University of Southampton

AN INVESTIGATION OF FACTORS INFLUENCING THE SPATIAL AND TEMPORAL DISTRIBUTION OF SURFACE PHYTOPLANKTON IN THE ENGLISH CHANNEL AND BAY OF BISCAY IN 2003 AND 2004

By

Mohammed Ali B. Qurban

This thesis is submitted for
Doctor of Philosophy

Faculty of Engineering, Science and Mathematics

School of Ocean and Earth Sciences

February 2009

UNIVERSITY OF SOUTHAMPTON

ABSTRACT

FACULTY OF ENGINEERING, SCIENCE AND MATHEMATICS

SCHOOL OF OCEAN AND EARTH SCIENCES

Doctor of Philosophy

AN INVESTIGATION OF FACTORS INFLUENCING THE SPATIAL AND TEMPORAL DISTRIBUTION OF SURFACE PHYTOPLANKTON IN THE ENGLISH CHANNEL AND BAY OF BISCAY IN 2003 AND 2004

By Mohammed Ali Qurban

Throughout 2003 and 2004 continuous autonomous observations of surface temperature, conductivity and chlorophyll fluorescence were recorded on the P&O "Pride of Bilbao" ferry between Portsmouth, UK and Bilbao Spain. Different conditions over the shelf, slope and deep waters along the route were detected and studied - from eutrophic harbour waters to the southern Bay of Biscay, which is oligotrophic in summer. During the two years, 21 manned crossings on the ferry provided information on nutrients, phytoplankton biomass and speciation. Measurements include chlorophyll *a* concentrations (calibration of the fluorimeter is discussed), High Performance Liquid Chromatography (HPLC) determined pigments concentrations, phytoplankton species abundance (biomass and identification) and nutrients. Data was also available from satellite images for estimates of chlorophyll (SeaWIFS), zooplankton abundance from CPR (Continuous Plankton Recorder) tows, wind speed and direction and irradiance. This has enabled phytoplankton populations to be related to-: (1) nutrient supply (2) grazing pressure (3) fresh water influences, (4) hydrography and (5) climatic conditions.

The distributions of hydrographic properties and of plankton were analysed on the basis of four generalised regions (i) well-mixed, (ii) northern summer stratified, and (iii) southern summer stratified on the shelf and (iv) oceanic region in the Bay of Biscay water. There were differences between the two years in the timing of seasonal changes and in the abundance of phytoplankton species. Chlorophyll *a* values were generally higher in shelf waters compared to oceanic water in both years.

The spring phytoplankton bloom reached its peak during March 2003 in the Bay of Biscay and during April on the continental shelf with maximum chlorophyll values of 2-4 mg m^{-3}. Whereas, the strong SW wind in Bay of Biscay in winter 2004 may have delayed growth in this region. In the shelf regions in 2004 low salinity values off western France and high solar irradiance in the north are likely to have led to earlier phytoplankton biomass than in 2003. During early summer, the coccolithophore, *Emiliania huxlyei* (>1000 cells ml^{-1}) was widespread in northern stratified regions, more so in 2003 than in 2004. In the summer of 2003 an exceptional dinoflagellate bloom occurred in the western English Channel. The bloom was composed of a monspecific surface population of *Karenia mikimotoi*, giving cell densities up to 8000 cells ml^{-1} and chlorophyll *a* concentrations up to 70 mg m^{-3}. Development of this dinoflagellate bloom in the western English Channel could be explained in terms of physical stability, and

low wind speed together with sufficient light and a supply of inorganic nutrients favouring growth of the cells. By contrast, in 2004, the abundance of diatoms was higher than 2003 and *K. mikimotoi* was common but not at bloom levels (chlorophyll *a* ~4.0 mg m^{-3}). A mixed diatom-dinoflagellate community was the dominant the final stage in the succession, as the summer thermocline was less well developed. The phytoplankton biomass and composition in 2003 matches the classical model of phytoplankton seasonal succession in temperate waters (Margalef, 1978; Smayda, 1980) but this was not obvious in 2004.

In general, the FerryBox system on the Pride of Bilbao in 2003 and 2004 was successful and improved understanding of the relationship between the phytoplankton population and hydrographic regimes in 2003 and 2004 between Portsmouth and Bilbao. Improvements in future might include continuous observations of oxygen and nutrients and more work can be done to link FerryBox data, satellite and CPR based observations.

ACKNOWLEDGEMENTS

This section of my thesis should probably be the most read, as there are so many people who have helped me on the road to my thesis who require special mention. To my supervisors, Professor Patrick Holligan and Dr. David Hydes, despite appearing to be overloaded with projects and post-graduate students, you were supportive and helpful. I would like to thank Prof. Holligan for providing invaluable guidance, experience and comments on this thesis. I would like to express my gratitude to Dr. Hydes for his guidance, encouragement and patience throughout this work even over Christmas and New Year. I would like to thank Dr. Duncan Purdie for providing invaluable guidance in this thesis, helping and supporting me in the analytical techniques.

I would like to express my sincere gratitude to Professor Harry Bryden for his help and support. I would also like to thank Dr. Antony Jensen for his help and support in multivariate analysis.

I am truly grateful to King Fahd University of Petroleum and Minerals (KFUPM) for the financial support and scholarship that made it possible for me to obtain this degree. Thanks must go to Dr. Alla-Aldeen Bukhari, Director of Centre for Environmental and Water, for his support and encouragement. The financial support for "FerryBox" work came from the EU (project EVK2-2001-00230 FerryBox) and the NERC CSP BICEP. This work would not have been possible without the help of many people with the sampling Charlie, Mark, Sue, Mia, Lina, Steff, Claire, Sue, Young, Jim, Andy and particularly P&O Ferries and the crews of the "Pride of Bilbao". Special thanks go for Dr. Anthony Walne from Marine Biological Association (MBA) for the CPR data.

I would like to say a word of gratitude also to National Oceanography Centre (NOC) for the use of facilities, laboratories and library. Special thanks go for Dr. Doug Connelly and Dr. Boris Kelly-Gerreyn for their useful discussions regarding my thesis work. I also need to thank Dr. John Gittins for helping me in the HPLC work. I would like to thank Kate Davis for her help in graphics. I am indebted to Dr. Osama Alamri, Dr. Hanan Al-Buflasa and Mr. Mohammed El-hajjar for their massive help and support in MATLAB. I appreciated Dr. Saed Al Ghamdi for his help in statistics.

I have a special feeling of gratitude in my heart for my parents (Baha Qurban and Faridah Dakak), sisters, and my brother. Their loving support and counsel have always been beyond compare. I need to thank my parents in law (Abdul roof Yghamour and Fowziah Dakak) and for their emotional support and taking care of my children in Saudi Arabia will be always remembered. Special thanks go for my brother in law for their support and phone calls. I would like to express my deep appreciation to my best friends Dr. Nabeel Abu-Zaid and Saad Alholiba (Abu Ryyan) for their supports, help and phone calls all years of my study.

To my dearest wife, you have helped me in more ways than you will ever know. You always supported and stood by me, no matter what the situation, and for this I am eternally grateful. You alone made me believe that finishing this degree was more than possible. Thanks so much for your love and support. Special thanks go to my children Hayat, Baha, Danyah, Ryyan and Fares for their patience during my study and being away from our country.

To my friend Turki Alsied, my office mate through the last years. You helped me with the discussions in our office surrounding the applicability and importance of our individual projects. You helped me whenever I was doubting the worth of my work and for this I cannot thank you enough. Also to Ibrahim Altisan, we worked together for the first year of my project, and you have been very supportive. I also wish to thank my friends Lyla Hazeem, Thamer Al-rashedi and Turki Alradadi for their support.

GRADUATE SCHOOL OF THE SOUTHAMPTON OCEANOGRAPHY

This PhD dissertation by

Mohammed Ali Qurban

has been produced under the supervision of the following persons;

Supervisor/s

Professor Patrick M. Holligan
Dr. David J. Hydes

Chair of Advisory Panel

Dr. Duncan A. Purdie

DECLARATION

This thesis is the result of work done wholly while under registered postgraduate candidature.

THESIS CONTENTS

LIST OF FIGURES

LIST OF TABLES

CHAPTER 1

1.GENERAL INTRODUCTION

1.1 Background

The oceans occupy about 70 percent of the earth's surface. The marine environment contributes about 40-50 % of annual global photosynthesis (Field *et al.*, 1998), even though it represents a small proportion of the plant biomass compared with terrestrial plants (Falkowsk, 1994; Williams, 1998). In the open ocean and shelf seas, the dominant primary producers are unicellular, chain-forming or colonial planktonic (free-floating) microalgae. The cells of marine phytoplankton range in diameter from < 1 micron to several hundred microns, with most species < 70 μm, and are differentiated by their morphology, structure and chemical composition (Jeffrey and Vesk, 1997; Porra *et al.*, 1997). They are often categorised by size into the pico- (< 2 μm), nano- (2-20 μm) and micro-phytoplankton (> 20 μm diameter) (Sieburth, 1979), with the small size classes generally dominant in oligotrophic (nutrient-poor) waters (Zubkov *et al.*, 1998) and micro-phytoplankton most abundant in eutrophic (nutrient-rich) waters (Chisholm, 1992).

Phytoplankton form the base of the marine food chain (Fenchel, 1988; Miller, 2004), supplying organic carbon in particulate or dissolved forms to consumer organisms that range from relatively large metazoans such as herbivorous copepods (the 'classical' foodweb) to small heterotrophic bacteria (the microbial foodweb Azam *et al.*,(1983) ; Kirchman, (2000)). The development of phytoplankton populations is controlled by the resources required for plant growth in the sea, in particular light and inorganic nutrients, and by mortality due to predators and pathogens. These two types of control are generally referred to as 'bottom-up' and 'top-down' respectively. At temperate and polar latitudes, where there are strong seasonal variations in solar irradiance and the depth of surface mixing, the increase of phytoplankton abundance in spring can be largely attributed to the enhanced availability of light and nutrients at this time of year (Holligan, 1989). However, it appears that top-down processes are more important than generally thought in determining the structure of marine pelagic

ecosystems (Verity and Smetacek, 1996). Recent observations from the Southern Ocean suggest that cell size may also be important, with variations in the abundance of large (micro-) phytoplankton cells reflecting bottom-up control and those of small (nano- and pico-) phytoplankton cells reflecting control by grazers (Smith and Lancelot, 2004).

The sensitivity of phytoplankton growth to environmental factors (Behrenfeld *et al.*, 2008) means that, within a particular geographic or climatic region, phytoplankton abundance is variable at time scales ranging from a few days (storms, tides etc.) to annual (year-to-year differences in climatic conditions), decadal (climatic oscillations) and millennial (climate change). This variability has important consequences for the marine food chain, including fish production, and for the global cycles of elements such as carbon, nitrogen and sulphur (Falkowski *et al.*, 1998). Furthermore, it is strongly affected by ecological (top-down control) and biogeochemical (effects of greenhouse gases such as CO_2 on the climate system) feedback processes. (Note that within the context of this thesis, the term 'climate' is applied to both long term and year-to-year changes in the weather patterns).

Large scale observational systems are beginning to provide some understanding of the nature of the complex interactions between ocean biota and environment. For example, satellite measurements of ocean colour (a measure of phytoplankton chlorophyll) are providing new information about how climate affects both the physiology of phytoplankton (Behrenfeld *et al*., 2008) and about the capacity of the upper ocean ecosystem to export organic carbon to depth (the biological carbon pump) (Falkowski *et al*., 1998). However, regional studies, which attempt to relate year-to-year variability in plankton abundance to measurements of environmental factors are rarely made (a notable exception being the Continuous Plankton Recorder (CPR) survey described in Section 1.5.2), mainly because of the logistical difficulties and high costs of making appropriate observations. Lack of knowledge of the nature and causes of such relative short term 'natural' variability is a source of considerable uncertainty for the interpretation of longer term records and for the prediction of the impacts of global change on ocean biology.

1.2 Characteristics of marine phytoplankton

More than 500 genera and 4000 species of marine phytoplankton have been identified (Sournia and Chretiennot-Dinet, 1991). Many show ubiquitous distributions in the world's oceans and, with the exception of heterotrophic dinoflagellates (see below), almost all are autotrophic (or mixotrophic) and contain chlorophyll *a* as the main light harvesting pigment.

1.2.1 *Taxonomy*

Phytoplankton are classified on the basis of their morphology, life cycles, and biochemical constituents including photosynthetic pigments (Van-Den-Hoek and Mann, 1997). Most marine phytoplankton belong to five major divisions: 1. Cyanophyta, 2. Prochlorophyta, 3. Bacillariophyta, 4. Dinophyta, and 5. Prymnesiophyta.

1) Cyanophyta: (Prokaryotic) are blue-green algae found as single cells (~1 µm in diameter, for example, *Synechococcus* sp.), large filamentous colonies (> 200 µm, *Trichodesmium* sp.), or as symbiotic associations within other phytoplankton cells. The water soluble phycobilins are important accessory pigments. Some types have an important role in nitrogen fixation (Azam *et al.*, 1983).

2) Prochlorophyta: (Prokaryotic) are the main free-living marine form being the unicellular *Prochlorococcus*, 0.6-0.8 µm in diameter, which is abundant in tropical and subtropical waters. Unlike the cyanophytes, this group contains chlorophyll *b* but lacks phycobilins.

3) Bacillariophyta: (Diatoms) are characterised by a siliceous cell wall (frustule) and found as single cells or chains with cell size in the range 2-200 µm (Jeffrey and Vesk, 1997). The major accessory pigment is fucoxanthin, which gives the cells a brown colour. They are widespread and often abundant in the oceans.

4) Dinophyta: (Dinoflagellates) are mainly motile flagellates, variable in size and brownish in colour due to the presence of the accessory pigment, peridinin. However, many species lack chloroplasts and are heterotrophic. The cells are often covered in thecal plates made of cellulose. They are widespread but relatively rare in polar waters.

5) Prymnesiophyta: (Unicellular flagellates), are 2-50 µm in diameter, and including the coccolithophores which produce external plates, or coccoliths, of calcium carbonate. Pigments are similar to those of the diatoms but the fucoxanthin derivative, 19'-hexanoyloxyfucoxanthin, is often important.

1.2.2 *Distributions of main taxonomic groups*

Due to changes in the availability of light and inorganic nutrients in surface water, the temporal distribution of the main taxonomic groups tends to follow a well described seasonal pattern in temperate, polar and upwelled waters (Margalef, 1978). Early in the year diatoms tend to be dominant under conditions of high light and inorganic nutrient availability. As nutrients become depleted, diatoms are replaced by coccolithophores (particularly the globally-abundant species, *Emiliania huxleyi*) and then by dinoflagellates. These ecological shifts reflect increasing stratification of the water column during spring and summer approaches and depletion of nutrients in surface water. By midsummer, the maximum phytoplankton biomass (usually measured as chlorophyll *a*) is often associated with the seasonal thermocline and, on continental shelves, with frontal boundaries between mixed and stratified water (Pingree *et al.*, 1976). The dominant species groups in these boundary environments between light and nutrient-limited conditions (Pingree *et al*., 1976) may be coccolithophores, dinoflagellates or, when light is low, small flagellates.

This seasonal pattern for the distributions of phytoplankton biomass and species groups was documented for a station in the western English Channel by Holligan and Harbour, (1977). It conforms to the hypothesis of Margalef, (1978) that relatively turbulent, nutrient-rich environments are characterised by fast growing species (diatoms) whereas under stable, nutrient-poor conditions slow growing motile species (dinoflagellates) tend to be relatively abundant. Coccolithophores appear to be intermediate in their ecophysiological requirements.

