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Partition of the Ocean into Ecological Provinces: Role of Ocean-Colour Radiometry

Edited by:

Mark Dowell and Trevor Platt

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Preface

The IOCCG Monograph and Report Series has already covered a broad range of topics, in both the theory and the application of remotely-sensed data on ocean-colour radiometry (OCR). The present volume is concerned with a topic whose development has been intimately associated with the application of OCR data, namely the partition of the ocean ecosystem to reveal its underlying functional structure. Although the discipline of biogeography has a long tradition in marine science, its further refinement to the method of biogeochemical provinces, as epitomised by Longhurst's (1998) majestic survey, would probably not have been possible without the availability of ocean-colour data. It is another example of the growing stature of optical applications in oceanography. Indeed, in a review of landmark achievements in biological oceanography over the last fifty years, Barber and Hilting (2000) considered ocean colour as the application that most profoundly affects all biological oceanographers, and indeed each citizen of the planet.

Often, remotely-sensed observations of the ocean are applied at large geographical scales. For example, remotely-sensed data on ocean colour may be applied at the ocean-basin scale to determine primary production. In such applications, a suitable protocol or algorithm has to be implemented on each and every pixel in the domain or biome of interest. More particularly, an equation (transfer function) has to be invoked, together with the requisite parameters, on all pixels. At large geographical scales, the assumption that the requisite parameters were constant over the biome of interest might not be robust.

The question then arises, if the parameters are not constant over the biome of interest, how can their variation be specified? The extreme expression of the question is reached when issues of global scale are involved. Are the ecological rate parameters of the ocean biota constant over all the world oceans, and if not, in what way do they change with position? Although these are questions that have arisen in the application of ocean-colour data, they also have a more general significance. For example, in the development of coupled circulation-ecosystem models of the ocean at global scale, it is appropriate to ask whether the ecological parameters will be held constant everywhere at all seasons, or whether some spatial or temporal variability will be introduced.

More directly we can ask whether, from the point of view of its ecological structure and function, the ocean is everywhere the same. If not, is it a continuum, or is it composed of a series of internally-uniform regions separated by boundary discontinuities? If it is the latter, how or where should the boundaries be drawn? These questions are in themselves of sufficient importance to the ocean-colour community (for interpretation of data) to warrant particular scrutiny. If it is further realised that OCR data provide the ideal tool for tracing the putative boundaries in a synoptic manner, then the significance of the matter is beyond question.

Against this background, the IOCCG established a Working Group to explore the

issues raised above. The present monograph is the report of that working group which outlines the state of the art in ocean classification methods, both in the use of ocean-colour imagery and derived products in formulating ecosystem classifications, and also in the implementation of existing classifications in ocean-colour-related applications (e.g. primary production modelling).

Additionally, new and emerging methods that are available for defining dynamic province distributions in near-real time are addressed. If provinces are defined strictly on the basis of geospatial or temporal criteria (e.g. latitude zones, bathymetry, or season), the resulting maps exhibit discontinuities that are uncharacteristic of the real ocean. Although this may be useful for many purposes, it is unsatisfactory in that it does not capture the dynamic nature of ocean systems. Classifications in which the boundaries are fixed in time and space do not allow us to treat seasonal, inter-annual or longer-term variability (e.g., domain shifts, Karl *et al.* 1995) that may result, for example, from climate change. Fortunately, methods are now available (Devred *et al.* 2007) for delineation of the province boundaries in operational mode, which are also addressed in this report.

Chapter 1

Introduction

Trevor Platt and Mark Dowell

1.1 Importance of Ocean Colour

Ocean-colour radiometry (OCR) from Earth-orbiting spacecraft is more than thirty years old. The proof of concept, that biomass of phytoplankton could be observed over all the ocean on synoptic scales with useful accuracy and precision, has been made beyond all doubt. It is our only window into the ocean ecosystem on these scales. The results of such observations have revolutionised the field of biological oceanography, and have made important contributions to ocean biogeochemistry, physical oceanography, ocean modelling, fisheries oceanography and coastal management. It is a technology that has achieved much for a relatively modest investment.

By the nature of the technology, OCR is global in scope, as are many scientific problems of the day, such as those related to climate change. Because the ocean ecosystem can be observed at fine resolution (one kilometre or better) and high repeat frequency (one day or better) over the entire globe, this means we have a tool of the highest versatility to conduct research on a broad range of scales.

We have a responsibility to learn to exploit the resulting data to the fullest extent, so that the underlying investment will be justified as well as possible. This means that we should explore and understand the important issues that arise when we implement OCR data. One such major question is the relation between the structure of the ocean-colour field as seen from space and the ecological function that can be inferred from it. The present monograph is a contribution to resolving that question.

1.2 Background

For the terrestrial and marine biospheres, there is a well-developed discipline of biogeography. In terrestrial systems, it is quite easy to see that, at large scale, there is an array of habitats under different environmental conditions, from desert to rain forest, from coastal strip to high plateau, and a corresponding diversity of biota associated with each. Biogeography, a discipline in which taxonomy is

accorded great emphasis, is concerned with the description and characterisation of the habitats and their associated biotic communities.

In marine systems, where the biota is predominantly microscopic, distinctions between major habitats are less obvious to casual observation, but no less real. That the ocean ecosystem is highly structured in space, has been revealed with great clarity, and great beauty, using OCR data. Of course, spatial structure in the biomass field does not necessarily imply that biotic communities are similarly structured or that the functional properties are structured in the same way. But the OCR data are at least suggestive that this might be the case.

In many ocean analyses, for example in biogeochemistry, it is exactly the large-scale variations in ecosystem function that are important. In such cases, taxonomy is of little interest for its own sake, only indirectly in so far as the variations in biota have associated variations in functional dynamics. We pose the question: Is the functional response of the marine microbiota the same everywhere in the ocean? More precisely, if we can represent ecophysiological dynamics by equations, are the parameters of the equations the same everywhere? If we aim to construct the submarine light field from the bio-optical properties of the micro-organisms, are the relevant bio-optical properties the same everywhere? Related questions would include: Are the functional responses, parameters and bio-optical properties seasonally variable?

The imperative to address such questions provides the motivation for the present monograph. When we seek to quantify ecological or biogeochemical fluxes in the ocean, we want to know if the relevant processes act at the same rate everywhere for the same intensity of forcing. As a specific example, if a given marine autotrophic biomass, expressed as concentration of chlorophyll, is forced with a saturating irradiance, would the photosynthetic response (the assimilation number) be the same everywhere in the ocean and in all seasons?

If the assimilation number is not spatially uniform and constant in time, how might it be distributed? One possibility is that it could be a continuous function of an environmental property, such as temperature. In general, for the ecophysiological parameters of interest (e.g., the assimilation number), such functions, that would be robust everywhere, have not been discovered.

An alternative view is that the parameters we seek are not distributed in a continuous manner. Rather, we suppose that at the large scale, the ocean ecosystem comprises a suite of contiguous, autonomous regions whose biological structure and function are distinctive and serve to differentiate one from another. On this scale, parameters of interest might change abruptly at the boundaries between the regions (piecewise continuity). Within the regions, the magnitudes of the parameters would be determined by rules internal to the region concerned: parameters would be controlled more strongly by processes within the region than by interactions between regions.

A related set of issues can be collected under the question: In calibrating OCR

data for chlorophyll retrieval, should the retrieval algorithm be the same everywhere, or do different algorithms apply at different places on the globe? If the algorithm is not the same everywhere, how do we know where to change it?

1.3 History

In seeking approaches to the estimation of primary production using OCR data, Platt *et al.* (1991) noted the following identity

$$P = B \times P^B,$$

where P is the absolute rate of primary production, B is the phytoplankton biomass, expressed as a concentration of chlorophyll (such as could be obtained by OCR) and P^B is the specific primary production (primary production normalised to biomass, $P^B = P/B$). In nature, B is a highly variable property, with a dynamic range of more than four orders of magnitude. It is exactly this variability that can be observed by OCR on synoptic scales.

On the other hand, the normalised production P^B is a property with a much more narrow dynamic range, and by virtue of its normalisation factor, is not dependent on the biomass in the first order. Dimensionally, it corresponds to the assimilation number (P_m^B , where the subscript m means maximum): it is the photosynthetic response of unit chlorophyll biomass.

To calculate primary production at a given space-time point by OCR using the identity above, B can be assigned from the OCR data, but P_m^B must be assigned in some other way, since it cannot be measured by OCR. It was proposed (Platt and Sathyendranath, 1988) that P_m^B (and other parameters required for the calculation) were properties of the regional autotrophic assemblage, and that this would be an intrinsic characteristic of the oceanographic regime in which it was embedded. They perceived the ocean as an aggregate of such regimes, which they referred to as regions or provinces, and termed this type of partition a *dynamic biogeography*. In the literature, they have been called, variously, biogeographic provinces, biogeochemical provinces and ecological provinces. When primary production was calculated for a given ocean-colour image, the algorithm for production would be implemented for each pixel in the image using parameters that were assigned according the province in which the pixel lay, using whatever information was available about that province.

To follow the approach proposed by Platt and Sathyendranath (1988), the first requirement is a partition of the world oceans into provinces made according to some protocol. This task was undertaken by Longhurst (1995; 1998; 2006). His premise was that the partition could be based on commonality in physical forcing, in so far as that forcing was significant for the requirements of phytoplankton. At the first level of reduction Longhurst (1995; 1998) recognised four principal *biomes* (also referred to as *domains*, Longhurst 1995): the Polar Biome, where the seasonal

coverage by ice was the characteristic factor; the Westerlies Biome, where local forcing determines mixed-layer depth; the Trade-Winds Biome, where local physical structure might be determined by processes acting at long distance; and the Coastal Boundary Zone Biome, where interaction between local winds and local topography determines the intensity of physical forcing. These four Biomes are recognisable in every major ocean basin.

The individuality of the ocean basins is expressed at the next level of reduction, the partition into provinces (Figure 1.1), roughly ten for each basin¹. The partition could be used as a template for summarising the world database on the parameters needed to calculate primary production from OCR data. This structured database was then used to make parameter assignments in estimates of primary production in the Atlantic Ocean (Sathyendranath *et al.*, 1995) and of global, marine production (Longhurst *et al.* 1995).

It was understood from the beginning (Platt and Sathyendranath, 1988) that the boundaries of the provinces would not be fixed, but that they would move under seasonal and interannual changes in physical forcing. The boundaries were expected to be elastic, and the partition was referred to as dynamic. In this context, the elegant partition of Longhurst (1998), with its rectilinear boundaries (a convenience for computing), is to be seen as an intermediate step rather than a final solution. We know that the boundaries are not rectilinear and we know that they are not rigid.

The next step is to build on the Longhurst partition to create a truly dynamic partition in which the boundaries between the provinces are not constrained to be straight lines, and moreover are free to move as the forcing varies. The methods by which the dynamic partition can be achieved form the principal subject matter of this monograph. It will be seen that the most valuable tool available for us to reach the desired goal is the OCR data stream.

1.4 Significance

The concepts of oceanic biogeography and ecological classifications have existed for almost a century (see review in Longhurst 1998). Whether real or only conceptual, a classification into provinces provides a useful framework for understanding the mechanisms controlling biological, physical and chemical processes operating therein and the interactions between them. Criteria have been established for defining provinces based on physical forcings, availability of light and nutrients, complexity of the marine food web and other factors. The use of provinces as an aid to assessing marine primary production was exemplified by Longhurst *et al.* (1995). In general, such classification systems address the heterogeneous nature of

¹Shapefiles of the initial static boundaries of Longhurst's provinces, for use with ESRI/ArcGIS, SAGA GIS or any other open source GIS software, have been constructed by the Flanders Marine Data and Information Centre, and can be downloaded from:

<http://www.vliz.be/vmdcdata/vlimar/downloads.php>

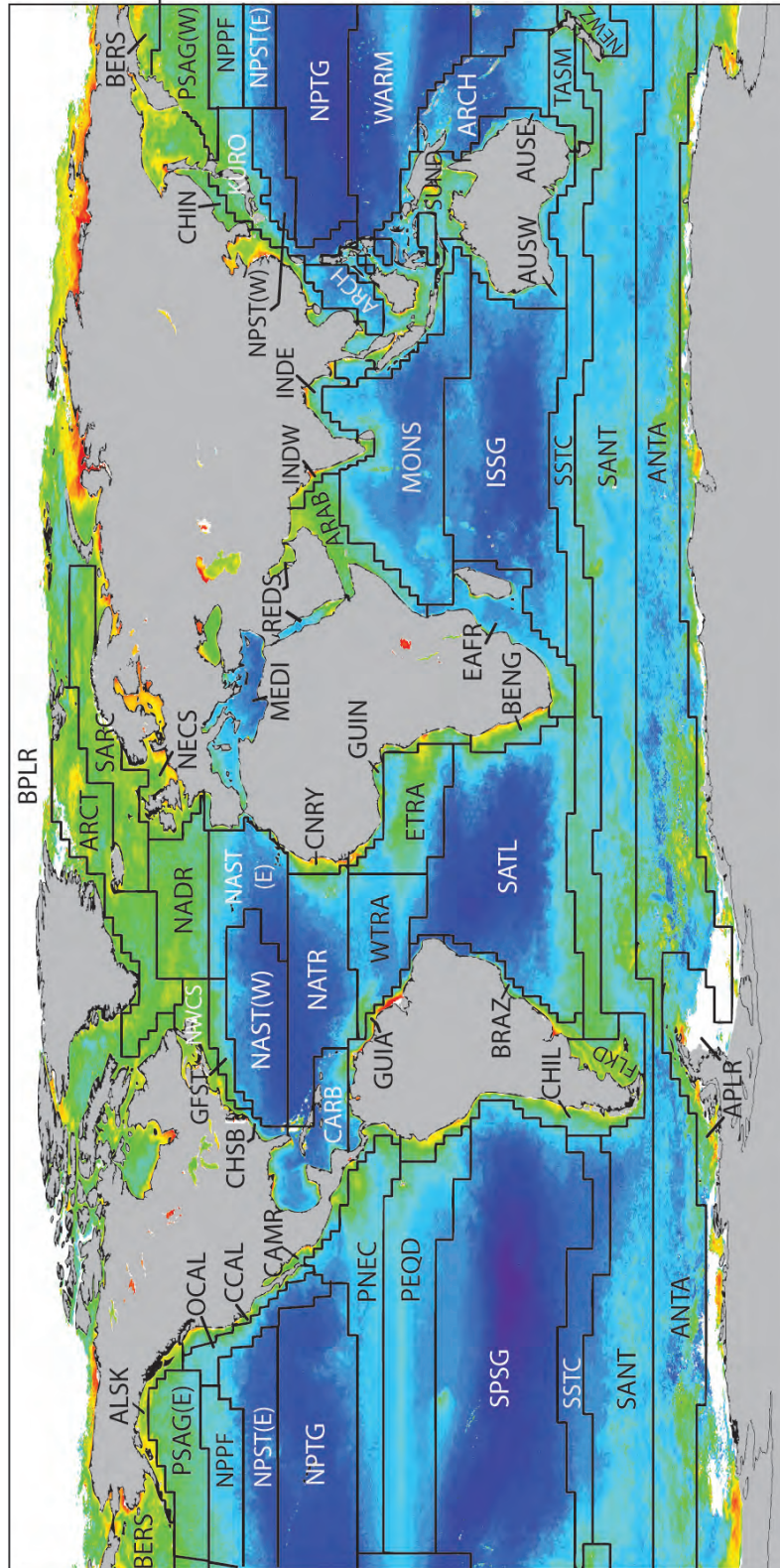


Figure 1.1 Global biogeochemical provinces, adapted from Longhurst (2006). See also <http://www.mar.dfo-mpo.gc.ca/science/ocean/BedfordBasin/Papers/Longhurst1998/Provinces/EcoTogicalTheSea.htm> for data on individual provinces.

the global ocean environment, and represent the effort of scientists to comprehend the whole system by understanding its homogeneous components. With the advent of the first global images of chlorophyll distribution from the CZCS sensor at the beginning of the 1980s, pelagic oceanographers had a new and formidable tool to identify basin scale boundaries between different marine biomes. Over more than twenty years, much work has been undertaken to define appropriate methods to optimise use of this and subsequent datasets in the context of marine biogeography and biogeochemistry.

1.5 Terminology

The act of defining boundaries on the ocean surface to separate areas with characteristic ecophysiological properties is referred to as making *a partition* or a *classification*. The areas so separated are called *provinces*, often qualified as *biogeochemical* or *ecological provinces*. The original Longhurst partition was based on commonality of physical forcing. Other implementations have used statistical procedures based on the recognition of *clusters* or *classes* in the input data. In some cases, the emphasis is on identifying areas with common bio-optical properties, in which case the resultant provinces may be called *optical water types* or *distinct optical water types*. Applied to provinces, the qualification *static* implies that the boundaries of the provinces are not allowed to vary with season or between years. When this restriction is relaxed, the provinces are said to be *dynamic*.

Chapter 2

Implementation Issues

Mark Dowell, Timothy Moore, Janet Campbell, Frédéric Mélin, Nicholas Hardman-Mountford, David Broomhead and Emmanuel Devred

2.1 Static/Traditional Approach

While recognising the value of species-specific global and regional maps of biogeography produced by several workers (Margalef 1961; Brinton 1962; Smayda 1980; Colebrook 1982), Longhurst (1998) considered them insufficient to provide the sole basis for ocean partition. He therefore proposed a primary and secondary hierarchical partitioning of the pelagic ocean into a suite of interconnecting, geographically-identifiable biomes and provinces as discussed in Chapter 1. Longhurst (1998) combined the following factors to define regional ecological biogeography: latitude, bathymetry, proximity of coastline, influence of coastal upwelling and land effluents, seasonal irradiance cycle, local wind and precipitation regime, remote forcing of pycnocline depth and nutrient supply to upper layer. A detailed example of the classification of ecological provinces in the Arabian Sea is given below.

2.1.1 Arabian Sea provinces

The Trade Wind biome is represented by the tropical oceans extending polewards from the equator to about the same latitude in each hemisphere (30°N - 30°S). Some of the important physical characteristics that determine its singular ecology are the relatively constant level of solar irradiance across seasons, presence of surface mixed layer throughout the year and larger, but fewer eddies towards the equator. Longhurst (1995; 1998) partitioned the Indian Ocean under the Trade wind biome into eight provinces, including the following four ecological provinces of the Arabian Sea which are based on detailed regional oceanographic characteristics (Figure 2.1):

1. Red Sea, Persian Gulf Province (REDS): The two adjacent evaporative basins are taken together as a single province, Red Sea extending up to the Straits of Bab-el-Mandeb and Persian Gulf within the Straits of Hormuz.
2. Northwest Arabian Upwelling Province (ARAB): this province includes the coastal areas of the northern Arabian Sea from Somalia to Pakistan and the deep northwestern Arabian Sea. Both areas are regions of strong biological en-

- hancement during the southwest monsoon due to coastal divergent upwelling and to winter convection and turbulent mixing during the northeast monsoon.
3. Western Indian Coastal Province (INDW): Coastal areas and continental shelf of western India and southern Pakistan extending from the mouth of the Indus at 25°N to the Gulf of Mannar in the south at about 7°N are included in this province. The regional circulation and biological response in this province are influenced both by local and remotely-forced wind-driven upwelling.
 4. Indian Monsoon Gyre Province (MONS): The MONS province extends from the hydrochemical front at 10°S to the northern part of Arabian Sea. It includes the offshore limits of coastal provinces. The most important characteristic of regional oceanography is seasonally-reversing monsoon winds and monsoon currents in this province.

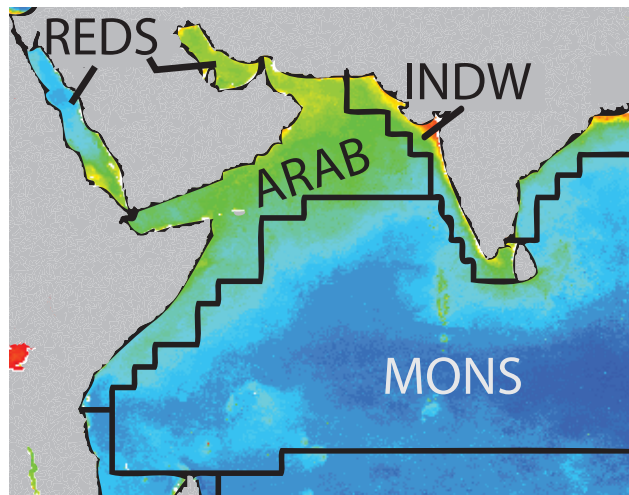


Figure 2.1 Biogeochemical provinces of the Arabian Sea, adapted from Longhurst (2006).

In Longhurst's initial scheme of partition, the provinces were fixed in space and time although it was acknowledged that they would shift from year to year as inter-annual forcings varied. The borders between the provinces were defined as a boundary, and the boundary relationship between the provinces was also considered to vary seasonally and between years. Although, the requirement of boundaries to be dynamic was explicit, the initial implementation did not achieve this. However, Longhurst strongly emphasized the need to locate boundaries between provinces in real time by defining features that are accessible using remote sensing. He suggested identifying discontinuities in sea surface temperature maps or ocean-colour maps generated from satellite data to locate boundaries between provinces, an approach that relies on the premise that boundaries are transition zones between provinces where a sharp or gradual change occurs in the ecological properties due to a change in the physical environment. The ecological characteristics in the provinces on either side of the boundary are distinct from each other. An advantage of adopting

the use of remotely-sensed data to locate the coordinates of boundaries is that the boundaries can be adjusted in real time to reflect changes in physical forcing. In other words, the boundaries between the provinces may migrate in response to changes in physical environment, or the ecological properties may be modified in a way that allow adjacent provinces to coalesce and become indistinguishable for longer or shorter time periods. Various protocols have been developed for dynamic partitioning, and several are elaborated in this section.

2.2 Dynamic Approaches

There have been a number of approaches addressing the problem of dynamic provinces in the ocean in recent years (Moore *et al.* 2001; Alvain *et al.* 2005; Devred *et al.* 2007; Oliver and Iriwn 2008). These approaches share the characteristic of comparing remotely-sensed data to pre-determined “classes”, which can be represented in different ways but nonetheless equate to provinces. The outcomes of these approaches yield spatial maps of the provinces that are not pre-determined, and allow for varying locations of province borders. Some of these approaches share input fields but differ in methodological implementation (e.g., Moore *et al.* 2001 and Alvain *et al.* 2005), while others produce a similar output product yet differ on input and implementation (Melin and Challis 2004; Devred *et al.* 2007; Oliver and Irwin 2008).

One key difference among the approaches is the concept of hard boundaries versus fuzzy boundaries. Of the methods, the province boundaries in Moore *et al.* (2001) take the form of fuzzy memberships. This approach differs from the others in this regard. Fuzzy memberships provide a solution to the problem of step-wise transitions across boundaries that are otherwise crisp (i.e. hard). The implementation of this approach is similar to that of Melin and Challis (2004), as both methods implement a distance estimator based on the Mahalanobis distance for assigning class membership. The major difference is an extra step in Moore *et al.* (2001), which feeds this distance calculation into a probability density function. This outcome produces the fuzzy membership. Thus, the difference between producing hard and fuzzy boundaries may not be that significant in terms of methodological implementation.

2.2.1 Fuzzy logic

Fuzzy logic was first introduced by Zadeh (1965) as a mathematical way to represent vagueness and imprecision inherent in data. The idea behind fuzzy sets simply states that an object can have partial membership in more than one set. This concept is a departure from classical set theory, which maintains that an object belongs exclusively to only one set. The degree of belonging to any given set is expressed mathematically by a membership function which ranges from 0 to 1. In fuzzy set

theory, full membership to exclusively one set is still permitted, and thus it is a superset of classical set theory.

Table 2.1 Characteristic values of sea surface temperature (SST), photosynthetically available radiation (PAR), and chlorophyll (CHL) for each class, and description of the associated provinces.

Class	SST	PAR	CHL	Province
Class 1	High	High	Very low	Sub-tropical gyres
Class 2	High	High	Low	Tropical
Class 3	Medium	Low	Low	Temperate deep mixed layer depth
Class 4	High	High	Medium	High nutrients, high latitude
Class 5	Low	Medium	Medium	Polar
Class 6	Medium	Very low	Medium	High Latitude, low light
Class 7	Medium	Low	High	Enclosed temperate seas
Class 8	High	High	High	Upwelling/ river plumes
Class 9	Low	Medium	Very high	Turbid coastal

Fuzzy logic has been applied to spectral reflectance measurements to identify optically-distinct water types (Moore *et al.* 2001, see also Chapter 4), with the aim of developing regional or class-specific bio-optical algorithms. Subsequently the method was applied to satellite ocean-colour observations to select and blend algorithm results. It was also applied to a comprehensive *in-situ* primary productivity data set (largely drawn from the data of Behrenfeld and Falkowski 1997) in which nine classes were identified based on the ranges of CHL, SST, and PAR within the data set. The motivation was to evaluate the performance of primary productivity algorithms within different environmental *niches*. Subsequently, the classification was applied to monthly-composited satellite data on CHL, SST, and PAR to map the global distribution of the nine classes. The resulting classes were spatially coherent and logically distributed within any given month, and yet temporally dynamic from month to month. The nine classes thus “scaled up” to represent nine large-scale dynamic provinces (Table 2.1).

The overall scheme, as depicted in Figure 2.2, consists of two steps illustrated by the two boxes. In the first step, applied strictly to *in-situ* data, distinct classes are defined on the basis of SST, PAR and CHL through an unsupervised cluster analysis. The database should ideally include a complete representation of all ecological biomes or provinces. The statistical properties of these three variables for each class then becomes the basis for defining membership to each class found in the satellite data. The second step, depicted in the lower box in Figure 2.2, illustrates the application of the method to satellite data. At each ocean pixel \mathbf{x} , we have satellite observations of CHL, SST, and PAR (as generated routinely with SeaWiFS data). A membership function, $f_i(\mathbf{x})$, is computed for each \mathbf{x} to each class i ($i = 1, 2, \dots, c$). The membership function (ranging from 0 to 1) expresses the likelihood that the vector of observations $\mathbf{V} = (\text{SST}, \text{PAR}, \text{CHL})$ at pixel \mathbf{x} was “sampled” from the

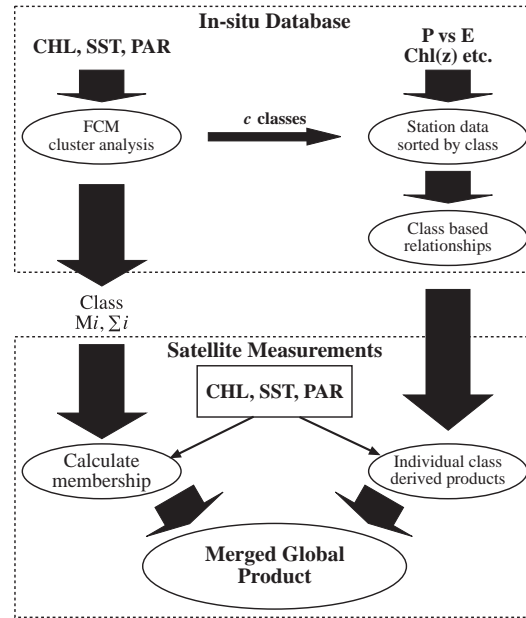


Figure 2.2 Schematic representation of the fuzzy logic procedure adopted. Top half of the flow chart shows analysis related to *in-situ* data and the bottom half shows that related to satellite data.

distribution of class i . Membership values are then used to weight variables derived from the corresponding class-specific models. In practice, only those classes with membership values above a certain threshold are considered to be plausible, and hence, models need not be applied for classes that are implausible.

An unsupervised, fuzzy, c -means (FCM) clustering algorithm (Bezdek 1981) was applied to the *in-situ* data to identify the classes. The FCM algorithm produces a fuzzy clustering of the data into a specified number of clusters (herein denoted as c). The clustering routine returns the means of SST, PAR and CHL for the c -classes, and a matrix U containing the memberships of each point in each class. The number of clusters, c , is an input to the FCM clustering routine, but the optimum number is not known in advance. We may vary c and evaluate the results with the aid of *cluster validity measures* (Bezdek *et al.* 1997). Once the clusters are identified, the individual stations are sorted according to the cluster (class) with the highest membership value (Figure 2.3). The mean (SST, PAR, CHL) vector, M_i , and reflectance covariance matrix, Σ_i , are calculated for each class i . These are subsequently used in the membership function (defined below).

The data set used in the cluster analysis was evenly distributed among the 9 classes (classes contained between 120 and 160 stations). This was not prescribed by the FCM clustering method used, and therefore is an indication that the mean and variance determined for the classes is representative of natural variability.

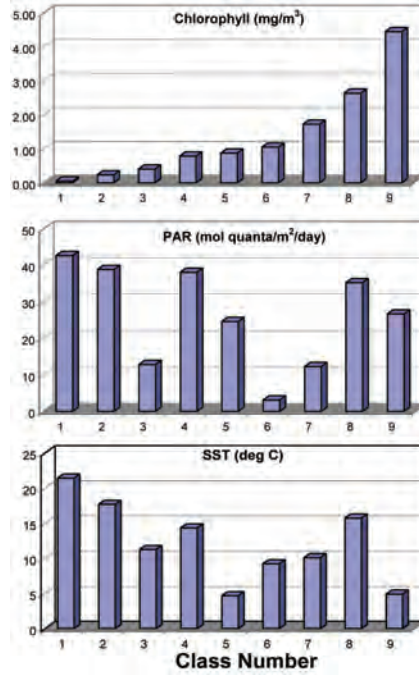


Figure 2.3 Plot showing the mean values of the three variables in each of the nine classes. The classes themselves have been ordered so that chlorophyll increases in concentration from Class 1 to Class 9.

Membership to the i^{th} class is defined by a fuzzy membership function. For any measured $V = (\text{SST}, \text{PAR}, \text{CHL})$, the fuzzy membership is defined in terms of the squared distance between V and the i^{th} class mean M_i . For this, we use the squared Mahalanobis distance given by:

$$Z_i^2 = (V - M_i)^t \Sigma_i^{-1} (V - M_i), \quad (2.1)$$

where t indicates the matrix transpose. The Mahalanobis distance is a generalized distance from V to M_i in units of standard deviations adjusted for covariance.

If the V vectors belonging to class i are multivariate normal, and if the observation was “sampled” from class i , then Z_i^2 has a χ^2 distribution with n degrees of freedom (where n is the dimension of the set). As a measure of likelihood that V is drawn from class i , we define the membership function to be:

$$F_i = 1 - F_n(Z_i^2), \quad (2.2)$$

where $F_n(Z^2)$ is the cumulative χ^2 distribution function with n degrees of freedom. When $V = M_i$, then $Z_i^2 = 0$, and $f_i = 1$. This would be interpreted as the pixel having full membership in class i . As V becomes more distant from M_i , f_i decreased from 1 to 0, indicating a diminishing likelihood that the pixel belongs to class i .

