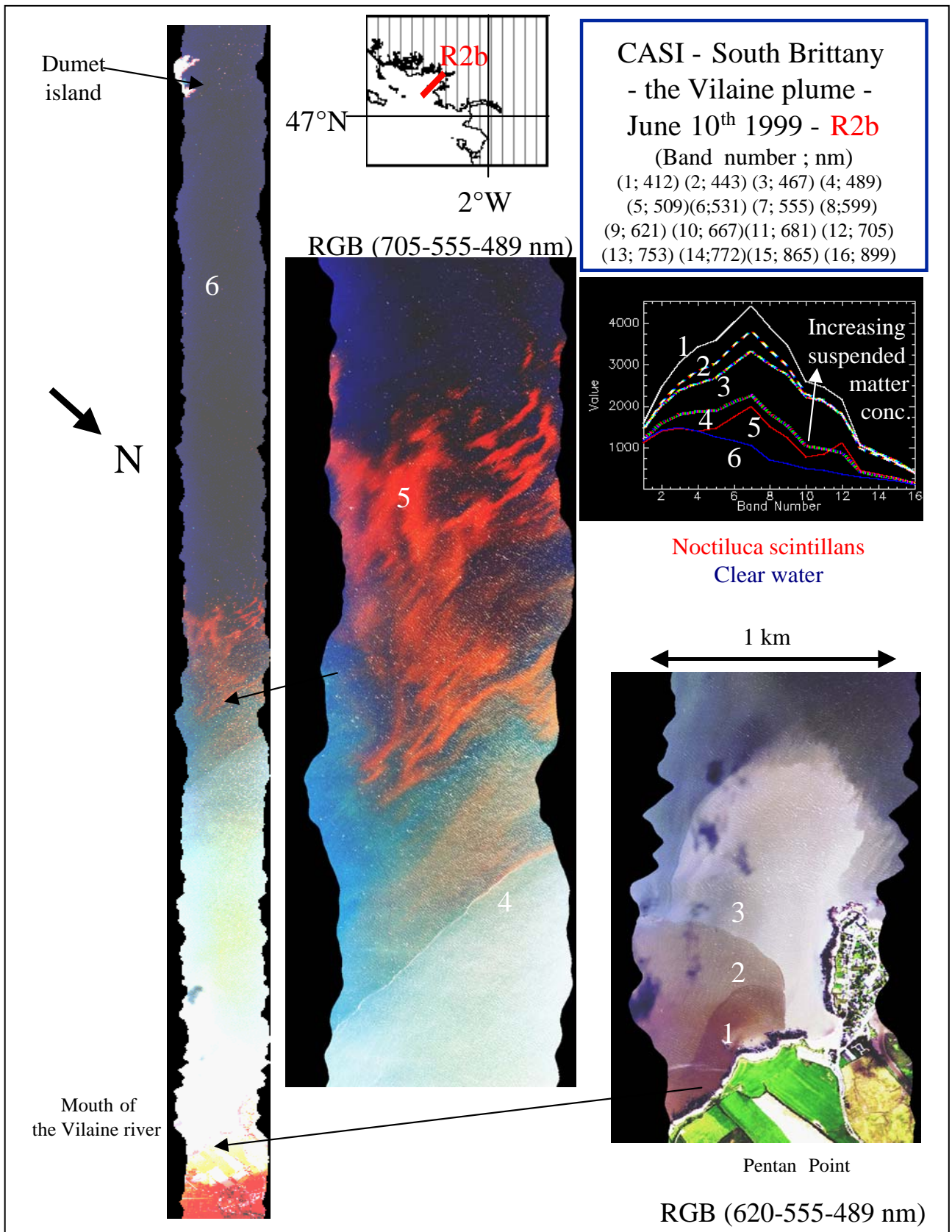


Figure 5

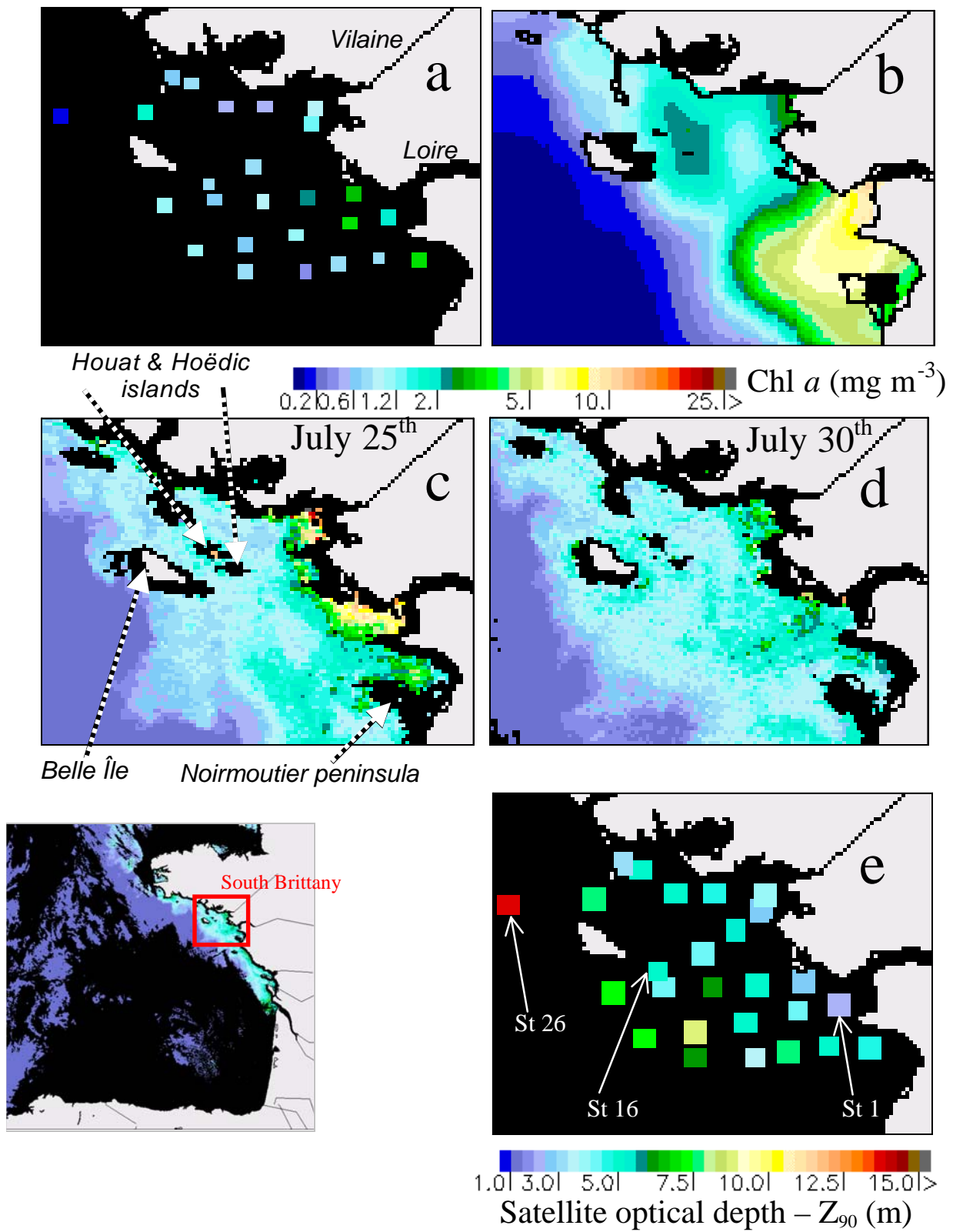