An anomalous phenomenon within the relationship between turbulence and phytoplankton succession described by Margalef, (1978) is the occurrence of monospecific surface blooms of dinoflagellates, commonly known as red tides. These are generally found in summer stratified waters, often close to fronts where the seasonal pycnocline is relatively shallow (< 20 m), and characterised by high plant biomass in

low nutrient water. Two possible causes of dinoflagellate blooms are recognised; the first is based on mechanisms of physical accumulation as might occur along frontal convergences for positively buoyant (or upwardly motile) cells (Le Fevre, 1986), and the second on the enhancement of nutrient fluxes across the seasonal pycnocline through vertical movements of motile cells (Pingree *et al*., 1977b; Holligan *et al*., 1984b). The physical mechanism is applicable only to relatively small scale blooms, whereas blooms that persist for weeks over spatial scales of 10 km or more require a large supply off nutrients that cannot be explained by lateral processes.

Within the context of this thesis (and of the wider scientific literature), it should be noted that the term phytoplankton 'bloom' has several meanings. The spring bloom refers to the relatively sudden growth of predictable diatom populations, giving typical maximum chlorophyll concentrations of 5-10 mg m^{-3} (e.g. Pingree *et al*., 1976), when light and nutrient conditions become favourable in the early part of each year. Within monospecific dinoflagellate blooms (see above) chlorophyll often exceeds 20 mg m^{-3}. The coccolithophore, *E. huxleyi*, also forms blooms with high cell densities but, as the cells are small (< 5μm in diameter), the maximum chlorophyll concentration is usually < 2 mg m^{-3} (Holligan *et al.*, 1983) and other phytoplankton species may also be present in significant numbers.

1.3 Control of marine phytoplankton biomass

The growth of marine phytoplankton is influenced by the availability of light and inorganic nutrients input as well as by water temperature (Holligan, 1989; Legendre and Rassoulzadegan, 1995). Except for cold (< 5^{o} C) polar seas, temperature is relatively unimportant as it is neither a limiting factor on growth or very variable over the annual cycle compared to the range experienced by many terrestrial ecosystems. For that reason, only light and nutrients are considered here.

1.3.1 *Phytoplankton photosynthesis*

The photosynthetic process is carried out within chloroplasts which contain light absorbing pigments, in particular chlorophyll *a,* (Kirk, 1994; Falkowski and Raven, 1997). The light-dependent part of photosynthesis, which yields chemical energy as ATP and NADPH from the photolysis of water, is composed of two components (photosystem I and photosystem II) (Falkowski and Raven, 1997), each of which

contains a reaction centre (RC) and a light-harvesting centre (LHC). The LHC is composed of various pigment-protein complexes, which absorb light (photons) from prevailing light field and transfer energy (electron transport) to the RC from higher to lower excitation states and between pigment-protein complexes. In general, the energy of photons striking the photosynthetic pigments of phytoplankton has three fates (Kirk, 1994; Falkowski and Raven, 1997): 1. transfer to chlorophyll *a* for photosynthesis, 2. re-emittion as fluorescence, or 3. lost as heat. The ability of phytoplankton to lose excess excitation energy as heat or fluorescence is thought to prevent photo-induced damage to the photosynthesis apparatus. However, various processes can change the relationship between absorption and fluorescence by chlorophyll both temporally and spatially (Dubinsky, 1992). Such processes include species succession and changes in nutrient concentrations, solar radiation and the physiological state of the phytoplankton.

The light-independent reactions of photosynthesis utilise chemical energy from the light-dependent reactions to produce organic matter through the reduction of carbon dioxide and inorganic nitrogen (nitrate) and phosphate. A generalised equation (Falkowski and Raven, 1997) for this process is:

$$106\,CO_2 + 112\,H_2O + 16\,NO_3 + PO_4 + 19\,H^+ \rightarrow (CH_2O)_{106}(NH_3)_{16}H_3PO_4 + 138\,O_2$$

The reverse reaction represents respiration. The relative proportions (by atoms) of 106C:16N:1P were first described by Redfield, (1934) as characteristic of the bulk composition of phytoplankton (and more generally of particulate organic matter in surface waters of the ocean). They are not only relatively constant but also approximate the ratio of N to P that is supplied as nitrate and phosphate from deep water to the surface in order to balance losses due to sinking organic matter. Without this resupply of nutrients through upwelling and winter mixing of the water column phytoplankton growth in the surface waters would be permanently nutrient limited.

1.3.2 *Light utilisation*

The rate of photosynthesis is related non-linearly with irradiance. Figures 1.1 shows the general relation (P-E curve) between the photosynthesis and irradiance and can be described by a set of mathematical equations (Kirk, 1994). Those that describe the P-E curve up to the maximum rate of photosynthesis (P_{max}) are:

$$P_g = \frac{P_{max}[E]}{K_1 + [E]} \quad (1)$$

$$P_n = \frac{P_{max}[E - E_c]}{K_1 + [E - E_c]} \quad (2)$$

where P_g and P_n are gross and net photosynthesis respectively and K_1 is the irradiance half-saturation constant . E is irradiance expressed as photosynthetically available radiation (PAR, 350-700 nm), and $[E-E_c]$ is the difference between ambient PAR and the compensation PAR (irradiance level at which the rate of phytoplankton photosynthesis equals the rate of phytoplankton respiration – see Figure 1.1). At high irradiance a significant decrease in photosynthesis (photoinhibition) can occur. Phytoplankton can recover relatively rapidly from photoinhibition when light intensity is reduced (Kirk, 1994).

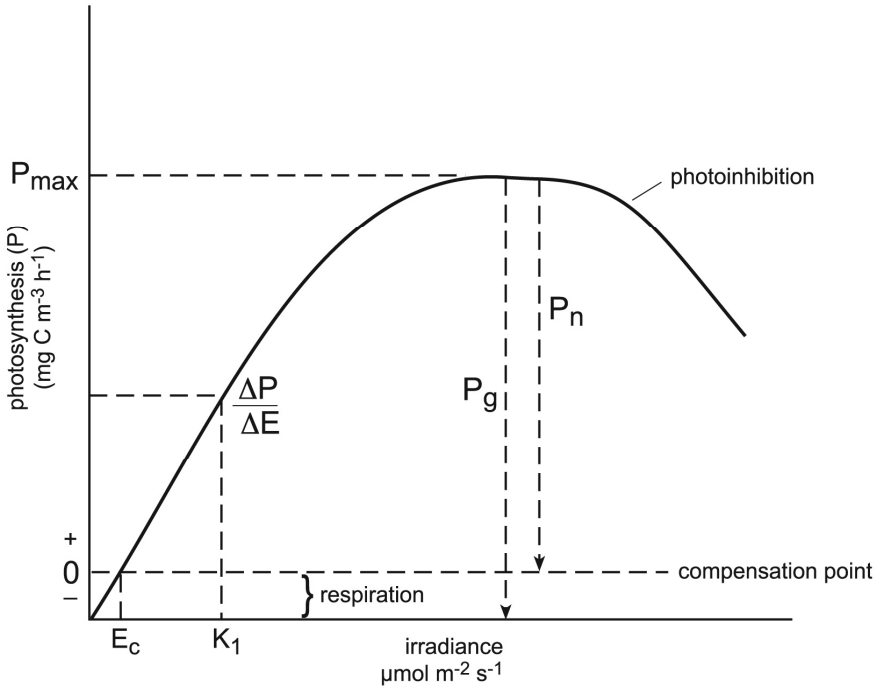


Figure 1.1: The response of photosynthesis (P) to change in light intensity (E) from Holligan, (1989) and Lalli and Parsons, (2001). Note that in this diagram irradiance is denoted as I rather than E.

The shape of the P-E curve varies with phytoplankton species, and values for P_{max} and the initial slope of the curve, $\alpha, \Delta P / \Delta E$ (Figure 1.1), reflect the physiological properties of the phytoplankton cells. α is a measure of the efficiency of light absorption (photoacclimation) whereas P_{max} reflects environmental conditions such as nutrient

concentration and temperature (Kirk, 1994). As different phytoplankton species are characterised by different P-E curves, changes in light and nutrient conditions will lead to a succession of different dominant species in the community. For example, diatoms tend to grow well at high irradiance whereas dinoflagellate population show efficient growth at low irradiances (Holligan, 1989; Smayda, 1997).

The availability of light to phytoplankton cells in the water column is determined by a combination of surface irradiance (sunlight), light penetration in the water and the depth of surface mixing (Kirk, 1994). Surface irradiance varies with climatic conditions, season and latitude. Light penetration is generally described as the extinction coefficient (kd, m^{-1}) for specific waveband(s) of PAR and is affected by the optical properties of water, and light-absorbing particulate (including phytoplankton cells) and dissolved materials. The depth of the surface mixed layer in the open sea ranges from hundreds of meters in winter where convective cooling and wind mixing are strong to a few tens of meters in summer where a stable warm surface layer forms by solar heating. This combination of factors, especially day length (combined with solar angle) and depth of mixing, means that over an annual cycle the mean daily irradiance experienced by phytoplankton cells is highly variable.

A conceptual basis for understanding how phytoplankton growth in the sea is controlled by light was given by Sverdrup, (1953) and is summarised in Figure 1.2. Assuming that the cells are evenly distributed with depth, profiles for gross photosynthesis (P_g) and dark respiration (R) can be drawn, given knowledge of the extinction coefficient and the P-E curve. Integration of these variables against depth then defines a depth, (the critical depth,) above which water column photosynthesis balances respiration. According to Sverdrup's hypothesis if the depth of mixing is less than the critical depth then there will be net growth of the population. Conversely, when the depth of mixing is greater than the critical depth phytoplankton biomass will not increase. Figure 1.2 also defines the compensation depth at which the rates of gross photosynthesis and respiration are equal. Above this depth, net photosynthesis (Pn) is positive.

Although the critical depth concept can be applied in a general sense (e.g. Pingree *et al*., 1976) its application to specific oceanographic conditions is limited by a

lack of data on phytoplankton respiration rates compared to P-E characteristics which are relatively easily determined using the ^{14}C technique (Langdon, 1988). Furthermore, as appreciated by Sverdrup, it is the relationship between community respiration (including heterotrophic organisms) and phytoplankton photosynthesis that will determine whether or not net growth of the phytoplankton occurs in the sea (Smetacek and Passow, 1990). Despite these limitations the critical depth hypothesis remains a useful basis for understanding how and when the spring diatom bloom is initiated (Siegel *et al.*, 2002).

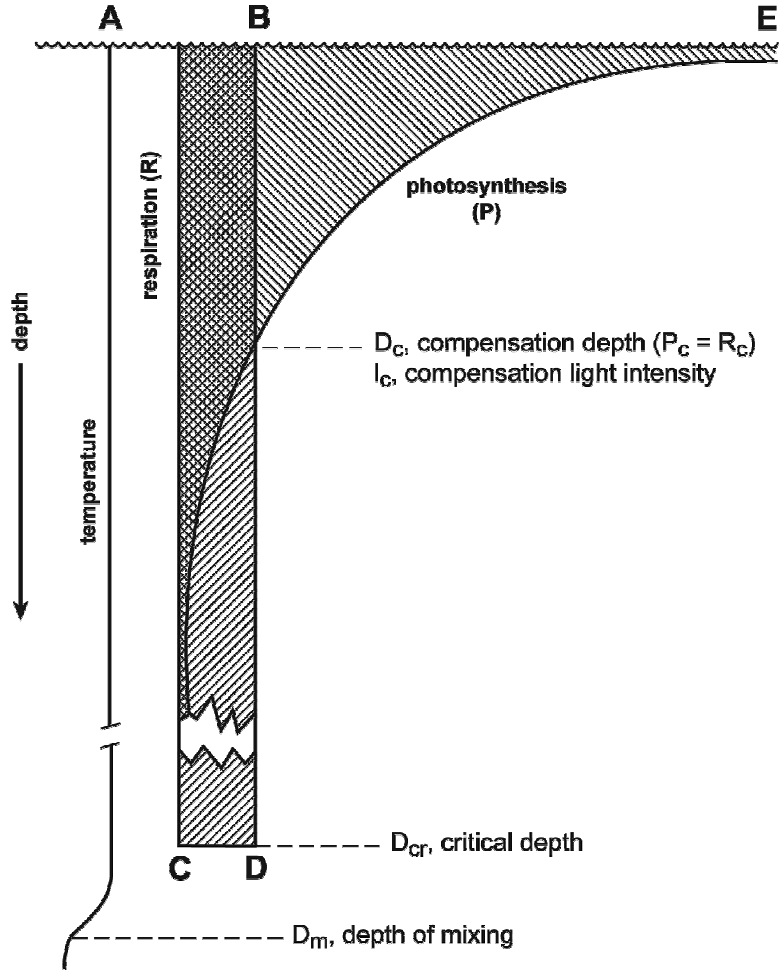


Figure 1.2: The relationship between mixing depth, compensation depth and critical depth (after Sverdrup, 1953).

1.3.3 *Nutrient utilisation*

A wide range of elements is essential for the growth of phytoplankton (Riebesell and Wolf-Gladrow, 2002; Arrigo, 2005). Nitrogen (N), and phosphorus (P) are considered to be the main macro-nutrients limiting phytoplankton abundance (Tyrrell,

1999) although in large areas of oligotrophic oceanic waters the availability of micro-nutrients such as iron is now known to be a key limiting factor. Also the availability of silica (Si) required for cell wall (frustule) formation by diatoms can determine the distribution of this group of organisms (DeMaster, 2001). In general, both observational and experimental data suggest that phytoplankton productivity is most often limited by inorganic fixed inorganic N (e.g. nitrate) (Falkowski *et al*., 1998) and, for that reason, nitrogen fixation (LaRoche and Breitbarth, 2005) is considered to play an important role in maintaining the nutrient balance of the oceans.

Nutrients are supplied to surface waters from a combination of external (e.g. deep ocean, atmosphere, rivers) and internal sources (Legendre and Rassoulzadegan, 1995). The internal source is determined by nutrient regeneration within the marine food chain through excretory (herbivores) and remineralisation (bacteria) processes. In the open sea, most of the N for phytoplankton growth is in the form of nitrate mixed upwards from depth and of ammonium and urea excreted by herbivores. These two sources are generally referred to as 'new' and 'regenerated' nitrogen (Dugdale and Goering, 1967).

Nutrient replenishment in the microenvironment of a phytoplankton cell occurs in three ways: 1. by diffusive transport, 2. by advective transport and 3. by chemical reaction in the diffusive boundary layer (Riebesell and Wolf-Gladrow, 2002). Nutrient assimilation by the cell can be described in terms of the Michaelis-Menten (and Monod) equation as follows:

$$\mu = \frac{\mu_{max}\, S}{K_R + S} \qquad (3)$$

where μ is growth rate or nutrient uptake rate, S is extracellular concentration of the rate-limiting nutrient (resource), and K_s is the half-saturation constant for uptake or growth rate. This relationship between ambient nutrient concentration and growth (uptake) rate is illustrated in Figure 1.3.

Factors affecting uptake rate include cell size, nutritional state of the cell, transport limitation across the cell membrane and toxicity effects (if abundance of nutrients is too high) (Riebesell and Wolf-Gladrow, 2002). Cell size is considered to be an important ecophysiological variable (Tilman and Kilham, 1982). When nutrient

concentrations are low, smaller algal cells generally have a competitive advantage compared to larger cells because of a higher affinity (low K_R) for uptake (Stolte *et al.*, 1994; Arrigo, 2005). Thus, small-sized species are generally dominant in oligotrophic water. The positive correlation between cell volume and storage capacity (Stolte and Riegman, 1995) provides an explanation for the greater abundance and higher growth rates of larger cells in nutrient enriched waters.

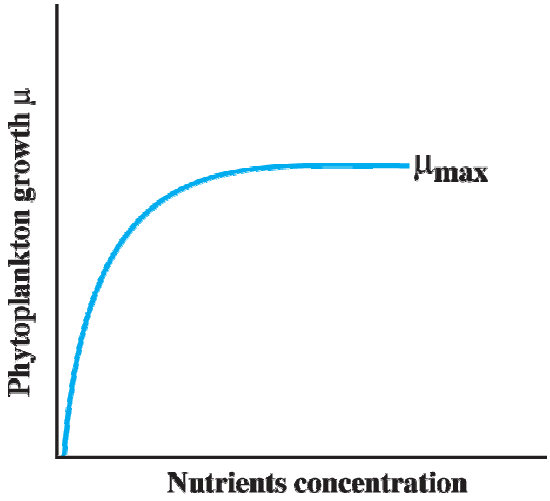


Figure 1.3: The effect of nutrient concentration on the phytoplankton growth rate.