Using the class statistics defined from the *in-situ* data, this method has been applied to monthly-composited satellite measurements of CHL and PAR from SeaWiFS,

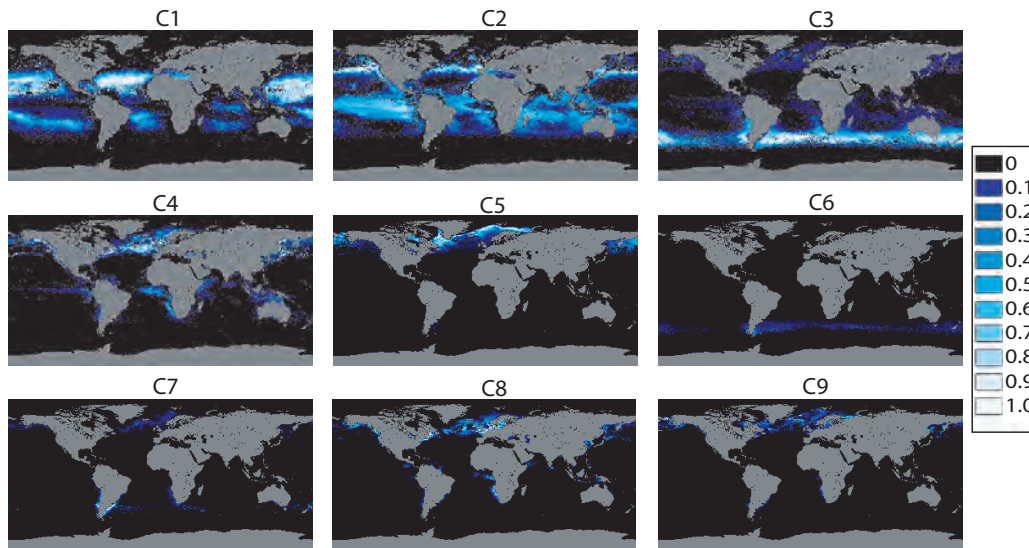


Figure 2.4 Fuzzy membership maps for July 2000, for the nine classes.

and SST from AVHRR. Fuzzy membership values were calculated for all pixels and all classes. For each month of global SeaWiFS and AVHRR data, nine membership maps were generated showing the distribution of the nine classes. The membership maps for July 2000 are shown in Figure 2.4, and maps for four months (January, April, July, and October 2000) showing the classes with the highest membership values (so-called “hardened” classes) are presented in Figure 2.5 to illustrate the seasonal variability in the location of the provinces.

2.2.2 Spatial principal component analysis

Ecological provinces can be thought of as coherent, co-varying spatial regions. As such, a theoretical approach to defining natural length scales in ecological systems has been defined, based on spatial “windows of correlation” (Keeling *et al.* 1997). On land, the spatial extent of such provinces varies little through time so it is easy to map. The dynamic nature of the oceans, however, means that the spatial extent of such provinces can vary significantly through time. Any attempts to describe these provinces need to account for both spatial and temporal variability together, specifically testing whether putative provinces vary in spatial extent coherently through time.

Principal Components Analysis (PCA), also called Empirical Orthogonal Function (EOF) analysis¹, is an objective statistical method for analysing modes of co-variability in multi-dimensional data sets. Spatial and temporal PCA (otherwise

¹The terms PCA and EOF analysis are used interchangeably here, usually based upon the term used in the study being reported.

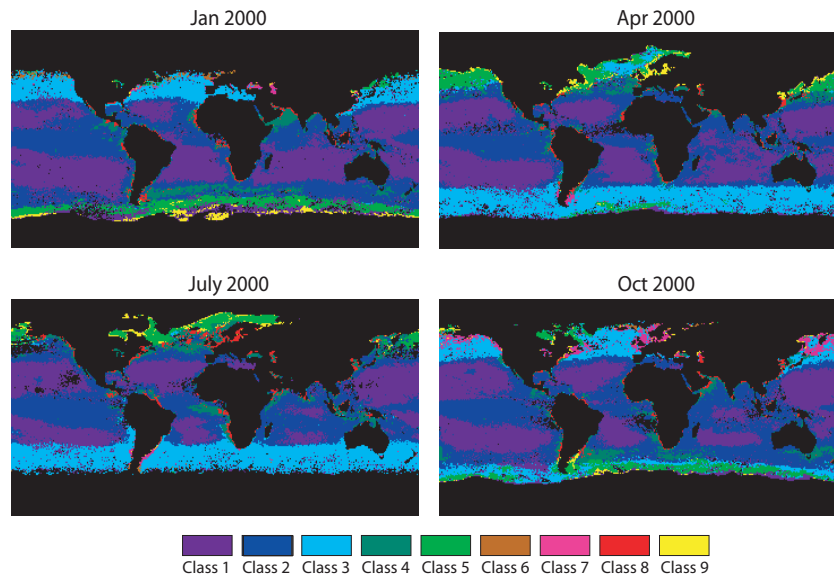


Figure 2.5 Seasonal variability in the geographic distribution of the nine classes in January, April, July and October 2000 based on monthly composites of the “hardened” classes (i.e. class with highest membership value).

known as T-mode and S-mode EOF analysis, respectively) are implementations of this method for dealing with spatio-temporal co-variability. Spatial PCA describes specifically how spatial modes vary in time, whereas temporal PCA describes how temporal modes vary in space. These methods have been proposed as a useful technique for the identification and investigation of marine ecological provinces.

EOF analysis of spatio-temporal data has been used routinely in physical oceanography and atmospheric studies, but much less frequently in biological oceanography since most remote sensing studies have used sea surface temperature (SST) data. S-mode EOF analysis (temporal PCA) has been the most commonly-used method and was, until recently, the only method applied to ocean-colour data (e.g. Garcia-Moliner and Yoder 1994; Ryan *et al.* 1999; Wilson and Adamec 2001; Yoder *et al.* 2002; Yoder and Kennelly 2003; Palacios 2004). However, a number of studies have suggested that T-mode EOF analysis (spatial PCA) is better suited to obtain spatial variance in areas where persistent spatial patterns with strong horizontal gradients are present (e.g. upwelling, fronts, persistent eddies; Lagerloef and Bernstein 1988; Paden *et al.* 1991; Fang and Hsieh 1993). The first direct application of spatial or temporal PCA to the determination of oceanic provinces was undertaken by Hardman-Mountford and McGlade (2002) for the Gulf of Guinea region of the eastern tropical Atlantic using Advanced Very High Resolution Radiometer (AVHRR) SST data. In this study, two biomes were used: the first covered the African coast from Mauritania to Namibia. The first principal component (PC1) of this region separated warm tropical waters from cooler subtropical waters and showed very little temporal variability, while

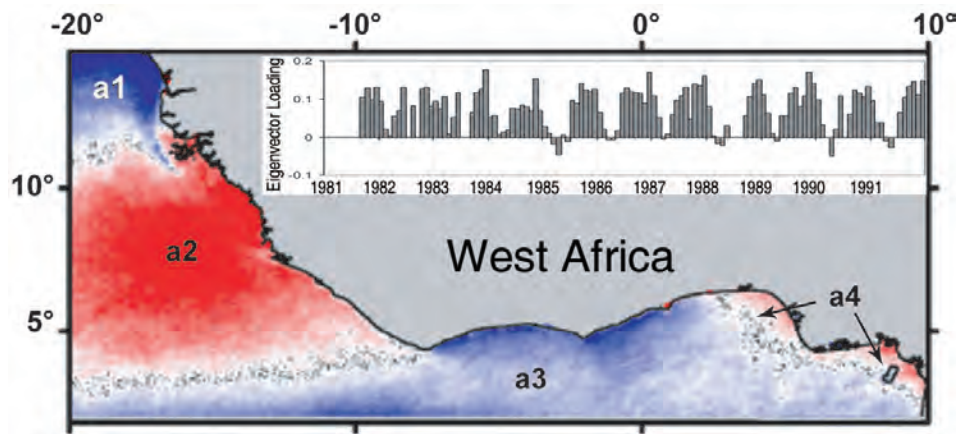


Figure 2.6 PC2 of the Gulf of Guinea region. The PCA has separated four distinct areas: A1= Senegalese upwelling influence, A2= Guinea Dome region, A3= Area of equatorial dynamics (equatorial and coastal upwelling and downwelling), A4= Area of strong freshwater input from the Niger Delta and Cameroon rivers. Adapted from Hardman-Mountford and McGlade (2002).

PC2 showed a seasonal oscillation of warming and cooling between the northern and southern hemispheres. The second biome focused on the coastal area of the Gulf of Guinea, in the equatorial Atlantic. This was entirely within the warm tropical region identified from PC1 of the larger biome and PC1 of the sub-biome showed the same inter-hemispheric seasonal pattern as PC2 of the larger biome. PC2 of the sub-biome showed further boundaries separating Gulf of Guinea waters from wind-driven upwelled waters originating off Ghana and the Ivory Coast to the north, and separating waters within the Gulf of Guinea into:

- ❖ those under the influence of equatorial upwelling,
- ❖ those in the vicinity of the Guinea dome and
- ❖ those with a large freshwater influence in the Bight of Biafra (see Figure 2.6).

Although these distinct regions could not all be determined through comparison of SST fields alone, they could be identified by the covariance of the SST fields through time. The nested spatial scales at which these distinct regions were identified also shows the power of this technique. It should be noted that, since SST only describes the physical variability of the region, PCA of satellite SST was used to test and refine system and subsystem boundaries proposed by other *in situ* descriptive studies using a wider range of biophysical variables.

A second study was undertaken by Hardman-Mountford *et al.* (2008) to apply this technique to delineating ocean provinces and biomes globally from a monthly climatology of SeaWiFS chlorophyll-a concentration (Chl-a) data. Other studies using spatial PCA, although not explicitly addressing this issue, have also shown results suggesting that this method is applicable to the investigation of marine ecological provinces. In areas with a persistent, strong spatial structure, this is often identified

in the first or second PC and is associated with a temporal signal that is of one sign (positive or negative), showing the spatial structure represented to be always present. When this spatial structure is seen in PC1 it can sometimes resemble the temporal mean and have very reduced, near constant temporal variability (Hernandez-Guerra and Nykjaer 1997; Armstrong 2000; Kuo *et al.* 2004). While statistically this is different from the mean field, it does represent a near-constant part of the variance. Its value lies in this pattern being a permanent, real part of the variance structure for the region being studied. Thus the strong spatial patterns represented may be interpretable in terms of ocean physical systems and provinces.

Hardman-Mountford *et al.* (2008) exploited this feature of PCA as the basis for their recent study. They argued that because (i) Chl-a represents an integration of both physical forcing and top down controls on the ecosystem, and (ii) that systems theory predicts that the spatial extent of ecosystems should be discernible from persistent patterns in ecosystem variables, then the near-constant spatial patterns identified across all seasons from Chl-a data in PC1 of their analysis are representative of ocean ecosystems or provinces. They supplemented this analysis with additional multivariate techniques (multi-dimensional scaling and cluster analysis) which identified the same spatial structure in global surface Chl-a, and also showed that sub-provinces of the higher level provinces exist at nested spatial scales. Regions of similar Chl-a were then classified globally according to their biome (6 classes covering the spectrum from eutrophic to oligotrophic waters, Figure 2.7), with the regional occurrence of a particular biome labeled a province. Comparison of these biomes with those of Longhurst (1998) showed a great deal of similarity. The major difference was that these objectively-defined provinces identified the equatorial regions as distinctly separate from the subtropical gyres, which Longhurst's classification lumps together under the 'Trades' biome.

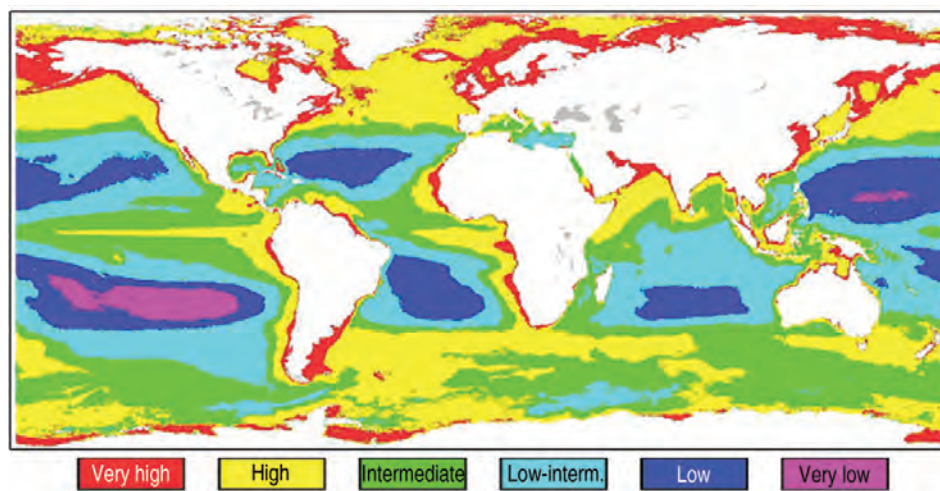


Figure 2.7 Classification of biomes from PC1 of chlorophyll-a, adapted from Hardman-Mountford *et al.* (2008).

Comparisons of temporal and spatial PCA have shown similar results, but with spatial PCA representing dominant spatial patterns more clearly (Hernandez-Guerra and Nykjaer 1997; Tseng *et al.* 2000; Bisagni *et al.* 2001). This may largely be due to the removal of the temporal mean, hence the dominant spatial structure, by temporal PCA. Nonetheless, temporal PCA has been applied to satellite ocean-colour data in a number of studies, and these results also highlight the applicability of PCA to the investigation of marine ecological provinces through the identification of strong spatial structure in ocean chlorophyll (e.g. Ryan *et al.* 1999; Wilson and Adamec 2001; Brickley and Thomas 2004). Ho *et al.* (2004) removed the spatial rather than temporal mean for an S-mode EOF analysis (temporal PCA), allowing the temporal amplitude of EOF1 to remain constant and showing the spatial variability structure represented to be always present.

The global-scale analysis of ocean colour by Yoder and Kennelly (2003) used S-mode EOF analysis (temporal PCA) to analyse the four-year time series of SeaWiFS Chl-a data for the period from January 1998 to December 2001. Their results showed EOF1 to be primarily associated with inter-hemispheric phase shifts in seasonality while EOF2 showed differences in seasonal bloom cycles between the Atlantic and Pacific Oceans and also highlighted a number of seasonal chlorophyll features. Most notable within the context of ecological provinces is the resolution of major ocean regions in EOF2 corresponding to the major high-latitude, temperate, sub-tropical and equatorial zones as well as reflecting inter-basin asymmetries.

A number of S-mode EOF analyses have compared results between SST and ocean-colour data, and found similar spatial patterns to be identified from both data sets (Garcia-Moliner and Yoder 1994; Baldacci *et al.* 2001; Palacios 2004), although sometimes in different EOFs (Bisagni *et al.* 2001). Yoder *et al.* (2002) found SeaWiFS and CZCS data showed similar patterns to each other, but these differed from those identified from SST data; however, they could be attributed to the same physical forcing processes. Longhurst (1998) described a number of physical factors that may underpin ecological provinces in the ocean, so such relationships between spatial patterns identified from physical (SST) and biological (ocean colour) data are significant and highlight the value of PCA for investigating these regions.

Limitations of PCA include orthogonality constraints and assumptions of linearity. Rotation of principal components and neural network-based non-linear PCA methods may be useful in considering these constraints. A more fundamental methodological issue is that it does not actually classify regions or clearly define boundaries between provinces, so a combination with other methods is required for these goals to be achieved (as implemented by Hardman-Mountford *et al.* 2008). Nonetheless, the objectivity of the method and its reliance upon only the inherent variability of the data make it useful for testing the applicability of the concept of ecological provinces in the ocean, specifically whether stable regions exist over large spatial scales in the dynamic marine environment, as well as for testing and refining provinces proposed by other methods.

2.2.3 Dynamic partitioning with subjectively-defined classes

There are numerous ways of dividing a given set of observations into a limited number of groups, or classes, that suit particular applications. If no *a priori* information is accounted for, techniques like clustering analysis may be used to bring out the important features present in the distribution. Other classification schemes have been proposed that integrate a varying level of empirical information, for example for the detection of some types of phytoplankton blooms (e.g., Subramaniam and Carpenter 1994) or a feature-based classification of water masses in a given region (Martin Traykovski and Sosik 2003). A partition of the global ocean into

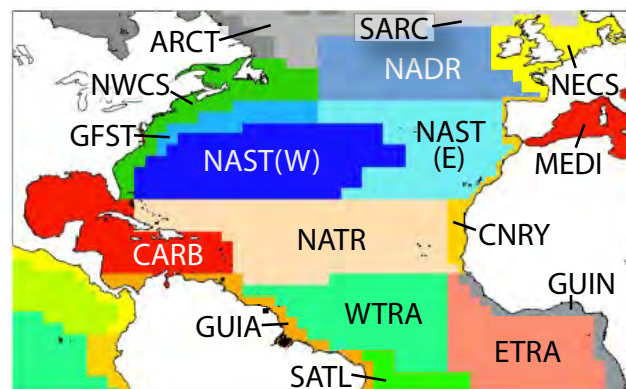


Figure 2.8 Location of ecological provinces in the northern Atlantic Ocean, described by Longhurst (1998) – see footnote for province names.

ecological provinces has been comprehensively described by Longhurst (1998)². This framework for a regional ecology of the ocean takes into account factors such as the light climate, the physical circulation patterns, the inputs of macro- and micronutrients, or the distance from continental masses. An application of this distribution has been the calculation of ocean primary productivity (Longhurst *et al.* 1995), by associating each province and season with a set of parameters that describe the phytoplankton photosynthetic performance and the vertical structure of chlorophyll-*a* concentration.

A partition is also a convenient way of defining an *a priori* knowledge of the main biophysical characteristics of an ocean basin, including the optical signature expressed by the spectrum of normalized water-leaving radiance $nL_w(\lambda)$. This framework can be used to illustrate a classification of an ocean basin (for example, the northern Atlantic Ocean) into distinct water masses on the basis of a subjectively

²Province nomenclature for NW Atlantic – ARCT: Atlantic Arctic; SARC: Atlantic Subarctic; NADR: North Atlantic Drift; NWCS: NW Atlantic Shelves; NECS: NE Atlantic Shelves; GFST: Gulf Stream; NAST(W): North Atlantic Subtropical Gyre (West); NAST(E): North Atlantic Subtropical Gyre (East); CNRY: Canary Coastal; CARB: Caribbean; NATR: North Atlantic Tropical Gyre; GUIN: Guianas Coastal; WTRA: Western Tropical Atlantic; GUIN: Guinea Current Coastal; ETRA: Eastern Tropical Atlantic; SATL: South Atlantic Gyral

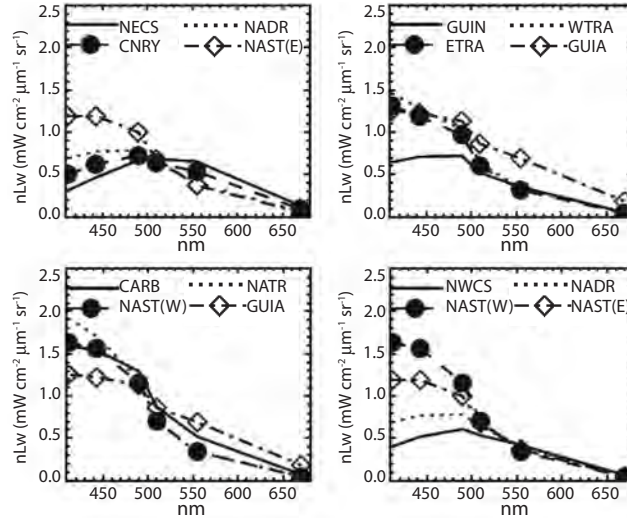


Figure 2.9 Mean $nL_w(\lambda)$ spectra for the climatological month of April, grouped by neighboring provinces.

defined training set. The working hypothesis is that the ensemble of $nL_w(\lambda)$ spectra given by the grid points located in a province captures features that are sufficiently distinct with respect to adjacent provinces.

For that purpose, the first 6 years of the SeaWiFS time-series have been used to derive a monthly climatology of the normalized water-leaving radiance spectrum $nL_w(\lambda)$. For each month and province in the biome (shown in Figure 2.8), the frequency distribution of $nL_w(\lambda)$ and its main statistical properties (mean, standard deviation, covariance matrix) were then computed. Figure 2.9 shows the mean $nL_w(\lambda)$ spectra for the climatological month of April, taken as a representative example, grouped by neighboring provinces. It appears that each province can be associated with characteristic optical properties, under the influence of different sources of absorption and scattering (phytoplankton pigments, detritus, minerals, coloured dissolved substances).

For a given climatological month, each province is taken as a class defined by the frequency distribution of log-transformed nL_w at 412, 490 and 555 nm (these wavelengths are believed to carry enough spectral information for the present purpose) of all grid points located in the province, and the corresponding mean μ and covariance matrix Σ . For any triplet x (a 3-wavelength vector), the Mahalanobis distance $\Delta^2 = (x - \mu)^T \Sigma^{-1} (x - \mu)$ quantifies the degree to which x is close to the distribution (D'Alimonte *et al.* 2003). Another indicator of membership is defined as:

$$p = \frac{1}{(2\pi)^{d/2} |\Sigma|^{1/2}} \cdot e^{-\frac{1}{2} (x - \mu)^T \Sigma^{-1} (x - \mu)} \quad (2.3)$$

where $|\Sigma|$ is the determinant of Σ and d is equal to 3. Strictly speaking, the expression of p can be interpreted in terms of probability of membership to the 3-dimensional

distribution represented by μ and Σ only if the distribution is normal (i.e., if the 3-dimensional distribution of $nL_w(412, 490, 555)$ is log-normal). In practice, the normality is not well verified for any of the provinces, which is easily understood: the high number of grid points constituting a province, and thus the size of the frequency distribution, requires a very tight fit to a theoretical gaussian distribution to satisfy classical tests of normality (e.g., Kolmogorov-Smirnov). The normality of these large distributions is impeded by the existence of organized structures (currents, fronts, eddies) in each province, as well as the initial inclusion of water masses that specific characteristics will eventually assign to another province. An extreme case is that of the province CARB (Caribbean Sea) initially defined on geographical terms rather than on oceanographic criteria. Consequently, p is used only as a index for classification, assuming that the intrinsic properties of a province are sufficiently well represented by μ and Σ so that they will prevail in the final partition.

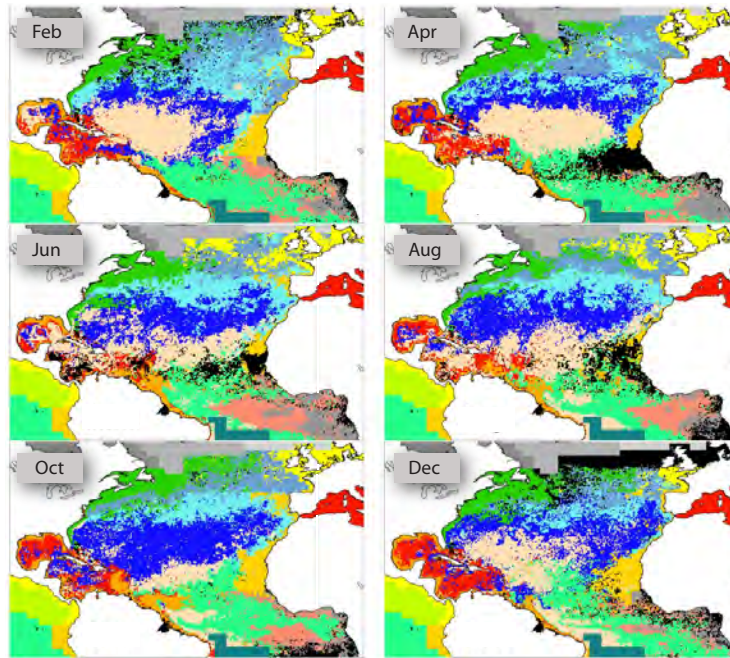


Figure 2.10 Dynamic distribution of ecological provinces in the northern Atlantic for six months of 1998 (same colour code as on Figure 2.8).

An example calculation is performed with the monthly maps of the year 1998. Each grid point is tested for membership to arbitrarily-defined candidate provinces (the province of the original membership as well as a selection of neighbour provinces, a selection that might itself vary with the location of the grid point). The grid point is eventually assigned to the most representative province, according to the value of p . The province GFST (Gulf Stream) is excluded from the lists of candidates in these calculations because it is a narrow region of variable oceano-

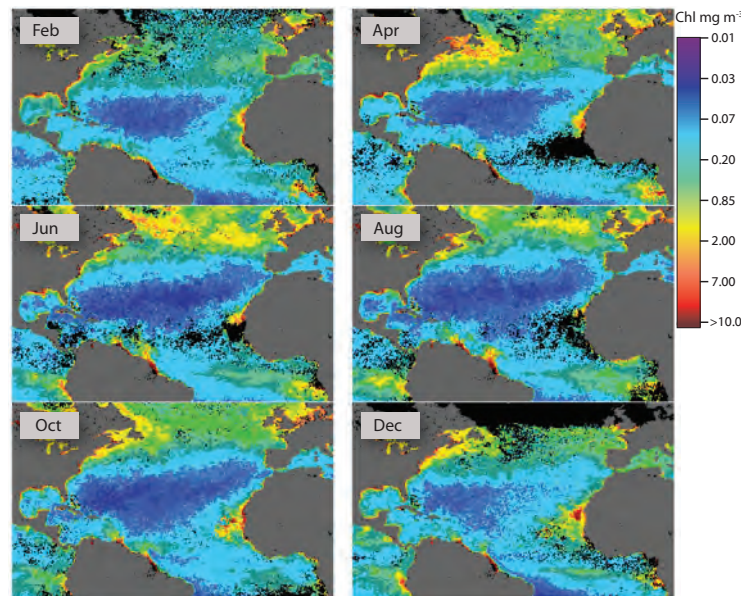


Figure 2.11 Chlorophyll distribution in the northern Atlantic for six months of 1998

graphic features between two water masses (continental shelf and open ocean) that are likely to display very different optical properties. Statistical properties of the province NECS are calculated without the Baltic Sea.

Figure 2.10 shows the resulting dynamic distribution for six months of 1998 (with the same colour code as on Figure 2.8). The monthly series shows very variable features that modulate large, more stable, biomes. Obviously, this distribution bears some resemblance to the variability displayed by the corresponding maps of chlorophyll-*a* concentrations (Figure 2.11). The most important variability is noticed in the respective surfaces of the gyre provinces NAST(W), NAST(E), WTRA and NATR. Other noticeable results include the clear distinction between the continental shelves NWCS and NECS and the deep Atlantic, the offshore extension of the upwelling CNRY biome, the signature of the South American rivers (Orinoco and Amazon), and the interplay in the tropical Atlantic between the oligotrophic waters, the upwelling regime and the influence from the coastal biome. As expected, the results obtained for CARB are rather complex. The interior grid points are associated with various combinations of CARB, NATR and NAST(W), and the coastal waters of the northern Gulf of Mexico are found closer to the properties of the coastal biome GUIA. The problems associated with CARB will likely be encountered in all archipelagic regions having deep internal basins.

This example shows how the application of a simple classification scheme depicts a more realistic separation of the water masses at the level of the North Atlantic, particularly in terms of the boundaries separating large scale ecological provinces. Using *a priori* information to define classes has the advantage of conserving the main

structures of the original fixed distribution, and therefore of keeping an association with its detailed description by Longhurst (1998) and the same modelling framework and parameter sets for primary productivity calculations. Concurrently, the analysis highlights the areas where a more refined partition is required.

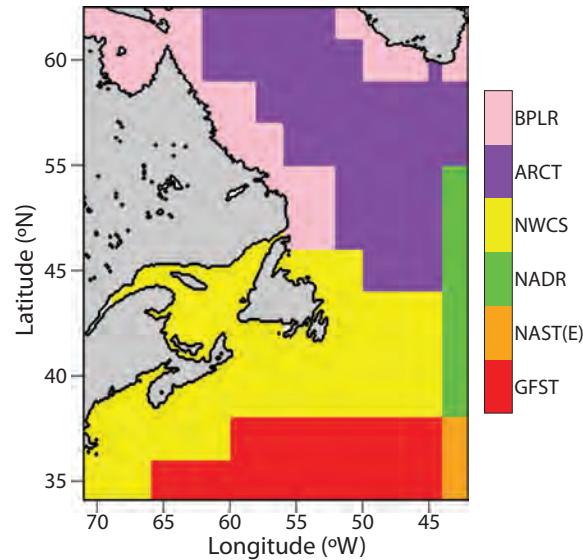


Figure 2.12 Static boundaries of ecological provinces in the NW Atlantic defined by Longhurst (1998). BPLR: Boreal Polar; ARCT: Atlantic Arctic; NADR: North Atlantic Drift; NWCS: NW Atlantic Shelves; GFST: Gulf Stream; NAST(E): North Atlantic Subtropical Gyre (East); NAST(W): North Atlantic Subtropical Gyre (West).

2.2.4 Dynamic provinces based on distribution function analysis

The Canadian SOLAS field programme in the NW Atlantic provided an excellent context for developing operational procedures to delineate the instantaneous boundaries of the biogeochemical provinces and establish their dynamic change with season (Platt *et al.* 2005; Devred *et al.* 2007). In this programme, expeditions were made in Spring, Summer and Fall 2003. Observations included vertical structure of temperature, salinity and fluorescence (proxy for chlorophyll concentration). Using the original, rectilinear partition of Longhurst (Longhurst *et al.* 1995; Longhurst 1998) as a starting point, the boundaries of provinces were traced for the study area (Figure 2.12).

To implement the partition of Longhurst, one must establish criteria by which individual pixels can be associated with a particular province. Longhurst provided only the rectilinear boundaries of the idealised case: he did not define the characteristics of points inside the provinces in a way that an arbitrary point could be identified as belonging to a particular province. So, the first step is to establish the

characteristics of the provinces in an operationally-useful form. Because the goal is

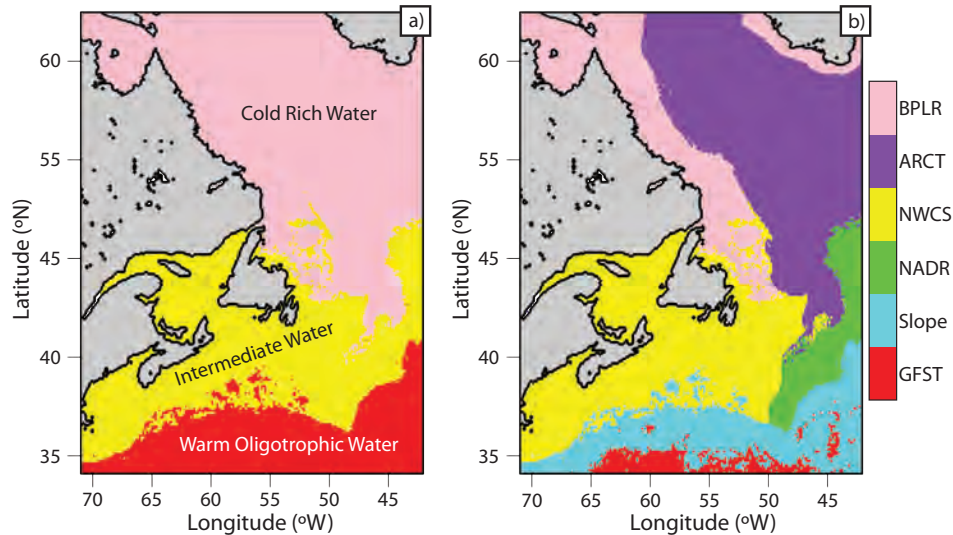


Figure 2.13 (a) Initial identification of water masses using a cluster analysis based on satellite-derived SST and chlorophyll-a concentration, bathymetry and location, for the October C-SOLAS 2003 cruise in the NW Atlantic. (b) Dynamical definition of ecological province borders for the October 2003 C-SOLAS cruise. BPLR: Boreal Polar province; ARCT: Arctic province; NWCS: NW Atlantic Shelves; NADR: North Atlantic Drift; Slope: Slope waters; GFST: Gulf Stream. Image provided by Emmanuel Devred, Dalhousie University, Canada.

to delineate the boundaries in real time, only a limited range of criteria is possible. These include water depth, chlorophyll concentration and sea-surface temperature, the last two being available from remote sensing. Using these variables, rules have to be constructed that will assign any pixel objectively and unambiguously to one and only one province.

The procedure used to refine the rules is first to partition the study area into three main water masses (an initial scheme) corresponding to the cold rich waters in the North, intermediate water and warm oligotrophic waters in the south. Figure 2.13a gives an example of the initial province scheme for the October C-SOLAS cruise in 2003. This first step allows acceleration of the statistical analysis and therefore a reduction in computing time, before performing a more detailed cluster analysis within each of these water masses to achieve the final partitioning (Figure 2.13b).