Figure 6

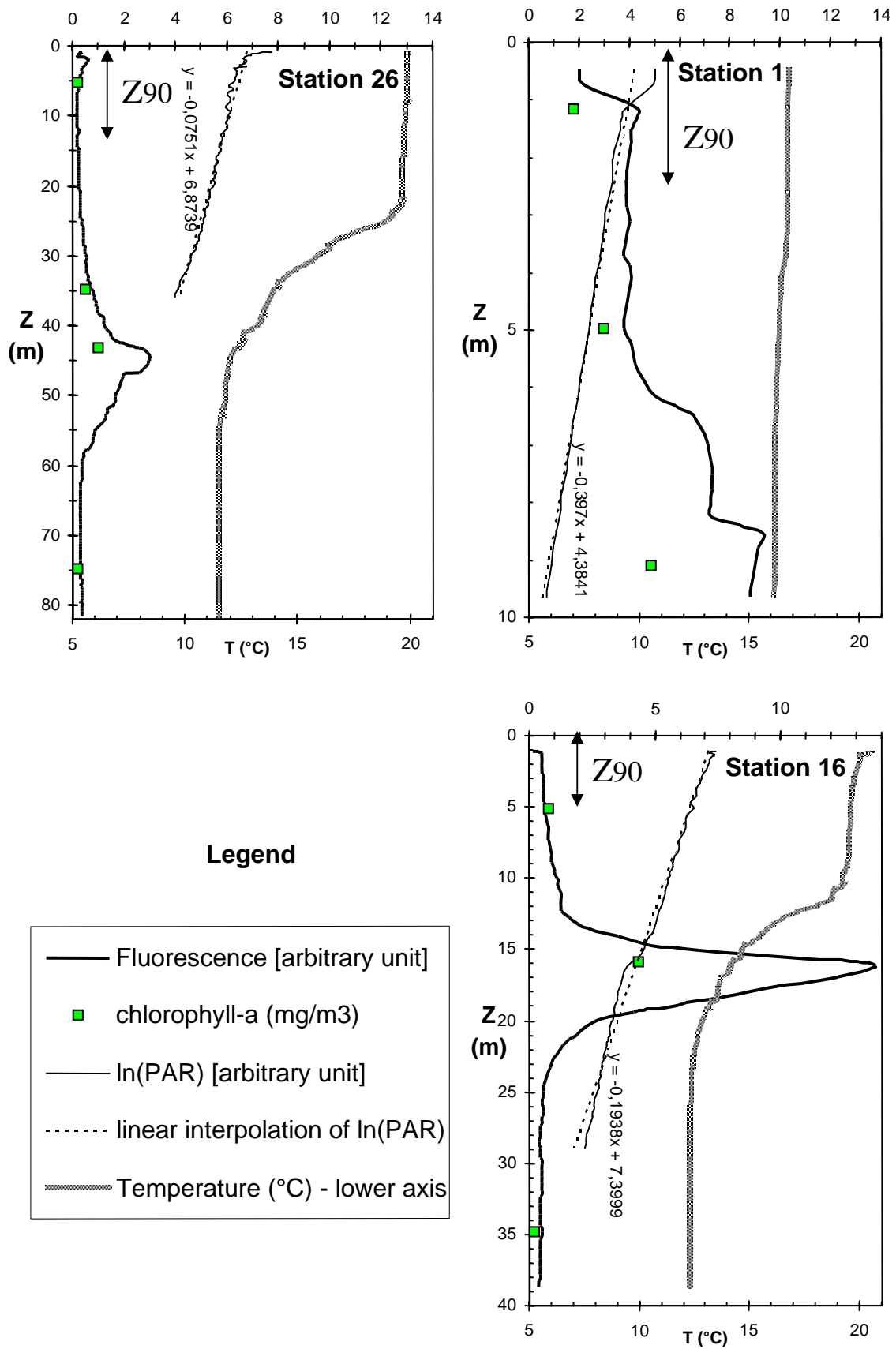


Figure 7