As discussed in the previous section (1.3.1), the Redfield ratio, C: N: P = 106:16:1, defines the elemental composition of healthy phytoplankton and, more generally, of particulate organic matter in surface ocean waters. Fluctuations in the ratio of N to P in phytoplankton or of nitrate-N to phosphate-P in water are often used as indicators of nutrient status or nutrient limitation (Geider and Roche, 2002; Riebesell and Wolf-Gladrow, 2002). For example, when the water N: P ratio is > 16 or < 16 growth is expected to be limited by P or N respectively. In most situations, the N:P ratio tends to decrease as nutrients are removed from the water (e.g. Pingree *et al.*, 1977a), reflecting the relatively rapid recycling of P, so that the phytoplankton becomes increasingly N-limited with time. Similar arguments can be applied to the interpretation of changes in the water N:Si (or P:Si) ratio when considering the growth of diatoms, based on an average N:Si ratio of 1:1 for nutrient replete cells (Brzezinski, 1985).

It should be noted that significant deviations from the Redfield ratio are observed both for phytoplankton in culture (Geider and Roche, 2002) and, to a lesser degree, for particulate organic matter in the sea (Arrigo, 2005). These are believed to

reflect biochemical differences between groups of algae and, for a given phytoplankton species, between cells in distinct physiological states. Thus, the Redfield ratio represents an average condition of the upper ocean ecosystem, which includes diverse groups of phytoplankton growing under a wide range of nutritional situations.

1.3.4 *Light and nutrient utilisation in stratified waters*

In temperate seas during winter, when surface irradiance is minimal, the depth of mixing greatly exceeds the critical depth. Phytoplankton biomass remains low and nutrients accumulate. With decreasing winds and increasing solar radiation during spring there is a marked change of conditions in the water column especially when the seasonal thermocline is established (Pingree, 1975). The depth of mixing becomes less than the critical depth, and the growth of phytoplankton (mainly diatoms) leads to rapid depletion of nutrients (e.g. Pingree *et al*., 1976; Siegel *et al*., 2002). Through the summer months, phytoplankton abundance tends to be nutrient-limited rather than light-limited until decreasing solar radiation and increasing winds in autumn lead to a breakdown of stratification. At this time of year, the combination of upward mixing of nutrients from below the seasonal thermocline and persistence until early winter of some degree of surface stabilisation can lead to renewed growth of phytoplankton in surface waters (Pingree *et al*., 1976). Finally, the depth of mixing will again exceed the critical depth to complete the annual cycle.

The summer thermocline and, on continental shelves, frontal boundaries between tidally well mixed and seasonally stratified waters (see Pingree and Griffiths, 1978) represent transitional regions between nutrient and light limitation of phytoplankton growth. Here relatively high chlorophyll concentrations may persist for weeks or even months (Holligan and Harbour, 1977; Holligan, 1981) as phytoplankton exploit, through behavioural (e.g. motility) and/or physiological adaptations, the continuing availability of both light and nutrients. The combination of the effects of internal tides and bottom topography at the edge of the continental shelf can also lead to a localised enhancement of vertical mixing and phytoplankton abundance (Sharples *et al.*, 2007).

The general consequences of seasonal stratification for planktonic ecosystems are now relatively well understood (e.g. Cushing, 1989; Tett *et al*., 1993; Gowen *et al*., 1995). In terms of phytoplankton abundance the major uncertainties relate to the precise

nature of physical processes (see van-Haren *et al*., 1998) that control the timing and rate of development of the spring bloom and to the role of herbivorous zooplankton in maintaining inputs of regenerated nutrients during summer period.

1.3.5 *Mortality*

The major processes determining phytoplankton mortality are grazing by herbivores, infection by viruses and sinking of living cells. Grazing is ubiquitous whereas both viral attack and sinking are likely to be more localised and dependent on the type of algal cells.

Herbivorous zooplankton (grazers) are an important cause of phytoplankton mortality, act as a source of regenerated nutrients and are determinants of the trophic structure of the marine food chain (Banse, 1995; Mousseau *et al.*, 2001). Herbivores influence the standing stock and growth of phytoplankton cells. For example, grazing control of diatom and dinoflagellate numbers is related to the zooplankton population growth rate (Calbet, 2001) and the consumption of phytoplankton by grazers strongly depends on relative sizes and relative growth rates (Sautour *et al.*, 1996); large cells are grazed by mesozooplankton (copepods) and small cells are mostly ingested by microzooplankton or microheterotrophic organisms (Marquisa *et al.*, 2007). Copepod grazing may have a relatively low impact on spring bloom if there is a time lag between the initial increase in phytoplankton and the response of the over-wintering copepod (mesozooplankton) population (Barquero *et al.*, 1998). On the other hand, high ingestion rates by microzooplankton (heterotrophic nanoflagellates and ciliates) can exceed the grazing rates of mesozooplankton and closely match the growth rates of small phytoplankton cells (Marquisa *et al.*, 2007).

Viruses are abundant members of the aquatic microbial community (Rodriguez *et al.*, 2000; Suttle, 2005, 2007) and tend to flourish in situations of high biological productivity (Rodriguez *et al.*, 2000). For example, during blooms of a single species, such as the prymnesiophytes *Emiliania huxleyi* and *Phaeocystis globosa*, a high proportion of infected cells has been used to infer high levels of viral-mediated mortality (Suttle, 2007). In summer, increasing water temperature enhances viral production (Rodriguez *et al.*, 2000). However, in autumn and winter, the role of viruses appears to be less important because of low phytoplankton biomass (Rodriguez *et al.*,

2000; Short and Suttle, 2003; Suttle, 2005). Short and Suttle, (2003) concluded from an annual study that, although not all eukaryotic algal species acted as hosts to viruses, the regular production of, and mortality from, algal viruses has a significant effect on phytoplankton community structure and dynamics.

Phytoplankton cells are typically 3 to 5 % denser than the sea water in which they live. Although many species with large (> 10 μm diameter) cells have special adaptations to reduce or prevent sinking, such as flagellae (Alexander, 1990), gas vacuoles, low-density storage compounds or external appendages, large and rapid losses of phytoplankton, especially diatoms, from the surface layer can occur via sinking (Billett *et al.*, 1983). Direct sinking of algal cells has important implications for the export of organic carbon from the surface ocean to deep water and the sediments (Legendre, 1990).

1.4 Phytoplankton functional groups

Attempts to interpret or predict patterns in phytoplankton distributions and their significance in relation to ecological or biogeochemical processes requires some classification of function, especially for a group of organisms that exhibit such a wide range in cell size. The most widely used approaches are based on allometry (size dependence of metabolic processes) and biochemical properties, both of which have important applications in numerical modelling of planktonic ecosystems (Anderson, 2005).

The maximum growth rate of unicellular organisms varies inversely with cell size, smaller cells growing faster than large ones at a given temperature, so that knowledge of the size spectrum of cells within a natural population can be used to infer information about production rates (Joint, 1991). Furthermore, patterns in phytoplankton size distribution and species richness are believed to reflect how energy flows through those communities from one trophic level to another (Cermeno and Figueiras, 2008) with the larger cells of particular importance for the transfer of organic carbon both to higher trophic levels (e.g. fish) and to deep water and the sediments (Legendre, 1990). For these reasons, changes in time and space in the proportions of pico-, nano- and micro-phytoplankton (Sieburth, 1979) are important indicators of shifts in the way the marine ecosystem is functioning.

In terms of both species succession (Margalef, 1978) and nutrition, diatoms which require Si for cell walls, coccolithophores which require Ca^{++} for coccolith formation and dinoflagellates which have no biomineral phase represent distinct functional groups that, at least to some degree, can be distinguished by ocean colour remote sensing (Raitsos *et al.*, 2008). Secondary characteristics, such as the tendency for diatoms to sink (Billet *et al*., 1983) and the role of coccolithophores in the global sulphur cycle (Holligan, 1992), mean that these groups have particular importance for biogeochemical studies. Phytoplankton populations could also be classified in terms of their cellular carbon-to-chlorophyll ratio (Geider, 1987; Geider *et al.*, 1997), a variable that reflects taxonomic affiliation, nutritional state and light history (photoacclimation). Thus, the carbon-to-chlorophyll ratio (C:chl) tends to be lower in diatoms than in dinoflagellates (and other flagellates), in nutrient-replete cells than in nutrient-deficient ones, and in cells growing under high light compared to low light. Cellular chlorophyll content also influences optical properties as detected by remote sensing.

1.5 Large scale observations of marine phytoplankton populations

Data on the large scale distributions of phytoplankton at the level of species or functional groups are still hard to obtain. Single stations with time series records are not necessarily representative of some broader geographic region, and research cruises can give spatially extensive information, but only cover a short time scale. Two widely applied methods do provide wide coverage in time and space, satellite remote sensing of ocean colour and the Continuous Plankton Recorder (CPR), bur both have significant limitations for ecological studies.

1.5.1 *Satellite remote sensing of ocean colour*

Satellite instruments measure ocean colour by detecting the reflected radiance as seen through the atmosphere in number of wavebands, which correspond to high, medium and low absorption by phytoplankton pigments. The launch in 1978 of the first ocean colour sensor, the Coastal Zone Color Scanner (CZCS), was an experimental NASA mission that ended in 1986. After a gap of several years, the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) was launched in August 1997. Compared to the CZCS, SeaWiFS was a much improved instrument in terms of a higher signal to noise ratio, on board calibration capabilities, and the detection of dissolved organic material which interferes with the estimation of chlorophyll (Joint and Groom, 2000). Subsequently, the

Moderate Resolution Imaging Spectroradiometer (MODIS) was launched in December 1999. MODIS represents an increase in capability compared to SeaWiFS with more wavebands and a higher signal to noise ratio for observing both ocean colour and (in the near infra-red) sea surface temperature. Examples of outputs from the CZCS, SeaWiFs and MODIS are given in Figure 1.4.

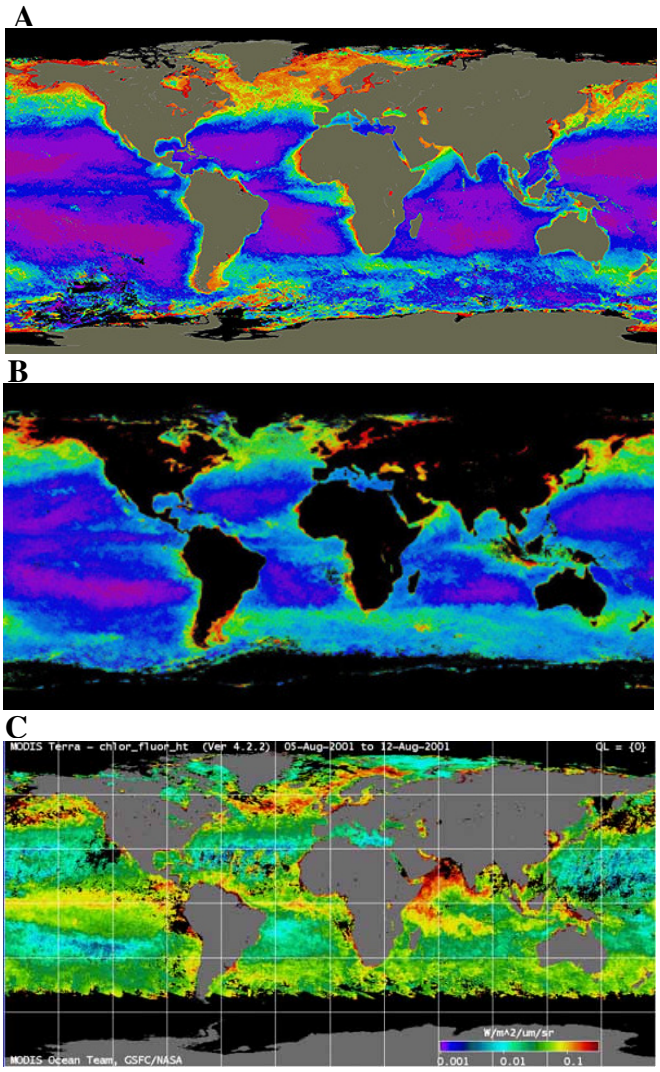


Figure 1.4: (A) The global distribution of chlorophyll averaged between 1978 and 1986 from CZCS data. (B) Global oceanic photoautotroph abundance, from September 1997 to August 2000, provided by the SeaWiFS Project, NASA/Goddard Space Flight Centre and ORBIMAGE. (C) A MODIS image for 12 August 2001, showing global chlorophyll distribution for a single day (http://www.pml.ac.uk).

Many studies have now been made of regional-scale distributions of chlorophyll using SeaWiFs and MODIS with respect to both seasonal and inter-annual variability (e.g. Joint and Groom, 2000; Brickley and Thomas, 2004) and to the processes that

initiate phytoplankton blooms (e.g. Henson *et al*., 2006). However, they provide no information about the vertical distribution or composition of phytoplankton populations in terms of species or functional groups, although attempts to resolve the latter are now just starting (Raitsos *et al.*, 2008).

1.5.2 *Continuous Plankton Recorder*

The Continuous Plankton Recorder (CPR) survey is the largest multi-decadal plankton monitoring programme in the world (Richardson *et al.*, 2006). CPRs are towed by merchant ships and weather ships and have been sampling the North Sea and North Atlantic since the 1930s (Batten *et al.*, 2003). This has enabled the study of large scale spatial and temporal variability in the abundance and species composition of phyto- and zooplankton populations (Batten *et al.*, 2003; Richardson *et al.*, 2006). The survey has an archive store in Plymouth, UK, of formalin-preserved samples dating continuously back to the 1960s (and for some areas the 1950s). Analysis is based on direct identification and counts of organisms caught on the moving silk of the CPR, which has a mesh size of about 200 µm. In addition, an assessment is made of total phytoplankton in terms of the greenness of the silk attributable to photosynthetic pigments, which is expressed as the Phytoplankton Colour Index (PCI).

In response to recent changes in climate (global warming), large scale changes in the distributions of plankton populations in the North Atlantic have been detected by the CPR survey (Beaugrand *et al.*, 2002; Richardson and Schoeman, 2004). In particular, it is evident that there has been a shift by about 10^{o} of latitude (~1000 km) of copepod communities since the 1980's with significant bottom-up effects on the distributions of carnivorous zooplankton. Corresponding changes in, and relationships to, phytoplankton populations are less easy to define, in part because uncertainty in the significance of smaller phytoplankton cells in determining PCI. In spite of these uncertainties, seasonal changes in phytoplankton abundance and in diatoms (spring) and dinoflagellates (summer) have been defined by CPR data (Leterme *et al.*, 2006; McQuatters-Gollop *et al.*, 2007). A general trend of increasing PCI for the NE Atlantic and North Sea has been described (Leterme *et al.*, 2005) which can be attributed in part to increasing abundance and/or proportion (compared to diatoms) of dinoflagellates. However, sub-areas of the NE Atlantic and North Sea appear to behave in different

ways reflecting the complexity of the relationship between environmental variables and phytoplankton abundance.

1.5.3 *Other time series*

Several marine laboratories established in the late 19th and early 20th centuries started monitoring programmes in nearby coastal waters. For example, the UK Marine Biological Association (MBA) started collecting hydrographic and plankton data at station E1, about 30 km south of Plymouth in 1902, and interpretation of the observations has made important contributions to our understanding the dynamics and variability of plankton populations (Southward *et al*., 2005).