Applying the method to the NW Atlantic had the interesting consequence that the solution could not be achieved without invoking the existence of an extra province over and above the set originally specified by Longhurst (1998). This was called the Slope Waters province: it is a transition province between cool water of the continental shelf and the warm oligotrophic water to the south. It is characterised by warm water with relatively high chlorophyll biomass.

A major significance of this study (Devred *et al.* 2007) is that it represents

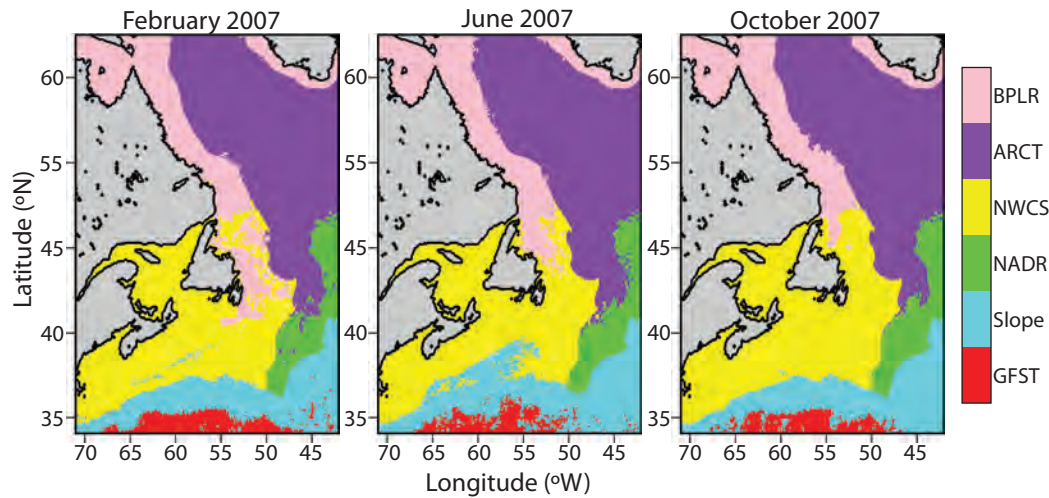


Figure 2.14 Dynamic borders of biogeochemical provinces in the NW Atlantic in February, June and October 2007. Image provided by Emmanuel Devred, Dalhousie University, Canada.

the first successful attempt to implement, in a dynamic sense, the partition of Longhurst *et al.* (1995), with the boundaries realistically reproducing the meandering structure of the currents (as opposed to the polygonal-shaped representation in Figure 2.12). It is a major step along the road to operational remote sensing using ocean-colour radiometry. It is not the definitive solution in the sense that it required the involvement of highly-skilled personnel such that real-time performance could not be achieved. However, it is an important advance that encourages the hope that the operational goal will be reached.

The second aspect of the work (Platt *et al.* 2005; Devred *et al.* 2007) was the demonstration of seasonal shift in the province boundaries (Figure 2.14). For example, as the season advances and water temperatures increase, the NWCS province (nomenclature of Longhurst *et al.* 1995) increases in size at the expense of the BPLR province. During summer, the slope water province intrudes into the NWCS province and an eddy is formed.

Such an analysis is of great value in the interpretation of field data, since it allows the investigator to determine, for each station occupied by the ship, the province in which that station was located. The partition provides a template, or intellectual framework, within which results can be discussed to advantage. The template is useful far outside the original focus (estimation of primary production).

Chapter 3

Regional Considerations

Nicolas Hoepffner and Mini Raman

The first implementation of biogeochemical provinces for the global ocean (Longhurst 1998) is magisterial in scope and treatment: it has been applied successfully to a variety of problems at global and regional scales. For certain regional problems, however, it may be necessary to examine more deeply the subtleties of forcing and its seasonal variations. The Longhurst template provides an ideal starting point in such cases. In this section, we examine the issue of oceanographic partition for selected regions with differing forcing, taking into consideration the alternatives that have been proposed and the applications that have resulted. Two regions, the Arabian Sea and the North Atlantic, have been of particular importance within International IGBP Programmes such as JGOFS (Joint Global Ocean Flux Study), and will be examined in this chapter.

3.1 Dynamic Structure and Function of the Arabian Sea

In this section, we consider various approaches to partition the Arabian Sea basin based on its regional oceanographic characteristics and as such, the focus is on the use of ocean-colour radiometry as a tool to delineate the boundaries of the provinces and to some extent, infer the taxonomic status of the communities contained therein. We begin by presenting an overall picture of the physical oceanography of the Arabian Sea to emphasize the unique characteristics of relevance to ecological partitioning. We consider the work carried out during the IIOE (International Indian Ocean Expedition) in 1959-1965, the JGOFS Arabian Sea Process Study from 1992-1997, and various relevant national and local sea campaigns. We then review the various methods that have been developed to partition the Arabian Sea and consider their utility in delineating the boundaries of the provinces.

3.1.1 Oceanography of the Arabian Sea

The landmasses of India and Sri Lanka separate the Indian Ocean into the Arabian Sea and the Bay of Bengal. Two adjoining seas are connected with the Arabian Sea;

the Red Sea through the strait of Bab el Mandeb, and the Persian Gulf through the Strait of Hormuz.

The IIOE expedition undertaken during 1959-65, was the first large-scale scientific expedition to study in detail the physical, chemical and biological oceanography of the region. Subsequently many such expeditions were conducted, particularly in the context of the JGOFS programme (1992-1997) that examined the complex biogeochemical processes in the Arabian Sea (Fasham 2003), and the World Ocean Circulation Experiment (1995-1996) with a comprehensive survey of the Indian Ocean physics (Field 1997). The influence of the huge land mass of the Asian sub-continent has resulted in unique circulation patterns in the Arabian Sea which are substantially different from those of other world oceans. A comparison with sea surface topographies of Atlantic and Pacific oceans reveal that the large gyres that exist in these two oceans are not found in the Arabian Sea. In addition, the unique monsoon atmospheric circulation affects the ocean surface circulation extending beyond Arabian Sea up to 10° south. Consequently, the Arabian Sea experiences a semi-annual reversal of the surface circulation in response to the changing wind system, a feature not found in either the Atlantic or Pacific Oceans (Wyrski 1973; Schott and McCreary 2001).

The seasonally-reversing monsoon winds are divided into southwest (June-September) and northeast (December to February) phases with two transition periods, spring inter-monsoon (March to May) and fall inter-monsoon (October and November). The large-scale open-ocean, seasonally reversing currents are known as monsoon currents. During summer, heating of land produces a region of low surface pressure over the Asian landmass, which results in the development of strong south-westerly winds over a broad region. Under the influence of southwest monsoon winds, vigorous and deep anti-cyclonic surface circulation develops in Arabian Sea. Coastal upwelling along the Arabian Peninsula occurs as a result of offshore transport of waters under the influence monsoon winds blowing parallel to the coast (Fischer *et al.* 2002).

During the northwest monsoon, cyclonic circulation occurs as a result of the north-south pressure gradient in the Arabian Sea. The monsoon current thus reverses its direction and flows from east to west north of the equator. During the northeast monsoon, oceanic circulation is only moderately strong compared with that during the southwest monsoon, while during the intermonsoon transition period, surface currents dissipate and hydrographic conditions in the Arabian Sea approach those of a well stratified and unperturbed tropical ocean.

The Red Sea and Persian Gulf are relatively shallow, narrow seas surrounded by arid land masses with negligible rainfall. High rates of evaporation result in a very high salinity in these basins. Characteristics of the Arabian Sea waters are thus the result of mixtures of various water masses, including the Indian Ocean Equatorial Water Mass.

The peculiar oceanographic characteristics of the Arabian Sea and the variety

of water masses described here provide the basis for partitioning using physical forcing concurrently with synoptic observations from satellite.

3.1.2 Satellite approach to a bio-physical partitioning of the Indian Ocean

Various taxonomical approaches have been used to partition the Indian Ocean, based on the distribution and composition of phytoplankton species. For example, Thorrrington-Smith (1970; 1971) grouped samples from the IIOE expedition according to their phytoplankton composition, using numerical taxonomic methods and cluster analysis. He noted that the study of phytoplankton associations in mixed waters is useful in tracing water masses since phytoplankton populations do not lose their identity by mixing. Furthermore, low species diversity is a useful indicator of the boundaries of phyto-hydrographic regions, since these regions are areas of environmental instability and only favour the growth of adaptable species.

Working along similar lines, Krey (1973) divided the Indian Ocean into eight geographical regions based on the hydrographical and meteorological properties of data collected during the Indian Ocean Expedition (1959-1965). Qualitative plankton associations or predominance in each geographic region, and their distribution in relation to prevailing patterns of oceanic circulation in the area were mapped to provide a composite picture of various plankton-geographical regions of Indian Ocean. Although no attempt was made to identify the boundaries of plankton-geographical regions, Krey (1973) stressed the importance of recognizing the seasonal variations of the ecological boundaries. Satellite-derived ocean-colour radiometry in combination with other databases has been demonstrated to be an essential tool to achieve such partitioning at appropriate spatial and temporal scales.

3.1.2.1 Biohydro-Optical Classification of the Arabian Sea

Following Longhurst's scheme of partitioning (see Section 2.1.1), Brock *et al.* (1998) used a combination of climatologies of the mixed layer, computed light field and archived satellite chlorophyll data (Coastal Zone Color Scanner) to develop province-specific rules to partition the Arabian Sea into three different biohydro-optical provinces. Chlorophyll concentrations derived from ocean-colour satellites are used in this classification scheme as an indicator of the phytoplankton biomass and also to determine whether the attenuation of the underwater light field is dominated by phytoplankton or by seawater. The euphotic zone is then calculated and related to the depth of the mixed layer.

The characteristic modes of plankton ecology in the classified provinces reflect the seasonal hydrography of the Arabian Sea. Low winds and high insolation at the start of the spring inter-monsoon season results in a shallow mixed layer where the algal growth is limited by the availability of nutrients. As the season advances, the stratification deepens driving the Arabian Sea towards a typical tropical structure

(TTS), which is clearly identified by Brock's classification method. Light attenuation in the upper mixed layer is dominated by seawater, allowing the downward penetration of light into the nitricline. The structure of the water column in such a province is typically a two-layered system with a pronounced vertical structure of phytoplankton biomass.

In the northwest Arabian Sea, at the onset of the southwest monsoon, the TTS is modified by the upward movement of nutrient rich waters into the mixed layer, where mean light levels are high. The combination of both triggers a rapid growth of phytoplankton. As a result, the distinct deep chlorophyll maximum (DCM) in the nitricline region ascends and decreases in amplitude until it dissipates in the well-mixed eutrophic waters.

Brock *et al.* (1998) capture such a "Mixed-Layer Bloom" province in the western and northern Arabian Sea during the southwest monsoon, where the use of a homogeneous vertical phytoplankton pigment profile equal to that observed by satellite for the upper attenuation depth can be used for regional parameterization of the local primary production algorithm.

A third province of this biohydro-optical classification identifies regions where phytoplankton dominate the attenuation of light in the mixed layer, but the base of the euphotic depth lies within the nitricline, below the mixed layer. This condition drives photosynthesis at depth and thereby maintains a DCM. Such a "transitional" class marks the leading edges or trailing borders of advancing or senescing mixed-layer blooms in the northern and western Arabian Sea, at the onset of fall inter-monsoon, and persists through out the season.

3.1.2.2 Bio-Physical Classification of the Arabian Sea

Watts *et al.* (1999) classified the Arabian Sea into a suite of biogeochemical provinces to estimate new production in northwest Arabian Sea. The underlying concept is that biogeochemical processes and eco-physiological rates are under physical control in a given region. The ocean basin could thus be partitioned into a suite of provinces by delineating regions which are under common physical forcing (Platt *et al.* 1995) with respect to factors influencing the growth of phytoplankton. The provinces can form a template upon which the eco-physiological rate parameters can be assigned for basin-scale modelling of oceanic primary production. Spatio-temporal variability of biogeochemical processes and biological properties in a province is subjected to changes in physical forcing, therefore the provinces have dynamic boundaries.

To identify the location of a dynamic boundary, Watts *et al.* (1999) proposed the use of sea-surface properties (sea-surface temperature, sea-surface chlorophyll) that can be measured synoptically by satellite. Watts *et al.* (1999) divided the Arabian Sea into six provinces, each being characterized by a unique combination of sea-surface temperature, sea-surface chlorophyll and maximum bottom depth as obtained from field measurements. The authors developed a flow diagram specifying province-

specific rules for partitioning the Arabian Sea based on these *in situ* measurements.

The classification scheme proposed by Watts *et al.* (1999) was applied to monthly composites of CZCS chlorophyll data, co-registered with NOAA/AVHRR SST data and bathymetry (Figure 3.1). Each pixel of the image was assigned to a particular province according to province-specific criteria, so that the extent of each province could be determined. This classification scheme combined with the use of satellite data allowed the real-time identification of dynamic province boundaries.

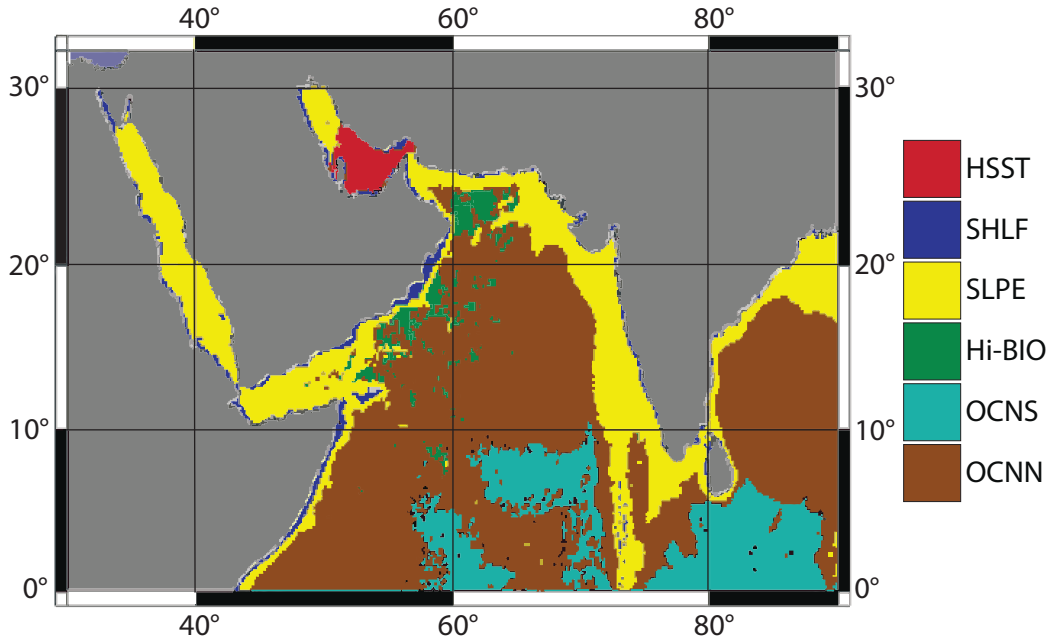


Figure 3.1 Areas occupied by the six biogeochemical provinces identified for the north-west Indian Ocean basin, for the monsoon month of September. Characteristics of the provinces: HSST - bottom depth > 200 m and < 2500 m, SST $\geq 28^{\circ}\text{C}$ to 30°C ; SHLF - bottom depth was ≤ 200 m, SST < 25°C ; SLPE - bottom depth > 200 m but < 2500 m, SST < 28°C to 30°C ; Hi-BIO - Chl > 0.9 mg m^{-3} , bottom depth > 2500 m; OCNS - bottom depth ≥ 4000 m, Chl $\leq 0.2\text{--}0.3\text{ mg m}^{-3}$, SST $\geq 27^{\circ}\text{C}$; OCN - bottom depth ≥ 2500 m, SST $\leq 27^{\circ}\text{C}$ and intermediate surface chlorophyll concentrations. Adapted from Watts *et al.* (1999).

3.2 Biogeography of the North Atlantic

The North Atlantic has been the focus of numerous studies because of its importance in the global climate and the carbon cycle. As a result, a significant amount of data has been generated over the years to characterize the physics and, to a lesser extent, the chemistry of the North Atlantic at a reasonable spatial resolution (e.g. 1° grid) and time scale (e.g. monthly averages). For biological studies and ecosystem assessment, however, both the lack of field data and poor regional/seasonal coverage still require the extrapolation of discrete measurements at much coarser spatial and

temporal scales. During the last two decades, satellite measurements of surface reflectances have contributed in many ways to solve the problem by providing broad spatial and temporal coverage of quantities directly related to biogeochemical distributions and processes. In addition, remote sensing of ocean colour has been extremely valuable to set the basis for a first identification of marine “provinces” likely to have peculiar biological systems, which then can be used as a template for extrapolating ship-based measurements.

3.2.1 Province delineation based on hydrodynamic-biology interactions

In an attempt to compute primary production in the North Atlantic, Sathyendranath *et al.* (1995) used a two-step partitioning of the study area based firstly on a general description of the regional oceanography, which was then extended to the consideration of other aspects of pelagic ecology. The North Atlantic circulation is essentially driven by wind stress and some meridional differences in the water density.

Three major wind regimes have been used by Sathyendranath *et al.* (1995) to define primary biogeochemical biomes in the North Atlantic: the Polar winds (Polar Biome), the Westerlies (West-wind Biome), and the Trade winds (Trade-wind Biome). Each of these biomes have unique physical characteristics with respect to mixed-layer dynamics and radiation budget, which will influence the phytoplankton ecology. A fourth biome (the Coastal-Boundary Biome) accounts for the specific physical structure of the water column due to the shelf-break and shallower bathymetry. In a second step, each biome is subdivided into “provinces” which are defined by local currents, fronts, topography and other recurrent features that can be visualized using remote sensing data, including surface chlorophyll fields. This type of division follows similar criteria to those implemented on a global scale by Longhurst (1995) to study the degree of seasonal coupling between production and consumption in the upper layers.

Some 18 provinces were then identified in the North Atlantic (Sathyendranath *et al.* 1995), together with their associated boundaries which could then be re-adjusted on the basis of more detailed statistical analysis on one or several measured properties that respond as directly as possible to changes in regional oceanography. Although the boundaries are allowed to vary to some degree when the parameters (in this case, parameters required for the computation of primary production) are assigned to each province for a given time scale, this regional partition of the North Atlantic can be viewed as rather *static* in relation to the large temporal variability of the forcing fields.

In the same way, Hoepffner *et al.* (1999) delineated the eastern tropical and sub-tropical North Atlantic to determine the depth-integrated primary production in this important upwelling system, largely influenced by the Trade-winds along the coast of Portugal and north-west Africa. In this case, the computation scheme for

primary production included the use of surface chlorophyll from satellite imagery to derive, on a pixel-by-pixel basis, the time-varying shape of the biomass profile in the water column. The photosynthetic parameters required in the calculation still had to be derived from field measurements. The paucity of these data enforced a grouping into pre-defined bio-geographical provinces which were selected according to a meticulous examination of the satellite-derived chlorophyll values and current knowledge of the local circulation and bathymetry (Figure 3.2).

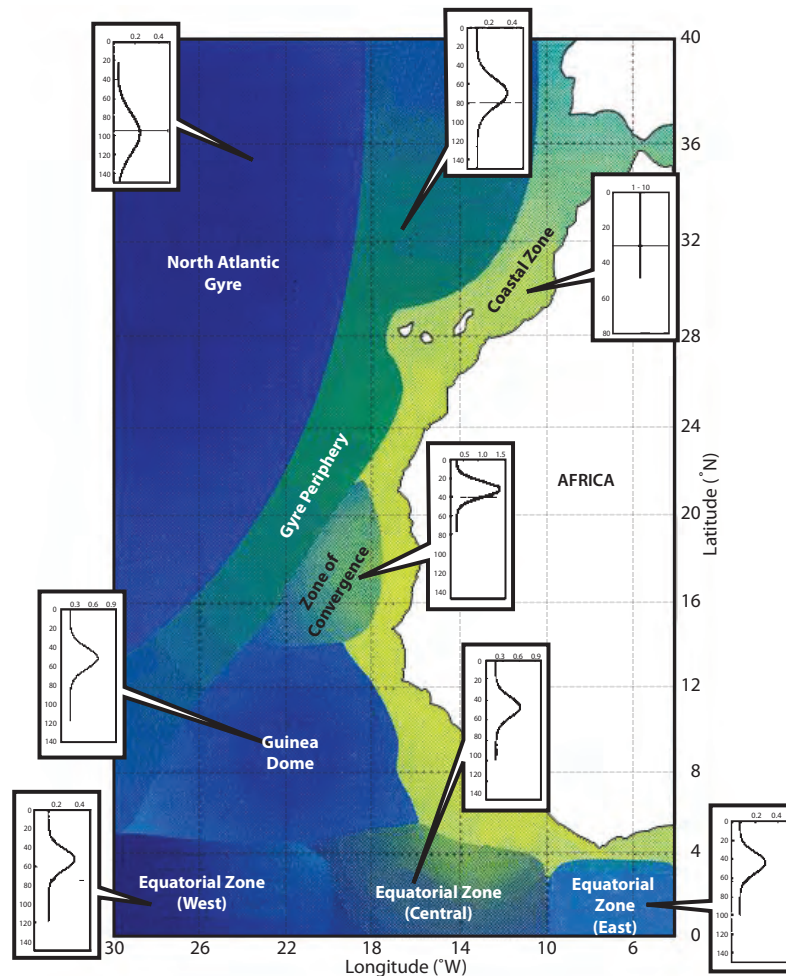


Figure 3.2 Delineation of oceanic regions in the eastern tropical and sub-tropical North Atlantic. A total of eight bio-physical provinces are identified on the basis of hydrographic properties and ocean-colour radiometry. Adapted from Hoepffner *et al.* (1999).

As in the previous work, the method used to partition the North Atlantic, although conducted to mirror as closely as possible the natural system, reflects a computational convenience to compensate for the deficit of biological quantities not accessible at satellite scales, but still important in modelling biogeochemical

cycles in the oceans. It is a “static” representation of the biogeochemical field in a sense that the province boundaries remained fixed and polygon-shaped, giving little perception as to the true variability of the ecosystems. One way to identify province boundaries, retaining the intrinsic dynamics of marine biological events, is to select environmental criteria or forcing variables that can be measured by remote sensing. The use of sequential images of bio-physical variables collected by one or multiple sensors enables direct visualization of changes in the distribution of the water masses, as well as the generation of decision-trees for a classification system that will reproduce the dynamic dimension of the province boundaries (Watts *et al.* 1999).

To estimate new production in part of the Northwest Atlantic Ocean, Sathyendranath *et al.* (1991) relied on satellite-derived sea surface temperature and the bathymetry field to identify mixed waters over the shallow area of Georges Bank, the stratified oceanic waters with high temperature in the mixed layer and deep water column, and the frontal system with upwelled cold waters surrounding the central part of Georges Bank. Satellite-derived chlorophyll concentrations may be added to the province identification process, as the three zones showed significantly different patterns with a gradual decrease in biomass from the central part of Georges Bank to the stratified oligotrophic Sargasso Sea waters. In this process, the province boundaries could vary at high temporal scales according to the availability of satellite images, providing much more accuracy in the assessment of ecological processes than relying on a delineation based on climatological observations.

A similar process was applied by Platt *et al.* (2005) and Devred *et al.* (2007) to study the interactions between physical forcing and phytoplankton distributions in the Northwest Atlantic Ocean, including the Scotian Shelf and the Labrador Sea (see Section 2.2.4). According to a static biogeographical division scheme (Sathyendranath *et al.* 1995; Longhurst *et al.* 1995), this area would include seven ecological provinces (see Figure 2.12 - the western part of the subtropical gyre is located just below 35°N). A dynamical re-adjustment of the static biogeographical division scheme using satellite-derived sea surface temperature and chlorophyll data vindicated this basic partition of the ocean, reflecting the prevailing role of physical forcing as a regulator of phytoplankton distribution. It also generated complementary detailed information on the changes in forcing at scales ranging from seasonal to that portraying storm events.

3.2.2 Regional classification based on optical properties

Theoretically, the ocean-colour signal or water-leaving radiance collected by the satellite-based sensor at different wavebands reflects the variation in the optically-active components in the water and the relative distribution of these constituents at a given time and location. Accordingly, Martin Traykowski and Sosik (2003) developed an automated method to distinguish different water types based on distinct clusters

in the water-leaving radiance feature space. After examination of a test satellite image in the western North Atlantic and a review of the local hydrography and bathymetry, six regions were selected as having implicit differences in their optical signatures. Each of these regions was represented by a cluster of water-leaving radiances and a mean value at three different wavelengths. The province boundaries were then calculated using two methods: the Euclidian Distance Classifier and the Eigenvector Classifier. Decision rules in both methods are based on a minimum distance between the data points and each class centre, assuming each class to be spherical and non-spherical in shape, respectively. The six regions are well defined

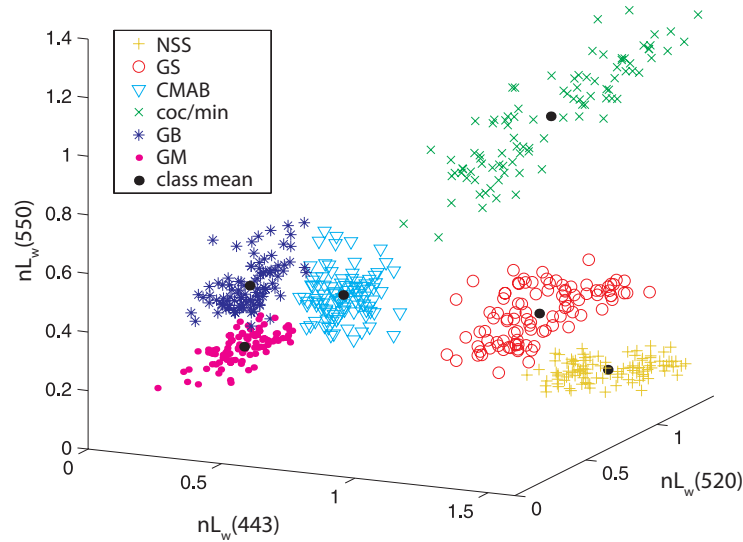


Figure 3.3 Water type classes for the NW Atlantic shown in a three-dimensional single band feature space (nL_w in $\text{mW sr}^{-1} \text{cm}^{-2} \mu\text{m}^{-1}$). The training set consists of $n_j = 100$ randomly chosen pixels from each of six different geographical regions. NSS = Northern Sargasso Sea waters; GS = Gulf Stream waters; CMAB = Central Mid-Atlantic Bight waters; coc/min = coccolithophore/mineral dominated waters; GB = Georges Bank waters; GM = Gulf of Maine waters. Adapted from Martin Traykovski and Sosik (2003.)

in a 3D plot of water-leaving radiances (nL_w) at 550, 443, and 520 nm (Figure 3.3), which illustrates the typical optical signature of the different water masses in the studied area, including some highly-scattering waters dominated by coccoliths or other mineral compounds. Applying one of the Classifier methods to two different satellite scenes (Figure 3.4) enabled the extent and the boundaries of each class to be mapped for the same region. Each pixel in the satellite scene was assigned to a class according to a given decision rule, yielding a dynamic view of the “optical provinces” when applied to a time-series of satellite-derived water-leaving radiances. In this method, a first selection of the regions was conducted, and a training dataset was allocated to each of the regions to define their optical characteristics. This is equivalent to a supervised classification, with the risk of obtaining unclassified

(or misclassified) pixel data. The number of misclassified pixels was significantly reduced using the Eigenvector Classifier technique. In this case, a completely unsupervised classification could also have been conducted, using the frequency distribution of satellite-derived chlorophyll as a way to separate distinct clusters (Esaias *et al.* 2000).

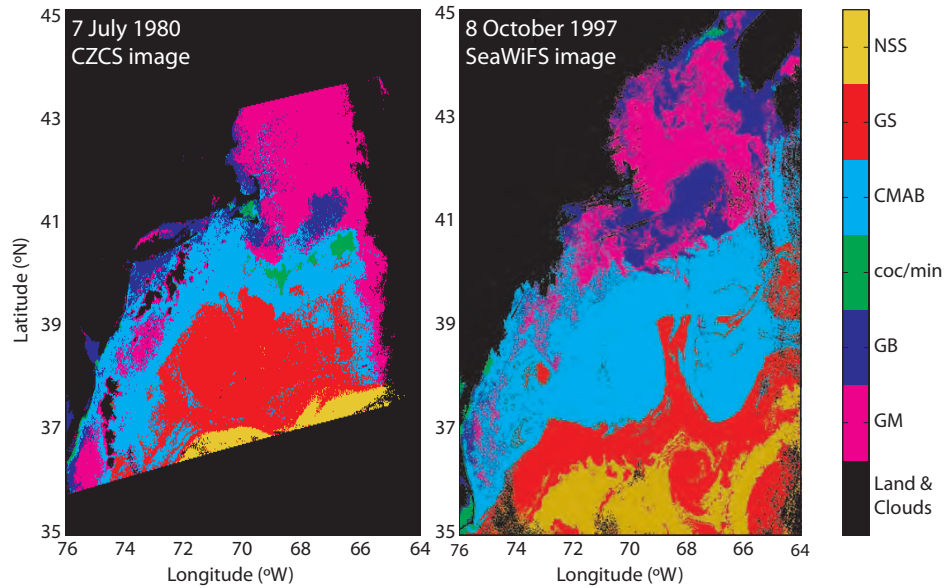


Figure 3.4 Classification results for the Euclidean Distance Classifier applied to the Northwest Atlantic on two different days: (left) 7 July 1980 (CZCS image) and (right) 8 October 1997 (SeaWiFS image). The water types are clearly distinguishable, and application of the classifier reveals that they form well-defined water masses. There are striking broad-scale similarities in the distribution of these water types between the two scenes, even though they are 17 years apart. Mesoscale physical oceanographic features are apparent; differences may represent seasonal and/or inter-annual variability. Adapted from Martin Traykovski and Sosik (2003).

Chapter 4

Retrieval of Phytoplankton Biomass, Optical Constituents and Primary Productivity

Mark Dowell, Timothy Moore, Trevor Platt

This chapter addresses two fundamental applications making use of provinces. The specific interest in documenting these two applications in a dedicated chapter is twofold: the first is that these two applications are the closest to the essence of ocean-colour radiometry (OCR) as a tool and a discipline; the second is that the estimation of phytoplankton biomass and primary production are the two applications making use of provinces that have made the most significant progress over the past 10 years. The origin for much of the research on this topic comes from the work of Alan Longhurst and colleagues. The global province distribution was formulated first in response to the requirement to parameterise a primary production model for implementation on many grid points. Likewise, many of the initiatives focused on the development of dynamic methods for province distribution have resulted from the operational requirement to define regional bio-optical inversion algorithms. The motivation stems from defining algorithms for different regions or distinct optical water types that can be subsequently blended together into seamless products.

4.1 Phytoplankton Biomass and Optical Constituents: Background

A clearly-demonstrated use of provinces - and a major stimulus for much of the ongoing work on methodological aspects of province distribution definition - is in their application to the retrieval of phytoplankton biomass and associated optical constituents. This was the primary focus of effort and resource initially invested in OCR, and it is thus fitting that the work on refining province distributions has contributed so much to this application.

4.1.1 Use of provinces as a template for data synthesis

A first example is the use of static provinces as a template for analyzing large *in-situ* datasets. This has been demonstrated as an effective approach for the North Atlantic

by Kyewalyanga and colleagues (1998) who analysed the spatial distribution of the specific absorption coefficient of phytoplankton (a_{ph}^*) across the basin using the Longhurst *et al.* (1998) provinces.

It should be emphasized at this point that there are historical optical classifications of the oceans in the literature, which have not been discussed up to this point, but which are of utmost importance in addressing this specific application. These optical classifications began with the pioneering work of Jerlov (1968) and Soviet scientists, which produced maps of the ocean on the basis of regional- and basin-scale differences in the diffuse attenuation coefficient.