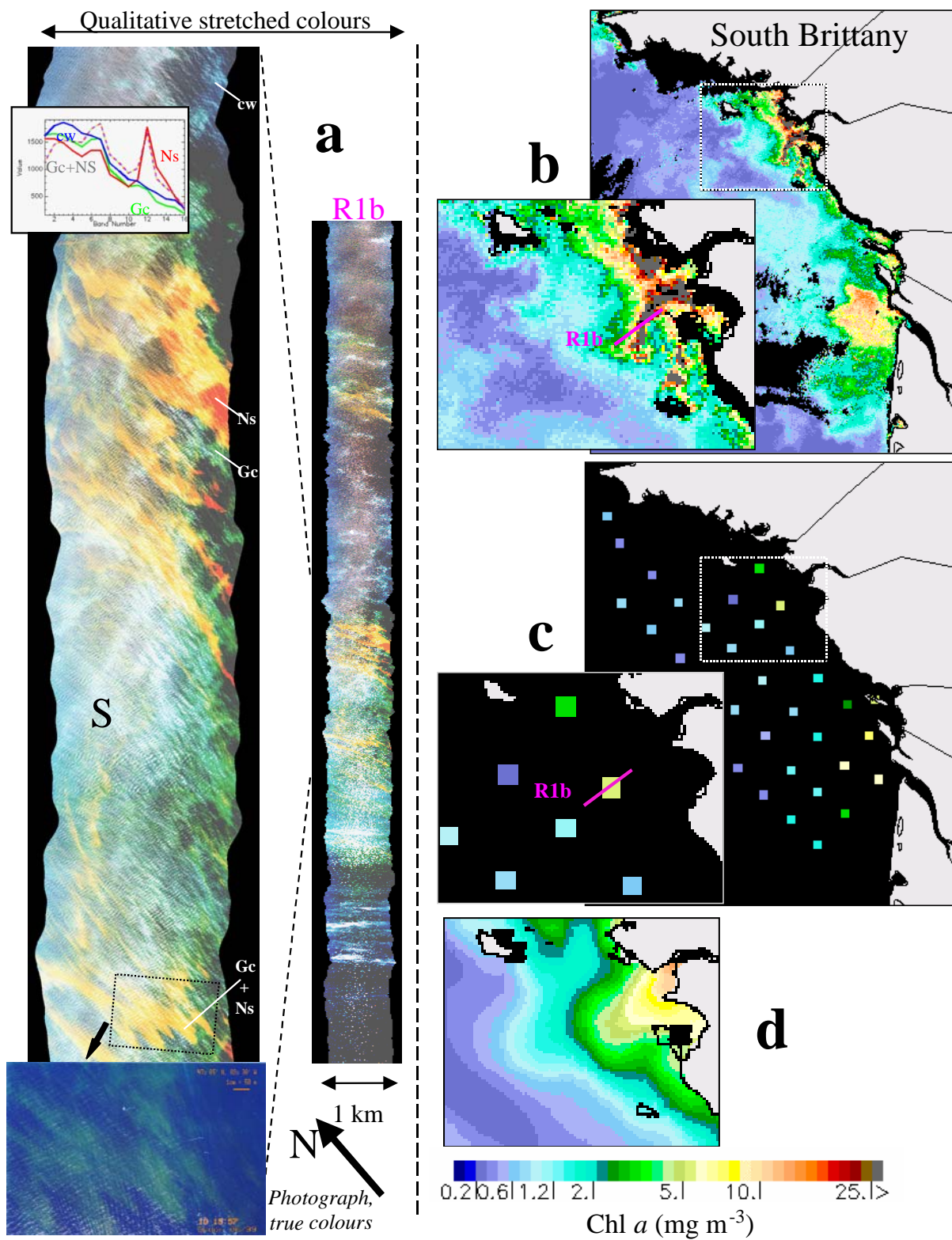


Figure 8

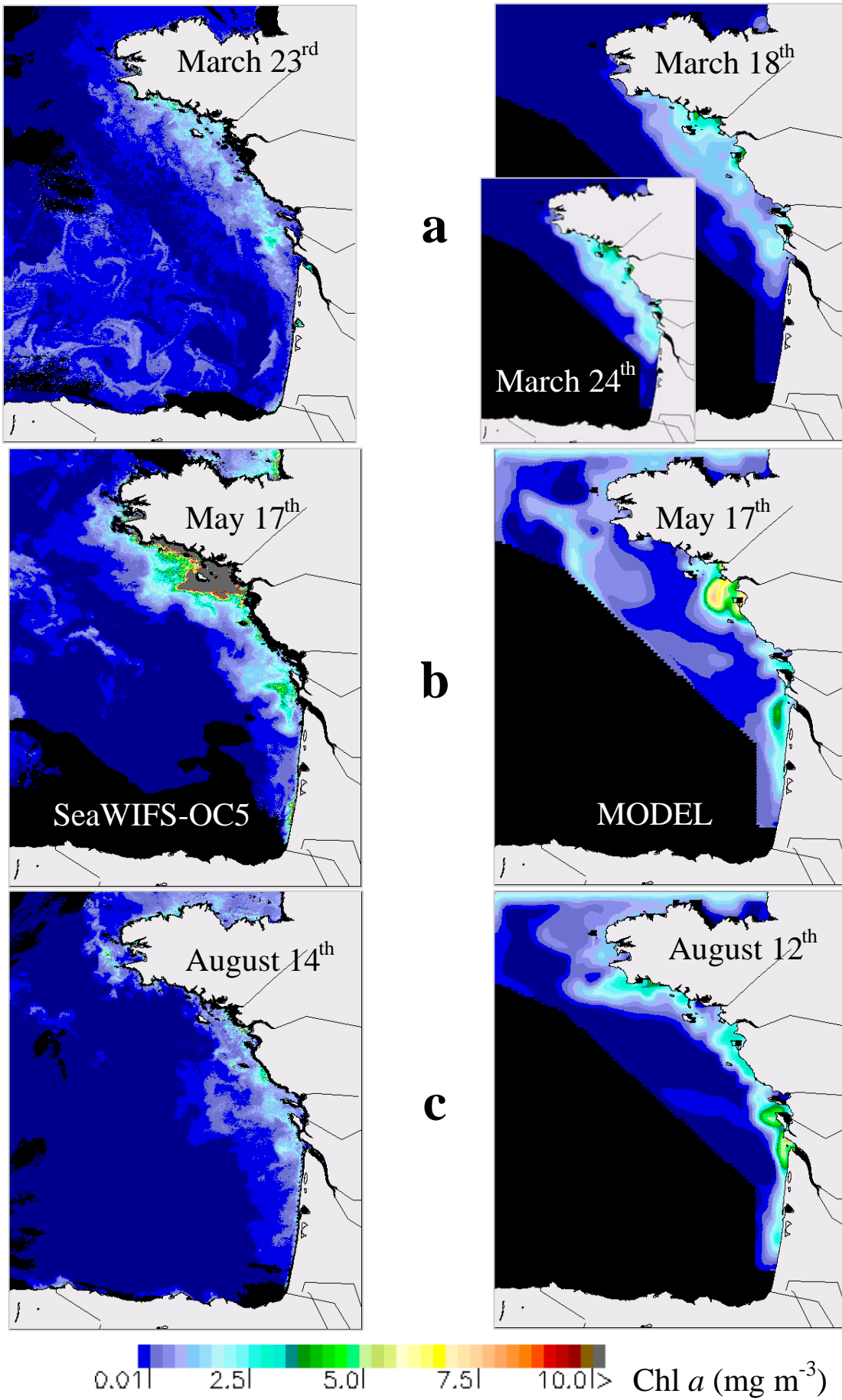