Recognition of the importance of global change in influencing planktonic ecosystems has led to a re-vitalisation of monitoring programmes. Thus, over the last 15 years, detailed observations on the plankton have been made at weekly intervals at station L4 about 15 km south of Plymouth (Rodriguez *et al*., 2000; http://www.pml.ac.uk). Variables measured include vertical profiles of temperature, salinity and chlorophyll fluorescence, total and size-fractionated chlorophyll, and phytoplankton and zooplankton species abundance. Despite the uncertainty about the degree to which a single station is representative of a wider area, it has been possible to relate variability in phytoplankton populations at L4 to the North Atlantic Oscillation (NAO) (Irigoien *et al.*, 2000).

1.6 The European FerryBox Project (Bay of Biscay)

The European FerryBox Project (2002-2005) was a multi-disciplinary research and development programme using measurements from ferries and other commercial ships to demonstrate the efficacy and application possibilities in European Seas (Petersen *et al.*, 2004). Ships-of-opportunity (Ferry) are being used to carry sets (boxes) of scientific instruments, hence the name FerryBox. The FerryBox instrumentation packages have several advantages compared to other types of measurement systems including (1) protection against harsh environment, e.g. waves and currents, (2) prevention of bio-fouling (inline sensors), (3) no energy restrictions (in contrast to buoys), (4) lower running costs since ship operation costs do not need to be calculated, and (5) the acquisition of spatially-extensive (i.e. transects) rather than single point data (Petersen *et al.*, 2005).

The FerryBox Project systematically collected data relevant to specific basic and applied issues, including (1) impacts of frontal systems on the biological activity, (2) changes in the physiological state of phytoplankton before, during and after blooms (3) variations in sediment transport, (4) validation of satellite data sets, and (5) data assimilation into numerical models (Petersen *et al.*, 2004; Petersen *et al.*, 2005).

In April 2002, a FerryBox system was installed by National Oceanography Centre, Southampton (NOCS) on the P&O European Ferries Ltd ship "M V Pride of Bilbao" which operates between Portsmouth, UK and Bilbao, Spain (Figure 1.5). The route was selected because it crosses a range of oceanic environments, is operational all year round, and has a high repeat rate (4 times per week) enabling most types of oceanographic event (storms, seasonal stratification, salinity anomalies, plankton blooms etc.) to be sampled. Background information on the area of study for this work are now discussed in details below.

1.7 Regional topography, hydrography and phytoplankton of the English Channel and Bay of Biscay

1.7.1 *Regional topography*

The study region for this thesis comprised the central and western English Channel and the Bay of Biscay (northern, central and southern) (Figure 1.5). The English Channel is a narrow body of water, separating England from France and is a pathway between the North Atlantic and the North Sea (Borges and Frankignoulle, 2003). The Bay of Biscay is bounded by France to the east, by Spain to the south and by the Celtic Sea to the north (Lavin *et al.*, 2006) (Figure 1.5). The continental shelf in the northern Bay of Biscay is delimited by the entrance of the English Channel with mean width of 150-180 km (Koutsikopoulos and Le-Cann, 1996) whereas the continental shelf along the Cantabrian coast (southern Bay of Biscay) is as narrow as 12 km, but widens westward (Valdes and Lavin, 2002; Lavin *et al.*, 2006).

Changes in water depth along the route are shown in Figure 1.6. The southern part of the transect is in the deep waters of the Bay of Biscay, whereas the northern part lies on the tidally-energetic NW European continental shelf. Regions of shallow (< 50 m) water are found only at the end and start of the route.

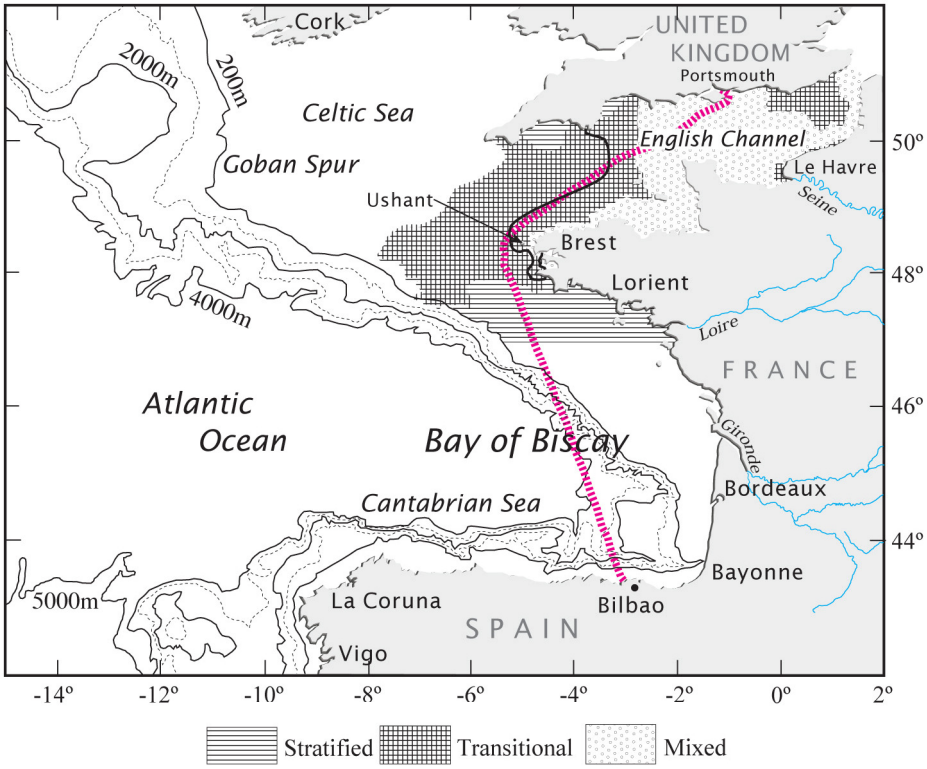


Figure 1.5: Bathymetry and topography of the Bay of Biscay. Red dashed line is the standard route of Pride of Bilbao. The hatched area represents the transitional zone between well-mixed and stratified waters, regions that are well mixed throughout the year are indicated by stippling, and heavy line represents stratified waters during the summer (after Pingree and Griffiths, 1978). The black line indicates the predicted position of tidal mixing front from Pingree and Griffiths (1978).

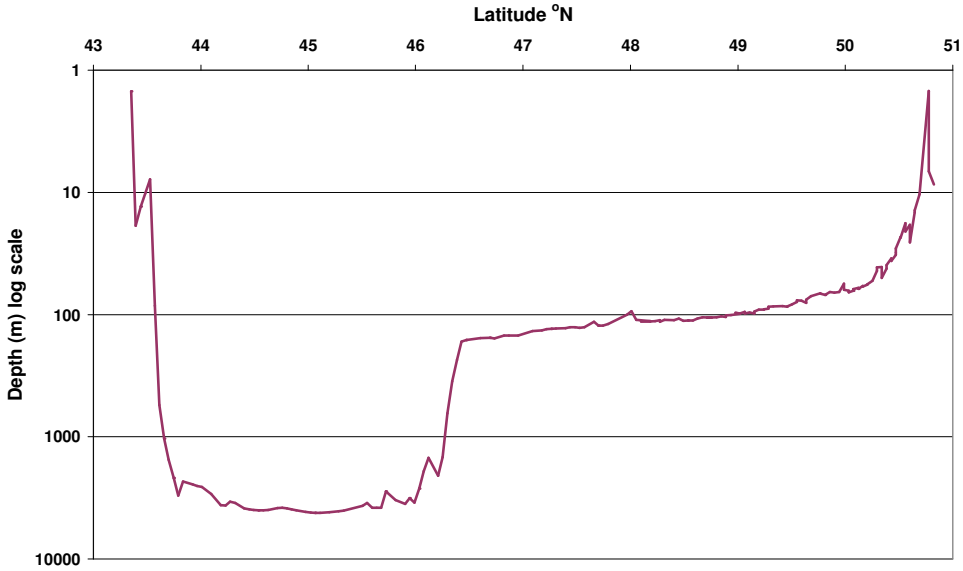


Figure 1.6: Plot of the bathymetry along the route of the Pride of Bilbao between Bilbao 43° N and Portsmouth 51° N. The deepest point along the route is 4210m. Data from GEBCO were provided by Peter Hunter (NOCS).

1.7.2 *Rivers*

The annual input of fresh water into the English Channel is about 25 km^3/y from a catchment area of 137,000 km^2 (Reid *et al.*, 1993), the main source being the river Seine (Hoch and Garreau, 1996). The Loire and Gironde Rivers with a combined mean annual outflow about 850 m^3 s^{-1} (Puillat *et al.*, 2004) dominate fresh water input to the Bay of Biscay. Each of them has peak runoff in winter or spring of about 3000 m^3 s^{-1} reducing in summer to about 200 m^3 s^{-1} (Lazure and Jegou, 1998; Puillat *et al.*, 2004).

1.7.3 *Winds*

The English Channel and Bay of Biscay have a temperate climate, which is strongly influenced by the Atlantic Ocean and lies between an anticyclonic zone south of 40° N near the Azores and a low pressure area at about 60° N. The prevailing winds are from west to southwest, stronger in winter and weaker in summer (Lavin *et al.*, 2006). The prevailing westerly wind has a considerable influence on water advection, vertical mixing and surface heat flux in the English Channel (Pingree, 1980). On the French continental shelf, south-westerly winds in autumn and winter promote downwelling whereas north-westerly winds in spring and summer induce upwelling (Puillat *et al.*, 2004; Lavin *et al.*, 2006). By contrast, northeast winds over the Cantabrian Sea lead to upwelling in spring and summer which becomes diminished under the influence of south-westerly winds in winter and autumn (Koutsikopoulos and Le-Cann, 1996; Cabanas *et al.*, 2003).

1.7.4 *General circulation and tides*

The surface waters of the North Atlantic Current flow east between 44-54° N towards NW Europe (Pingree *et al.*, 1977a). The complex pattern of surface currents on the continental shelf is influenced by wind, buoyancy due to freshwater input and seasonal heating, tides, and earth's rotation (Coriolis force).

The waters of the English Channel are derived partly from the west and partly from the English and French rivers. The western supply comes from the relatively salty and warm water of the Bay of Biscay, which enters from the south-west (Reid *et al.*, 1993; Sharples and Holligan, 2006). As illustrated in Figure 1.7 there is a slow and continuous flow from west to east (Reid *et al.*, 1993) reinforced by the tides (see below) so that the English Channel represents a transit area for oceanic water entering the

southern North Sea (Simpson, 1998). Various gyres and counter-currents are formed near the coast where depths are variable (Figure 1.7).

Tides play an important role in the distribution of hydrographic properties in the English Channel. The tidal wave results in M_2 current amplitudes of 1.0-1.5 m s^{-1} (Huntley, 1980; Pingree, 1980) with higher tidal ranges on the French coast than on the English coast due to geostrophic effects (Pingree, 1980). Regional variations in tidal strength and water depth lead to marked gradients in the degree of seasonal stratification of the water column (Pingree and Griffiths, 1978; Pingree, 1980). In the central part of the English Channel and along the French coast, the large tidal range and shallow water depth (30-70 m) maintain a well-mixed water column throughout the year. By comparison, in much of the western English Channel as well as the Celtic Sea to the west, weaker tides and greater depth allow a strong seasonal thermocline to develop during the summer months. The surface temperature gradient in summer between the warm stratified water and cold well mixed water is generally known as the Ushant front along which baroclinic instabilities and geostrophic shear tend to generate a series of irregular cyclonic eddies with scales of order ~ 20-40 km (Pingree, 1978).

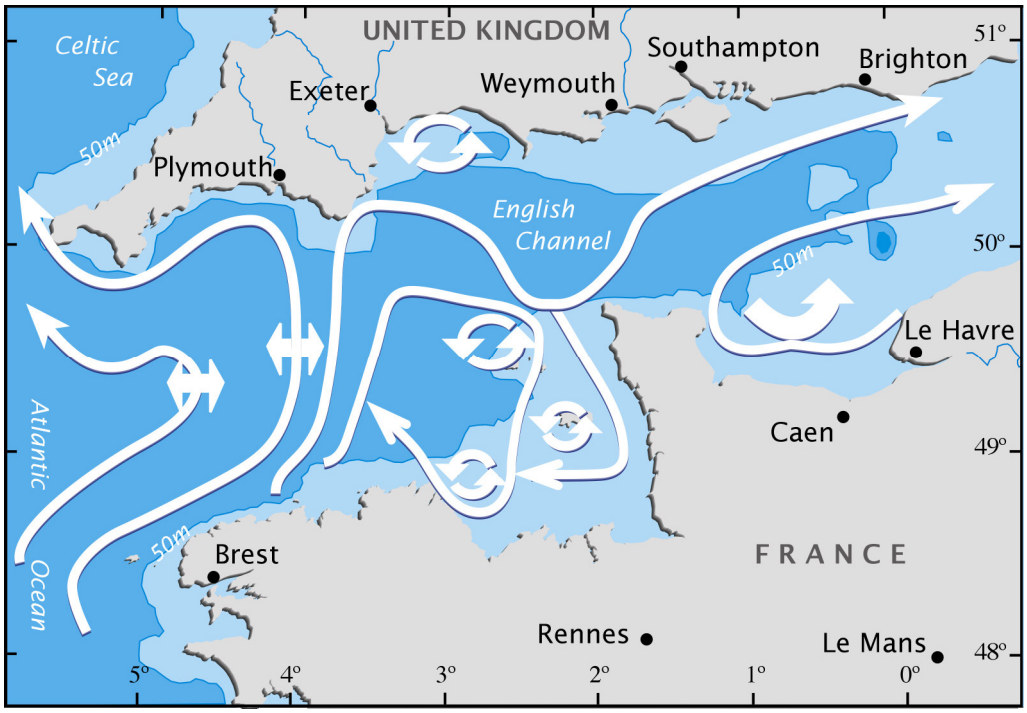


Figure 1.7: General circulation in the English Channel (after Reid *et al.*, 1993).

In the Bay of Biscay, the tidal amplitude increases from ~1.3 m on the open shelf to ~1.7 m close to the shore (Koutsikopoulos and Le-Cann, 1996; Lavin *et al.*,

2006). The tidal current strength is influenced by the bottom topography and the width of the continental shelf; the instantaneous tidal currents are weaker over the Cantabrian shelf (southern Bay of Biscay) (~ 15 cm s^{-1}) than over the Biscay shelf (northern Bay of Biscay) (~30 cm s^{-1}) (Pingree and Le-Cann, 1990). Along the continental slope at a depth of 500 m, sub-tidal residual currents are stronger (5-10 cm s^{-1}) and are mainly oriented poleward (Puillat *et al.*, 2004). However, these residual currents vary seasonally (Koutsikopoulos and Le-Cann, 1996).

Figure 1.8 shows the surface current systems in the Bay of Biscay. The oceanic waters towards the centre of Bay of Biscay are characterised by weak currents (1-2 cm s^{-1}) (Pingree and Le-Cann, 1992a; Koutsikopoulos and Le-Cann, 1996). The main feature of the oceanic area is the presence of cyclonic and anticyclonic eddies, which are shed by the slope current (Frouin *et al.*, 1990; Haynes and Barton, 1990). A warm, saline intrusion is often observed off the western Iberian coast during winter, flowing poleward (Pingree and Le-Cann, 1992b) and this tends to reach the Cantabrian slope around the Christmas period (Koutsikopoulos and Le-Cann, 1996). The residual currents over the shelf are influenced by the wind, tide, water density (Pingree, 1980) and off the Loire and Gironde estuaries, the density currents that are generated are affected by the wind.