Likewise there is a body of historical work addressing the separation of the oceans in areas of differing trophic state. This approach, initially proposed by Morel and Berthon (1989), was effectively used to define seven trophic biomes in the ocean exclusively based on chlorophyll profiles. The authors subsequently observed that this trophic delineation could actually be considered as a continuum, and as a consequence used this to define a continuous function for defining the parameters for a model of the vertical profile of chlorophyll-“a”. In more recent work, Hardman-Mountford *et al.* (2008) have re-analyzed the problem of discriminating trophic regimes. In their work, the authors used an objective method based on a spatial principal component analysis (see Section 2.2.2) applied to a time-series of satellite chlorophyll data.

4.1.2 Dynamic province assignment methods for ocean-colour algorithms

It is now widely accepted that a universal bio-optical algorithm applicable for all water types is not feasible. In a single ocean-colour image scene, there can be multiple water types with differing optical properties, which in turn require different algorithms. The historic example is the difference between Case-1 and Case-2 waters (Morel and Prieur 1977; IOCCG 2000). In Case-1 waters, the optical properties are dominated by phytoplankton, whereas in Case-2 waters the optical properties are governed by other constituents, such as suspended sediments and/or coloured dissolved organic matter. Case-1 algorithms often fail or return inaccurate retrievals in Case-2 waters. Among Case-2 waters, however, there are many different substances found globally that affect the optical properties of the water. A single parameterized Case-2 algorithm should be able to account for variability in the concentrations of two or three substances, but not variability due to the wide variety of substances found globally. Thus, we are often presented with different Case-2 algorithms derived for local waters, or for specific situations such as CDOM-dominated or sediment-dominated waters. Although there has been a lot of effort devoted to developing Case-2 algorithms, much less effort has been applied to address the problem of merging algorithms for different water types. A unifying scheme is needed that will not only choose which algorithm is best for a given

satellite pixel, but will blend retrievals from different algorithms in a manner that is physically meaningful.

The decision regarding which algorithm to apply may be viewed as a classification problem. The application of a hard classification scheme that selects only one algorithm and rules out the others can result in a “patchwork quilt” effect. This effect can be seen in retrieval images as discontinuities between water types, or it might also be manifested in ways that are not readily visible in the images but observable in other formats. The latter situation occurred in the standard processing of CZCS images where the algorithm switched between two different radiance-ratio algorithms. This produced discontinuities that were not obvious in the images, but clearly seen in discontinuous, bimodal chlorophyll histograms. In transition zones where pixels could belong to Case-1 or Case-2, one might have very different chlorophyll retrievals depending on which algorithm was applied. As a consequence, use of a hard classifier would result in uneven or discontinuous retrievals.

Ocean waters with different biogeochemical composition often have different optical properties. These different waters can be identified by their spectral reflectance characteristics. A first attempt at classifying waters based on optical characteristics with the objective subsequently to select and blend different bio-optical algorithms was presented by Moore *et al.* (2001), using an ocean-colour satellite image of the northwest Atlantic shelf. The approach is based on a fuzzy logic classification scheme applied to the satellite-derived water-leaving radiance data (see Chapter 2, Section 2.2.1). Local *in situ* bio-optical data were used by the authors to characterize optically-distinct water classes *a priori* and to parameterize algorithms for each class.

Although the algorithms can be of any type (empirical or analytical), this demonstration involves class-specific semi-analytic algorithms, which are the inverse of a radiance model. The semi-analytic algorithms retrieve three variables related to the concentrations of optically active constituents. When applied to a satellite image, the fuzzy logic approach involves three steps. First, a membership function is computed for each pixel and each class. This membership function expresses the likelihood that the measured radiance belongs to a class with a known reflectance distribution. Thus, for each pixel, class memberships are assigned to the predetermined classes on the basis of the derived membership functions. Second, three variables are retrieved from each of the class-specific algorithms for which the pixel has membership. Third, the class memberships are used to weight the class-specific retrievals to obtain a final blended retrieval for each pixel. This approach allows for graded transitions between water types, and blends separately-tuned algorithms for different water masses without suffering from the “patchwork quilt” effect associated with hard-classification schemes.

A different approach proposed by D’Alimonte *et al.* (2003) used the statistical method of novelty detection to identify the range of applicability of empirical ocean-colour algorithms. This method is based on the assumption that the level of

accuracy of the algorithm output depends on the representativeness of inputs in the training dataset. The effectiveness of the novelty detection method was assessed using two datasets: one representative of the northern Adriatic Sea coastal waters and the other representative of open ocean waters. The two datasets were used independently to develop neural network algorithms for the retrieval of chlorophyll-a concentration. The authors found the range of applicability of each algorithm which was applied to satellite data from SeaWiFS for three selected regions: the central Mediterranean Sea, the North Sea, and the Baltic Sea.

Lubac and Loisel (2007) recently presented a similar application. In this study they used data from intensive field bio-optical campaigns undertaken during spring and summer 2004. The geographic region covered by the measurements was the eastern English Channel and southern North Sea and the study aimed to assess the mechanisms regulating the ocean colour variability in a complex coastal environment. In-water hyperspectral remote-sensing reflectances (R_{rs}) were acquired simultaneously with measurements of optically-significant parameters at 93 stations. In their study, the authors incorporated the use of empirical orthogonal function (EOF) analysis. The prime result from this analysis demonstrated that 74% of the total variance of R_{rs} is explained by particulate backscattering (b_{bp}), while particulate and dissolved absorption only explain 15% of the ocean colour variability. Additionally, the authors applied an unsupervised hierarchical cluster analysis to their data set of normalized R_{rs} spectra. This resulted in five spectrally-distinct classes. Of the five classes, three classes had particularly distinct characteristics: one class corresponded to *Phaeocystis globosa* bloom events, whereas the other classes were associated with water masses dominated by mineral and non-living particles, respectively. Among the different bio-optical parameters, the particulate backscattering ratio, the chlorophyll concentration and the particulate organic carbon-to-chlorophyll ratio exhibited a high degree of class-specific behaviour.

4.1.3 Using provinces to develop cal/val strategies

A fundamental aspect of operational ocean-colour radiometry is the post-launch calibration of the sensors in orbit, and the routine validation of derived products (at Level 2 and higher) as provided by the space agencies. There are various criteria that are used to define an appropriate strategy for the selection of locations and the general geographic distribution of these locations. One of the fundamental aspects is the nature of the optical characteristics of the location, and the stability (or variability) of the water properties at this location over time. The prescribed criteria may in fact be considerably different for calibration and validation requirements. For example, calibration activities may require regions where the variability of optical water types is low (i.e. stable). It should be noted, in the context of calibration, there are also important considerations to be made on the variability of atmospheric properties. This however is beyond the scope of the present report and will not be

considered further.

On the contrary, for validation purposes it may be preferable to look for areas where temporal or spatial optical variability throughout the year is highest, so as to obtain a validation dataset covering the widest dynamic range of optical variability possible.

We now consider the potential of the methods presented in Chapter 2 to address some of these issues. Specifically, we used the fuzzy logic method described in Section 4.1.2, and applied it to a global *in-situ* dataset called NOMAD (Werdell and Bailey 2005). The classification identified objectively eight distinct optical water types from this data set. Based on a 48-month global time-series of these optical water types, we analyzed the persistency of each individual class. Figure 4.1 shows a global map of the class persistency > 70% for the time-series considered. It is proposed that information of this type may provide an avenue into better allocation of resources for optimizing the collection of *in-situ* data for calibration and validation purposes.

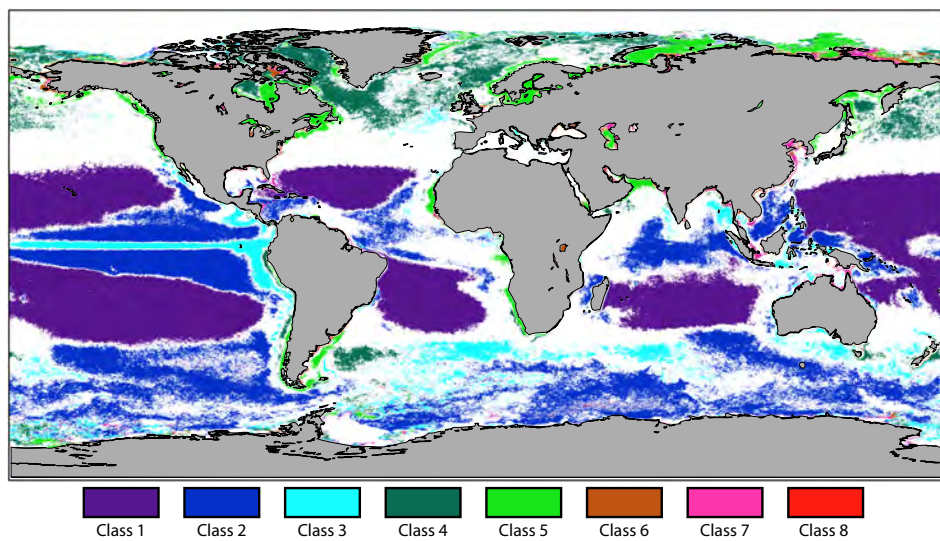


Figure 4.1 Map showing global persistence of optical water type for regions exhibiting membership to a certain class more than 70% of the time over a 48 month time-series. Image courtesy of Mark Dowell, Joint Research Centre, EC.

Additionally, a further requirement - which is requested frequently by users of ocean-colour data - is the need to have spatial information on uncertainties for the products provided. At present, there are global uncertainty budgets assigned to the individual products derived from bulk validation estimates over global or basin scale datasets, but what would be preferable would be to assign uncertainty on a pixel-by-pixel basis. There are several ongoing initiatives to undertake such an analysis routinely (e.g. GlobColour - <http://www.globcolour.info/>) but we demonstrate here that to a first order this can be estimated using the province distributions. Specif-

ically, we use the global province distributions presented above (based on fuzzy logic). For each of the optical water classes, the relative error and RMS error values estimated for the OC3M algorithm for the NOMAD v2 dataset are shown in Table 4.1. The resulting global distribution of relative error, based on the information in Table 4.1 and the fuzzy memberships maps, are shown in Figure 4.2.

Table 4.1 Error distribution across the eight optical water types as characterized using the MODIS-Aqua validation data set.

Optical water type	Average relative error	RMS log error	Bias log error	Number of points	Average Chl	Minimum Chl	Maximum Chl
1	16 %	0.090	-0.002	37	0.075	0.033	0.147
2	48 %	0.252	-0.125	33	0.257	0.077	0.703
3	51 %	0.265	-0.033	23	0.361	0.090	0.748
4	68 %	0.280	0.066	132	2.45	0.05	29.00
5	60 %	0.259	0.041	105	2.27	0.25	19.93
6	123 %	0.366	0.216	104	7.05	0.46	29.05
7	52 %	0.297	0.046	14	1.05	0.29	6.12
8	81 %	0.307	0.116	93	9.97	0.96	50.84
All	73 %	0.289	0.078	541	4.17	0.033	50.84

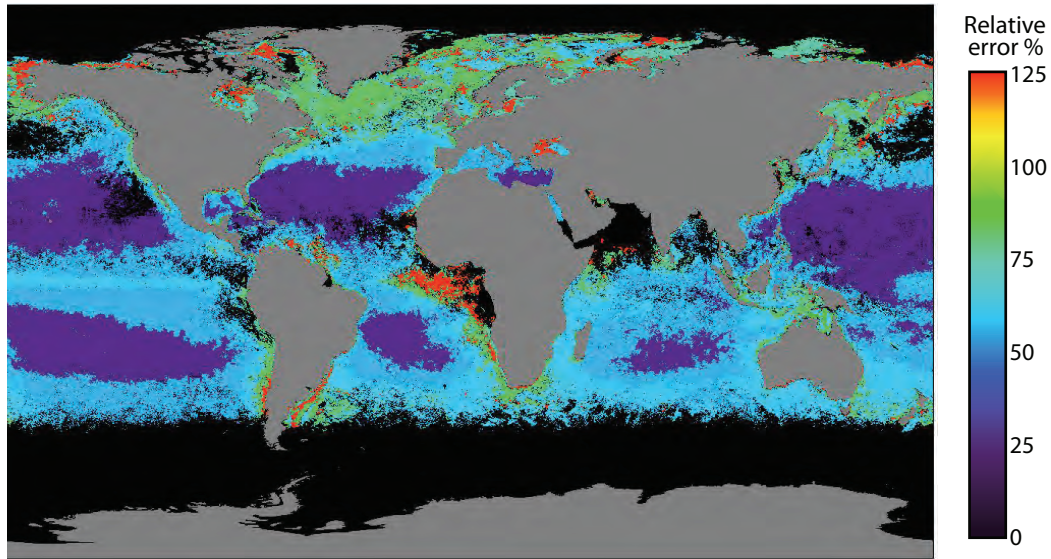


Figure 4.2 Global maps of the MODIS-Aqua chlorophyll uncertainty (relative error, %) for July 2005. Black represents areas with no data, grey represents land. Image courtesy of Mark Dowell, Joint Research Centre, EC.

4.1.4 Future developments

Application of the methods presented in this report for addressing the retrieval of chlorophyll concentration and other optically-active constituents demonstrates their value in improving the retrieval of the primary products from ocean-colour radiometry. Whether the technique is based strictly on the spectral properties of the water-leaving radiances, or whether it uses existing province distributions as templates for analysis, the prime motivating factor to use a classification methodology with OCR algorithms is to reduce the variance of the model-derived parameters associated with the optical properties of phytoplankton (e.g. the specific absorption coefficient). At present, the use of optical classification schemes to refine and constrain OCR algorithms is a topic of ongoing research and requires specific attention to ensure awareness and applicability of the method.

4.2 Estimation of Phytoplankton Production using OCR Data

The calculation of phytoplankton production at large spatial scales poses a problem that provided the original stimulus for developing the method of biogeochemical provinces. The calculation is based on the application of fundamental photo-physiology of algae, which can be represented by robust mathematical models. The models are forced by irradiance, and in the simplest case (assumption of vertical homogeneity) need a minimum of two (chlorophyll) biomass-normalised photosynthesis parameters, for which the existing database is not rich on a world scale. The models are implemented on a pixel-by-pixel basis and the problem arises that the parameters have to be assigned on each and every pixel, usually based on only limited information. The resolution of the problem was to postulate a suite of provinces within each of which the ecophysiological rates were characteristic (Platt *et al.* 1991). The required parameters were then assigned according to the province (and season) within which the pixel lay.

This was the approach used in the first calculation of global phytoplankton production using OCR data (Longhurst *et al.* 1995) and in a detailed calculation for the Atlantic Ocean (Sathyendranath *et al.* 1995). An important element of the approach is to construct the partition of the ocean itself. This task was accomplished brilliantly by Longhurst (1998) in a book that has influenced the science of oceanography far beyond the limited subject area of phytoplankton production.

4.2.1 Operational-mode remote sensing of primary production

In operational or routine estimation of primary production by remote sensing, the biome of interest is usually smaller than an ocean basin. The spatial resolution needed in the result is usually higher than that needed in basin-, and global-scale

calculations. Fixed protocols are applied on a regular basis to produce routine results that can be used directly in practical applications.

Platt *et al.* (2008) developed such a protocol for routine calculation of phytoplankton production from remotely-sensed data, using data from the Northwest Atlantic Ocean. Firstly, they constructed a local algorithm to generate reliable estimates of primary production, using information on forcing variables, physiological parameters for photosynthetic response to available light, and shape parameters for the vertical chlorophyll profile. Secondly, they established a protocol for extrapolation of the local algorithm to large horizontal scale, i.e. all pixels in the target image, using an archive of photosynthesis parameters and vertical structure of the chlorophyll profile for the region. Parameters were assigned according to matches between the remotely-sensed image data (chlorophyll, surface temperature) and the archived station data of ship observations for the same region. This approach was referred to as the “nearest-neighbour method”.

4.2.2 Application of the nearest-neighbour method

The rationale for the approach is that the magnitudes of the photosynthesis parameters that would be observed at a particular time and place would be determined by a suite of factors including the kinds and size of the cells present in the phytoplankton assemblage, their growth history, including light environment, the nutrient regime, temperature, degree of vertical mixing and so on. These variables can also help to set the local chlorophyll biomass. The combined effect of all the variables will be encoded in the parameter magnitudes, which can be estimated from archived data on the parameters from the same area, arranged according to the environmental context in which they were collected.

Of course, an important element of environmental context is that arising from the seasonal cycle of stratification and species succession. The former is associated with the annual cycle of surface temperature and the latter with changes in phytoplankton biomass (chlorophyll concentration). Fortunately, both these properties are accessible to remote sensing and are available routinely on synoptic scales. This is the basis of the nearest-neighbour method for parameter assignment: the remotely-sensed information about a given space-time point can be used as an entrance into the regional archive of parameters, and an average can be calculated for the parameters of the nearest neighbours of archived points.

The biomass B' , sea surface temperature T' , water depth z' and the day number t' are known for any pixel in the remotely-sensed images (the primes indicate properties of the image pixels), and are also available in the archived data (without primes) along with the parameters of the photosynthesis-light curve, and the parameters of the chlorophyll profile when it is fitted to a standard shape.

The strategy for the protocol is to enter the archive with the values of biomass and surface temperature for any given pixel in the remotely-sensed image, and find

the archive station with the closest coordinates of biomass and surface temperature. The chlorophyll profile and photosynthesis parameters for that archive station will be the first-order estimates of the parameters for that pixel. Note that the values of B , B' , T and T' must be scaled so that they have similar ranges to ensure that B and T are given equal weight in calculation of the Euclidean distance between the two points.

This procedure can be repeated with the parameters of the nearest neighbours of archived points (around 10) with the closest coordinates in the biomass-temperature plane, and the average parameter values can be calculated over this set. Furthermore, it should be taken into consideration that the archive station data and the image may have been taken in different seasons, so the archived station should be weighted according to the difference in day number between it and the image, thereby constructing a weighted average of the parameters over the nearest neighbour set.

The advantage of this method developed by Platt *et al.* (2008) is that it exploits fully the intersection between the image data and the archive data, using information from both the ocean-colour and the sea-surface-temperature images.

Chapter 5

Applications to Biogeochemical Cycles and Global Climate Change

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The oceans play a crucial role in the cycling of carbon in the Earth system. The oceans contain 38,000 billion metric tons of carbon (Sarmiento and Gruber 2002); this is about 55 times as much as is in the atmosphere (Sarmiento and Gruber 2006). Carbon dioxide (CO₂) is constantly in flux between the atmosphere and the oceans, through chemical disequilibrium between the air and water. The *solubility pump* of carbon refers to the thermodynamic air-sea gas exchange of carbon dioxide into the ocean in regions of under-saturation and the subsequent physical advection and diffusion of this carbon enriched water to depth. There is, however, an additional “biological” pump that plays a role in the movement of carbon in the ocean. In the photic zone, carbon can be incorporated into phytoplankton cells as part of the process of photosynthesis. In fact, phytoplankton are responsible for about half the primary production of the Earth’s biosphere (Field *et al.* 1998). Some of the organic matter that is thus incorporated into the marine ecosystem is exported out of the photic zone as sinking decaying material and fecal matter. This export can be sequestered in the deep ocean, leading to a gradient of dissolved inorganic carbon between the surface and depth. This will, in turn, increase the efficiency of the solubility pump.

In pre-industrial times, it is thought that the net flux of carbon into the global oceans was essentially zero since the atmosphere and ocean were in steady-state. As the atmospheric CO₂ content increases as a result of anthropogenic release of carbon by burning of fossil fuels (at the rate of 7.8 Gt C y⁻¹ in 2005, IPCC Report, Forster *et al.* 2007) and land use changes, the role of the ocean as a potential sink of carbon becomes more important. The flux of anthropogenic CO₂ from the atmosphere to the ocean has been estimated to be 2.2 ± 0.4 Gt C y⁻¹ for the 1990s (IPCC report, Bindoff *et al.* 2007). How will the ocean continue to react to future increases in atmospheric CO₂, and the associated changes to the ocean physics and chemistry? Carbon utilization is also linked intimately with the cycling of other elements (e.g. nitrogen, phosphorus), particularly in relation to the biological pump. Biological

production is rarely, if ever, limited by carbon, but rather by the availability of other macro-nutrients such as nitrate and phosphate, and micronutrients such as iron. To fully understand the movement of carbon through the system and the impact of the ocean on the anthropogenic induced changes, we must understand the rest of the biogeochemical cycles - the pathways of elemental material through both their inorganic and organic phases. The latter requires a deeper knowledge of the marine ecosystem and its variability on both seasonal and inter-annual time scales.

In this chapter we review and conjecture on how biogeographical provinces and satellite data can aid us in understanding biogeochemical cycles in the ocean. The relative strength of the biological pump can be dependent on the dominant type of phytoplankton. Broad scale variations in the species composition and diversity of biogeochemical functions of the ocean ecosystem can be described through a combination of physical and biological criteria (e.g. Longhurst 1998). Clearly the interplay of the local physical and nutrient environments leads to the delineations of these provinces. Thus provinces can be determined by nutrient availability and types of dominant species (the subject of the next two sections). In the third section we give examples of how inter-annual variability affects province productivity and phytoplankton assemblages. Long term variability resulting from climate change remains difficult to determine. In the fourth section we consider how biogeochemical cycles (nutrient availability, primary production, phytoplankton assemblages, and their feedback on air-sea exchange of CO_2) are changing and how they may continue to change in the future.

5.1 Nutrient Availability

Biological production in the ocean surface waters is rarely limited by the availability of carbon. Other macro-nutrients such as nitrate (NO_3) and phosphate (PO_4) frequently limit phytoplankton growth. For instance the first-order pattern of high and low surface chlorophyll concentrations (Figure 5.1a) and nitrate concentration (Figure 5.1b) are remarkably similar. Upwelling regions with high macro-nutrients tend to support higher productivity and therefore also higher chlorophyll. The correspondence between these patterns, though, is not exact. There are other macro-nutrients (e.g. phosphate and silicic acid) and micro-nutrients (e.g. iron) that can become limiting to productivity in different regions of the world oceans. It is the pattern of these combined limitations that can lead to the delineation of biogeographical provinces.

At present, nutrient availability cannot be estimated directly by satellite. As a consequence, empirical relationships have been developed to associate world ocean nitrate (NO_3), phosphate (PO_4) and silicate (SiO_4) availability with satellite-derived predictors like temperature (Kamykowski and Zentara 1986, as modified in Kamykowski *et al.* 2002). Additionally, satellite-derived chlorophyll can also

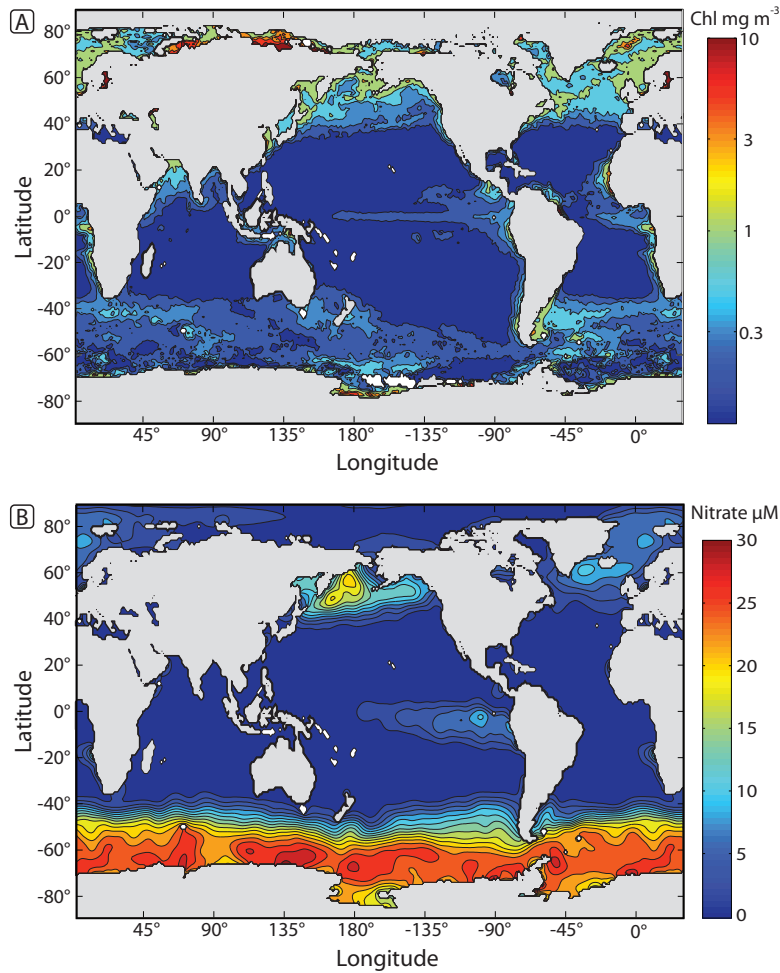


Figure 5.1 (a) Annual composite chlorophyll concentration (mg m⁻³) as derived by SeaWiFS; (b) Annual mean nitrate (μM) in the layer 0-10m (Conkright *et al.* 2002).

be combined with sea-surface temperatures (SST) to provide estimates of surface nitrate distributions (Goes *et al.* 1999; 2000; 2004).

Since supply of nutrients to the surface ocean outside terrestrial influence is mostly from colder depths by convection, mixing events or diffusion, there is often a negative correlation between SST and nutrient concentrations. The temperature-based approach of Kamykowski *et al.* (2002) estimates a Nutrient Depletion Temperature (NDT) at which colourimetrically-determined nitrate, phosphate and silicate become unmeasurable for each 2-degree latitude by longitude grid cell in the world ocean. Three NDTs result, one specific for each nutrient (i.e. NO₃, PO₄, and SiO₄ depletion temperatures). Nutrient availability is determined by subtracting each NDT from SST (e.g. [SST-NO₃, DT], [SST-PO₄ DT] and [SST-SiO₄ DT]). Additionally iron depleted areas from 40°N to 40°S can be inferred using aerosol concentrations

measured by AVHRR blended with precipitation measured by the Tropical Rainfall Measuring Mission's (TRMM) Microwave Imager (TMI). Sixteen nutrient availability categories, defined by the presence/absence of the four nutrients were mapped in the world ocean each month over a sixteen month period. For two offset annual cycles (Figure 5.2), nitrate, phosphate and silicate were all available in the oceanic Ekman upwelling areas and in coastal upwelling zones. These nutrients are selectively unavailable along the margins of these zones, and all unavailable in the central gyres. Atmospheric iron availability, which depended on an available dust source region and prevailing wind patterns, is prominent in the Atlantic Ocean off Africa and in the Northern Indian Ocean. More remote oceanic regions (specifically the Southern Ocean, and much of the Pacific) are low in iron. Where the low iron deposition areas coincide with upwelling and high macro-nutrients, there is a comparatively low concentration of chlorophyll. These regions are frequently denoted as "High Nitrate, Low Chlorophyll" (HNLC) regions. Monthly plots (Kamykowski *et al.* 2002) show a more dynamic relationship among the four nutrients.

5.2 Functional Groups

Biogeographic provinces are often described by the suite of organisms that dominate the region. From a biogeochemical perspective it is convenient to consider *functional groups* in which species are organized according to a specific biological function, for example diazotrophs, with the ability to fix nitrogen, or coccolithophores which produce calcium carbonate structural material. Different functional groups of plankton have differing capabilities for exporting organic matter (including carbon) to depth. For instance, those that build silica-based structures (e.g. diatoms) tend to export more organic material than many other phytoplankton types, and are therefore relatively more important to the biological pump. Hence it is important to understand where the different functional groups can be found and how these vary inter-annually and how they might respond to climate change. Recently it has become possible to identify types of phytoplankton from ocean-colour data (Subramaniam *et al.* 2002; Sathyendranath *et al.* 2004; Balch *et al.* 2005; Alvain *et al.* 2005; 2006; Uitz *et al.* 2006; Westberry and Siegel 2006; Aiken *et al.* 2007; Hirata *et al.* 2008).

A nutrient-depletion-temperature-based approach (NDT) toward phytoplankton functional group identification (Kamykowski *et al.*, 2002) examined the simultaneous availability of nitrate, phosphate and silicate, predicted by respective [SST-NDT] calculations using SST measured with the Advanced Very High Resolution Radiometer (AVHRR), and the availability of iron. The phytoplankton classes most likely associated with each of the 16 nutrient-availability categories were then identified and mapped based on a marine adaptation of the Plankton Ecology Group model for freshwater systems (Sommer 1989). For example, diatoms were expected only when

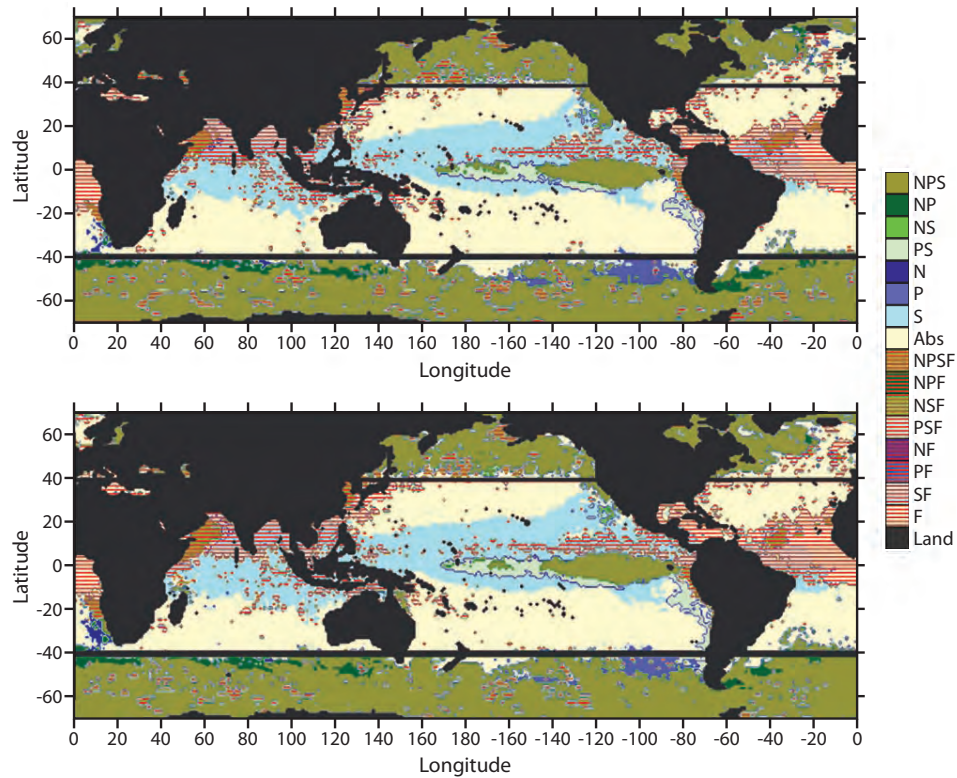


Figure 5.2 Two world ocean contour plots derived from a 16-month nitrate (N), phosphate (P), silicate (S) and iron (F) data set for two 12-month periods, (a) from March 1999 to February 2000 and (b) from July 1999 to June 2000. The annual representation was derived by calculating the mode for each 1° latitude by 1° longitude square for each 12-month period. Note that NPS implies only iron is unavailable, Abs indicates all nutrients are unavailable, NPSF indicates all nutrients are available, F indicates only iron is available. The black lines at 40°N and 40°S mark the limits of the precipitation data. Adapted from Kamykowski *et al.* (2002)

silicate was available with limited stress from other nutrients (NPS, NS, PS, NPSF, NSF, PSF), nitrogen-fixers were expected when other nitrogen sources were severely limiting (PF, SF, F), and oligotrophic phytoplankton were expected when adequate iron was not available (N, P, S, Abs). A second NDT-based approach toward phytoplankton functional group identification (Kamykowski and Zentara 2003) concentrated on the actual value of the $[\text{SST-NO}_3 \text{ DT}]$ calculation. The greater the negative result, the greater the inferred surface nitrate concentration; the greater the positive result, the greater the inferred stratification separating subsurface nitrate from surface waters. Two proof-of-concept trials organized phytoplankton community structure along the $[\text{SST-NO}_3 \text{ DT}]$ X-axis. In the first (based on samples collected off La Jolla, CA and analyzed using traditional microscope-based taxonomy), samples were successively distributed along the X-axis using maximum counts of centric diatoms, pennate diatoms and dinoflagellates as well as partitioned chlorophyll. In the second (based

on samples collected along the Atlantic Meridional Transect and analyzed using HPLC), maxima in nanoflagellates, large eukaryotes and prokaryotes successively distributed samples along the X-axis. These results suggest that phytoplankton functional group identification can indeed be inferred from satellite-derived [SST-NO₃ DT] values.