Figure 9

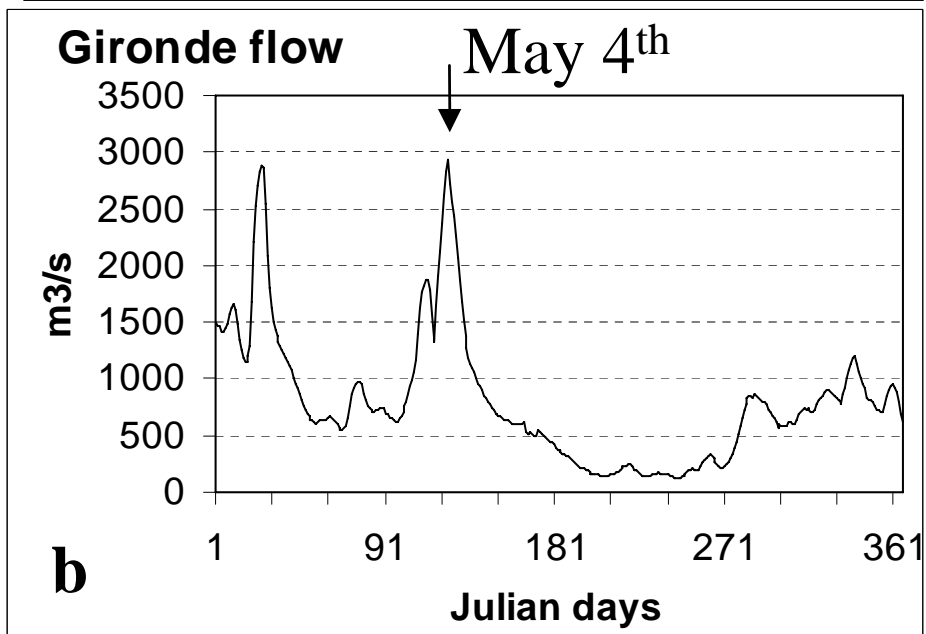