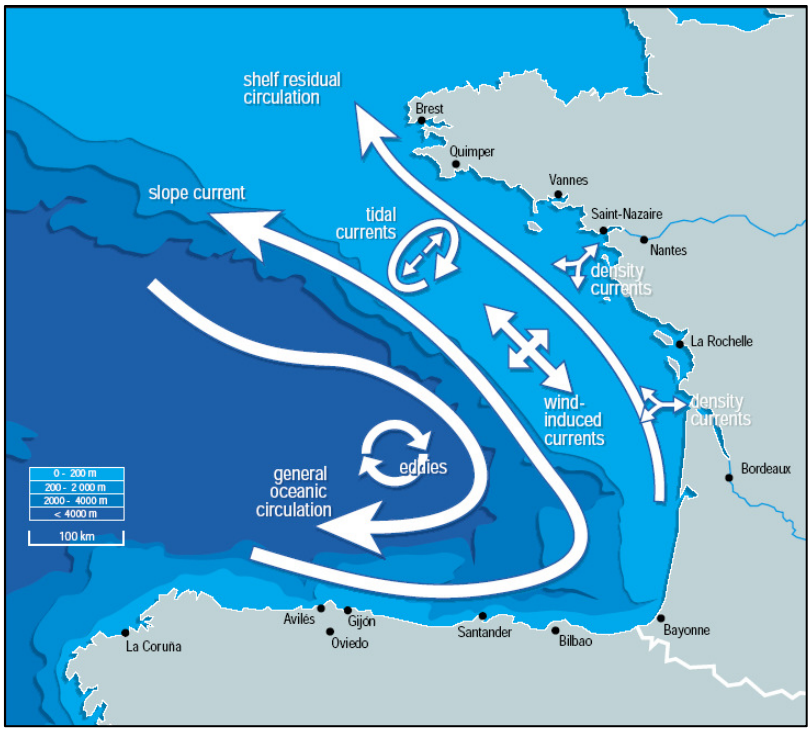


Figure 1.8: General circulation in the Bay of Biscay (after Koutsikopoulos and LeCann, 1996).

1.7.5 *Temperature and salinity*

The causes of interannual variability in temperature and salinity in the western English Channel and Bay of Biscay have been related to climatic factors including the strength of the North Atlantic Oscillation (NAO) (e.g. Southward *et al*., 2005).

The long temperature and salinity time series in the English Channel and Bay of Biscay (Table 1.1) have been well studied (Southward, 1960; Southward and Butler, 1972; Pingree, 1980; Becker *et al.*, 1997; Koutsikopoulos *et al.*, 1998; Lazure and Jegou, 1998; Southward *et al.*, 2005). Early analysis of water temperature data from E1 (50.02^{o} N, 4.22^{o} W) in the western English Channel showed a trend in temperature for the period from 1900 to 1970 when temperature increased (1900 and 1961), followed by a period of cooling (Southward and Butler, 1972). A previous study by Southward, (1960) found a rise of 0.5^{o} C between 1921 and 1959 at E1. The highest surface temperature measured between 1923 and 1987 at E1 occurred during the summers of 1983 and 1984 when the maximum temperatures were 19.2 and 18.8^{o} C respectively (Jordan and Joint, 1998).

Table 1-1: Summary of physical and chemical variables for the English Channel and Bay of Biscay.

Physical and chemical variables	S. Biscay	C.Biscay	N. Biscay	W. Channel	C. Channel
Temperature winter/summer	12.8/20.0 [1 and 2]	11.0/22.0 [5]	11.0/17.5[1]	9.0/15.0-19.0 [8]	8.0/14.5 [10]
Salinity	35.7 [3]	35.65[4]	spring <35.0/ summer 35.4 [6]	35.4 [9]	35.1 [9]
Nitrate winter/summer	4.7/<0.1[4 and 2]	4.0/<0.1[4]	7.0/<0.1 [7]	5.0-9.0/<0.1 [8]	7.0/<0.1 [9]
Phosphate winter/summer	0.3/0.05 [4 and 2]	0.3/0.05[4]	0.37/0.05 [7]	0.3-0.7/0.04 [8]	0.5/0.05 [9]
Silicate winter/summer	3.0/<1.0 [4]	2.0/<1.0 [4]	4.0/<1.0 [7]	3.5/0.1 [9]	6.0/0.2 [9]

1 and 2 Koutsikopoulos *et al*., (1998) and Llope *et al*., (2007); 3 Fernandez and Bode, (1991); 4 Treguer *et al*., (1979); 5 Pingree and Le-Cann, (1990); 6 Puillat *et al*., (2004); 7 Loyer *et al*., (2006); 8 Jordan and Joint, (1998); 9 Tappin *et al*., (1993); 10 Pingree *et al*., (1986).

Sea surface temperature (SST) time series measurements from 1854 to 1985 on the northwest European shelf were analyzed by Becker *et al*., (1997). They showed that winter temperatures in the Bay of Biscay have been rising since 1950 and the variability in summer temperature seems to be lower during the last 30 years of the measurements. The maximum Bay of Biscay SST was in 1950 and the coldest years were 1860 and 1923 (Becker *et al.*, 1997). A time series spatial grid of sea surface temperature data provided by the archives of Meteo-France and covering the period 1972-1993 at different locations in the Bay of Biscay confirmed the existence of a long-term increasing trend in the SST, but this trend was not homogeneous over the entire region (Koutsikopoulos *et al.*, 1998). The south-eastern part of the Bay of Biscay shows a

stronger warming trend and this decreases in the northern Bay of Biscay (Koutsikopoulos *et al.*, 1998). Maximum temperatures were reached in August and the mean SST was roughly 2.0^{o} C higher in the southern Bay of Biscay (~44.0^{o} N) than the northern Bay of Biscay (~47.0^{o} N) (Koutsikopoulos and Le-Cann, 1996; Koutsikopoulos *et al.*, 1998). The Bay of Biscay region is warmer than the western English Channel and the warm period in the 1940 and 1950s was more pronounced in the Bay (see Figure 9 in Southward *et al*., 2005).

Annual and seasonal variations in salinity in the western English Channel (E1) have been described and discussed by Pingree, (1980). The freshwater flux from river run-off, precipitation and water movement influence the seasonal change in salinity. Low salinity lenses (< 35.0), which appear at the southern entrance to the western English Channel (near Ushant region) at the end of winter in some years (Dietrich, 1962; Armstrong *et al.*, 1974; Morin *et al.*, 1991) can be linked to high freshwater input from French rivers (Loire and Gironde) (Poole and Atkins, 1929; Lazure and Jegou, 1998; Puillat *et al.*, 2004).

1.7.6 *Seasonal changes in stratification and fronts*

As noted previously, the water column in winter is well mixed in both the English Channel and the Bay of Biscay (Pingree *et al.*, 1976; Koutsikopoulos and Le-Cann, 1996). This mixing is influenced by tides from below and by wind and convection from heat loss at the surface (Pingree *et al.*, 1976). The outflow of fresh water from the French rivers in late winter is responsible for the presence of strong horizontal gradients in salinity over the continental shelf (Castaing *et al.*, 1999) and a thermohaline front appears along the mid-shelf from the Ushant region down to ~44.0^{o} N (Puillat *et al.*, 2004). The surface waters of the southern Bay of Biscay are eventually influenced by intrusion of warm and saltier Atlantic waters advected from west of the Iberian Peninsula (Fernandez *et al.*, 1993; Lavin *et al.*, 2006).

In spring, a seasonal thermocline is established throughout the Bay of Biscay, Celtic Sea and the western English Channel (Pingree, 1980) and persists until autumn. By May, much of the western English Channel has thermocline at approximately 20 m (Reid *et al.*, 1993). In the summer on the continental shelf, tidal mixing fronts (see Figure 1.5) separate the seasonally stratified waters from the continuously mixed

waters in the central English Channel (Sharples and Holligan, 2006). Summer satellite images of sea surface temperature show the separation of seasonally stratified (warm) and permanently mixed (cool) regions in the English Channel (Sharples and Holligan, 2006). The mixed waters in the central English Channel are typically ~2.0^{o} C colder than the stratified waters in the western English Channel which show a surface to bottom temperature differences of 3.0-5.0^{o} C in the summer (Holligan *et al.*, 1984a).

Thermal stratification in the Bay of Biscay occurs from May until September with a warm surface layer of 30-50 m (Koutsikopoulos and Le-Cann, 1996; Koutsikopoulos *et al.*, 1998). Below the seasonal thermocline, a cold pool (Bourrelet froid) of comparatively homogenous water (11.0-12.0º C) from ~40-50 m to the bottom, occurs on the north Biscay shelf and extends down to a latitude of ~45.0^{o} N (Koutsikopoulos and Le-Cann, 1996).

1.7.7 *Surface nutrient availability and irradiance*

The major factors determining the distribution of nutrients in the English Channel and the Bay of Biscay are inputs from rivers and exchange with the open ocean, biological regenerative processes and exchange due to water advection and mixing (there will also be a minor input from the atmosphere).

River and ocean inputs: the Loire and Gironde rivers account for 80 % of fresh water inputs of nitrogen and phosphorus along the French Atlantic coast (Loyer *et al.*, 2006). The phosphorus input from the Gironde is larger than from the Loire due to the relatively high quantity of suspended particulate matter (Gil *et al.*, 2002). Reid *et al.*, (1993) noted that the river Seine contributes ~85 % of the fresh water inputs of nutrients to the English Channel. The importance of the open ocean as a source (or sink) for nutrients on the continental shelf depends on surface winter gradients across the shelf break (Hydes *et al.*, 2004). In general, it appears that, at the latitude of the southern Celtic Sea and Bay of Biscay, oceanic waters are a relatively weak source of nutrients to the shelf except locally at the shelf edge where upwelling (e.g. along the Cantabrian coast of northern Spain) or mixing due to internal tides occur (Sharples *et al.*, 2007). Differences in nitrate-to-phosphate ratios mean that the ocean may act as a source for one but not the other (Hydes *et al.*, 2004).

Biological control: Nutrient concentrations decrease in the spring and early summer as assimilation into the planktonic food chain exceeds regeneration in the water column and from bottom sediments, and then rise again in autumn and winter as regeneration from detritus and dissolved organic matter exceeds assimilation (Reid *et al.*, 1993). During the summer months, relatively high nutrient concentrations below the seasonal thermocline lead to a slow upward flux associated with vertical mixing processes, which is largely utilised within the subsurface chlorophyll maximum (Pingree and Pennycuick, 1975; Sharples *et al.*, 2001).

Advection and mixing: Horizontal advection and exchange will act as a source of nutrients along gradients associated, for example, with freshwater plumes and frontal boundaries. Tides are the main cause of vertical mixing on the shelf and affect nutrient exchange between the bottom sediments and overlying water (Trimmer *et al.*, 1999). In the ocean upward vertical motion associated with mesoscale eddies is a source of nutrients to the surface water (Pingree and Le-Cann, 1992a, 1992b).

A summary of typical winter and summer inorganic nutrient (nitrate, phosphate and silicate) concentrations in the English Channel and Bay of Biscay is presented in Table 1.1. The spatial variability of inorganic nutrients in winter from a survey covering most of the English Channel waters was reported by Tappin *et al*., (1993). They showed a south to north gradient in inorganic nutrients in the western English Channel. The seasonal decline in nitrate concentration in the summer and increase in winter is clear at station E1 in the western English Channel (Armstrong *et al.*, 1974; Pingree *et al.*, 1977a; Jordan and Joint, 1998). Jordan and Joint, (1998) re-examined the historical nutrient data from station E1 from 1923 to 1987 and showed a high degree of variability in the nitrate: phosphate ratios. The latter analysis revealed that mid-summer values of phosphate increased for short periods of time while nitrate concentrations remained low, but there was no clear explanation (Jordan and Joint, 1998). Pingree *et al*., (1977a) considered that nitrate was limiting phytoplankton growth at E1. In regions where the waters are permanently well mixed by tidal action, such as the central English Channel and Ushant region, nutrients are not depleted (Wafar *et al.*, 1983).

The Bay of Biscay is characterised by a homogeneous water mass, relatively rich in nutrients during the winter (Treguer *et al.*, 1979). Freshwater inputs (Loire and

Gironde rivers) contribute to the nutrients in the northern Bay of Biscay (Loyer *et al.*, 2006). The winter nitrate supply persists throughout spring and nitrate concentrations are depleted in the summer (Loyer *et al.*, 2006). By using a monthly time series (1993-2003) of nutrient data from the southern Bay of Biscay, all nutrients showed important seasonal variations and decreasing trend overall (Llope *et al.*, 2007).

The regional consequences of seasonal changes in solar radiation and water column stratification on plankton distributions and nutrient utilisation have been described by Lavin *et al*., (2006) for the Bay of Biscay and Sharples and Holligan (2006) for the Celtic Sea and western English Channel. In the winter, phytoplankton biomass is low, as growth is light limited due to low solar radiation and deep mixing. In the northern Bay of Biscay, increased phytoplankton abundance early in the year (February-March) has been associated with shallow haloclines in plumes of the Gironde and Loire Rivers (Pingree *et al.*, 1986; Labry *et al.*, 2001; Hureta *et al.*, 2007) that carry relatively high nutrient and suspended sediment loads. The effects of these plumes occasionally extend around Ushant into the western English Channel.

In spring, with increased heating of the surface water resulting from increased daily insolation, thermal stratification occurs and combined with the increase in irradiance and the availability of nutrients in the water, leads to an increase in phytoplankton biomass in most regions in the western English Channel and Bay of Biscay. In regions where the waters are permanently mixed by tidal action, such as the central English Channel and Ushant region, a stratification-induced spring bloom does not occur and the phytoplankton population only reaches its maximum in the summer, when irradiance intensity is such that the euphotic depth becomes comparable to the water depth (Wafar *et al.*, 1983). The balance between the effects of vertical turbulence and the increasing of spring irradiance determines the start of spring bloom (Van-Haren *et al.*, 1998). However, when wind mixing is weak, the spring bloom can begin even before thermal stratification is established (Henson *et al.*, 2006).

Development of spring and autumn surface phytoplankton blooms, as well as summer blooms associated with tidal fronts are well documented by ocean colour satellite imagery (Joint and Groom, 2000). Enhanced chlorophyll levels associated with internal wave activity at the Celtic Sea shelf break in summer have recently been

investigated by Sharples *et al*., (2007). In all cases, increased phytoplankton biomass can be attributed to a relatively stable surface layer in which light and nutrients are sufficient for growth to exceed losses. The only feature of the annual distribution of phytoplankton that cannot be resolved by satellite is the subsurface chlorophyll maximum (SCM) associated with the seasonal thermocline (Sharples *et al*., 2001). It should be noted however, that the dynamics of the SCM is largely a function of mixing at the base of the thermocline and is relatively unaffected by the nutrient properties of the surface water.

1.7.8 *Plankton distributions*

There have been many publications on the plankton of the western English Channel and Celtic Sea (Holligan and Harbour, 1977; Holligan *et al.*, 1984a; Southward *et al.*, 2005; Sharples and Holligan, 2006), the Bay of Biscay (Varela, 1996; Albaina and Irigoien, 2004; Lavin *et al.*, 2006; Albaina and Irigoien, 2007), and the Cantabrian shelf (Fernandez and Bode, 1991; Bode and Fernandez, 1992; Fernandez *et al.*, 1993; Valdes and Moral, 1998). Reference to these papers and others will be made as appropriate later in the thesis. Information on the reported dominant species of phytoplankton in these regions is summarised in Table 1.2.

Several studies have reported changes in the species composition of phytoplankton across hydrographic boundaries including river plumes (Albaina and Irigoien, 2004), tidal fronts (Holligan, 1981, Holligan *et al*., 1984a and b), and shelf break (slope) fronts (Fernandez *et al*., 1993; Albaina and Irigoien, 2004; Sharples *et al*., 2007). An analysis of CPR data between the eastern English Channel and NW Spain (La Coruna) for the period 1979 to 1995 by Beaugrand *et al*., (2000) showed 5 distinct biogeographic zones, consistent with boundaries listed above, which corresponded to the coastal waters off England, tidally-mixed waters in the central English Channel, a narrow zone off NW France close to the position of the Ushant tidal front, summer stratified shelf waters extending to just beyond the shelf break and, finally, oceanic waters of the Bay of Biscay. Thus, any analysis of plankton distributions along a shelf-ocean transect is likely to show similar patterns. Beaugrand *et al*., (2000) also demonstrated that year-to-year variations in plankton abundance on the continental shelf were greater than in the oceanic waters of the Bay of Biscay, and were related to some

degree to the North Atlantic Oscillation (NAO). More specifically, Irigoien *et al*., (2000) reported that the percentage of diatoms during the spring phytoplankton bloom in the English Channel at station L4 is significantly correlated with the NAO. Both studies provide evidence for external climatic forcing of marine plankton abundance in these waters.