5.3 New Production

New production represents that part of primary production resulting from the assimilation by phytoplankton of nutrients newly added to the euphotic layer. As such, it is opposed to the *regenerated production* which emerges from nutrient recycling within that same upper layer of the ocean (Dugdale and Goering 1967). The *f*-ratio (Eppley and Peterson 1979) specifies the fraction of total production due to new production. Assuming a steady state, new production must be balanced by an equivalent amount of organic matter exported from the mixed layer. As defined, new production and the *f*-ratio are of particular importance, representing both an indicator of water column productivity for a given region, as well as an estimate of the ability of the pelagic ecosystem to export carbon from the surface waters to the deep ocean (the biological pump). The latter becomes even more important as atmospheric CO₂ rises.

Exogenous nitrogen inputs to the euphotic zone often occur when colder nutrient-rich waters are brought from the deep ocean. The processes involved can be winter convective mixing, wind-induced upwelling, or simple diffusion at a density gradient. In all cases, an inverse correlation between temperature and nitrate concentration (SST-NO₃ relationship) is found, enabling the determination of large-scale surface nitrate concentration using satellite-derived sea surface temperature (Kamykowski *et al.* 2002). In turn, clear relationships were also established between the *f*-ratio and nitrate concentration (Platt and Harrison 1985). Together these relationships can be exploited further to determine new production at different marine locations.

Dividing the Georges Bank area into three zones on the basis of satellite-derived biomass and SST fields, Sathyendranath *et al.* (1991) estimated new production to represent 31%, 55%, and 27% of the total production in the mixed, frontal and stratified regions, respectively. For that calculation, relationships between nitrate and temperature, on the one hand, and between nitrate and the *f*-ratio, on the other hand, were established for the Georges Bank province using field measurements. Other sets of these relationships were drawn from a province in the northwest African upwelling-center (Dugdale *et al.* 1989) and for one off the coast of California (Dugdale *et al.* 1997).

In the Pacific, the addition of surface chlorophyll to the SST-NO₃ relationship resulted in a significant improvement of nitrate retrieval, hence, new production prediction (Goes *et al.* 2000). The apparent stability of this new formulation, and the

access through satellite remote sensing of nutrient predictors such as temperature and chlorophyll, has shown to be very promising in generating maps of nitrate over the global ocean using a single set of parameters obtained after aggregating data over seasons and regions (Goes *et al.* 2004). In that study, however, the response of nutrients, f -ratio, and new production to changes in the environment is assumed to rely on a smooth and simple function. This, however, screens out the considerable variations commonly observed in those relationships. Harrison *et al.* (1987) for instance, observed a dynamic range up to a factor of 40 in some coefficients relating the f -ratio to the ambient nitrate concentration. Henson *et al.* (2003) could not demonstrate any correlations between temperature and nitrate in the spring and summer in the Irminger Basin, although a strong relationship was observed with the winter datasets.

In addition, some phytoplankton functional groups may have the capacity to fix nitrogen compounds in different ways and in different forms. Moreover, the sources of new nutrients into the productive layer of the ocean may differ drastically from the classical view of an enrichment from deep waters. As an example, Herut *et al.* (1999) estimated that the atmospheric inputs of bio-available N could represent 8 to 20% of new production in the southeast Mediterranean Sea. There is no reason to believe that such an input of new nutrient would be associated with a change in sea surface temperature. Furthermore, in summer in the western North Atlantic, Coles *et al.* (2004) observed a maximum in chlorophyll and significant new production due to the fixation of atmospheric nitrogen by *Trichodesmium*, with a clear decoupling between phytoplankton and the vertical nutrient flux in that area. Their study even suggested a positive relationship with temperature. High N-fixation rates were also recorded in the eastern tropical North Atlantic (Voss *et al.* 2004), enhanced by the supply of iron from atmospheric dust deposition.

It therefore becomes evident that relationships between satellite-derived indicators of nutrients and the f -ratio in the ocean are sufficiently variable and most valuable when results are separated into specific spatial and temporal patterns. The periodical nature of these properties (e.g. Henson *et al.* 2003) can be further exploited in the context of an ecological partition of the oceans to retrieve new production estimates over large areas using remote sensing data or regional modelling schemes.

5.4 Inter-annual Variability

It is crucial in any attempt to understand the effects of global climate change to understand first the natural year-to-year changes in any system. Studies of variability of ocean-colour data and the boundaries of biogeographical provinces find that many of the signals can be tied to large-scale phenomena such as El Niño/La Niña cycles (e.g. Yoder and Kennelly 2003) and the North Atlantic Oscillation (NAO) (Ueyama

and Monger 2005). Here we highlight as examples (1) inter-annual variability in the Pacific (much of which is influenced by El Niño) and (2) inter-annual variability in the North Atlantic (mostly from Continuous Plankton Recorder, CPR, data) and its looser ties to the NAO.

5.4.1 Pacific Ocean

The Pacific Ocean has a well-documented record of inter-annual variability affecting the characteristics and the distribution of its constituent biogeographical provinces. Much of this variability, especially in equatorial and tropical regions, follows the El Niño cycle. The El Niño Southern Oscillation (ENSO) evolves upon a background of interdecadal oscillations that affect physical and biological fields, including upper trophic levels (Mantua *et al.* 1997). In particular, the analysis of the strong 1997-1998 El Niño event benefited from an appropriate coverage by ocean-colour sensors that complemented other sources of data i.e. remote sensing and arrays of *in situ* measurements.

The equatorial Pacific can be split into two main regions, the warm pool (WARM) and the Pacific Equatorial Divergence (PEQD). The boundary between these regions displays clear gradients of sea surface salinity, temperature (to a lesser extent), $p\text{CO}_2$, and surface concentration of nitrate, biomass and productivity (Le Borgne *et al.* 2002). The surface concentration and the vertical structure of chlorophyll fields also differ. WARM is depleted in macronutrients (at least for NO_3 and PO_4) and a deep chlorophyll maximum is found around 80-100 m. PEQD, on the other hand, has high nutrients (from upwelled water) together with low-to-medium chlorophyll concentration (a classical HNLC regime). The location of the boundary between these regions undergoes large inter-annual variability. The signal of the strong El Niño of 1997-1998 and the moderate El Niño of 2002-2003 are clearly visible in the movement of this boundary (Figure 5.3). Previous studies have also found evidence of the El Niño signal in the boundary.

Using zonal sections from CZCS data, Halpern and Feldman (1994), found an increase in surface chlorophyll in the warm pool and a decrease in the central Pacific in November 1982 (El Niño). In February 1991 and April-May 1996, the surface concentration of chlorophyll was rather homogeneous in the eastern and central equatorial Pacific, and west to at least 165°E (Le Borgne *et al.* 2002). In contrast, Rodier *et al.* (2000), using Flupaq transects, found a strong chlorophyll gradient at 169°W , near the salinity gradient (172°W) during a period of negative Southern Oscillation Index. The 0.2 mg m^{-3} isopleth for the surface chlorophyll concentration was seen at 166°W . This isopleth was also observed by Matsumoto *et al.* (2004) at $161\text{-}162^\circ\text{E}$ in December 1999 and January 2001 (cold phases) and at 177°W in January-February 2002 (initiation of warm phase).

The hydrographic front (particularly salinity and $p\text{CO}_2$) and the western limit of the HNLC area do not always coincide. In warm phases, the latter can be several

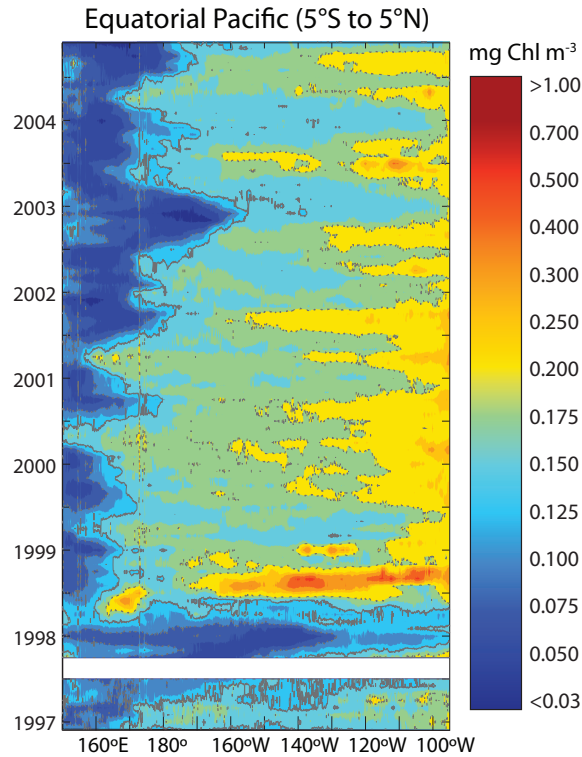


Figure 5.3 Time-longitude plot of chlorophyll-a concentration, averaged over the band 5°S - 5°N along the equatorial Pacific, and obtained from the OCTS and SeaWiFS time series. Image courtesy of Frédéric Mélin, Joint Research Centre, EC.

degrees east of the hydrographic front. During strong El Niño events, the high nitrate conditions in the PEQD can be completely eliminated west of the Galapagos archipelago. Longhurst (1998) suggested that a single province (WARM-ENSO) could be considered in such cases (see Figure 5.3). Conversely, the transition to a cold phase, accompanied by a renewed influx of nutrients after the long and intense warm phase of 1997-1998, and combined with the effects of the propagation of a tropical instability wave, resulted in a spectacular migrating phytoplankton bloom (e.g. Ryan *et al.*, 2002), a phenomenon atypical for the equatorial provinces.

The development of the ENSO cycle is not constrained to the equatorial Pacific but rather associated with large scale atmospheric and oceanic anomalies (e.g. Schwing *et al.* 2002). Connections with the North American west coast have been well documented. Particularly the boundary between areas of high concentrations of chlorophyll along the coast and the open ocean has been shown much closer to the continent during El Niño events, as seen with CZCS (Thomas and Strub 2001) or SeaWiFS (Chavez *et al.* 2002). Conversely, offshore Baja California, the extent of the mesotrophic biome ($0.2\text{--}1\text{ mg m}^{-3}$) approximately doubled (Kahru and Mitchell 2000) in 1997-1998. These modifications on primary producers and the changes in

the physical conditions in the California Current System had a noticeable impact on higher trophic levels, from zooplankton to cetaceans (Benson *et al.* 2002; Marinovic *et al.* 2002), that included the northern intrusion of warm water species. Such changes have counterparts along the coast of South America. For instance, Iriarte and González (2004) document the extension of oligotrophic characteristics to inshore waters during the second half of 1997 in northern Chile. Further north, the water masses of the North East Pacific also show inter-annual fluctuations linked to the ENSO variability. Whitney *et al.* (1998), on the basis of data collected along Line P (from Vancouver to Ocean Station Papa), distinguish three water types: the coastal zone, which is under the influence of summer upwelling, the open ocean, which is classified as HNLC, and the transition zone, which experiences nitrate depletion in summer.

The seasonal fluctuations of nitrate undergo significant inter-annual variability. For instance at the end of a warm phase in 1994, the area of nitrate depletion in summer extended much further into oceanic waters (600 km offshore). A similar extension was seen in 1997 and 1998 with respect to 1999. These extensions corresponded to a contraction of the band of high chlorophyll coastal waters seen in the ocean-colour record (Whitney and Welch 2002).

The subtropical North Pacific has also shown manifestations of inter-annual and inter-decadal variations (Venrick *et al.* 1987; Karl *et al.* 2001), with evidence of an increase in phytoplankton biomass and productivity in the gyre waters north of Hawaii. However, some changes affecting the functioning of the phytoplankton compartment are not observable by remote sensing. For instance, Karl *et al.* (1995) reported a strong increase in primary production from 1990 to 1991-92, and an increased abundance of diazotrophs, yet without a corresponding increase in surface chlorophyll concentration. Another example is provided by Leonard *et al.* (2001) with transects along 158°W sampled in April 1998 and 1999: the South Subtropical Front was encountered at 28-29°N and 31°N in 1998 and 1999, respectively. At the location of the front, the depth of the subsurface chlorophyll maximum (0.3 mg m^{-3}) shoaled by 20 m (it was found at 100 m in the south part of the gyre). This front and its inter-annual shift were not associated with any surface signature. Conversely, further north, the Subtropical Front outcropped at the surface, and was associated with the Transition Zone Chlorophyll Front (TZCF) and a clear ocean-colour signal (gradient from 0.1 to 0.3 mg m^{-3}). This front was located at 29°N and 32°N at the end of winter (most southerly displacement of the front) in 1998 and 1999, respectively (Bograd *et al.* 2004). In 1998, the TZCF was not only further south but showed a considerable meandering with respect to 1999 (Polovina *et al.* 2001). These conditions were associated with large increases in catch rates for albacore (large predators such as tuna and turtles migrate along this front).

Ocean colour will remain an important tool to follow the evolution of the Pacific Ocean particularly as it has shown signs of entering a new climate regime since 1998 (Bond *et al.* 2003; Peterson and Schwing 2003). McClain *et al.* (2004), for instance,

found that the surface area of the North Pacific subtropical gyre (defined as the area of SeaWiFS derived chlorophyll concentration below 0.07 mg m^{-3}) increased at a rate 3% per year over 6 years. Similarly, Polovina *et al.* (2008) documented the expansion of the low-chlorophyll regions in the tropical Pacific. In another study, Oliver and Irwin (2008) demonstrated that temporal changes in the equatorial Pacific provinces are tightly coupled to the ENSO indexes, with a lag of about one month, indicating that provinces are dynamic reporters of climate conditions.

5.4.2 North Atlantic

Long-term datasets are essential to identify inter-annual variability and relationships between climate fluctuations and both changes in species abundance and biodiversity, and changes in the structure and functioning of aquatic and terrestrial ecosystems. These datasets should also encompass a large range of regions to appreciate spatial variability in the response of ecosystems to climate change. Such datasets are unfortunately rare. For the marine pelagic environment, the Continuous Plankton Recorder (CPR) survey is the only plankton monitoring programme that allows examination of the long-term changes of more than 400 plankton species or taxa over many regions in the North Atlantic Ocean and its adjacent seas. The CPR programme is operated by a high-speed plankton recorder that is towed behind voluntary merchant ships at a depth of approximately 6 to 7 m. Plankton are filtered by a slowly moving band of silk with an average mesh size of $270 \mu\text{m}$. A second band of silk covers the organisms to form a sandwich that is reeled into a tank containing 4% formaldehyde. Further details on methods and the dataset are provided by Warner and Hays (1994) and Reid *et al.* (2003).

Results from the CPR survey have shown that major biological changes have taken place in the plankton over the last few decades mainly in the north-eastern part of the North Atlantic Ocean, including the North Sea. Using species assemblage indicators of calanoid copepods, Beaugrand *et al.* (2002a; b) reported substantial changes during the period 1960–1999 in the spatial distribution patterns of calanoid copepod assemblages at ocean basin scales, and provided evidence that this might have been influenced by the combined effect of climate warming of the Northern Hemisphere, and the North Atlantic Oscillation (NAO). Maps of the mean number of species present in an area for all species assemblages (Figure 5.4) demonstrate that major biogeographical shifts for all species assemblages have taken place since the early 1980s to the south-west of the British Isles and from the mid 1980s in the North Sea. The mean number of warm-temperate and pseudo-oceanic temperate species increased by about 10 degrees of latitude. In contrast, the mean number of cold-temperate mixed water, subarctic and arctic species decreased toward the north. All the biological assemblages show consistent long-term changes, including neritic species assemblages which also moved marginally northward. These changes have been correlated to Northern Hemisphere Temperature (NHT) anomalies and

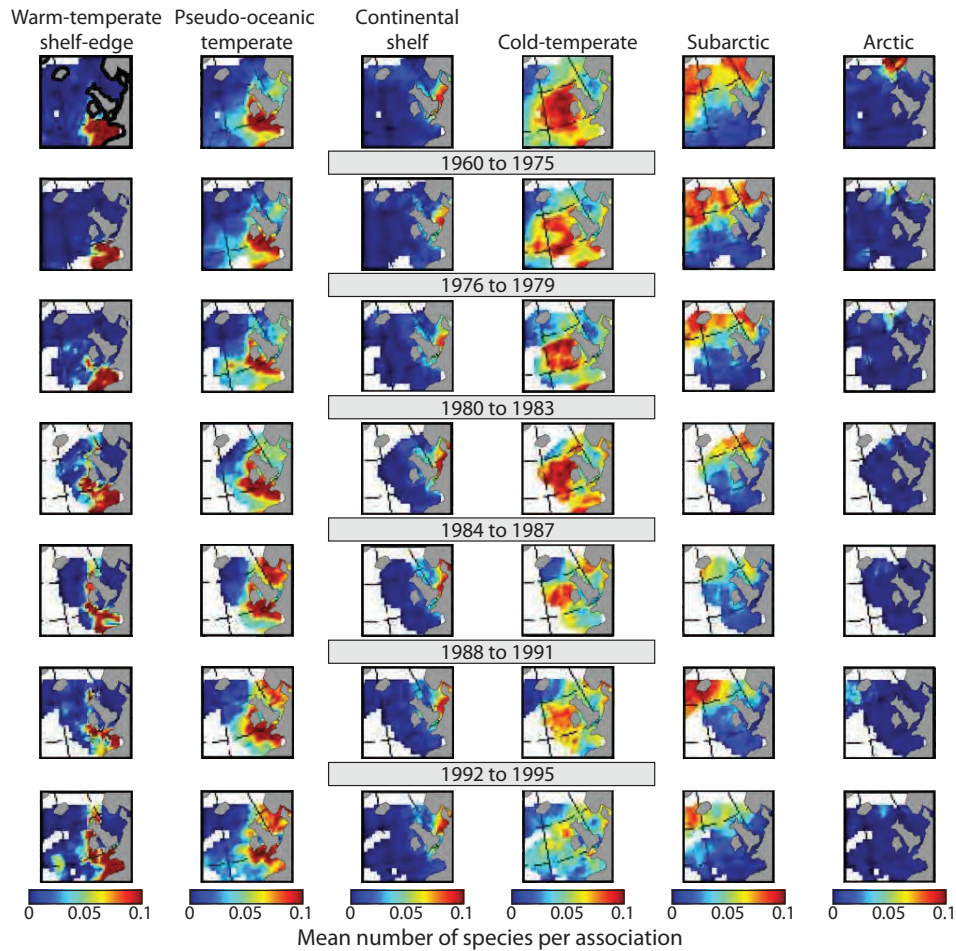


Figure 5.4 Long-term changes in the spatial distribution of the calanoid copepod species assemblages around the United Kingdom. Note the northward movement of the warm-water species associated with a decrease in the mean number of cold-water species. Adapted from Beaugrand *et al.* (2002b).

to a lesser extent the winter NAO index. West of the mid-Atlantic ridge, especially in the Labrador Sea, the trend was opposite and the number of both subarctic and arctic species increased while the number of warm-water oceanic species decreased. This result indicates a possible move of north-west Atlantic ecosystems toward a colder-biological dynamic regime. The opposing trends found in the eastern and western side of the North Atlantic indicate that the response of the biosphere to inter-annual variability may exhibit complex behaviour. This type of response is mediated through complex regional interactions with existing hydro-climatic channels such as the North Atlantic Oscillation. Indeed, the inverse response of ecosystems to climatic features on the two sides of the North Atlantic Ocean is consistent with the spatially heterogeneous nature of the climatic manifestations

induced by this dominant mode of atmospheric variability (Dickson *et al.* 1996; Drinkwater 1996).

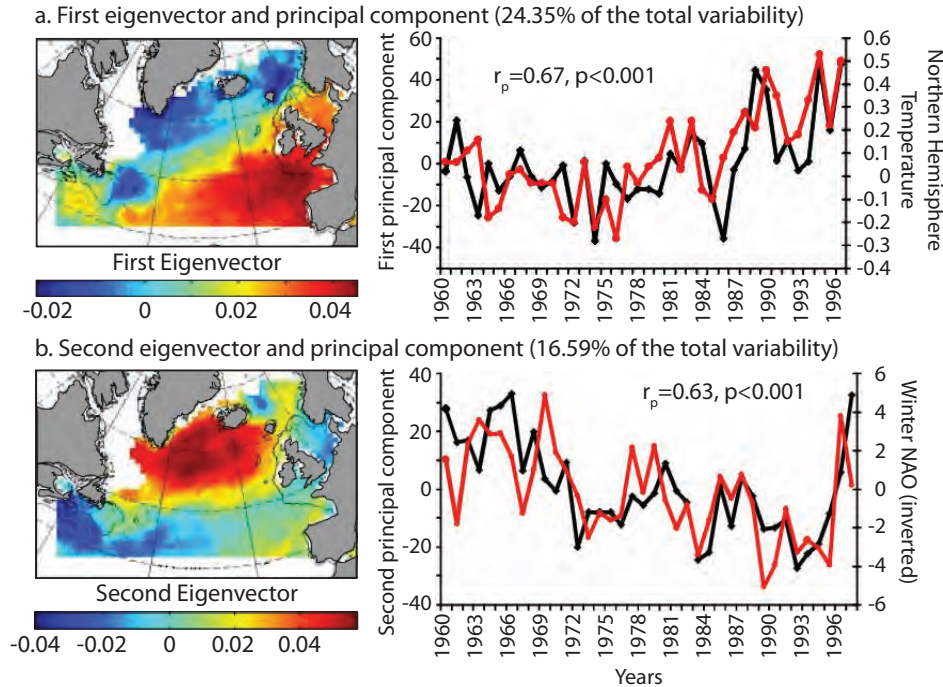


Figure 5.5 Principal Component Analysis of long-term changes in sea surface temperature in the North Atlantic Ocean. (a) Long-term changes in Northern Hemisphere Temperature (NHT) anomalies and Pearson correlation coefficient between the first principal component and NHT anomalies are indicated. (b) Long-term changes in the winter North Atlantic Oscillation (NAO) and the Pearson correlation coefficient between the second principal component and the NAO index are indicated. The signal displayed by the first principal component (PC) is highly correlated positively with NHT anomalies ($r_p = 0.69$, $p < 0.001$). In the subarctic gyre, the values of the second PC decreased until about 1993 and then increased. The long-term change in the second PC is highly correlated negatively with the NAO index ($r_p = -0.63$, $p < 0.001$). Modified from Beaugrand *et al.* (2002b).

To better understand how large-scale hydro-meteorological processes may have influenced the biogeographical shifts observed in the studied area, long-term changes in Sea Surface Temperature (SST) were investigated. Figure 5.5 displays the first two eigenvectors and principal components representing 40.9% of the total variability. The region south of a line from 40°N, 45°W to 60°N, 5°E and especially in the West European Basin was characterized by a decrease in SST from 1960 to about 1975 and then a strong continuous increase until 1997. Long-term changes in this signal are correlated positively with NHT anomalies. In the subarctic gyre the second principal component negatively co-varied with the NAO, showing a decrease until 1993 and then an increase.

5.5 Anthropogenic Induced Climate Change

Coupled ocean-atmospheric models (e.g. Covey *et al.* 2003; Dutkiewicz *et al.* 2005b; Russell *et al.* 2006; IPCC Report - Meehl *et al.* 2007) have suggested that the physics of the ocean will change quite dramatically over the next few hundred years as the climate system becomes increasingly affected by the greater abundance of greenhouse gases (e.g. carbon dioxide, methane) accumulating in the atmosphere. Some of these changes are:

- ❖ increased water temperature, especially sea surface temperatures,
- ❖ reduced sea-ice coverage,
- ❖ increase in sea level,
- ❖ increased surface stratification, and
- ❖ reduced production of North Atlantic Deep Water, leading to a slowing down of the meridional overturning cell in the North Atlantic
- ❖ changes to overturning in response to shifting wind patterns (e.g. the intensification and poleward shift in the Southern Ocean westerlies).

Increased sea surface temperatures will lead to enhanced surface stratification. This together with a slowing meridional overturning will lead to a potential slowing of the transport of carbon away from the surface waters. However, highly increased atmospheric CO₂ will lead to a large influx of carbon into the surface waters. What will happen to the “biological” pump? Models (e.g. Bopp *et al.* 2001; Boyd and Doney *et al.* 2002; Sarmiento *et al.* 2004a; Dutkiewicz *et al.* 2005b; IPCC Report, Meehl *et al.* 2007) suggest the following:

- ❖ a decrease in surface nutrients, due to increase stratification (e.g. Figure 5.6b),
- ❖ changes to light due to changes in cloud cover and particularly to changes in the sea-ice cover,
- ❖ changes to the growth season, due to both changes in the temperature and changes to the stratification,
- ❖ an increase in the acidity (lower pH) of the surface waters as larger amounts of carbon are dissolved into the surface (e.g. Figure 5.6c), and
- ❖ changes in species, in response to changes in temperatures, light and pH.

Such changes will have an effect on biogeographical provinces. Province boundaries will shift as the physical attributes of the upper ocean change, along with associated changes in nutrient and plankton distributions. The modelling study of Sarmiento *et al.* (2004a) demonstrates the utility of using biogeographical provinces as a means of tracking and possibly quantifying the impacts of climate change. However, more difficult questions address the impacts of changing plankton assemblages. Will these lead to completely new provinces and if so, how will these new and altered provinces compare in their ability to export carbon from the surface?

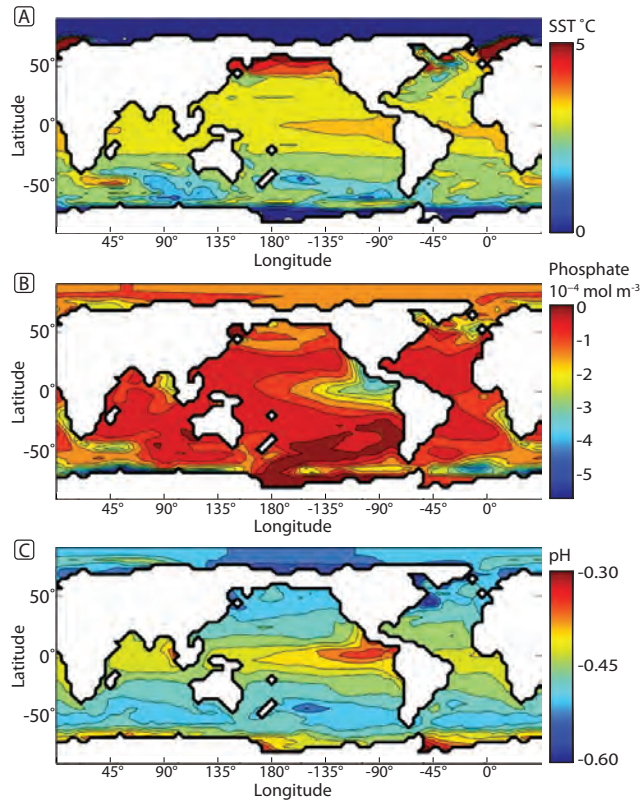


Figure 5.6 Model results from the Integrated Global System Model 2 (IGSM2) which is run with a 2-dimensional atmospheric model with active chemistry, 3-dimensional ocean model, carbon cycle models for ocean, and land vegetation and ground water models as well as land and sea-ice models. (a) Difference in Sea Surface Temperatures ($^{\circ}\text{C}$) 2100-1860. Contour interval 0.5°C . Areas with small difference near the poles are regions with significant sea-ice coverage. (b) Difference in surface phosphate ($10^{-4} \text{ moles m}^{-3}$) 2100-1860. Contour interval $0.5 \times 10^{-4} \text{ moles m}^{-3}$. (c) Difference in surface pH 2100-1860. Contour interval 0.025 units. Adapted from Dutkiewicz *et al.* (2005b).

5.5.1 Nutrient availability

There is increasing evidence that surface nutrients in the ocean are decreasing. A Nutrient Depletion Temperature based approach (see Section 5.1) showed an overall trend of decreasing world ocean nitrate availability through the 20th century and a receding front of nitrate availability in the High Nutrient Low Chlorophyll (HNLC) regions along the Equator and along the equator-ward margins at higher latitudes (Kamykowski and Zentara 2005; 2006). A more detailed analysis compared nitrate availability in a representative cold year, 1909, to that in a representative warm year, 2002, just after the end of the century (Figure 5.7). A general decrease in nitrate availability occurred through the 20th century, but regional increases occurred in a few areas. The overall spatial complexity in nitrate availability was

related to reported co-variation in broadly-separated regional fisheries (Klyashtorin 2001). Results suggested that the changing nitrate availability acted on fisheries as a bottom-up control influencing phytoplankton community structure. An overriding question remained unanswered: in the next relatively cool phase of the interdecadal cycle, will available nitrate return to levels capable of supporting the ecosystems that occurred under those conditions earlier in the 20th century?

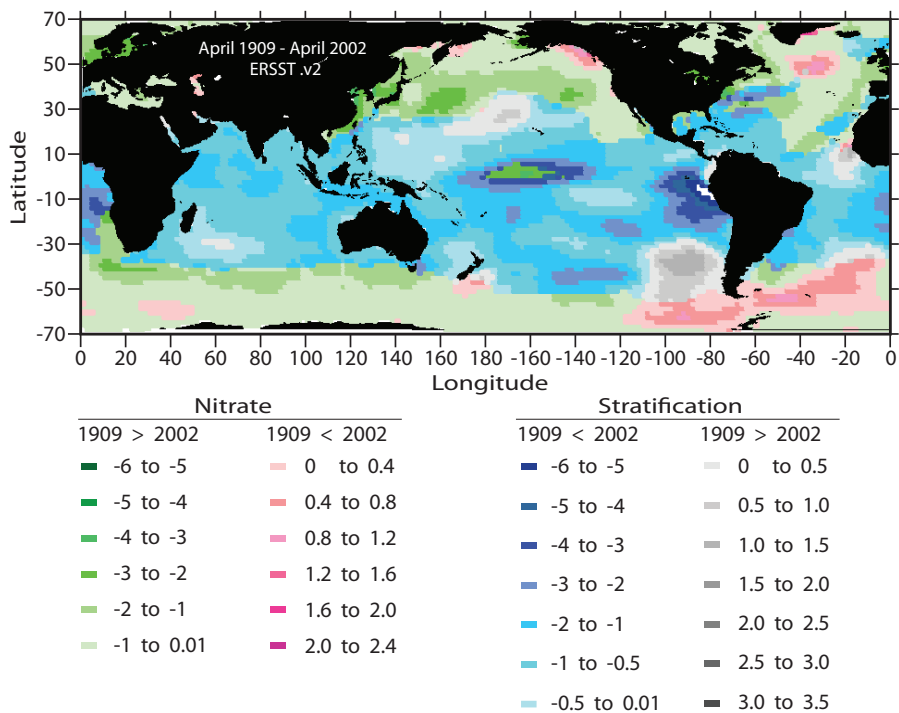


Figure 5.7 A classed post map comparing nitrate availability changes between April 1909 and April 2002 using [SST-NDT] values based on Sea Surface Temperature (SST) from the Extended Reconstruction Sea Surface Temperature, version 2 data set (ERSSTv.2) minus the National Oceanographic Data Center based (NODC-based) NDTs. Negative [SST-NDT] values or nitrate present at the surface are represented by green (1909 nitrate > 2000 nitrate) and red (1909 nitrate < 2002 nitrate). Positive [SST-NDT] values or the temperature stratification between the surface and the nitricline are represented by blue (1909 stratification < 2002 stratification) and gray (1909 stratification > 2002 stratification). Darker colours in each series represent greater differences between the years. Adapted from Kamykowski and Zentara (2005).