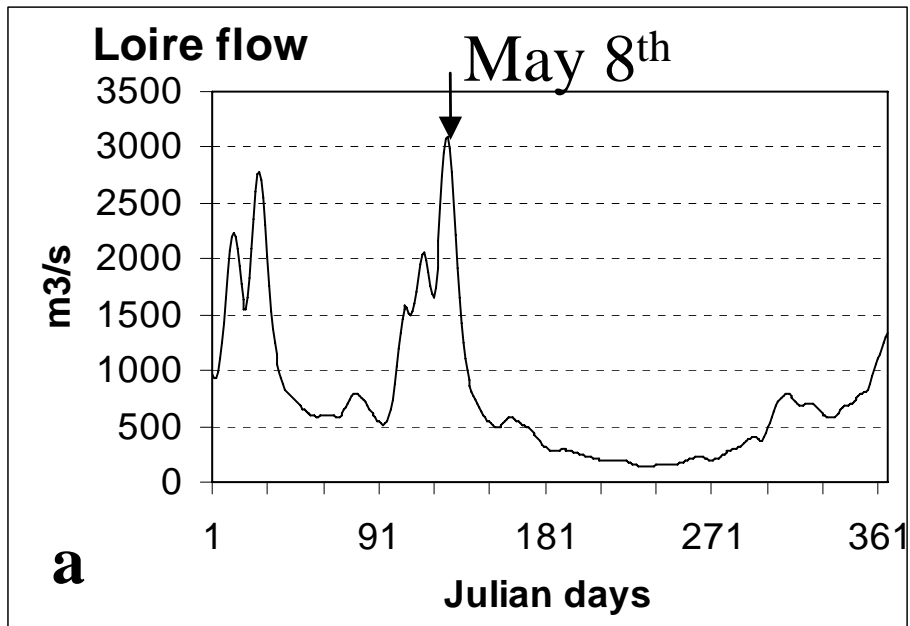
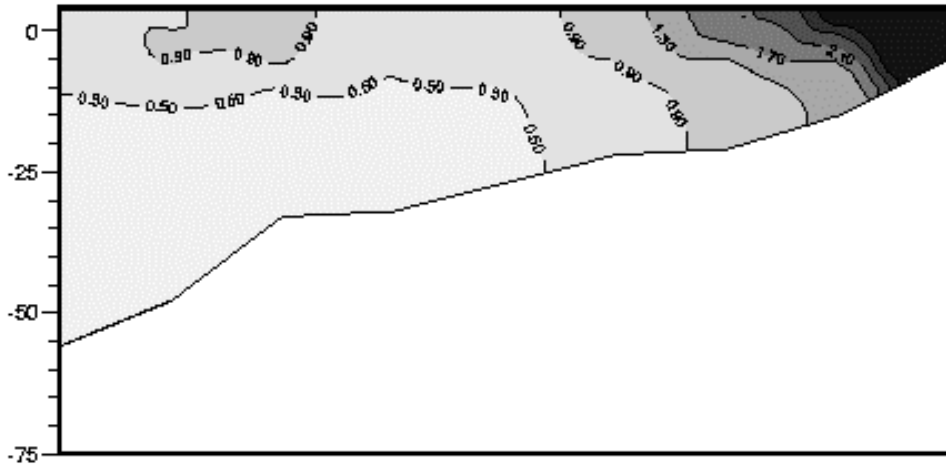