Table 1-2: Dominant phytoplankton species in the English Channel, Celtic Sea and the Bay of Biscay.

Dominant species		Location	Time of survey	References
Diatoms:	*Rhizosolenia alata, Rhizosolenia delicatula, Rhizosolenia stolerfothii,*	Western English Channel	May-June-77	Holligan and Harbour, (1977)
	Thalassiosira sp., *Cerataulina pelagica*	Celtic Sea 48-50° N	Apr-Aug-83	Joint *et al*., (1986)
	Nitzchia sp., *Thalassionema* sp., *Chaetoceros* sp.	Celtic Sea 48.5°-49.5° N	Apr-94	Rees *et al*., (1999)
	Chaetoceros danicus; Coscinodiscus sp.*; Nitzschia* sp.*; Skeletonema* sp.	North-western Bay of Biscay 46°- 47° N	Feb-Mar-00	Gohin *et al*., (2003)
Coccolithophore:	*Emiliania huxleyi*	Celtic Sea and Armorican Shelf	May-82	Pingree *et al*., (1982); Holligan *et al*., (1983)
Dinoflagellate:	*Karenia mikimotoi* (*Gyrodinium aureolum*); *Procentrum micans; Scrippsiella* sp.	Approaches to the English Channel	Jul-75	Pingree *et al*., (1975); Gohin *et al*., (2003)
	Karenia mikimotoi (Gyrodinium aureolum)	Western English Channel	Jul-81	Holligan *et al*., (1983) and (1984a and b); Jordan and Joint, (1984)

1.8 Aims of thesis

Use of the National Oceanography Centre (NOC) FerryBox system on the ferry between Portsmouth and Bilbao has enabled the acquisition of data on the distribution and succession of phytoplankton over two annual cycles along a transect between oceanic and shelf waters in the North East Atlantic that could not have been obtained by remote sensing or with the Continuous Plankton Recorder. These observations, including differences between the two years (2003 and 2004), will be described and interpreted with respect to the climatological, hydrographic and biological variables that influence variability in phytoplankton species abundance. Data coverage in space and

time enabled the validity of previous ideas about phytoplankton growth and succession under a range of environmental conditions to be evaluated.

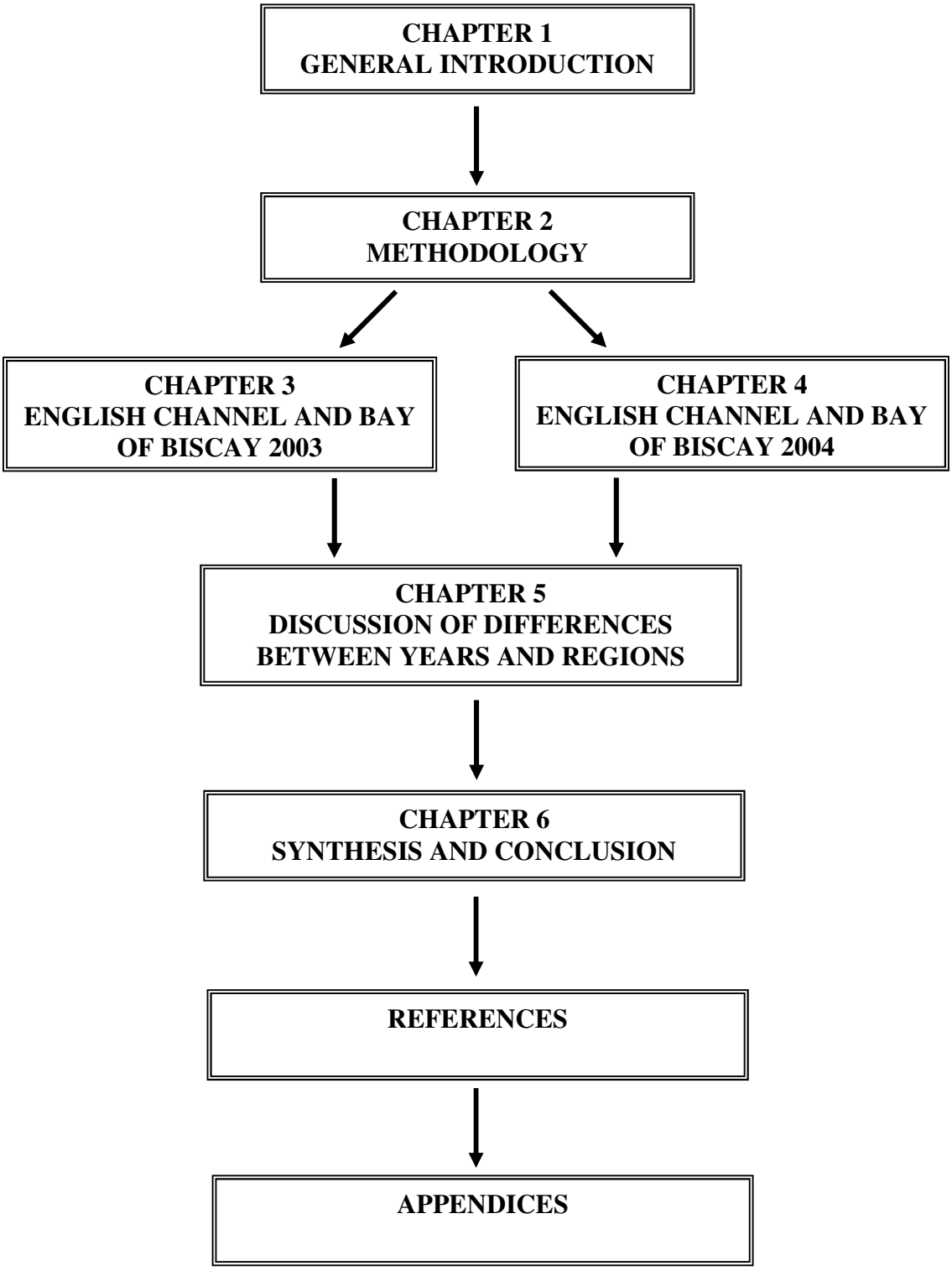
In particular, information provided by the FerryBox system will be used to:-

1) describe and delineate phytoplankton communities along the route with respect to known hydrographic provinces and to the seasonal changes in temperature and nutrient levels.
2) relate variations in phytoplankton abundance to the availability of light and nutrients and to zooplankton distributions.
3) interpret annual differences in phytoplankton community structure in relation to climatological and hydrographic conditions.

The main research questions of this thesis are:-

- Does surface irradiance determine the timing and intensity of the spring phytoplankton bloom?
- Is the summer distribution of phytoplankton determined by nutrient limitation or by grazing?
- Are internal (e.g. hydrographic) or external (e.g. climatic) factors the main cause of annual variability in phytoplankton abundance?

1.9 Thesis structure



CHAPTER 2

2.METHODOLOGY

2.1 The Pride of Bilbao and area of study

The FerryBox instruments were installed in April 2002 on the P&O ferry ship 'MV Pride of Bilbao' (POB) (Figure 2.1). The weight and length of the POB is 37583 tons and 177 m respectively, and its normal cruising speed is between 20 and 22 knots.

Figure 2.1: The P&O ferry "MV Pride of Bilbao".

The POB operates between Portsmouth, UK (50.8^{o} N, 1.1^{o} W) and Bilbao, Spain (43.4^{o} N, 3.0^{o} W), and generally does the round trip once per week from early February to mid-March and twice weekly from mid-March to early January. The annual refit is carried out during January. The distance between Portsmouth and Bilbao is approximately 1000 km and the journey time is about 35 hours per crossing and 72 hours per round trip. The crossings made by the POB in 2003 and 2004 are shown in Figure 2.2.

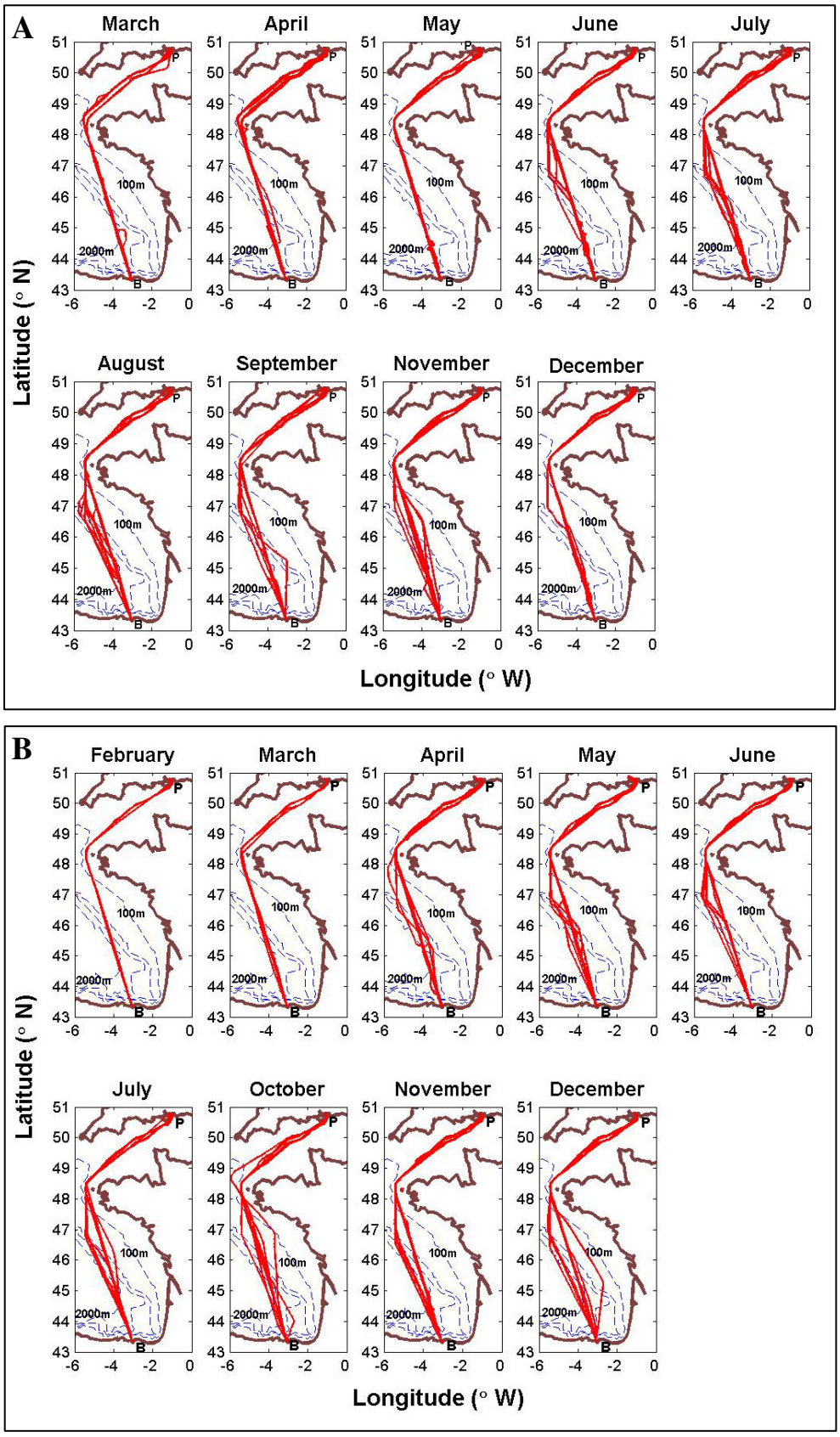


Figure 2.2: The crossings of Pride of Bilbao on which oceanographic data were collected between Portsmouth (P) and Bilbao (B) in A. 2003 and B. 2004. The Ferry-Box was not carried in February and October of 2003 and in August and September of 2004.

Figure 2.3 shows the standard route of Pride of Bilbao between Portsmouth and Bilbao. As listed in Table 2.1, the transect includes (1) eutrophic UK coastal waters (50.3-50.8° N), (2) the central English Channel (49.7-50.3° N) where water remains tidally well mixed year round, (3) the western English Channel (49.0-49.7° N) where waters are thermally stratified in summer, (4) Ushant region (47.8-49.0° N) close to French coast where strong tides also maintain well mixed water throughout the year despite a water depth of up to 130 m, (5) the wide shelf of the northern Bay of Biscay (46.4-47.8° N) extending to the 200 m isobath, (6) the central Bay of Biscay (45.0-46.4° N) with a maximum water depth > 4000 m, (7) and the southern Bay of Biscay (43.6-45.0° N which includes the narrow continental shelf off northern Spain, and (8) eutrophic Spanish coastal waters. The range of water depth along the route is shown in Figure 2.4.

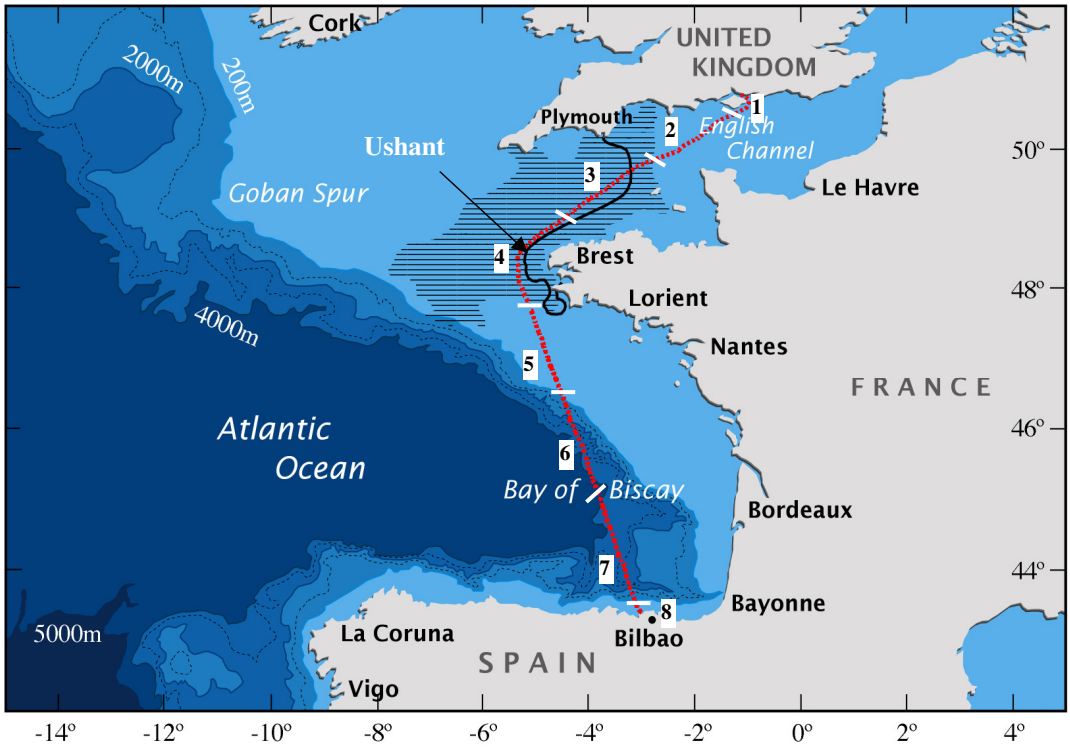


Figure 2.3: The standard route of Pride of Bilbao (red dashed line) for 2003 and 2004 from Portsmouth to Bilbao is marked to indicate the regional segments listed in Table 2.1. The hatched area represents the transitional zone between well-mixed waters in the eastern English Channel and along the coast of NW France and seasonally well-stratified waters in the western English Channel (Pingree and Griffiths, 1978). The black line indicates the predicted position in summer of the tidal front between mixed and stratified waters.

Table 2-1: Geographic regions of the Portsmouth to Bilbao route.