It is likely that other macro-nutrients (e.g. phosphate, silicic acid) are also becoming less available in the surface ocean. It has also been estimated that iron deposition has decreased over the last couple decades (Gregg *et al.* 2003, using the modelled mineral dust deposition results of Ginoux *et al.* 2001), although modelling studies of future atmospheric dust loading suggest a range of 20% increase in dust (Tegen *et al.* 2004) to a 60% decrease (Mahowald and Luo 2003).

5.5.2 Chlorophyll and productivity

How will the changes to the ocean, especially decreased nutrients (macro and micro), affect phytoplankton growth? Though some studies suggest that global surface chlorophyll may have increased especially relative to the CZCS era (Gregg *et al.* 2002; Gregg *et al.* 2005; Antoine *et al.* 2005); Behrenfeld *et al.* (2006) found a global mean decline in satellite derived chlorophyll and net primary production (NPP) over the 2000s. Distinct regions where NPP decreased were associated with increased SST. Additionally Gregg *et al.* (2003) found a 6% decline in the surface primary productivity as determined by ocean-colour data between the CZCS years (early 1980's) and the 1997-2002 SeaWiFS years. This decline corresponded to a 0.2°C increase in sea surface temperature (with accompanying increased stratification and implied decreased macro-nutrients) and a 25% decrease in iron deposition. Most of the decline in productivity occurred at higher northern latitudes. A particularly vulnerable region appears to be around Antarctica: Montes-Hugo *et al.* (2009) found a striking 12% decrease in the summertime chlorophyll along the western shelf of the Antarctica Peninsula due to shifting patterns of ice, clouds and winds that affect the mixing. Another striking shift in provincial boundaries is evident from McClain *et al.* (2004), who found that the North Pacific and North Atlantic subtropical oligotrophic gyres (defined as areas with SeaWiFS-derived chlorophyll $< 0.07 \text{ mg m}^{-3}$) had increased by 3% per year and 4% per year respectively between 1996 and 2003. Associated with this areal increase was a decrease in chlorophyll in those regions of 1% and over 2.5% per year, respectively. Further study is required to determine if these shifts in province boundaries are part of a long-term trend associated with climatic warming and reduced nutrients?

However, not all ocean provinces appear to have had a decline in productivity. Montes-Hugo *et al.* (2007) found that receding sea-ice extent since the 1970's led to some shifts in boundaries that led to increase in chlorophyll in the southern region of the western shelf of the Antarctic Peninsula. Gregg *et al.* (2003) suggest that the primary production did increase in some equatorial regions, and Behrenfeld *et al.* (2006) found that in the 1999 to 2004 time period some areas had an increase in NPP, and often these regions also had associated decreased SST. The Behrenfeld *et al.* (2006) study only considered changes for the lower latitudes. The modelling study of Bopp *et al.* (2001) found that although the total ocean productivity decreased in a world where the atmospheric CO₂ was doubled from present, some high latitude regions actually had an increase in productivity. This increase was attributed to the decrease in light limitation brought on by a longer growing season induced by the increased stratification (i.e. shallower mixed layers). The decreased light limitation outweighed the decreased nutrients in the upwelling high latitudes regimes. However, the Gregg and Conkright (2002) satellite analysis together with a model study (Gregg 2002) found that any enhancement of the spring bloom due to increased stratification in the last two decades led to a more severe nutrient

limitation later on in the season. The net annual result was lower productivity. How will this combination of light and nutrient limitation play out in these regions in the future? How will individual provinces continue to change, and in particular how will the boundaries of the provinces continue to shift?

Sarmiento *et al.* (2004a) used six different coupled climate models to investigate the response in the boundaries of biogeographical provinces (here determined by basin, model upwelling, winter mixing, ice cover, divergent flow) to climate change by the year 2050. Each province had associated with it an empirical chlorophyll model, and associated estimates of primary production. Changes to stratification, maximum mixed layer depths and water mass also brought significant shifts in province boundaries. Globally the models predicted a 0.7% to 8.1% decrease in primary productivity. However the individual model boundary shifts were not very comparable, the most consistent response between models came from changing the boundaries of the highly productive marginal sea-ice province. We have already seen some boundary shifts in the real oceans: how will individual provinces continue to change, and in particular how will the boundaries of the provinces continue to move?

Increased surface stratification is definitely not the only change that will affect ocean productivity. Nutrient supply for instance does not only come from vertical processes: lateral processes are important in maintaining nutrient budgets (e.g. Sarmiento *et al.* 2004b; Dutkiewicz *et al.* 2005a; Williams *et al.* 2006). Future changes in wind stresses (and therefore Ekman transport) and changes to productivity of upwelling regions, will therefore also have an effect on supply of nutrients to, and hence productivity in, downstream provinces.

5.5.3 Plankton

The above studies have taken broad methods of estimates of change over the global oceans. They have not addressed the more complex consequence of shifts in species in response to climate change. Boyd and Doney (2002) summarized some of the regime shifts seen in the Pacific biogeographical provinces, that can be attributed to increased stratification and shallower mixed layers that will be associated with global warming. For instance, they cite the more persistent coccolithophore blooms in the Bering Sea (Napp and Hunt 2001). The year 1997 saw profound changes in the functioning of the eastern Bering Sea: Vance *et al.* (1998) reported the first recorded occurrence of a large coccolithophore bloom that summer, a phenomenon observed in subsequent years with *in situ* sampling and SeaWiFS imagery (Iida *et al.* 2002). Another long-term shift in functional regime appears to have occurred in the North Pacific subtropical gyre through the late 1980s and early 1990s: Karl *et al.* (1997) found a dramatic increase in nitrogen fixers with more stratified conditions. Nitrogen fixers are unique in converting the abundant inert nitrogen to a biologically-available form. An increase in nitrogen fixing will potentially dramatically alter

nutrient stoichiometry. Such shifts will profoundly affect nutrient (and carbon) cycling in the region. Boyd and Doney (2002) also cite increased diatom blooms in the Equatorial Pacific as a response to shoaling of the upper ocean thermocline (Chavez *et al.* 1999). Such a shift will lead to greater export in that regime. Also cited are several studies showing shifts in the Southern Ocean communities in response to shoaling mixed layers (e.g. Boyd *et al.* 2000; Blain *et al.* 2001). In particular Arrigo *et al.* (1999) documented a shift from *Phaeocystis* to diatoms along the current ice shelf in the Southern Ocean, which could result in a decrease in the amount of carbon fixed per unit nitrogen.

Ecosystems of the north-east North Atlantic have changed over the past couple of decades toward a warmer dynamical regime. The observed biogeographical shifts in calanoid copepod distributions may have serious consequences for the whole ecosystem from phytoplankton to fish. Beaugrand and Reid (2003) detected similarities between the long-term changes in a Continuous Plankton Recorder (CPR)-derived index of phytoplankton biomass and abundance of small copepods, abundance of *Calanus finmarchicus*, euphausiids, the Atlantic salmon, SST, North Hemisphere Temperature (NHT) anomalies and, to a lesser extent, the winter North Atlantic Oscillation (NAO) index.

Richardson and Schoeman (2004) have shown that climate warming has involved an increase in the abundance of phytoplankton species in cooler regions and a decrease in warmer regions. They suggest that the impact has propagated to copepod herbivores and carnivores. The authors found evidence of a bottom-up control in the pelagic ecosystem of the eastern part of the North Atlantic. Those changes have been accompanied by species/group dependent phenological changes. For example, although the timing of diatom blooms seem to be fairly constant, that of dinoflagellates and meroplankton occurred earlier.

The current response of pelagic ecosystems to climate warming may have strong consequences for the ecosystem functioning and biogeochemical cycles. These biogeographical modifications paralleled a northward extension of the ranges of many warm water fishes in the same region (Quero *et al.* 1998; Stebbing *et al.* 2002). These results tend to indicate a shift of marine pelagic ecosystems toward a warmer dynamic regime in the north-eastern North Atlantic. Similar changes in spatial distribution and phenology have been detected for many species of plants in western Europe (Fitter and Fitter 2002), butterflies (Parmesan *et al.* 1999), amphibians (Beebee 1995) and birds (Thomas and Lennon 1999), and were attributed to climate warming. If the increase in Northern Hemisphere temperature predicted by the Intergovernmental Panel on Climate Change (IPCC Report 2001) continues, a marked change in the organisation of pelagic ecosystems from phytoplankton to fish can be expected with a possible impact on biogeochemical cycles. The current climate warming may manifest itself directly on SST. However, the opposite response of marine ecosystems to climate change observed over the Labrador Sea (Beaugrand *et al.* 2002a) shows that climate warming may also exhibit complex behaviour.

This kind of response is mediated through complex regional interactions with existing hydro-climatic channels such as the NAO. Furthermore, climate change may affect pelagic ecosystems by influencing either their stable-biotope component (e.g. modification in wind intensity and direction) or their substrate-biotope component (e.g. modifications in oceanic currents). It may also trigger a nonlinear response of marine ecosystems, possibly associated with hysteresis behaviour (Paillard 2001; Scheffer *et al.* 2001). Such a response has occurred in the North Sea after circa 1987 (Reid *et al.* 2001).

5.5.4 Feedback to air-sea fluxes of CO₂

The ability of the ocean to take up CO₂ will change significantly in a future high atmospheric *p*CO₂ world. Many of these modulations will arise from changes in the physical and chemical processes, but these changes are very complex and may compete. For instance CO₂ is less soluble in warmer water; increased stratification will lead to reduced mixing between surface and deep water, and therefore reduced movement of CO₂ by physical processes to depth; but increased winds might increase ventilation of carbon-rich water and reduce uptake (possibly already observed in the Southern Ocean, Le Quéré 2007). In addition, biological changes, not yet well understood, will occur as a result of the ocean's response to climate change.

Lower rates of primary production are predicted as a response, in part, to decreased nutrients in many regions of the ocean. Model studies (e.g. Woods and Barkmann 1993; Matear and Hirst 1999; Parekh *et al.* 2006) suggest that this will lead to a positive feedback (i.e. reduced ocean carbon uptake). However reduced ventilation of the deep ocean also means less exposure of deep water with high dissolved carbon concentration (deep water accumulates carbon as part of the biological pump), which could have the opposite feedback. The balance of the two processes will lead to either a total positive or negative biological pump sequestration feedback (Matear and Hirst 1999).

In addition, more complex feedbacks will arise as a result of changes to the structure and biogeochemistry of marine ecosystems. Calcifying organisms may increase due to warmer conditions (Holligan and Robertson 1996), or decrease due to the more acidic conditions associated with higher ocean CO₂ concentrations (Riebesell *et al.* 2000). A decrease in coccolithophores will probably result in a negative feedback (i.e. increased uptake of CO₂ by the oceans): reduced carbon sinks to depth in the form of CaCO₃ shells, but also less dissolved CO₃ removed, resulting in an increase in alkalinity and a greater solubility of CO₂. This scenario, and the corresponding opposite response for increased calcifiers, was found in the modelling study of Chuck *et al.* (2005), although the feedbacks were fairly small. More stratified conditions could lead to phytoplankton populations more suited to oligotrophic conditions. These plankton are often associated with a tighter recycling loop and less export of organic material to depths. Chuck *et al.* (2005) found that an

increased proportion of “export” species led to an additional uptake of atmospheric CO₂, while increased recycling led to a decreased ocean uptake and subsequently even higher atmospheric CO₂ levels.

It is likely that biological provinces will each have differing shifts in their functional groups. We must first understand the impacts in each region before we can determine their integrated response and the feedbacks to the net global CO₂ air-sea flux.

5.6 Summary

The regional, seasonal, inter-annual and future variations and efficiency of the oceanic carbon pumps are determined to a large extent by the types of phytoplankton that dominate. The efficiency of export of organic matter from the euphotic zone and the depth at which it is remineralized are both influenced by the composition of the organic detritus which, in turn, is influenced by variations in the phytoplankton community. Species dominance is dictated by the complex interplay of the local physical and nutrient environments, and ecological competitiveness. In this chapter we have provided an overview of the uses of biogeographic provinces and satellite data to elucidate some of these controls and their variability. As we enter an era of a rapidly changing climate system, it becomes all the more important to understand biogeochemical cycles and their control on phytoplankton productivity and carbon fluxes. In this regard it is essential to maintain satellite monitoring of the world's oceans as a means of detecting biological regime shifts.

Chapter 6

Applications to Marine Resources and Biodiversity

Jesus Morales, Shubha Sathyendranath, Gregory Beaugrand, Nicholas Hoepffner, Antonio Mata

6.1 Introduction

Fisheries and agriculture are among the oldest and most extensive professional activities around the world. For centuries it was commonly accepted that the marine resources would be inexhaustible, however, in the last few decades the ocean fisheries catch reports have shown that the marine yield has reached a plateau in some regions, with a clearly decreasing pattern in many other areas. Many local, national and international programmes for conservation and management of marine resources have been proposed since then; most of those programmes were based on precautionary principles issued using the statistical analysis of population dynamics.

In the last 15 years, fisheries oceanography has provided increasing knowledge about the relationship between marine life and habitat; this new vision for fisheries management received international support during the FAO (Food and Agriculture Organization) International Fisheries Conference held at Reykjavik in 2001. The Reykjavik Declaration considered *ecosystem-based management* as the way to “.....ensure sustainable yields while conserving stocks and maintaining the integrity of ecosystems and habitats on which they depend”. The general acceptance of this new approach for fisheries management was supported by the World Summit on Sustainable Development (WSSD) (Johannesburg 2002) through its Implementation Plan (Art. 29d) encouraging the application by 2010 of the ecosystem approach.

The ecosystem-based management proposal evolved into the concept of an ecosystem-based approach (FAO, 2003), extending the original single management idea to a wider approach involving a better understanding of the processes and ocean dynamics relevant for fisheries management in a close relationship between physical and biological oceanography and ecosystem trophodynamics. The linkage between physical forcing and its biological consequences is the basis of the biogeochemical provinces proposed by Longhurst (1998) and forms the basis for some recent applications concerning marine resources (Pauly *et al.*, 2000; Watson *et al.*, 2003).

Methodological approaches used to address the structure and function of pelagic

ecosystems have evolved to use satellite oceanography, especially for applications related to fisheries and marine resources. The original approach linked fishing grounds to thermal fronts (Lasker *et al.* 1981; Laurs *et al.* 1984) using NOAA-AVHRR imagery as input data, establishing an important link between physical oceanography and fisheries biology. The crucial linkage between the physical barrier represented by thermal fronts and the concentration of plankton elements (phytoplankton, zooplankton) was also observed with the use of CZCS imagery for fisheries applications (Yamanaka 1982).

More recently, the close relationship between physical oceanography and pelagic food webs has been studied extensively with the progressive assimilation of other remotely-sensed data in addition to that of sea surface temperature (SST) and ocean-colour data, such as altimetry-derived currents, sea surface height (SSH) and/or sea level anomalies (SLA). As a result of this integrated approach, the number of physical barriers and mesoscale processes actually accepted as critical features in the fisheries biology of pelagic species has grown significantly, including salinity (density) fronts, eddies, shelf-break fronts and upwelling process.

The dynamical approach involved in data assimilation analysis of coastal and marine mesoscale processes for fisheries applications represents a significant improvement in the understanding of the real functioning of pelagic ecosystems, close to the “ecosystem-based approach” proposed by the international organizations. In this chapter we review the current knowledge and potential use of ocean-colour information and the derived eco-regions concept for plankton (phyto- and zooplankton) and fisheries research.

6.2 Phytoplankton

Until recently, ocean-colour data have been used primarily for mapping concentrations of the major phytoplankton pigment, chlorophyll-a, which in turn is used for computation of primary production at the global scale. But recently, it has also become possible to map the distribution of some major phytoplankton groups using ocean-colour data. This new development has followed the advent of improved satellite sensors with higher spectral resolution than the first-generation CZCS sensor, coupled with improvements in ocean-colour models and in our understanding of how variations in phytoplankton community structure influence the inherent optical properties of phytoplankton, and hence the water-leaving signal.

Over the past few years a number of publications have advanced the identification of dominant phytoplankton groups from satellite data. Sathyendranath *et al.* (2004) used the flatter absorption spectrum of diatoms to discriminate them from other algal groups, while Alvain *et al.* (2006) relied on the relationship of the spectral shape of the specific water-leaving radiance (nL_w) to the biomarker pigments of five phytoplankton groups. Similarly, Aiken *et al.* (2007) applied the

empirical relationships developed for the chemical size fractioning of phytoplankton populations to the analysis of MERIS image data. They compared *in situ* data with the satellite-derived information and obtained some promising results discriminating between high- and low-scattering microphytoplankton (diatoms and dinoflagellates respectively) as well as high-scattering coccolithophores and other nanoflagellates. Furthermore, Uitz *et al.* (2006) used the surface chlorophyll-a concentrations for the assessment of the phytoplankton community composition and Hirata *et al.* (2008) have used an IOP approach based on $a_{ph}(443)$ to derive dominant phytoplankton size classes.

The standard ocean-colour products provided by NASA now include a flag indicating the presence or absence of coccolithophores and *Trichodesmium* blooms. The presence or absence of coccolithophore blooms is determined on the basis of the high reflectance that is associated with the calcium plates that become detached from the organism, and cause the waters to turn a turquoise blue colour when present in large quantities. Subramaniam *et al.* (1999a; b; 2002) studied the reflectance properties of *Trichodesmium* and proposed ocean-colour algorithms for their identification, based on their optical characteristics.

Platt *et al.* (2005) demonstrated that there is a close link between dynamically-assigned boundaries of provinces in the North-West Atlantic and the distribution of diatom blooms in the region. As suggested by Margalef (1967), the dynamics of the surface layer of the ocean influences not only the amount of phytoplankton present in the water, but also the type of community that survives and flourishes there. Since the biogeochemical provinces as proposed by Longhurst (1998) are assigned on the basis of large-scale forcing fields, it does not come as a surprise that the extent and location of provinces are related to the distributions of major phytoplankton types.

Information on phytoplankton community can also be obtained indirectly. In the open ocean, it has been shown that Case-1 waters typically prevail. That is to say, in such waters, optical properties can be modelled as a function of the main phytoplankton pigment, chlorophyll-a. This does not imply that chlorophyll is the only property that can be derived from ocean-colour data in Case-1 waters. In fact, it is now understood that there is a natural progression in phytoplankton community structure, as we move from oligotrophic to eutrophic waters. Typically, the phytoplankton populations change from small prokaryotes in oligotrophic waters, to large eukaryotes in eutrophic waters. Related changes in cell size and pigment composition are summarised in Table 6.1, which can be extended to include general trends in other diagnostic pigments. Macro-ecological studies have also shown some general trends in phytoplankton community structure, as a function of total biomass (Bouman *et al.* 2005) and temperature. Thus, it would always be possible to infer some information on phytoplankton community if we knew the total biomass from ocean-colour data. But one has to recognise that deviations do occur from the general trends, and that caution must be exercised when making

use of such trends. Such analyses will not allow one to distinguish between, say, blooms of diatoms and prymnesiophytes that can occur at the same time, in different locations of the Labrador Sea (Stuart *et al.* 2000).

Table 6.1 General trends in phytoplankton community structure along a gradient from a low-biomass environment to a high-biomass environment in the open ocean. (PPP=photoprotective pigments).

Low Biomass Environment	High Biomass Environment
High specific absorption	Low specific absorption
Small cells	Large cells
High PPP/Chl-a	Low PPP/Chl-a
High Chl-b/Chl-a	Low Chl-b/Chl-a
Low Chl-c/Chl-a	High Chl-c/Chl-a
Low fucoxanthin/Chl-a	High fucoxanthin/Chl-a

To take the analyses beyond the general trends, one has to rely on small spectral differences in the optical characteristics of different types of phytoplankton, as in the case of the models of diatoms, coccolithophores and *Trichodesmium*. Limitations in atmospheric correction procedures and in the spectral resolution of the signal are the main factors that limit the performance of such algorithms. One anticipates that this family of algorithms will develop further as radiometric accuracy and spectral resolution of ocean-colour data improve. Another area where additional development is needed is in the area of classifying the spectral optical characteristics of major phytoplankton groups. Furthermore, there are also indications that the same group of phytoplankton from different regions may have differing optical properties, reflecting regional differences in dominant species and size (Stuart *et al.* 2000). Ideally, such differences would be accounted for in ocean-colour algorithms designed to derive species information, in addition to biomass information.

6.3 Zooplankton

Since 1906, the global mean temperature has warmed by a mean of 0.74°C (IPCC 2007). There is new and stronger evidence that most of the warming observed over the last 50 years is attributable to human activities. Key questions for biologists and ecologists are (1) are we already observing a response of ecosystems to climate warming and (2) what could be the consequences for ecosystems, exploited resources and biogeochemical cycles?

Effects of both global warming and the increase in CO₂ concentration on ecosystems have started to appear in the scientific literature and many aspects of this influence are still poorly understood (Hughes 2000). Such effects may influence

organisms in a direct way by acting on the physiology (e.g. photosynthesis, Keeling *et al.* 1996; Myneni *et al.* 1997) or on the species phenology (e.g. seasonal cycle, Crick *et al.* 1997; McCleery and Perrins 1998). It may also influence biological systems in indirect ways by modifying abiotic factors involved in interspecific relationships between organisms. This, in turn, may affect the spatial distribution of species and modify the whole community at the ecosystem level.

In the marine environment, zooplankton play an important role in the functioning of marine ecosystems and in biogeochemical cycles (Roemmich and McGowan 1995). Interannual changes of their species assemblages often reflect an integrated response of the ecosystem to hydro-climatic forcing. Recently, findings have suggested that augmentation of greenhouse gases in the atmosphere could be the cause of the increase in the ocean heat content observed over recent decades (Barnett *et al.* 2001; Levitus *et al.* 2001). However, any response of marine organisms to increasing temperature still remains poorly documented. The possibility that marine ecosystems are being modified by climatic warming (Barry *et al.* 1995) had been based on either a restricted spatial coverage of data or a narrow time window, which strongly limited unequivocal interpretation (Hughen *et al.* 2000).

Beaugrand *et al.* (2002a) decomposed the diversity of calanoid copepods, one of the most abundant taxonomic groups sampled by the Continuous Plankton Recorder (CPR) survey, into species assemblages. This decomposition was done utilizing geostatistics and multivariate analyses, in combination with the “Indicator Values” method designed by Dufrêne and Legendre (1997). At the scale of the North Atlantic basin and a spatial resolution approaching the meso-scale, nine species assemblages were identified using three criteria: (1) spatial distribution of species, (2) similarity in the seasonal variability of species and (3) their diel and ontogenic variations. The nine species assemblages were closely related to a stable-biotope component (e.g. geographical location, van der Spoel 1994) or a substrate-biotope component (e.g. water mass, van der Spoel 1994). As a result, a new partition of the North Atlantic pelagic environment was outlined. Beaugrand *et al.* (2002a) thus proposed utilisation of the mean number of species belonging to each species assemblage as an indicator to monitor modifications in the structural organization of North Atlantic marine ecosystems, possibly linked to climate change.

Beaugrand *et al.* (2002b) reported substantial changes in the spatial distribution of calanoid copepod assemblages at an ocean basin scale during the period 1960–1999 using those species assemblage indicators. They also provided evidence that this might have been influenced by the combined effect of the climatic warming of the Northern Hemisphere and the North Atlantic Oscillation (see also Chapter 5). These large-scale biogeographical changes have deeply impacted the diversity of calanoid copepods in the North Sea (Beaugrand 2003; 2004). Diversity has increased in that region and changes in the structure of the north pelagic ecosystems have been observed (Beaugrand 2004). These changes may have a strong impact on the functioning of the ecosystems, biogeochemical cycles and exploited resources.

Using a plankton index indicator of the quality and quantity of prey available for

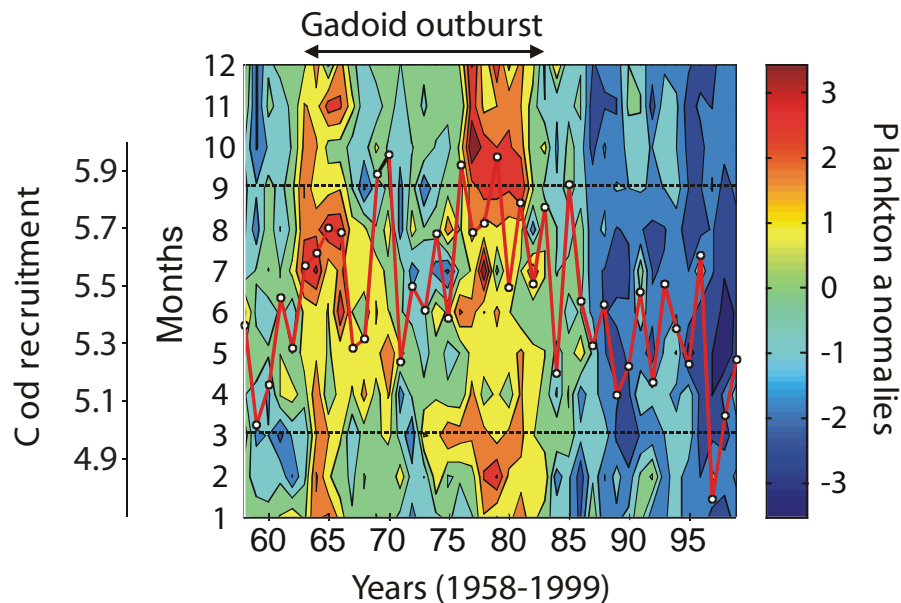


Figure 6.1 Long-term monthly changes (1958-1999) in the plankton index of larval cod survival and recruitment at age one (1-year lag; red). A negative anomaly in the index indicates a low value for *Calanus finmarchicus*, euphausiids, mean size of calanoid copepods with the exception of *C. helgolandicus* (opposite pattern) and *Pseudocalanus* spp. (no relationship). A positive anomaly indicates a high abundance of prey (and prey of suitable size). The period of the Gadoid Outburst (Cushing 1984) is also indicated. Modified from Beaugrand (2005).

larval cod survival in the North Sea, Beaugrand *et al.* (2003) showed that long-term changes in the index paralleled changes in cod recruitment at age 1 and therefore larval cod survival (Figure 6.1). The index revealed a clear distinction between the periods 1963-1983 and both the periods 1984-1999 and 1958-1962. The period 1963-1983 (Gadoid Outburst, Cushing 1984) was characterized by high abundance of prey for larval cod (positive anomalies in the biomass of calanoid copepods, in the abundance of *C. finmarchicus*, euphausiids and *Pseudocalanus* spp.) and a high mean size of calanoid copepods. Larval cod survival decreased from the mid-1980s, coincident with unfavourable changes in the plankton ecosystem, compared to the earlier period 1963-1983. These results provide evidence that changes in the plankton ecosystem are the probable cause of the increased recruitment during the period 1963-1983, which was called the “Gadoid Outburst”. Similar trends have been found with other gadoids and the Atlantic Salmon especially in the North Sea and the north-east Atlantic although processes at work are still to be identified (Beaugrand and Reid 2003; Beaugrand and Ibanez 2004).

6.4 Fisheries: Long-term management

6.4.1 Historical review

Only few attempts have been made to partition the world ocean into biogeographical regions for fisheries applications. Initially, the divisions were considered for comparative statistical catches analysis such as the FAO (Food and Agriculture Organization) classification of Fishing Areas. The evolution in the number of FAO Fishing Areas between 1956 and 1970 followed that of regional fishery bodies. Until the late 1960s FAO did not collect national catch data systematically by fishing area. Initially, FAO regional data sets were special *ad hoc* compilations. Once the collection of data in major fishing areas became systematic, all annual catch data in the historical time series were re-assigned by FAO to relevant fishing areas in consultation with countries as appropriate (Crispoldi, personal communication). Since the early 1970s the number of fishing areas remained stable, but as the need arose, some changes to the borders between areas were implemented, in consultation with Regional Fishery Bodies and countries.

The North Atlantic region was divided by ICES into a number of sub-areas and divisions for collection and presentation of fisheries statistics. This system has evolved over the past century: a refinement was introduced in some of the divisions to accommodate the statistics for deep water fishing and the requirements for reporting by EEZs, and eco-regions have been proposed to follow an ecological approach.

LMEs are relatively large regions, $\sim 200,000 \text{ km}^2$, characterized by a distinct bathymetry, hydrography, productivity and trophically-dependent populations (Sherman 1991; 1993; Sherman and Duda 1999). Currently there are 64 LMEs (<http://www.lme.noaa.gov/>) which produce 95% of the world's annual marine fishery biomass yields. In an interesting approach, Garibaldi and Limongelli (2003) adapted FAO capture data within the borders of 50 LMEs, and obtained good agreement between both classification systems. However, a major constraint in the use of LMEs in operational fisheries is the limited use of physical oceanography in the definition of the ecosystems, i.e. LMEs provide a limited knowledge about the dynamics of fisheries habitats within an ecosystem approach.

LMEs and ICES methodologies use fixed boundaries in the definition of the regions; the obvious advantage of this approach is the possibility of comparing similar data sets over time in trend studies. On the other hand, the fixed-boundaries approach fails to represent the hydrodynamic processes developed within the regions and in the transition zones; furthermore, since much of the fisheries activity in the pelagic ecosystem is related to dynamic oceanographic features (eddies, fronts, advection processes, etc.), the establishment of a fixed boundary could confound the environmental interpretation of catch data, foraging habitat or migration patterns.

Longhurst's (1995; 1998; 2006) partitioning of the world ocean into 4 biomes

and 57 biogeochemical provinces¹ was based physical forcing to which there is a characteristic response of the pelagic ecosystem (Platt and Sathyendranath 1988). As input data for the analysis, Longhurst used remote-sensing data from the CZCS ocean-colour sensor. This is essentially an ecological approach, since it considers the physical oceanography and marine productivity as major input information for the identification and definition of the provinces. A major innovation in the Longhurst approach was the use of flexible boundaries in the definition of the provinces, based on a statistical analysis of the input data. In many cases, Longhurst's biogeochemical provinces are too large to be used in an operational fisheries ecosystem approach.

Table 6.2 Comparative data of various projects using a partitioning of the sea with fisheries/biodiversity applications.

Author/ Institution	Geographical Coverage	Number of Units	Marine Biomes	Main Application
Longhurst (1998; 2006)	Global	57	All	Biogeochemistry
FAO	Global	18	All	Fisheries Statistics
LME	Global	64	Continental Shelf	Fisheries, Pollution, Productivity
ICES	North Atlantic	14	All	Fisheries
Eco-regions-200	Global	24(*)	All	Biodiversity

(*) In the marine environment

Table 6.2 summarizes the information on biomes and provinces used in the most common ocean partitioning schemes. The integration of the different classification systems for fisheries applications has been proposed by the "Sea Around Us" Project (<http://www.seaaroundus.org/>) which uses LMEs and Longhurst's biogeochemical provinces for research, while statistical catches reported by agencies such as ICES and FAO are allocated to a half-degree geographical system to produce catch maps.

6.4.2 Potential application of the satellite-derived biogeochemical provinces in regional fisheries

The fisheries application of ecological provinces at the regional level is a matter of scale. Most of the fishing activities and/or critical stages in the biological cycle of commercial species are linked to mesoscale or large scale physical and/or biological processes, e.g. fronts, eddies and upwelling processes. Bakun (1998) proposed a triad (enrichment, concentration and retention) involving different physical or chemical processes to enhance the development of intensive phytoplankton populations as a basis for important recruitment and/or forage areas. In most cases Bakun's

¹See Figure 1.1, also: <http://www.mar.dfo-mpo.gc.ca/science/ocean/BedfordBasin/Papers/Longhurst1998/Provinces/EcologicalGeographyOfTheSea.htm>

triad involves mesoscale processes that can be used in the definition of regional ecosystems for fisheries. In the definition of operational fisheries eco-regions on a Bakun-type scale, the ocean-colour remote-sensing approach of Longhurst (1995; 1998; 2006) may be complemented with other remote-sensing data such as SST or altimetry.