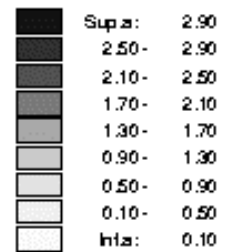
Figure 10

(a) Suspended matter - Loire plume

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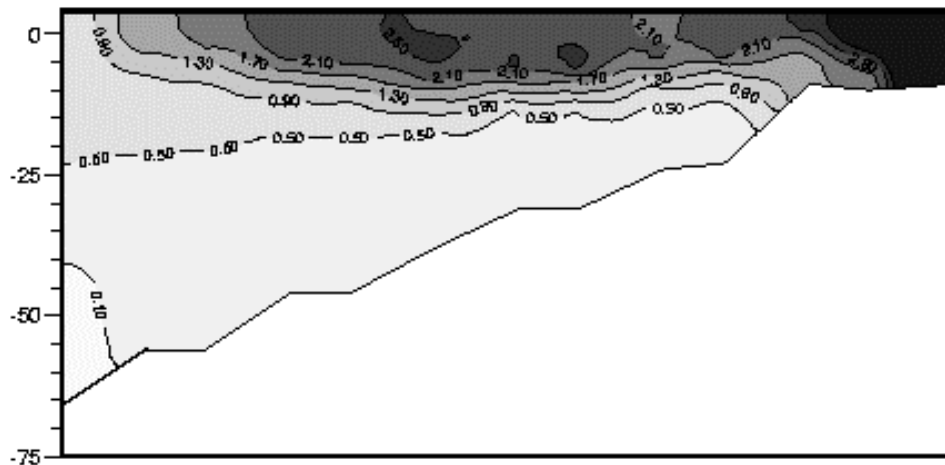


mg.l⁻¹



(b) Suspended matter - Gironde plume

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mg.l⁻¹

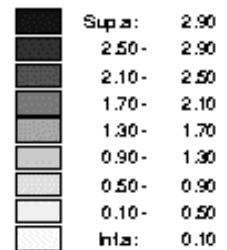


Figure 11