Region no.	Latitude (°N) range	Region description
1	50.3 - 50.8	Coastal English Channel
2	49.7 - 50.3	Central English Channel
3	49.0 - 49.7	Western English Channel
4	47.8 - 49.0	Ushant Region
5	46.4 - 47.8	Northern Bay of Biscay
6	45.0 - 46.4	Central Bay of Biscay
7	43.6 - 45.0	Southern Bay of Biscay
8	43.3 - 43.6	Coast of Spain

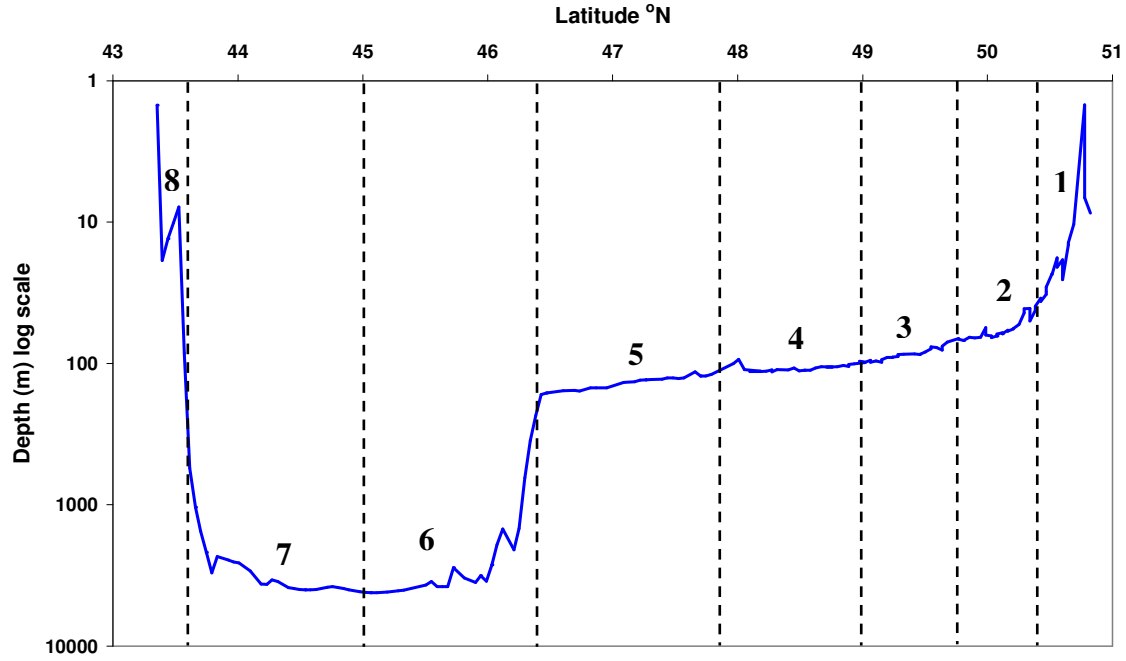


Figure 2.4: Plot of the bathymetry along the route of the Pride of Bilbao between Portsmouth and Bilbao. The deepest point along the route is 4210 m. The route is subdivided into the seven regions listed in Table 2.1 Data from GEBCO were provided by Peter Hunter NOCS.

2.2 FerryBox system

The FerryBox system is intended to be fitted permanently on the ship and provides measurements of conductivity (salinity), temperature, and chlorophyll (fluorescence) as well as time and the ship's position. The system has four key components: (1) a flow through system where the sensors are in contact with seawater, (2) a data logging system to collect the data from the sensors, (3) a data transmission system to send data from ship to shore (NOCS), and (4) a data logging and visualisation

system on shore. The relationship between the first three components on the POB is shown in Figure 2.5.

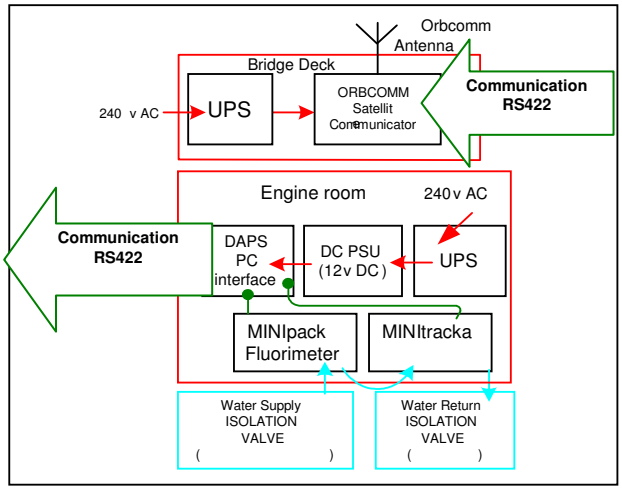


Figure 2.5: Schematic diagram of the components of the NOCS FerryBox system on the MV Pride of Bilbao.

2.2.1 *Sensors*

The water source is that used by the ship for the cooling of its refrigerator spaces and for air conditioning with an intake depth of 5m. The water take-off point is located prior to the refrigerator heat exchangers and returned to the main supply after these exchangers. The pressure drop between these two points induces flow past the FerryBox sensors. The internal pressure in the system is 2 Bar. By maintaining the system at this pressure bubbling does not occur and the data logged is therefore free from bubble noise. It also means that the system is mechanically simple. A tap is fitted at the point where the line to the FerryBox sensors joins the ship's system and is used for taking waters samples. A new flow-through manifold was specifically designed for this project in order to avoid areas of 'deadspace' where sediment may collect and cause erroneous readings in the optical channels. This was achieved by designing the input and output ports so that flow passes across the sensors and internal volumes are kept to a minimum. Attention was also given to making removal and refitting of the MiniPack and Minitracka flow cells as simple as possible in order that the sensor heads could be cleaned regularly while ensuring that the system would not suffer "wear and tear". Figure 2.6 shows the system installed in the engine room. The MiniPack CTD-F provides the information on conductivity, temperature, pressure and chlorophyll fluorescence. Its performance (see Table 2.2) and compact structure enabled easy

mounting of the unit to the flow though system. A MiniTracka II fluorometer was also fitted to the FerryBox system but data from this instrument have not been used for this study.

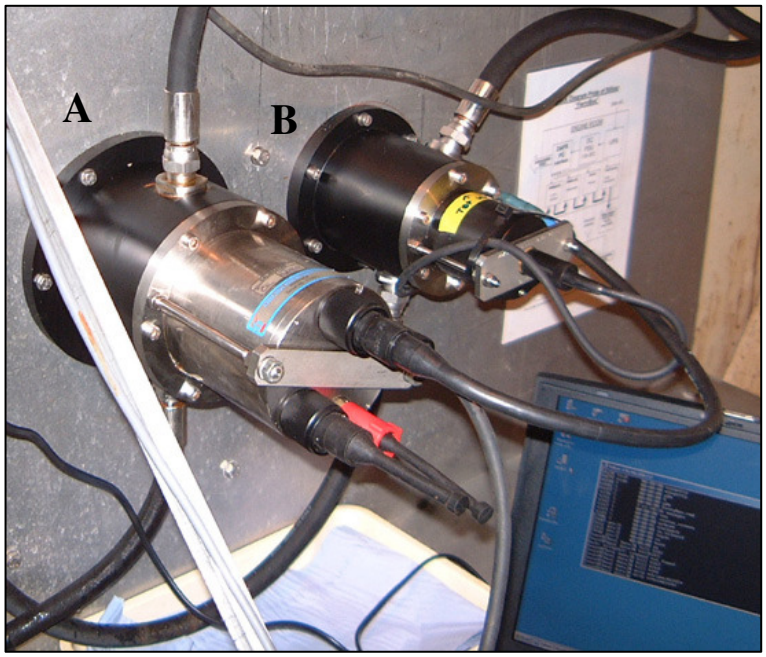


Figure 2.6: The MiniPack (A) and Minitracka (B) installed into the FerryBox flow housing on the MV Pride of Bilbao.

Table 2-2: Sensor performance details.

Variables	**Methods**	**Sensor**	**Units**	**Detection range**	**Resolution**	**Recorded range (min - max)**
Temperature	Pt resistance	"MiniPack"	° C	-2 to + 35	0.0005	8-25
Conductivity	Induction Cell	"MiniPack"	mhos/cm	0 to 70	0.001	25-45
Chlorophyll	fluorescence excitation	"MiniPack"	mg m^{-3}	0.03-100	0.01	0 - 100
	Maintenance Procedure	**Quality assessment**				
Temperature	Calibration check annual			Compared with SBE 48 & satellite data		
Conductivity	Weekly cleaning, monthly water samples			Salinity calibrated against monthly samples		
Chlorophyll	Weekly cleaning, monthly water samples			Acetone extracted chlorophyll *a* & HPLC.		

2.2.2 *Data acquisition*

All data from individual sensors were directed into the NOCS unit "PENGUIN" (Practical Environmental Network for Grouping Underwater Instrumentation Nodes).

This is a modular and scalable system built around a single board computer (SBC). It interfaced the sensors in the engine room to an Orbcomm satellite communicator (Panasonic Subscriber Communicator KX-G7100) which is located in the radio room behind the ship's bridge. The SBC ran DAPS (Data Acquisition and Processing Software) previously developed for shipboard acquisition at National Oceanography Centre, Southampton (NOCS). The attached sensors were configured to generate ASCII format data messages at a chosen sampling interval (typically 1 Hz), and these were gathered, interpreted, time-stamped with the DAPS system time and then stored to individual data files on a local 20GB hard disk. In addition to the data files for each instrument, log files containing other useful information related to data transfers, such as data timeouts, were also stored locally on disk. Associated with each instrument being logged by the system was an ASCII Instrument Control Variables (ICP) file, which was interpreted by the data acquisition software to determine the various logged variables. For example, the 'Orbcomm-interval' parameter in these files determines the number of seconds between data transfers to the Orbcomm unit on the bridge. These transfers were not direct to the Orbcomm unit, but were sent using an Inter Process Communication (IPC) protocol between the various acquisition processes.

The Orbcomm data was received at NOCS as an e-mail message approximately every 10 minutes. This message was automatically processed and the information was written to a MYSQL data base. These uncalibrated data were then made available via a public access web page http://www.soc.soton.ac.uk/ops/ferrybox_index.php so that operation of the system could be checked from anywhere in the world with web access. The web page displays the latest reported position of the ship and the positions of data points successfully received from the current ferry crossing. The data were visualised as three maps generated in MATLAB which display the evolution of temperature, salinity and fluorescence fields through time (y-axis) and distance between Portsmouth and Bilbao (x-axis) and were updated every half-hour.

Servicing of the system on the POB was carried out once a week and took about one hour between entering and leaving the engine room. The MiniPack CTD-F and MiniTracka II were removed in turn from their flow-through housing and all the surfaces were wiped clean with "Kleenex" tissues. The fluorometer windows were carefully cleaned and washed with "Decon 90" solution. Using this schedule on what

was essentially a "blue water" route, no significant shifts in sensor calibration due to cleaning events could be detected. After the sensors had been cleaned, the full 1 Hz data set stored on the "Penguin" hard drive was downloaded.

2.3 Water sampling

Water samples were collected for calibration of the conductivity sensor (salinity) and fluorometer (chlorophyll *a*), for nutrient and phytoplankton pigment measurements, and for phytoplankton cell counts (Table 2.3).

Table 2-3: Numbers of samples collected each month for measurements of salinity, chlorophyll *a*, nutrients, phytoplankton pigments, and phytoplankton cell counts between Portsmouth and Bilbao for A. 2003 and B. 2004. Each set of samples represents one return journey.

A

2003 Months	Salinity	Chlorophyll *a*	Nutrients	HPLC Pigments	Phytoplankton Taxonomy
March I	33	65	128	16	16
March II	35	68	134	18	18
April	32	59	114	20	20
May	34	60	117	18	18
June	35	66	131	17	17
July	33	60	115	18	18
August	35	68	131	20	20
September	35	67	131	16	16
November	32	60	115	18	18
December	40	69	136	16	16
Total	344	642	1252	177	177

B

2004 Months	Salinity	Chlorophyll *a*	Nutrients	HPLC Pigments	Phytoplankton Taxonomy
February	28	51	120	15	15
March	31	50	99	12	12
April	34	64	127	18	18
May I	--	55	55	26	26
May II	33	64	128	14	14
June	32	62	125	16	16
July	31	62	124	21	21
October	28	51	101	14	14
November	31	62	123	14	14
December	33	65	130	16	16
Total	281	586	1132	166	166

2.4 Statistical analyses

Non-multivariate standard statistics have been carried out by the using of Statistical analysis system (SAS) software. The computer software package PRIMER (Plymouth Routines In Multivariate Ecological Research) version 6, developed at the Plymouth Marine Laboratory was implemented as recommended by Clarke and Warwick, (2001) , and Clarke and Gorley,(2006) , to perform multivariate analysis statistical analyses for this work.

2.4.1 *Standard statistical analysis*

Analysis of variance (ANOVA) was used to test for differences between the storage methods for the determination of chlorophyll *a* in Section 2.4.2. Tukey's comparison test was used to check for significant difference between the storage methods. The Spearman Rank Correlation Coefficient was used for the comparisons of total chlorophyll *a* and total accessory pigments in Section 2.4.3 as well as the comparisons of chlorophyll *a* measurements from the fluorometer (acetone extractions) and HPLC. The relationships between in vivo fluorescence and chlorophyll *a* were described by regression analysis and a chi-squared test (χ^2) was used to test for significant differences between the regression lines.

The data in Chapter 5 for hydrographic variables (temperature, salinity, nitrate, and silicate) and biological variables (chlorophyll *a* and herbivorous copepods) were shown not to be normally distributed following the Kolmogorov-Smirnov test. Therefore, a nonparametric test (F-approximation to Friedman's test) rather than two-way ANOVA was used to test for significant differences in hydrographic data (temperature, salinity, and nutrients) and in biological data (chlorophyll *a* and herbivorous copepods) for the four regions over the two years (2003 and 2004). Duncan's Multiple Range Test for the ranked data was used to compare differences between regions for both years. The level of significance was set as $p < 0.05$ for all statistical analyses.

2.4.2 *Multivariate methods*

The basis for the multivariate techniques used in this study was the calculation of a similarity matrix, which describes the relationships between variables and samples. The pattern of the relationships between variables can either be described by cluster

analysis (classification of the variables into hierarchical categories on the basis of similarity matrix) or by ordination (non-metric multidimensional scaling) which is the reduction of a matrix of similarities among variables to one or a few dimensions (James and McCulloch, 1990) . The cluster analysis was based on the correlation matrix (Clarke and Warwick, 2001). The Multivariate methods were used in this study to reduce the complexity of the high dimensional phytoplankton community and environmental variables data. The cluster routine allows a choice of single 'nearest neighbour' linkage, which defines how the resemblance between two groups of sample is calculated from the cross-group resemblances of pairs of samples (Clarke and Gorley, 2006). The similarity profile analysis SIMPROF was used to characterise statistically significant cluster groupings of the assemblages for the phytoplankton and environmental data. A one-way analysis of similarity using the ANOSIM routine (PRIMER v6; Clarke and Warwick, 2001) was used to test for differences between groups of (multivariate) samples in the phytoplankton and environmental data.

Phytoplankton species data

In community analysis, several data transformation, such as presence/absence (PA) matrix and square root (SQRT) transformation may be applied to weight the contributions of dominant and rare phytoplankton species in non-parametric multivariate representations. Depending on the nature of phytoplankton species and ecological hypotheses, the choice of transformation can have a significant influence on the final ordination or clustering display. The phytoplankton biomass data in this study were transformed using presence/absence (PA) transformation to down-weight the importance of the more abundance species. In this study, PA transformation has been accompanied by the removal of rare components, following the suggestion of Clarke and Warwick, (2001).