Satellite OCR has also been used effectively to identify, study, and monitor the Transition Zone Chlorophyll Front (TZCF), an important basin-scale ecosystem habitat (Polovina *et al.* 2001; Bograd *et al.* 2004; Polovina *et al.* 2004; Polovina and Howell 2005). The TZCF is the basin-wide chlorophyll front located at the boundary between the low chlorophyll subtropical gyres and the high chlorophyll subarctic gyres. Global satellite maps of surface chlorophyll clearly show this feature in all oceans. In the North Pacific, the front is over 8000 km long and seasonally migrates north and south about 1000 km. In the winter this front is located at about 30-35°N latitude and in the summer at about 40-45°N. It is a zone of surface convergence where cool, vertically-mixed, high chlorophyll, surface water on the north side sinks beneath warm, stratified, low chlorophyll water on the south side (Figure 6.2).

Satellite telemetry data on movements of loggerhead turtles and detailed fisheries data for albacore tuna show that both apex predators travel along this front as they migrate across the North Pacific. The front is easily monitored with ocean-colour satellite remote sensing. A change in the position of the TZCF between 1997 and 1998 appears to have altered the spatial distribution of loggerhead turtles. The position and dynamics of the front varied substantially between the 1998 El Niño and the 1999 La Niña. For example, from May to July 1999 the TZCF remained between about 35°N and 40°N latitude showing very little meandering, whereas in 1998, during the same period, the TZCF exhibited considerable meandering and greater monthly latitudinal movement. Catch rates for albacore tuna were considerably higher in 1998 than in 1999, and it is likely that a meandering TZCF creates regions of convergence, which enhances the foraging habitat for apex predators along the front.

Changes in the zooplankton population as a result of climate change (see Section 6.3) also has other important implications within the pelagic food web; the quality of food available for the herbivores or for the larval stages of many pelagic species may be a critical issue for the application of ocean-colour data in operational fisheries. Parsons and Lalli (2002) have demonstrated two alternative pathways in pelagic food-webs according to the type and size of phytoplankton available. One of the food chains leads to fisheries (phytoplankton dominated by microphytoplankton species), while the other, dominated by pico- and nanophytoplankton leads to gelatinous zooplankton (e.g. jellyfish).

The use of the functional ecology approach to study natural marine phytoplankton populations is a research field adopted by an increasing number of scientists (Iglesias-Rodríguez *et al.* 2002; Reynolds *et al.* 2002; Vila and Masó 2005; Alvain *et al.* 2005; Le Quéré *et al.* 2005; Aiken *et al.* 2007; Alves de Souza *et al.* 2008;

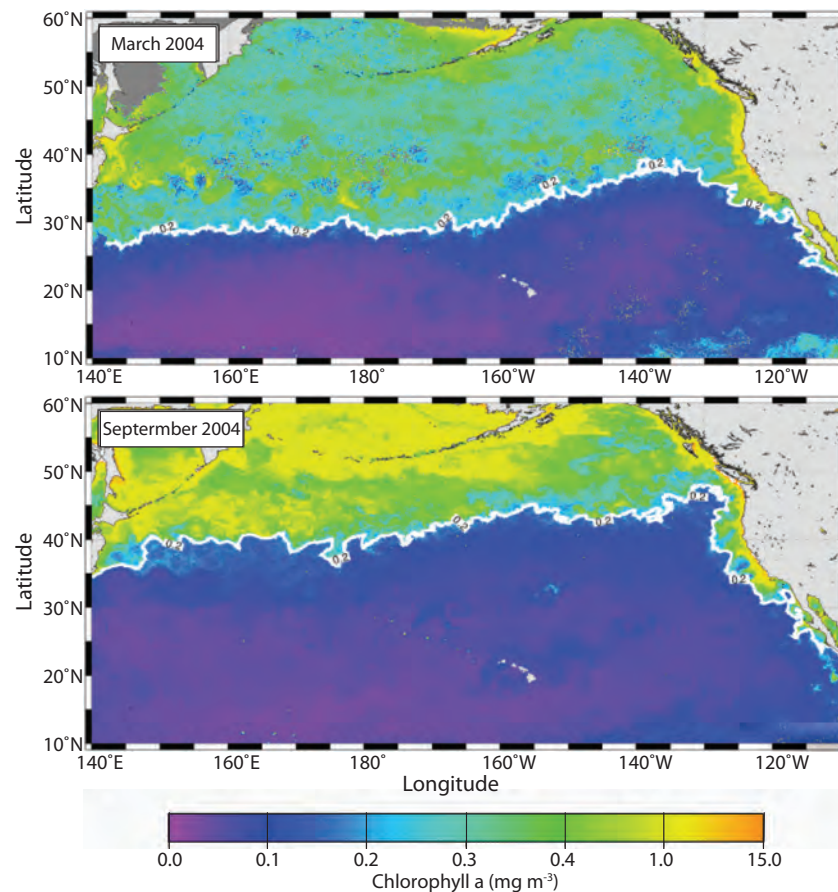


Figure 6.2 MODIS 4-km resolution surface chlorophyll distributions for the North Pacific in March (top) and September (bottom) 2004, showing the Transition Zone Chlorophyll Front (TZCF) as a white line representing a boundary between the high surface chlorophyll to the north and low surface chlorophyll to the south.

Aiken *et al.* 2009 - see also Sections 5.2 and 6.2). A critical issue for the practical application of functional ecology in phytoplankton studies is the identification of operational functional traits: grouping natural phytoplankton assemblages by size-classes was an initial step, but more recently a further step has been introduced with the use of bio-optical functional traits, derived from the microalgal pigment composition (Aiken *et al.* 2008). Hirata *et al.* (2008) have developed an absorption model (bio-optical functional trait) based on *in situ* pigment composition, for the determination of phytoplankton size classes (size functional trait) from satellite ocean-colour data. Nair *et al.* (2008) have recently reviewed the theoretical and operational background regarding the remote sensing identification of marine phytoplankton functional types, and the IOCCG Working Group on “Phytoplankton Functional Types” is preparing a report on this topic. Platt and Sathyendranath (2008) have proposed a number of ecological indicators of the pelagic ecosystems

based on the remote-sensing analysis of natural phytoplankton populations, with direct applications in the regional and temporal analysis of marine food webs.

Operational fisheries activities supported by ocean-colour data is an emerging field, and is currently widely used in India to provide forecasts of Potential Fishing Zones. An IOCCG monograph on this topic (Remote Sensing in Fisheries and Aquaculture: The Societal Benefits) will be published shortly. Many researchers have improved their analysis with the integration of NOAA-AVHRR sea surface temperature (SST) and ocean-colour information. However, only few large companies and government agencies are able to provide services at a global scale (e.g. CLS-Catsat, Orbimage).

Table 6.3 summarizes some examples of operational applications of remotely-sensed data, including ocean colour, in support of fisheries activities. In this short review, the selection criteria were the methodological approaches used by the different groups, ranging from simple calculations to sophisticated methods applying artificial intelligence tools (Iglesias *et al.* 2005).

Table 6.3 Examples of the operational use of ocean-colour data for the determination of potential fishing zones.

Sensor	Additional Parameters	Technique	GIS	Target Species	Country	References
SeaWiFS	SST + fishing logs	Fuzzy logic	YES	Small pelagics	Chile	Silva <i>et al.</i> 2000 Yañez <i>et al.</i> 2001
SeaWiFS	SST + fishing logs	Tropical fish forecasting system	YES	–	Malaysia	Mansor <i>et al.</i> 2001
OCM	SST	Data assimilation	NO	Small pelagics	India	Solanki <i>et al.</i> 2003
OCM	SST + wind	Data assimilation	NO	Small pelagic	India	Solanki <i>et al.</i> 2005
SeaWiFS	SST + SHA	Data assimilation	NO	Tuna	Japan	Zainuddin <i>et al.</i> 2002
SeaWiFS	SST + SLA + wind	Multivariate analysis	NO	Tuna	Spain	Coca & Ramos 2004
SeaWiFS	SST + SHA	ANN + expert systems	NO	Shark, tuna	Spain	Iglesias <i>et al.</i> 2005

In most of the case studies the majority (>90%) of the target species are small pelagics or large migratory pelagic species. In the case of small pelagic species (e.g. sardine, anchovy, horse mackerel) the fishing fleet is an artisanal fleet with a small geographical coverage, and limited resources. Their activities are supported by governmental and/or public institutions at no cost to the users. In the case of

large migratory pelagic species (e.g. tuna fish, swordfish) the higher value of the catches increases the market potential of this application, although there are no published data about the number of commercial users of satellite data.

A critical question arises: if the methodological approaches are available, why are ocean-colour data not more widely used in operational fisheries applications? The answer is probably different for each country or geographical region. For example, in the case of India and Japan operational services for fish harvesting are provided for artisanal fisheries and commercial fisheries, respectively. Thus, while the provision of potential fishing zone maps is a governmental service delivered at low cost, or no cost to the fishing communities in India, in Japan a commercial service is provided by private companies to fishing fleets harvesting high value species, which can justify the additional expense. The public availability of processed ocean-colour images through international programmes (e.g. ChloroGIN) or national agencies (e.g. NASA) could contribute at a more extensive use of this technology, although an intermediate step should be the planning of capacity building programs on image interpretation with applications on the management and exploitation of marine living resources. Remote sensing researchers are working on the development of new ocean-colour derived products, such as the identification of 'phytoplankton functional types' (PFTs) which will provide invaluable information about the trophic condition of pelagic ecosystems and consequently about their food webs.

6.4.3 Biogeography distribution

The partitioning of the pelagic ecosystem into biogeochemical provinces can represent the distribution of marine resources in a more ecological fashion, although to date there has been no attempt to integrate ocean biogeochemical provinces with flexible boundaries with the synoptic distribution of marine species.

Three international projects are investigating the biogeographic distribution of marine species. The Census of Marine Life (CoML) is the most ambitious and is comprised of five elements including the "Ocean Biogeographic Information System" (OBIS) which is most relevant for ocean biogeography. OBIS is part of the marine component of the Global Biodiversity Information System, and links to marine databases around the world via the internet to provide geo-referenced biodiversity data in relation to ocean habitats in a multidimensional geographic context (Grassle 2000; Decker and O'Dor 2003).

Aquamaps (<http://www.aquamaps.org>), a joint project of Fishbase and SeaLifeBase, is a new electronic atlas with standardized (half-degree cell) maps of the probability of occurrence for all marine organisms. The data will be available in FishBase, OBIS, Hexacoral, Sea Around Us and other online initiatives. Because of the standardization it will be possible to correlate species occurrence with environmental parameters such as primary production, temperature or salinity, or even to produce lists of species with a likelihood of occurrence for any area of the ocean (LMEs, Longhurst

provinces, EEZs). Currently 9,000 species of fish, marine mammals and invertebrates are represented.

In a different approach, the World Wildlife Fund (WWF) developed a classification scheme to identify a large number of terrestrial, freshwater and marine eco-regions for conservation purposes. Eco-regions are large areas of land or water that contain a characteristic assemblage of natural communities that share the majority of their species, dynamics, and environmental conditions. The WWF project has identified 232 marine eco-regions covering all major habitat types: polar, temperate shelves, temperate upwelling, tropical upwelling, tropical coral, pelagic (trades and west-erlies), abyssal, and hadal (ocean trench). However, this classification of marine eco-regions is limited by lack of knowledge of biogeographic boundaries and bio-diversity information for the major marine habitat types, although there is some evidence for the potential use of these eco-regions as a scheme for fisheries management in the Sulu-Sulawesi Sea fisheries project (Indonesia, Malaysia, Philippines - Ingles and Ballesteros 2004).

Chapter 7

Recommendations

Trevor Platt and Mark Dowell

The value of partitioning the ocean, according to its functional structure, into a suite of provinces has been demonstrated. The partition can be used as a template for making weighted calculations over regions, basins or over the global ocean, a priceless tool in marine biogeochemistry and in fisheries oceanography. In particular, we have seen that OCR data play a fundamental role in the delineation of the province boundaries, providing yet another reason to advocate a strong commitment to maintenance of long-term, high-quality streams of ocean-colour data. Currently, the CEOS Ocean-Colour Radiometry constellation (with representation from all agencies that have launched, or intend to launch an ocean-colour sensor), under the leadership of the IOCCG, is striving to coordinate ocean-colour missions on a global scale and encourage agencies to invest in data-merging protocols.

The ecophysiological basis for the partition into provinces is associated with corresponding bio-optical characteristics, which impact on the physics behind the retrieval of essential climate variables (geophysical properties), such as chlorophyll concentration. Therefore, researchers are encouraged to investigate the development and calibration of regional algorithms for property retrieval using the provinces as an underlying template. Although much progress has been made in the delineation and application of the province template, it is not considered to be a closed question, and research aimed at refining the provinces approach is encouraged.

Given the growing importance of operational oceanography, and given the value of the partition as an aid to interpretation of data, research aimed at improving the methodology for real-time, dynamic partition with a view to providing it to the operational oceanographic community should also be promoted. Given the global consensus that stewardship of marine resources should be carried out under ecosystem-based management, the development of appropriate ecosystem indicators that can be derived from OCR data and projected onto the template of provinces will provide a logical way forward.

The method of provinces has its origin in the issue of parameter assignment in ecosystem analyses, which remains a fundamental problem in the application of OCR data to oceanographic questions and in marine modelling in general. Therefore, research on the use of the province template for parameter assignment is

encouraged, moving the emphasis from piecewise uniform to piecewise continuous.

It is expected that the application of the provinces method will continue to grow in importance. Eventually a requirement will arise for a consensus on the optimal template for use in management, policy or legal contexts. An expert group competent to advise in the definition of a basic partition for community use could perhaps be established by agencies to anticipate this requirement. The ideal template to use for particular problems depends on the space and time scales involved. Choosing the optimal template requires subtle judgements. Therefore, the development of guidelines for the selection of optimal partitions to address oceanographic questions at different scales should also be supported.

Because of the value of the approach in ecosystem and biogeochemical analyses of the ocean, scientists are encouraged to adopt the provinces method for weighted calculations of regional, basin and global scale fluxes.

References

- Aiken J, Pradhan Y, Barlow R, Lavender S, Poulton A, Holligan P, Hardman-Mountford NJ (2009) Phytoplankton pigments and functional types in the Atlantic Ocean: A decadal assessment, 1995-2005. *Deep-Sea Res. II* doi: 10.1016/j.dsr2.2008.09.017
- Aiken J, Fishwick JR, Lavender SJ, Barlow R, Moore GF, Sessions H, Bernard S, Ras J, Hardman-Mountford NJ (2007) Validation of MERIS reflectance and chlorophyll during the BENCAL cruise October, 2002: preliminary validation and new products for phytoplankton functional types and photosynthetic parameters. *International Journal of Remote Sensing* 28: 497-516
- Aiken J, Hardman-Mountford NJ, Barlow R, Fishwick J, Hirata T, Smyth T (2008) Functional links between bioenergetics and bio-optical traits of phytoplankton taxonomic groups: an overarching hypothesis with applications for ocean colour remote sensing. *Journal of Plankton Research* 30: 165
- Alvain S, Moulin C, Dandonneau Y, Bréon F (2005) Remote sensing of phytoplankton groups in case I waters from global SeaWiFS imagery. *Deep-Sea Research Part I* 52: 1989-2004
- Alvain S, Moulin C, Dandonneau Y, Loisel H, Bréon FM (2006) A species-dependent bio-optical model of case I waters for global ocean color processing. *Deep-Sea Research Part I-Oceanographic Research Papers* 53: 917-925
- Alves-de-Souza C, González MT, Iriarte JL (2008) Functional groups in marine phytoplankton assemblages dominated by diatoms in fjords of southern Chile. *Journal of Plankton Research* 30: 1233-1243; doi:10.1093/plankt/fbn1079
- Antoine D, Morel A, Gordon HR, Banzon VF, Evans RH (2005) Bridging ocean color observations of the 1980s and 2000s in search of long-term trends. *Journal of Geophysical Research-Oceans* 110: C06009, doi:10.1029/2004JC002620
- Armstrong EM (2000) Satellite derived sea surface temperature variability off California during the upwelling season. *Remote Sensing of Environment* 74:1-17
- Arrigo KR, Robinson DH, Worthen DL, Dunbar RB, DiTullio GR, VanWoert M, Lizotte MP (1999) Phytoplankton community structure and the drawdown of nutrients and CO₂ in the Southern Ocean. *Science* 283: 365-367
- Bakun A (1998) Ocean triads and radical interdecadal variation: bane and boon to scientific fisheries management. In: Pitcher TJ, Hart PJB, Pauly D (eds) *Reinventing fisheries management*. Kluwer Academic Publisher, Dordrecht pp 331-358
- Balch W, Gordon H, Bowler B, Drapeau D, Booth E (2005) Calcium carbonate measurements in the surface global ocean based on Moderate-Resolution Imaging Spectroradiometer data. *Journal of Geophysical Research-Oceans* 110: C07001
- Baldacci A, Corsini G, Grasso R, Manzella G, Allen JT, Cipollini P, Guymer TH, Snaith HM (2001). A study of the Alboran sea mesoscale system by means of empirical orthogonal function decomposition of satellite data, *Journal of Marine Systems* 29: 293-311
- Barber RT, Hilting AK (2000) Achievements in biological oceanography. In: *50 Years of Ocean Discovery*. Ocean Studies Board, National Academy Press, Washington DC, pp 11-21
- Barnett TP, Pierce DW, Schnur R (2001) Detection of anthropogenic climate change in the World's Oceans. *Science* 292: 270 - 274 doi: 10.1126/science.1058304
- Barry JP, Baxter CH, Sagarin RD, Gilman SE (1995) Climate-related, long-term faunal changes in a California rocky intertidal community. *Science* 267: 672-675
- Beaugrand G (2004) The North Sea regime shift: evidence, causes, mechanisms and consequences. *Progress in Oceanography* 60: 245-262

- Beaugrand G (2005) Monitoring pelagic ecosystems using plankton indicators. *ICES Journal of Marine Science* 62: 333-338
- Beaugrand G, Ibanez F (2004) Monitoring marine plankton ecosystems II: Long-term changes in North Sea calanoid copepods in relation to hydro-climatic variability. *Marine Ecology-Progress Series* 284: 35-47
- Beaugrand G, Reid PC (2003) Long-term changes in phytoplankton, zooplankton and salmon linked to climate change. *Global Change Biology* 9: 801-817
- Beaugrand G, Brander KM, Lindley JA, Souissi S, Reid PC (2003) Plankton effect on cod recruitment in the North Sea. *Nature* 426: 661-664
- Beaugrand G, Ibañez F, Lindley JA, Reid PC (2002a) Diversity of calanoid copepods in the North Atlantic and adjacent seas: species associations and biogeography. *Marine Ecology-Progress Series* 232: 179-195
- Beaugrand G, Reid PC, Ibañez F, Lindley JA, Edwards M (2002b) Reorganization of North Atlantic marine copepod biodiversity and climate. *Science* 296: 1692-1694
- Beebee TJC (1995) Amphibian breeding and climate. *Nature* 374: 219-220
- Behrenfeld MJ, Falkowski PG (1997) Photosynthetic rates derived from satellite-based chlorophyll concentration. *Limnology and Oceanography* 42: 1-20
- Behrenfeld M, O'Malley R, Siegel D, McClain C, Sarmiento J, Feldman G, Milligan A, Falkowski P, Letelier R, Boss E (2006) Climate-driven trends in contemporary ocean productivity. *Nature* 444: 752-755
- Benson A, McFarlane G, Allen S, Dower J (2002) Changes in Pacific hake (*Merluccius productus*) migration patterns and juvenile growth related to the 1989 regime shift. *Canadian Journal of Fisheries and Aquatic Sciences* 59: 1969-1979
- Bezdek JC (1981) Pattern recognition with fuzzy objective function algorithms. Kluwer Academic Publishers Norwell, MA, USA
- Bezdek JC, Li WQ, Attikiouzel Y, Windham M (1997) A geometric approach to cluster validity for normal mixtures. *Software Computing* 1: 166-179
- Bindoff N, Willebrand J, Artale V, Cazenave A, Gregory J, Gulev S, *et al.* (2007) Observations: oceanic climate change and sea level. In: *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*, Solomon, S *et al.* (eds.). Cambridge University Press. Cambridge, UK
- Bisagni JJ, Seemann KW, Mavor TP (2001) High-resolution satellite-derived sea-surface temperature variability over the Gulf of Maine and Georges Bank Region, 1993-1996. *Deep Sea Research II* 48: 71-94
- Blain S, Tréguer P, Belviso S, Bucciarelli E, Denis M, Desabre S, Fiala M, Martin Jézéquel V, Le Fèvre J, Mayzaud P (2001) A biogeochemical study of the island mass effect in the context of the iron hypothesis: Kerguelen Islands, Southern Ocean. *Deep-Sea Research Part I* 48: 163-187
- Bograd SJ, Foley DG, Schwing FB, Wilson C, Laurs RM, Polovina JJ, Howell EA, Brainard RE (2004) On the seasonal and interannual migrations of the transition zone chlorophyll front. *Geophysical Research Letters* 31: L17204, doi:10.1029/2004GL020637
- Bond N, Overland J, Spillane M, Staben P (2003) Recent shifts in the state of the North Pacific. *Geophysical Research Letters* 30: 2183, doi:10.1029/2003GL018597
- Bopp L, Monfray P, Aumont O, Dufresne J, Le Treut H, Madec G, Terray L, Orr J (2001) Potential impact of climate change on marine export production. *Global Biogeochemical Cycles* 15: 81-100
- Bouman H, Platt T, Sathyendranath S, Stuart V (2005) Dependence of light-saturated photosynthesis on temperature and community structure. *Deep-Sea Research I* 52: 1284-1299
- Boyd PW, Doney SC (2002) Modelling regional responses by marine pelagic ecosystems to global climate change. *Geophysical Research Letters* 29: 53-1, doi: 10.1029/2001GL014130
- Boyd PW, Watson AJ, Laws CS, Abraham ER, Trull T, Murdoch R *et al.* (2000) Mesoscale phytoplankton bloom in the polar Southern Ocean stimulated by iron fertilization. *Nature* 407: 695-702
- Brickley P, Thomas AC (2004) Satellite-measured seasonal and interannual chlorophyll variability in the Northeast Pacific and coastal Gulf of Alaska. *Deep Sea Research* 51: 229-245
- Brinton E (1962) Variable factors affecting the apparent range and estimated concentration of euphausiids in the North Pacific. *Pacific Science* 16: 374-408

- Brock JC, Sathyendranath S, Platt T (1998) Biohydro-optical classification of the northwestern Indian Ocean. *Marine Ecology Progress Series* 165: 1-15
- Chavez F, Pennington J, Castro C, Ryan J, Michisaki R, Schlining B *et al.* (2002) Biological and chemical consequences of the 1997-1998 El Niño in central California waters. *Progress in Oceanography* 54: 205-232
- Chavez FP, Strutton PG, Friederich GE, Feely RA, Feldman GC, Foley DG, McPhaden MJ (1999) Biological and chemical response of the equatorial Pacific Ocean to the 1997-98 El Niño. *Science* 286: 2126-2131
- Chuck A, Tyrrell T, Totterdell IJ, Holligan PM (2005) The oceanic response to carbon emissions over the next century: investigation using three ocean carbon cycle models. *Tellus* 57B: 70-86
- Colebrook JM (1982) Continuous plankton records: seasonal variations in the distribution and abundance of plankton in the North Atlantic Ocean and the North Sea. *Journal of Plankton Research* 4: 435-462
- Coles V, Hood R, Pascual M, Capone D (2004) Modeling the impact of *Trichodesmium* and nitrogen fixation in the Atlantic Ocean. *Journal of Geophysical Research* 109: C06007, doi:10.1029/2002JC001754
- Conkright ME, Gregg WW, Levitus S (2000) Seasonal cycle of phosphate in the open ocean. *Deep Sea Research I* 47: 159-175
- Conkright ME, Locarnini RA, Garcia HE, O'Brien TD, Boyer TP, Stephens C, Antonov JI (2002) *World Ocean Atlas 2001: vol. 4, Nutrients*, NOAA Atlas NESDIS 52, NOAA, Silver Spring, MD.
- Covey C, AchutaRao K, Cubasch U, Jones P, Lambert S, Mann M, Phillips T, Taylor K (2003) An overview of results from the Coupled Model Intercomparison Project. *Global and Planetary Change* 37: 103-133
- Crick HQP, Dudley C, Glue DE, Thomson DL (1997) UK birds are laying eggs earlier. *Nature* 388: 526
- Cushing DH (1984) The gadoid outburst in the North Sea. *Journal du Conseil* 41: 159-166
- D'Alimonte D, Melin F, Zibordi G, Berthon J (2003) Use of the novelty detection technique to identify the range of applicability of empirical ocean color algorithms. *IEEE Transactions on Geoscience and Remote Sensing* 41: 2833-2843
- Decker CJ, O'Dor R (2003) A census of marine life: unknowable, or just unknown? *Oceanology Acta* 25: 179-186
- Devred E, Sathyendranath S, Platt T (2007) Delineation of ecological provinces in the North West Atlantic using visible spectral radiometry (ocean colour). *Marine Ecology Progress Series* 346: 1-13
- Dickson R, Lazier J, Meincke J, Rhines P, Swift J (1996) Long-term coordinated changes in the convective activity of the North Atlantic. *Progress in Oceanography* 38: 241-295
- Drinkwater K (1996) Atmospheric and oceanic variability in the northwest Atlantic during the 1980s and early 1990s. *Journal of the Northwest Atlantic Fisheries Science* 18: 77-97
- Dufrêne M, Legendre P (1997) Species assemblages and indicator species: the need for a flexible asymmetrical approach. *Ecological Monographs* 67: 345-366
- Dugdale R, Davis C, Wilkerson F (1997) Assessment of new production at the upwelling center at Point Conception, California, using nitrate estimated from remotely sensed sea surface temperature. *Journal of Geophysical Research* 102: 8573-8586
- Dugdale RC, Goering JJ (1967) Uptake of new and regenerated forms of nitrogen in primary productivity. *Limnology and Oceanography* 12: 196-206
- Dugdale RC, Morel A, Bricaud A, Wilkerson FP (1989) Modeling new production in upwelling centers: a case study of modeling new production from remotely sensed temperature and color. *Journal of Geophysical Research* 94: 18,119-118,132
- Dutkiewicz S, Follows MJ, Parekh P (2005a) Interactions of the iron and phosphorus cycles: A three-dimensional model study. *Global Biogeochemical Cycles* 19
- Dutkiewicz S, Sokolov A, Scott J, Stone P (2005b) A three-dimensional ocean-sea-ice-carbon cycle model and its coupling to a two-dimensional atmospheric model: uses in climate change studies, Joint Program on the Science and Policy of Global Change Report 122. Massachusetts Institute of Technology, Cambridge, USA

- Eppley RW, Peterson BJ (1979) Particulate organic matter flux and planktonic new production in the deep ocean. *Nature* 282: 677-680
- Esaías W, Iverson R, Turpie K (2000) Ocean province classification using ocean colour data: Observing biological signatures of variations in physical dynamics. *Global Change Biology* 6: 39-55
- Fang W, Hsieh WW (1993) Summer sea surface temperature variability off Vancouver Island from satellite data *Journal Geophysical Research* 98: 14391-14400
- FAO (2003) Report of the twenty-fifth session of the Committee on Fisheries. Rome, 24-28 February 2003. FAO Fisheries Report. No.702. Rome, FAO. 2003, 89 p
- Fasham MJR (ed) (2003) *Ocean Biogeochemistry: The Role of the Ocean Carbon Cycle in Global Change*. Joint Global Ocean Flux Study Springer-Verlag, Berlin 297 p
- Field A (1997) WOCE Indian Ocean expedition. *Geophysical Research Letters* 24: 2539-2540
- Field C, Behrenfeld M, Randerson J, Falkowski P (1998) Primary production of the biosphere: integrating terrestrial and oceanic components. *Science* 281: 237-240
- Fischer A, Weller R, Rudnick D, Eriksen C, Lee C, Brink K, Fox C, Leben R (2002) Mesoscale eddies, coastal upwelling, and the upper-ocean heat budget in the Arabian Sea. *Deep Sea Research II* 49: 2231-2264
- Fitter AH, Fitter RSR (2002) Rapid changes in flowering time in British plants. *Science* 296: 1689 - 1691
- Forster P, Ramaswamy V, Artaxo P, Bernsten T, Betts R, Fahey D *et al.* (2007) Changes in atmospheric constituents and in radiative forcing. *Climate Change*: 129-234
- García-Moliner G, Yoder J (1994) Variability in pigment concentration in warm-core rings as determined by coastal zone color scanner satellite imagery from the Mid-Atlantic Bight. *Journal Geophysical Research* 99: 14,277-14,290
- Garibaldi L, Limongelli L (2003) Trends in oceanic captures and clustering of large marine ecosystems: Two studies based on the FAO capture database, as reported to the FAO by official national sources. FAO Fisheries Technical paper 435. Food and Agriculture Organization of the United Nations. Rome
- Ginoux P, Chin M, Holben B, Lin S, Tegen I, Prospero J, Dubovik O (2001) Sources and distributions of dust aerosols simulated with the GOCART model. *Journal of Geophysical Research* 106: 20255-20273
- Goes JJ, Saino T, Oaku H, Ishizaka J, Wong CS, Nojiri Y (2000) Basin scale estimates of sea surface nitrate and new production from remotely sensed sea surface temperature and chlorophyll. *Geophysical Research Letters* 27: 1263-1266
- Goes JJ, Saino T, Oaku H, Jiang DL (1999) A method for estimating sea surface nitrate concentrations from remotely sensed SST and chlorophyll *a* — A case study for the Pacific Ocean using OCTS/ADEOS data. *IEEE Transactions on Geoscience and Remote Sensing* 37: 1633-1644
- Goes JJ, Sasaoka K, Gomes HDR, Saitoh S, Saino T (2004) A comparison of the seasonality and interannual variability of phytoplankton biomass and production in the Western and Eastern Gyres of the subarctic Pacific using multi-sensor satellite data. *Journal of Oceanography* 60: 75-91
- Grassle JF (2000) The Ocean Biogeographic Information System (OBIS): an on-line, worldwide atlas for accessing, modeling and mapping marine biological data in a multidimensional geographic context. *Oceanography* 13: 5-7
- Gregg W (2002) A coupled ocean-atmosphere radiative model for global ocean biogeochemical models. Technical Report Series on Global Modeling and Data Assimilation, NASA Technical Memorandum 104606, vol. 22, Goddard Space Flight Center, Greenbelt, Maryland
- Gregg W, Conkright M (2002) Decadal changes in global ocean chlorophyll. *Geophysical Research Letters* 29: 20-21
- Gregg WW, Casey NW, McClain CR (2005) Recent trends in global ocean chlorophyll. *Geophysical Research Letters*, 32: L03606, doi:03610.01029/02004GL021808
- Gregg WW, Conkright ME, Reilly JE, Patt FS, Wang MH, Yoder JA, Casey NW (2002) NOAA-NASA Coastal Zone Color Scanner reanalysis effort. *Applied Optics* 41: 1615-1628
- Gregg W, Ginoux P, Schopf P, Casey N (2003) Phytoplankton and iron: validation of a global three-dimensional ocean biogeochemical model. *Deep-Sea Research Part II* 50: 3143-3169

- Halpern D, Feldman GC (1994) Annual and interannual variations of phytoplankton pigment concentration and upwelling along the Pacific equator. *Journal of Geophysical Research* 99: 7347-7354
- Hardman-Mountford NJ, McGlade JM (2002) Defining ecosystem structure from natural variability: application of principal components analysis to remotely sensed SST. In: McGlade JM, Cury P, Koranteng KA, Hardman-Mountford NJ (eds) *The Gulf of Guinea Large Marine Ecosystem*. Elsevier Amsterdam, pp 67-82
- Hardman-Mountford NJ, Hirata, T, Richardson KA, Aiken J (2008) An objective methodology for the classification of ecological pattern into biomes and provinces for the pelagic ocean. *Remote Sensing of Environment* 112: 3341-3352
- Harrison WG, Platt T, Lewis MR (1987) *f*-Ratio and its relationship to ambient nitrate concentration in coastal waters. *Journal of Plankton Research* 9: 235-248
- Henson SA, Sanders R, Allen JT, Robinson IS, Brown L (2003) Seasonal constraints on the estimation of new production from space using temperature-nitrate relationships. *Geophysical Research Letters* 30: 1912, doi: 10.1029/2003GL017982
- Hernandez-Guerra A, Nykjaer L (1997) Sea surface temperature variability off north-west Africa: 1981-1989. *International Journal of Remote Sensing* 18: 2539-2558
- Herut B, Krom M, Pan G, Mortimer R (1999) Atmospheric input of nitrogen and phosphorus to the Southeast Mediterranean: Sources, fluxes, and possible impact. *Limnology and Oceanography* 44: 1683-1692
- Hirata T, Aiken J, Hardman-Mountford NJ, Smyth TJ Barlow RG (2008). An absorption model to determine phytoplankton size classes from satellite ocean colour. *Remote Sensing of the Environment* 112(6): 3153-3159. doi: 10.1016/j.rse.2008.03.011
- Ho C-R, Zheng Q, Kuo N-J (2004) SeaWiFs observations of upwelling south of Madagascar: long-term variability and interaction with East Madagascar Current. *Deep Sea Research II* 51: 59-67
- Hoepffner N, Sturm B, Finenko Z, Larkin D (1999) Depth-integrated primary production in the eastern tropical and subtropical North Atlantic basin from ocean colour imagery. *International Journal of Remote Sensing* 20: 1435-1456
- Holligan PM, Robertson JE (1996) Significance of ocean carbonate budgets for the global carbon cycle. *Global Change Biology* 2: 85-95
- Hughen KA, Southon JR, Lehman SL, Overpeck JT (2000) Synchronous radiocarbon and climate shifts during the last deglaciation. *Science* 290: 1951-1954
- Hughes L (2000) Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution* 15: 56-61
- Iglesias Nuno A, Arcay B, Cotos JM, Varela J (2005). Optimisation of fishing predictions by means of artificial neural networks, anfis, functional networks and remote sensing images. *Expert Systems with Applications* 29(2): 356-363
- Iglesias-Rodríguez MD, Brown CW, Doney SC, Kleypas J, Kolber D, Kolber Z (2002) Representing key phytoplankton functional groups in ocean carbon cycle models: Coccolithophorids. *Global Biogeochemistry Cycles* 16: doi:10.1029/2001GB001454
- Iida T, Saitoh S, Miyamura T, Toratani M, Fukushima H, Shiga N (2002) Temporal and spatial variability of coccolithophore blooms in the eastern Bering Sea, 1998-2001. *Progress in Oceanography* 55: 165-175
- Ingles JA, Ballesteros J (2004) Using the ecoregion approach to manage fisheries: A case study for the Sulu-Sulawesi marine ecoregion (SSME) fisheries program. Paper presented at the WWF Ecoregions 200 partners meeting (<http://www.wwf.org>), 9 p
- IOCCG (2000) Remote Sensing of Ocean Colour in Coastal, and Other Optically-Complex, Waters, Sathyendranath, S (ed). Reports of the International Ocean Colour Coordinating Group, No. 3, Dartmouth, Canada 140 p
- IPCC (2001) Climate Change 2001: The Scientific Basis. Contribution of Working Group 1 to the Third Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK
- IPCC (2007) Climate Change 2007: Synthesis Report. Contribution of Working Groups I, II and III to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change [Core Writing Team, Pachauri, R.K and Reisinger, A. (eds.)]. IPCC, Geneva, Switzerland, 104 p

- Iriarte J, González H (2004) Phytoplankton size structure during and after the 1997/98 El Niño in a coastal upwelling area of the northern Humboldt Current System. *Marine Ecology Progress Series* 269: 83-90
- Jerlov NG (1968) *Optical Oceanography*. Elsevier Publishing Company, Amsterdam, London, New York
- Kahru M, Mitchell BG (2000) Influence of the 1997-98 El Niño on the surface chlorophyll in the California Current. *Geophysical Research Letters* 27: 2937-2940
- Kamykowski D, Zentara SJ (1986) Predicting plant nutrient concentration from temperature and sigma-*t* in the world ocean. *Deep-Sea Research I* 33: 89-105
- Kamykowski D, Zentara SJ (2003) Can phytoplankton community structure be inferred from satellite-derived sea surface temperature anomalies calculated relative to nitrate depletion temperatures? *Remote Sensing of Environment* 86: 444-457
- Kamykowski D, Zentara SJ (2005) Changes in world ocean nitrate availability through the 20th century. *Deep Sea Research I* 52: 1719-1744
- Kamykowski D, Zentara SJ (2006) Corrigendum to "Changes in world ocean nitrate availability through the 20th century". [*Deep Sea Research I* 52 (2005) 1719-1744]. *Deep-Sea Research I* 53: 1578-1579
- Kamykowski D, Zentara SJ, Morrison J, Switzer A (2002) Dynamic global patterns of nitrate, phosphate, silicate, and iron availability and phytoplankton community composition from remote sensing data. *Global Biogeochemical Cycles* 16: 1077
- Karl DM, Bidigare RR, Letelier RM (2001) Long-term changes in plankton community structure and productivity in the Pacific Subtropical Gyre: The domain shift hypothesis. *Deep-Sea Research II* 48: 1449-1470
- Karl DM, Letelier R, Hebel D, Tupas L, Dore J, Christian J, Winn C (1995) Ecosystem changes in the Pacific subtropical gyre attributed to the 1991-1992 El Niño. *Nature* 373: 230-234
- Karl D, Letelier R, Tupas L, Dore J, Christian J, Hebel D (1997) The role of nitrogen fixation in biogeochemical cycling in the subtropical North Pacific Ocean. *Nature* 388: 533-538
- Keeling MJ, Mezic I, Hendry RJ, McGlade J, Rand DA (1997) Characteristic length scales of spatial models in ecology via fluctuation analysis. *Philosophical Transactions of the Royal Society* 352(1361): 1589-1601
- Keeling RF, Piper SC, Heimann M (1996) Global and hemispheric CO₂ sinks deduced from changes in atmospheric O₂ concentration. *Nature* 381: 218 - 221 doi:210.1038/381218a381210
- Klyashtorin L (2001) Climate Change and Long-Term Fluctuations of Commercial Catches. The Possibility of Forecasting, FAO Fisheries Tech. Paper No. 410
- Krey J (1973) Primary production in the Indian Ocean In: *The Biology of the Indian Ocean: Ecological Studies, Analysis and Synthesis*, Zeitzschel, B (ed.) Springer, New York: 115-130
- Kuo NJ, Zheng Q, Ho CR (2004) Response of Vietnam coastal upwelling to the 1997-1998 ENSO event observed by multisensor data. *Remote Sensing of Environment* 89: 106-115
- Kywalyanga MN, Platt T, Sathyendranath S, Lutz VA, Stuart V (1998) Seasonal variations in physiological parameters of phytoplankton across the North Atlantic. *Journal of Plankton Research* 20: 17-42
- Lagerloef GS, Bernstein RL (1988) Empirical orthogonal function analysis of Advanced Very High Resolution Radiometer surface temperature patterns in Santa Barbara Channel. *Journal of Geophysical Research* 63: 6863-6873
- Lasker R, Pelaez J, Laurs RM (1981) The use of satellite infrared imagery for describing ocean processes in relation to spawning of the northern anchovy (*Engraulis mordax*). *Remote Sensing of Environment* 11: 439-453
- Laurs RM, Fiedler PC, Montgomery DR (1984) Albacore tuna catch distributions relative to environmental features observed from satellites. *Deep-Sea Research* 31: 1085-1099
- Le Borgne R, Feely RA, Mackey DJ (2002) Carbon fluxes in the equatorial Pacific: a synthesis of the JGOFS programme. *Deep-Sea Research II* 49: 2425-2442
- Leonard CL, Bidigare RR, Seki MP, Polovina JJ (2001) Interannual mesoscale physical and biological variability in the Pacific Central Gyre. *Progress in Oceanography* 49: 227-244
- Le Quéré C, Harrison SP, Prentice IC, Buitenhuis ET, Aumont O, Bopp L *et al.* (2005) Ecosystem dynamics based on plankton functional types for global ocean biogeochemistry models. *Global Change Biology* 11: 2016-2040

- Le Quéré C, Rodenbeck C, Buitenhuis E, Conway T, Langenfelds R, Gomez A *et al.* (2007) Saturation of the Southern Ocean CO₂ sink due to recent climate change. *Science* 316: 1735
- Levitus S, Antonov JI, Wang J, Delworth TL, Dixon KW, Broccoli AJ (2001) Anthropogenic warming of Earth's climate system. *Science* 292: 267 - 270 doi: 210.1126/science.1058154
- Longhurst A (1995) Seasonal cycles of pelagic production and consumption. *Progress in Oceanography* 36: 77-167
- Longhurst A (1998) *Ecological Geography of the Sea*. Academic Press, San Diego 398 p
- Longhurst A (2006) *Ecological geography of the sea* (2nd Edition). Elsevier, Amsterdam 543 p
- Longhurst A, Sathyendranath S, Platt T, Caverhill C (1995) An estimate of global primary production in the ocean from satellite radiometer data. *Journal of Plankton Research* 17: 1245-1271
- Lubac B, Loisel H (2007) Variability and classification of remote sensing reflectance spectra in the eastern English Channel and southern North Sea. *Remote Sensing of Environment* 110: 45-58
- Mahowald N, Luo C (2003) A less dusty future? *Geophysical Research Letters* 30: 1903
doi:10.1029/2003GL017880
- Mantua N, Hare S, Zhang Y, Wallace J, Francis R (1997) A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society* 78: 1069-1079
- Margalef R (1961) Hidrografía y fitoplancton de un área marina de la costa meridional de Puerto Rico. *Invest. Pesq.* 18: 33-96
- Margalef R (1967) Some concepts relative to the organization of plankton. *Oceanography and Marine Biology Annual Review* 5: 257-289
- Marinovic B, Croll D, Gong N, Benson S, Chavez F (2002) Effects of the 1997-1999 El Niño and La Niña events on zooplankton abundance and euphausiid community composition within the Monterey Bay coastal upwelling system. *Progress in Oceanography* 54: 265-277
- Martin Traykovski LVM, Sosik HM (2003) Feature-based classification of optical water types in the Northwest Atlantic based on satellite ocean color data. *Journal of Geophysical Research - Oceans* 108: doi:10.1029/2001JC001172
- Matear RJ, Hirst AC (1999) Climate change feedback on the future oceanic CO₂ uptake. *Tellus* 51B: 722-733
- Matsumoto K, Uyama Y, Hayano T, Uematsu M (2004) Transport and chemical transformation of anthropogenic and mineral aerosol in the marine boundary layer over the western North Pacific Ocean. *Journal of Geophysical Research - Atmosphere* 109: D21206
- McClain CR, Signorini SR, Christian JR (2004) Subtropical gyre variability observed by ocean-color satellites. *Deep-Sea Research Part II-Topical Studies in Oceanography* 51: 281-301
- McCleery RH, Perrins CM (1998) ...temperature and egg-laying trends. *Nature* 391: 30-31
- Meehl G, Stocker T, Collins W, Friedlingstein A, Gaye A, Gregory J *et al.* (2007) Global climate projections. In: Solomon, S, Qin D, Manning, M *et al.* (Eds.) *Climate Change 2007: The Physical Science Basis. Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change*. Cambridge University Press, Cambridge UK and New York, USA
- Mélin F, Challis, J (2004) A simple method for a dynamic partition of the North Atlantic into biological provinces *Proceedings Ocean Optics XVII*, Fremantle, Australia, pp 11
- Montes-Hugo M, Doney SC, Ducklow HW, Fraser W, Martinson D, Stammerjohn SE and Schofield O (2009) Recent changes in phytoplankton communities associated with rapid regional climate change along the western Antarctic Peninsula. *Science* 323: 1470
- Montes-Hugo M, Vernet M, Smith R, Carder K (2007) Phytoplankton size- structure on the Western shelf of the Antarctic Peninsula: A remote sensing approach. *Journal of Remote Sensing* 29: 801-829
- Moore TS, Campbell JW, Feng H (2001) A fuzzy logic classification scheme for selecting and blending satellite ocean color algorithms. *IEEE transactions on Geoscience and Remote Sensing* 39: 1764-1776
- Morel A, Berthon JF (1989) Surface pigments, algal biomass profiles, and potential production of the euphotic layer: Relationships reinvestigated in view of remote-sensing applications. *Limnology and Oceanography* 34: 1545-1562
- Morel A, Prieur L (1977) Analysis of variations in ocean color. *Limnology and Oceanography* 22: 709-722

- Myneni RB, Keeling CD, Tucker CJ, Asrar G, Nemani RR (1997) Increase plant growth in the northern high latitudes from 1981-1991. *Nature* 386: 698-702
- Nair A, Sathyendranath S, Platt T, Morales J, Stuart V, Forget M, Devred E, Bouman H (2008) Remote sensing of phytoplankton functional types. *Remote Sensing of Environment* 118: 3366-3375
- Napp J, Hunt G (2001) Anomalous conditions in the south-eastern Bering Sea 1997: linkages among climate, weather, ocean, and biology. *Fisheries Oceanography* 10: 61-68
- Oliver MJ, Irwin AJ (2008). Objective global ocean biogeographic provinces. *Geophysical Research Letters*, 35: L15601, doi:10.1029/2008GL034238.
- Paden CA, Abbot MR, Winant CD (1991) Tidal and atmospheric forcing of the upper Gulf of California: 1. Sea surface temperature variability. *Journal of Geophysical Research* 96: 18,337- 318,359
- Paillard D (2001) Glacial hiccups. *Nature* 409: 147-148
- Palacios DM (2004) Seasonal patterns of sea-surface temperature and ocean color around the Galápagos: regional and local influences. *Deep-Sea Research Part II — Topical Studies in Oceanography* 51: 43-57
- Parekh P, Follows MJ, Dutkiewicz S, Ito T (2006) Physical and biological regulation of the soft tissue carbon pump. *Paleoceanography* 21: doi:10.1029/2005PA001258
- Parmesan C, Ryrholm N, Steganescu C, Hill JK, Thomas CD, Descimon H *et al.* (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature* 399: 579-583
- Parsons TR, Lalli CM (2002) Jellyfish population explosions: Revisiting a hypothesis of possible causes. *La mer* 40: 111-121
- Pauly D, Christensen V, Froese R, Palomares ML (2000) Fishing down aquatic food webs: industrial fishing over the past half-century has noticeably depleted the topmost links in aquatic food chains. *American Scientist* 88: 46-51
- Peterson WT, Schwing FB (2003) A new climate regime in northeast pacific ecosystems. *Geophysical Research Letters* 30: 1896, 10.1029/2003GL017528
- Platt T, Bouman H, Devred E, Fuentes-Yaco C, Sathyendranath S (2005) Physical forcing and phytoplankton distributions. *Scientia Marina* 69: 55-73
- Platt T, Caverhill C, Sathyendranath S (1991) Basin-scale estimates of oceanic primary production by remote sensing: The North Atlantic. *Journal of Geophysical Research* 96: 15,147-15,159
- Platt T, Harrison WG (1985) Biogenic fluxes of carbon and oxygen in the ocean. *Nature* 318: 55-58
- Platt T, Sathyendranath S (1988) Oceanic primary production: Estimation by remote sensing at local and regional scales. *Science* 241: 1613-1620
- Platt T, Sathyendranath S (2008) Ecological indicators for the pelagic zone of the ocean from remote sensing. *Remote Sensing of Environment* 112: 3426-3436
- Platt T, Sathyendranath S, Forget M-H, White GN, Caverhill C, Bouman H, Devred E, Son S (2008) Operational mode estimation of primary production at large geographical scales. *Remote Sensing of Environment* 112: 3437-3448
- Platt T, Sathyendranath S, Longhurst A (1995) Remote sensing of primary production in the ocean: Promise and fulfilment. *Philosophical Transactions of the Royal Society. London. Series B.* 348: 191-202
- Polovina JJ, Howell EA (2005) Ecosystem indicators derived from satellite remotely sensed oceanographic data for the North Pacific. *ICES Journal of Marine Science* 62: 319-327
- Polovina J, Howell E, Abecassis M (2008) Ocean's least productive waters are expanding. *Geophysical Research Letters* 35: L03618 doi:10.1029/2007GL031745
- Polovina JJ, Howell EA, Brainard RE (2004) On the season and interannual migrations of the transition zone chlorophyll front. *Geophysical Research Letters* 31: L17204, 17210.11029/12004GL020637
- Polovina JJ, Howell E, Kobayashi DR, Seki MP (2001) The transition zone chlorophyll front, a dynamic global feature defining migration and forage habitat for marine resources. *Progress in Oceanography* 49: 469-483
- Quero J-C, Du Buit M-H, Vayne J-J (1998) Les observations de poissons tropicaux et le réchauffement des eaux dans l'Atlantique européen. *Oceanologica Acta* 21: 345-351
- Reid PC, Edwards M, Beaugrand G, Skogen M, Stevens D (2003) Periodic changes in the zooplankton of the North Sea during the twentieth century linked to oceanic inflow. *Fisheries Oceanography* 12: 260-269

- Reid PC, Holliday NP, Smyth TJ (2001) Pulses in the eastern margin current and warmer water off the north west European shelf linked to North Sea ecosystem changes. *Marine Ecology Progress Series* 215: 283-287
- Reynolds CS (2002) Ecological pattern and ecosystem theory. *Ecological Modelling* 158: 181-200
- Richardson AJ, Schoeman DS (2004) Climate impact on plankton ecosystems in the Northeast Atlantic. *Science* 305: 1609-1612
- Riebesell U, Zondervan I, Rost B, Tortell PD, Zeebe RE, Morel FMM (2000) Reduced calcification of marine plankton in response to increased atmospheric CO₂. *Nature* 407: 364-367
- Rodier M, Eldin G, Le Borgne R (2000) The western boundary of the equatorial Pacific upwelling: Some consequences of climatic variability on hydrological and planktonic properties. *Journal of Oceanography* 56: 463-471
- Roemmich D, McGowan J (1995) Climatic warming and the decline of zooplankton in the California current. *Science* 267: 1324-1326
- Ryan JP, Polito PS, Strutton PG, Chavez FP (2002) Unusual large-scale phytoplankton blooms in the equatorial Pacific. *Progress in Oceanography* 55: 263-285
- Russell JL, Stouffer RJ, Dixon KW (2006) Intercomparison of the Southern Ocean circulations in IPCC coupled model control simulations. *Journal of Climate* 19: 4560-4575.
- Ryan JP, Yoder JA, Cornillon PC (1999) Enhanced chlorophyll at the shelfbreak of the Mid-Atlantic Bight and Georges Bank during the spring transition. *Limnology and Oceanography* 44: 1-11
- Sarmiento JL, Gruber N (2002) Sinks for anthropogenic carbon. *Physics Today* 55: 30-36
- Sarmiento JL, Gruber N (2006) *Ocean biogeochemical dynamics*. Princeton University Press, Princeton, NJ, pp 503
- Sarmiento J, Gruber N, Brzezinski M, Dunne J (2004b) High-latitude controls of thermocline nutrients and low latitude biological productivity. *Nature* 427: 56-60
- Sarmiento J, Slater R, Barber R, Bopp L, Doney S, Hirst A *et al.* (2004a) Response of ocean ecosystems to climate warming. *Global Biogeochemical Cycles* 18: GB3003, doi:10.1029/2003GB002134
- Sathyendranath S, Longhurst A, Caverhill CM, Platt T (1995) Regionally and seasonally differentiated primary production in the North Atlantic. *Deep-Sea Research I* 42: 1773-1802
- Sathyendranath S, Platt T (1988) The spectral irradiance field at the surface and in the interior of the ocean: A model for applications in oceanography and remote sensing. *Journal of Geophysical Research* 93: 9270-9280
- Sathyendranath S, Platt T, Horne EPW, Harrison WG, Ulloa O, Outerbridge R, Hoepffner N (1991) Estimation of new production in the ocean by compound remote sensing. *Nature* 353: 129-133
- Sathyendranath S, Watts L, Devred E, Platt T, Caverhill C, Maass H (2004) Discrimination of diatoms from other phytoplankton using ocean-colour data. *Marine Ecology Progress Series* 272: 59-68
- Scheffer M, Carpenter S, Foley JA, Folke C, Walker B (2001) Catastrophic shifts in ecosystems. *Nature* 413: 591-596
- Schott F, McCreary J (2001) The monsoon circulation of the Indian Ocean. *Progress in Oceanography* 51: 1-123
- Schwing F, Murphree T, DeWitt L, Green P (2002) The evolution of oceanic and atmospheric anomalies in the northeast Pacific during the El Niño and La Niña events of 1995-2001. *Progress in Oceanography* 54: 459-491
- Sherman K (1991). The Large Marine Ecosystem concept: research and management strategy for living marine resources. *Ecological Applications* 1: 350-360
- Sherman K. (1993). Large marine ecosystems as global units for management: An ecological perspective. In: Sherman, K., Alexander, L.M., Gold, B.D. (Eds.), *Stress, Mitigation and Sustainability of Large Marine Ecosystems*. Proceedings of Symposium on Large Marine Ecosystems, 1-6 October 1990, Monaco. Washington, DC: AAAS Press, p 3-14.
- Sherman K, Duda AM (1999) An ecosystem approach to global assessment and management of coastal waters. *Marine Ecology Progress Series* 190: 271-287
- Smayda TJ (1980) Species Succession, In: Morris I (ed) *The Physiological Ecology of Phytoplankton*. Univ. Calif. Press, Berkeley, CA, pp 493-570
- Sommer U (1989) Maximal growth rates of Antarctic phytoplankton: Only weak dependence on cell size. *Limnology and Oceanography* 34: 1109-1112

- Stebbing AD, Turk SMT, Wheeler A, Clarke KR (2002) Immigration of southern fish species to south-west England linked to warming of the North Atlantic (1960-2001). *Journal of the Marine Biology Association of the United Kingdom* 82: 177-180
- Stuart V, Sathyendranath S, Head EJH, Platt T, Irwin B, Maass H (2000) Bio-optical characteristics of diatom and prymnesiophyte populations in the Labrador Sea. *Marine Ecology Progress Series* 201: 91-106
- Subramaniam A, Brown CW, Hood RR, Carpenter EJ, Capone DG (2002) Detecting *Trichodesmium* blooms in SeaWiFS imagery. *Deep-Sea Research II* 49: 107-121
- Subramaniam A, Carpenter EJ (1994) An empirically derived protocol for the detection of blooms of the marine cyanobacterium *Trichodesmium* using CZCS imagery. *International Journal of Remote Sensing* 15: 1559-1569
- Subramaniam A, Carpenter EJ, Falkowski PG (1999b) Bio-optical properties of the marine diazotrophic cyanobacteria *Trichodesmium* spp. II. A reflectance model for remote sensing. *Limnology and Oceanography* 44: 618-627
- Subramaniam A, Carpenter EJ, Karentz D, Falkowski PG (1999a) Bio-optical properties of the marine diazotrophic cyanobacteria *Trichodesmium* spp. I. Absorption and photosynthetic action spectra. *Limnology and Oceanography* 44: 608-617
- Tegen I, Werner M, Harrison S, Kohfeld K (2004) Relative importance of climate and land use in determining present and future global soil dust emission. *Geophysical Research Letters* 31: L05105, doi:10.1029/2003GL019216
- Thomas A, Strub PT (2001) Cross-shelf phytoplankton pigment variability in the California Current. *Continental Shelf Research* 21: 1157-1190
- Thomas CD, Lennon JJ (1999) Birds extend their ranges northwards. *Nature* 399: 213
- Thorrington-Smith M (1970) Some new and little-known planktonic diatoms from the West Indian Ocean. *Nova Hedwigia Beih.* 31: 815-835
- Thorrington-Smith M (1971) West Indian Ocean phytoplankton: a numerical investigation of phyto-hydrographic regions and their characteristic phytoplankton associations. *Marine Biology* 9: 115-137
- Tseng C, Lin C, Chen S, Shyu C (2000) Temporal and spatial variations of sea surface temperature in the East China Sea. *Continental Shelf Research* 20: 373-387
- Ueyama R, Monger B (2005) Wind-induced modulation of seasonal phytoplankton blooms in the North Atlantic derived from satellite observations. *Limnology and Oceanography*: 1820-1829
- Uitz J, Claustre H, Morel A, Hooker SB (2006) Vertical distribution of phytoplankton communities in open ocean: An assessment based on surface chlorophyll. *Journal of Geophysical Research-Oceans* 111: doi: 10.1029/2005JC003207
- Vance T, Baier C, Brodeur R, Coyle K, Decker M, Hunt Jr G, *et al.* (1998) Anomalies in the ecosystem of the eastern Bering Sea: including blooms, birds and other biota. *EOS, Transactions of the American Geophysical Union* 79: 121-126
- van der Spoel S (1994) The basis for boundaries in pelagic biogeography. *Progress in Oceanography* 34: 121-133
- Venrick E, McGowan J, Cayan D, Hayward T (1987) Climate and chlorophyll a: long-term trends in the central North Pacific Ocean. *Science* 238: 70-72
- Voituriez B, Herbland A (1977) Production primaire, nitrate et nitrite dans l'Atlantique tropical. II — Distribution du nitrate et production de nitrite. *Cahiers O.R.S.T.O.M. série. Océanographie* 15: 57-65
- Vila M, Masó M (2005) Phytoplankton functional groups and harmful algae species in anthropogenically impacted waters of the NW Mediterranean Sea. *Scientia Marina* 69: 31-45
- Voss M, Croot P, Lochte K, Mills M, Peeken I (2004) Patterns of nitrogen fixation along 10° N in the tropical Atlantic. *Geophysical Research Letters* 31: L23S09
- Warner AJ, Hays GC (1994) Sampling by the continuous plankton recorder survey. *Progress in Oceanography* 34: 237-256
- Watson R, Pauly D, Christensen V, Froese R, Longhurst A, *et al.* (2003) Mapping fisheries onto marine ecosystem for regional, oceanic and global interactions. In: Hempel G, Sherman K (eds) *Large*

- Marine Ecosystems of the World: Trends in Exploration, Protection, and Research. Elsevier, Amsterdam, pp 375-395
- Watts LJ, Sathyendranath S, Caverhill C, Maass H, Platt T, Owens NJP (1999) Modelling new production in the north west Indian Ocean region. *Marine Ecology Progress Series* 183: 1-12
- Werdell PJ, Bailey SW (2005) An improved *in situ* bio-optical data set for ocean color algorithm development and satellite data product validation. *Remote Sensing of Environment* 98: 122-140
- Westberry T, Siegel D (2006) Spatial and temporal distribution of *Trichodesmium* blooms in the world's oceans. *Global Biogeochemical Cycles* 20: GB4016, doi:10.1029/2005GB002673
- Whitney F, Welch D (2002) Impact of the 1997-1998 El Niño and 1999 La Niña on nutrient supply in the Gulf of Alaska. *Progress in Oceanography* 54: 405-421
- Whitney F, Wong C, Boyd P (1998) Interannual variability in nitrate supply to surface waters of the Northeast Pacific Ocean. *Marine Ecology Progress Series* 170: 15-23
- Williams R, Roussenov V, Follows M (2006) Nutrient streams and their induction into the mixed layer. *Global Biogeochemical Cycles* 20: GB1016, doi:10.1029/2005GB002586
- Wilson C, Adamec D (2001) Correlations between surface chlorophyll and sea surface height in the tropical Pacific during the 1997-1999 ENSO event. *Journal Geophysical Research* 106: 31,175-31,188
- Woods J, Barkmann W (1993) The plankton multiplier-positive feedback in the greenhouse. *Journal of Plankton Research* 15: 1053-1074
- Wyrtki K (1973) Physical oceanography of the Indian Ocean. In: Zeitzschel, B (ed) *The Biology of the Indian Ocean*. 18-36 pp
- Yamanaka I (1982) Application of satellite remote sensing to fishery studies in Japan. *NAFO Science Council Studies* 4: 41-50
- Yoder J, Kennelly M (2003) Seasonal and ENSO variability in global ocean phytoplankton chlorophyll derived from 4 years of SeaWiFS measurements. *Global Biogeochemical Cycles* 17: 1112, doi: 10.1029/2002GB001942
- Yoder JA, Schollaert SE, O'Reilly JE (2002) Climatological phytoplankton chlorophyll and sea surface temperature patterns in continental shelf and slope waters off the northeast US coast. *Limnology and Oceanography* 47: 672-682
- Zadeh L (1965) Fuzzy sets. *Information and Control* 8: 338-353

Acronyms and Abbreviations

ARAB	NW Arabian Upwelling province
AVHRR	Advanced Very High Resolution Radiometer
BPLR	Boreal Polar province
CaCO ₃	Calcium Carbonate
CARB	Caribbean province
CDOM	Coloured Dissolved Organic Matter
CNRY	Canary Coastal province
CoML	Census of Marine Life
CPR	Continuous Plankton Recorder
CZCS	Coastal Zone Color Scanner
DCM	Deep Chlorophyll Maximum
DT	Depletion Temperature
EEZ	Exclusive Economic Zone
ENSO	El Niño Southern Oscillation
EOF1/EOF2	First or second Empirical Orthogonal Function
ETRA	Eastern Tropical Atlantic province
FAO	Food and Agriculture Organization
FCM	Fuzzy, <i>c</i> -means clustering algorithm
GFST	Gulf Stream province
GUIA	Guianas Coastal province
GUIN	Guinea Current Coastal province
HNLC	High Nitrate, Low Chlorophyll
HPLC	High Performance Liquid Chromatography
ICES	International Council for Exploration of the Sea
IGBP	International Geosphere-Biosphere Programme
IIOE	International Indian Ocean Expedition
INDW	West India Coastal province
IOCCG	International Ocean Colour Coordinating Group
IOP	Inherent Optical Properties
IPCC	Intergovernmental Panel on Climate Change
JGOFS	Joint Global Ocean Flux Study
LME	Large Marine Ecosystems
MERIS	Medium Resolution Imaging Spectrometer

MODIS	Moderate Resolution Imaging Spectroradiometer
MONS	Indian Monsoon Gyre province
NADR	North Atlantic Drift province
NAO	North Atlantic Oscillation
NASA	National Aeronautics and Space Administration (USA)
NAST(E)	North Atlantic Subtropical Gyre (East) province (also referred to as NASE or STGE)
NAST(W)	North Atlantic Subtropical Gyre (West) province (also referred to as NASW or STGW)
NATR	North Atlantic Tropical Gyre province
NDT	Nutrient Depletion Temperature
NECS	North East Atlantic Shelves province
NHT	Northern Hemisphere Temperature
nL _w	Normalized water-leaving radiance
NO ₃	Nitrate
NOAA	National Oceanic and Atmospheric Administration (USA)
NODC	National Oceanographic Data Center
NOMAD	NASA bio-Optical Marine Algorithm Data set
NPP	Net Primary Production
NWCS	North West Atlantic Shelves province
OBIS	Ocean Biogeographic Information System
OCR	Ocean-Colour Radiometry
PAR	Photosynthetically Available Radiation
P^B	Primary production normalised to biomass
PC1/PC2	First or second Principal Component
PCA	Principal Components Analysis
PEQD	Pacific Equatorial Divergence
PO ₄	Phosphate
REDS	Red Sea Persian Gulf province
RMS	Root Mean Square
SARC	Atlantic Subarctic province
SATL	South Atlantic Gyral province
SeaWiFS	Sea-viewing Wide Field-of-view Sensor
SiO ₄	Silicate
SLA	Sea Level Anomaly
SOLAS	Surface Ocean Lower Atmosphere Study
SSH	Sea Surface Height
SST	Sea Surface Temperature
TRMM	Tropical Rainfall Measuring Mission
TTS	Typical Tropical Structure
TZCF	Transition Zone Chlorophyll Front
WSSD	World Summit on Sustainable Development
WTRA	Western Tropical Atlantic province