Within this study, the Bray-Curtis Similarity index was used for the phytoplankton species data to reflect the difference between samples in different or similar stations at different times. The Bray-Curtis Similarity index is similar to other indices and compares the species composition of different samples, so that the theoretical range of the percent similarity index is from 0 % for samples with no similarity between species to 100 % for identical associations (Clarke and Warwick,

2001). The value of 100 % similarity is unlikely to occur because species abundance fluctuates in the field and sampling errors in the laboratory reduce the index (Venrick, 1982) . Phytoplankton species contributing greater than 1 % of the total biomass were retained, whereas rare species (less than 1 %) were excluded.

Cluster analysis was used to indicate the similarities in the distribution and occurrence of phytoplankton species. Clustering of phytoplankton can be represented by a dendrogram, with the x axis representing different groups of phytoplankton species and y axis defining a percentage similarity level. The similarity percentage (SIMPER) was used to calculate the similarity and dissimilarity between all pairs of inter-group phytoplankton species (Clarke and Warwick, 2001).

Non-metric MDS (Kruskal's non metric procedure) produces a map or ordination plot to describe the samples or group of samples in two or three dimensions with consideration of all conditions imposed by the rank (dis)similarity matrix. An MDS plot is validated by its stress value, which is a measure of the difficulty of compressing the inter-sample relationship into 2-dimensional space (Clarke and Warwick, 2001). The MDS algorithm calculates the stress and reanalyses the data to reduce the degree of stress. Clarke and Warwick, (2001) recommended that the critical stress values for MDS are: less than 0.05 indicates excellent ordination, no prospect of misinterpretation; less than 0.1indicates good ordination, no real prospect of misinterpretation; less than 0.2 indicates useful two dimensional cross-check (e.g. clusters); greater than 0.2 - 0.3 indicates points close to being randomly placed in two dimensions.

Environmental variables

Physical data (irradiance, temperature, and salinity), and chemical data (nitrate, phosphate, and silicate) were used as variables in the multivariate analysis. There are many differences between hydrographic and biological variables. Abiotic data are usually on mixed measurement scale and the Bray-Curtis coefficient is not suitable. The variables were normalised and transformed as log (v+1) for Euclidean distance. Cluster and non-metric MDS analyses were preformed using log transformed data and normalised Euclidean distance. Environmental variables (as bubble plots) have been

superimposed on the MDS ordination, in order to demonstrate the distribution of each variable between the groups.

2.5 Pigment measurements

2.5.1 *Chlorophyll a sample collection and fluorescence measurements*

Duplicate water samples for chlorophyll *a* analysis were collected every hour and immediately filtered through 25 mm diameter glass fibre filters (Whatman GF/F). Filters were folded in half twice and placed immediately into 13-ml screwed capped centrifuged tubes containing 5 ml 90 % acetone and stored at -32^{o} C in the dark for up to 4 days.

On return to the laboratory, chlorophyll *a* was determined by the fluorescence method of Welschmeyer, (1994). This method uses special filters for the excitation and emission spectra (436 and 680 nm respectively) in order to minimise interference from chlorophyll *b* and phaeopigments (Jeffrey and Vesk, 1997). Arar, (1994) has shown that the Welschmeyer technique compares favourably with the conventional fluorescence acidification, and with the spectrophotometric methods. In situations where there are large amount of chlorophyll *b*, the acidification technique underestimates chlorophyll *a* concentrations (Trees *et al.*, 1985). Welschmeyer's (1994) selection of excitation and emission light-filters was specifically aimed at correcting the error in the acidification technique due to fluorometric interference of the chlorophyll *a* signal by divinyl chlorophyll *a*, chlorophyll *b*, chlorophyll *c* and phaeopigments (Tree *et al*., 1985; Welschmeyer, 1994). Although the Welschmeyer (1994) method is not affected by phaeopigments and chlorophyll *c*, it cannot distinguish between chlorophyll *a* and chlorophyllide *a* due to their identical spectral properties (Welschmeyer, 1994). In this study, the designation " chlorophyll *a*" is used and will include both chlorophyll *a* and chlorophyllide *a* (Welschmeyer, 1994).

Preparation of chlorophyll extracts was carried out under subdued light. The samples were carefully sonicated for 30 seconds using Vibra Cell sonicator to disrupt the phytoplankton cells. Then they were centrifuged at 3000 rpm for 10 minutes to remove debris using a MSE Mistral 2000 centrifuge. The fluorescence of each extracted sample was measured with a Turner Designs Model 10AU Series fluorometer fitted with a F4T41/2B2 lamp, a 436 nm excitation filter and a 680 nm emission filter. The Turner fluorometer was calibrated using dilutions of a standard chlorophyll *a* solution

(Sigma Chemical Co.) in 90 % acetone determined spectrophotometrically following Jeffrey and Humphrey, (1975). Absorption values at 630 nm (E_{630}), 647 nm (E_{647}) and 664 nm (E_{664}) were measured using 1 cm cell, corrected for turbidity by subtracting the 750 nm reading and the chlorophyll *a* concentration calculated as:

$$\textbf{Chl } a = 11.85E_{664} - 1.54E_{647} - 0.08E_{630} \quad (1)$$

The concentration of total chlorophyll *a* was calculated from the fluorometer readings without correction for phaeopigments, as recommended by Edler (1979) and later applied by Welschmeyer, (1994), using the following equation:

$$\textbf{Chl } a \ (\mu g\ l^{-1}) = (F * CF) * v/V \quad (2)$$

where F is the fluorometer reading, CF is the calibration factor (if applicable), v is the volume of extract (in 90 % acetone), and V is the volume of water sample filtered.

2.5.2 *Storage tests of chlorophyll a samples*

The chlorophyll samples had to be stored for a short time (up to 4 days) before analysis in the laboratory, and a number of combinations of sample storage and extraction methods were tested for recovery of chlorophyll *a* since enzyme reactions are known to degrade pigments (Moreth and Yentsch, 1970). During manned crossings in March, August, October, 2003 and February, 2004, five different methods of storage were used: 1-2) filters were stored in 90 % acetone at -32° C, and 0° C filters were stored dry at -32° C, 0° C, and room temperature (25° C). In a separate experiment in April 2005, water samples were collected from Southampton Dock for chlorophyll *a* analysis. Chlorophyll was determined for five replicate filters either instantly or after storage for one month under three conditions: 1-2) in 90 % acetone at -32° C, -80° C, 3) as dry filters at -80° C.

The results from February 2004 of the comparison of different storage methods for the determination of chlorophyll *a* are shown in Figure 2.7, and those from March, August and October, 2003 are given in Appendix 1. The chlorophyll *a* values were found to be significantly different (one-way ANOVA, $p < 0.05$) between the five storage methods. A Tukey's comparison test ($p < 0.05$) showed that the chlorophyll *a* values were significantly higher for filters stored in 90 % acetone at -32° C than for filters stored dry at 0° C, and room temperature (25° C). The differences between samples stored in acetone at -32° C and at 0° C were relatively small and between

samples stored in acetone at -32° C and as dry filters at -32° C were not significant. The maximum difference in the estimates of chlorophyll *a* obtained for filters stored in acetone at -32° C and dry at 0° C and 25° C was 54 % (Figure 2.7).

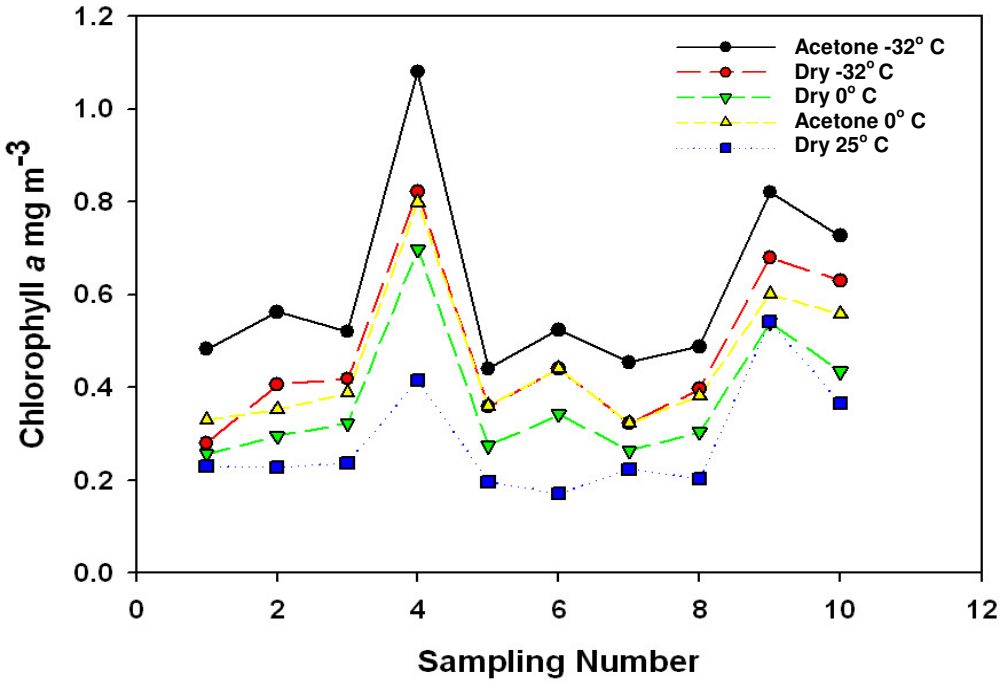


Figure 2.7: Comparison of chlorophyll *a* using different sample storage methods in February 2004.

The results of the April 2005 experiment with water samples from Southampton Dock are shown in Figure 2.8. A one-way ANOVA showed significant differences between the different storage methods ($p < 0.05$, n = 10), with higher chlorophyll *a* values for filters stored in 90 % acetone at -80° C than for filters stored in acetone at -32° C, and in dry at -80° C (Tukey's comparison test, $p < 0.05$). The difference in chlorophyll *a* values for filters stored in acetone at -32° C and dry at -80° C was insignificant ($p > 0.05$).

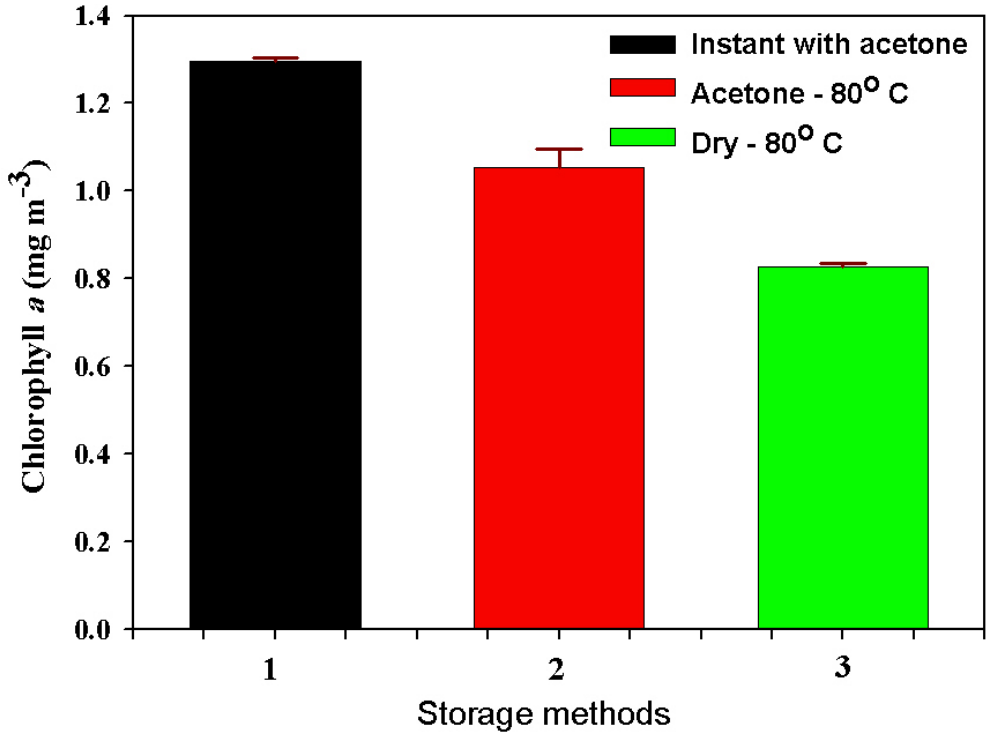


Figure 2.8: Comparison of total chlorophyll *a* values for samples collected from Southampton Dock and 1) measured instantly, 2) stored for one month in 90 % acetone at -80° C or 3) stored for one month as dry filters at -80° C (n = 5 for each treatment).

In this study, storage of the chlorophyll *a* filters was unavoidable. The best recovery of chlorophyll *a* was obtained for filters stored in 90 % acetone at -32° C in agreement with the work of Wasmund *et al*., (2006) and it is estimated that losses were < 10 % provided the storage period was no longer than 4 days (see Section 2.4.1).

2.5.3 *High performance liquid chromatograph (HPLC) pigments analysis*

Water samples (0.5-1.5 L) were collected every 2 hours and filtered through 25 mm diameter glass fibre filters (Whatman GF/F). The filters were then frozen immediately in a freezer at -32° C on board ship and transferred to a -80° C freezer on return to NOCS.

High performance liquid chromatography (HPLC) was used for the separation of the important phytoplankton pigments as described by Mantoura and Llewellyn, (1983) and modified by Barlow *et al*.,(1993). A Perkin Elmer C-18 HPLC column and Thermoquest HPLC system (gradient pump, vacuum degasser, autosampler, a dual solvent pump, UV detector, a fluorometer, and integration software) were used. The mobile phase consisted of a binary eluant system using solvent A: 80 % methanol and 20 % 1M ammonium acetate and solvent B: 60 % methanol and 40 % acetone. A linear

gradient was run from 100 % solvent A to 100 % solvent B over 10 minutes, followed by an isocratic stop at 100 % solvent B for 7.5 minutes. A second gradient of 2.5 minutes was used to return to the initial condition of 100 % solvent A.

The frozen filters were placed in 100 % acetone (3 ml), sonicated for 30 seconds and then centrifuged for 10 minutes at 3000 rpm to remove debris. The extracted samples were then filtered through 0.2 µm nylon filters. An aliquot of 500 µl of extract was mixed with 500 µl of 1M ammonium acetate and then 100 µl of the mixture was injected onto the HPLC column. Chlorophylls and carotenoids were detected by absorbance at 440 nm and phaeopigments were measured with a fluorescence detector using an excitation wavelength of 410 nm and an emission wavelength of 670 nm.

Peaks were identified by comparison with retention times for authentic pigment standards: chlorophyll *a*, chlorophyll *b*, and β-carotene from Sigma Chemical Company and chlorophyll c_2, chlorophyll c_3, peridinin, 19'-butanoyloxyfucoxanthin, fucoxanthin, 19-hexanoyloxyfucoxanthin, diadinoxanthin, diatoxanthin, violaxanthin, prasinoxanthin, alloxanthin, and zeaxanthin from DHI, Denmark (Table 2.4). The Chromquest software on a Dell 1100 computer was used for data collection and integration. The consistency of the retention values is within an error of ± 5 %, and the correlation coefficient (R^2) for chlorophyll *a* standards was 0.99 (Figure 2.9).

Table 2-4: Pigments lists of major pigments in algal division/classes, according to Jeffrey and Vesk, (1997).

Pigments	Abbreviations	Affiliations
Alloxanthin	Allo	Cryptophyta
β-Carotene	β-Car	All groups
19'-Butanoyloxyfucoxanthin	But-fuco	Dinophyta, Chrysophyta, Pelagophyta, Prymnesiophyta
Chlorophyll *a*	Chl *a*	All eukaryotic groups
Chlorophyll *b*	Chl *b*	Chlorophyta and Prasinophyta
Chlorophyll c_3	Chl c_3	Prymnesiophyta, Chrysophyta, Dinophyta, Bacillariophyta
Fucoxanthin	Fuco	Prymnesiophyta, Chrysophyta, Dinophyta, Bacillariophyta
19'Hexanoyloxyfucoxanthin	Hex-fuco	Prymnesiophyta, Dinophyta
Peridinin	Perid	Dinophyta
Zeaxanthin	Zea	Cyanophyta, Chlorophyta, Prasinophyta, Prochlorophyta

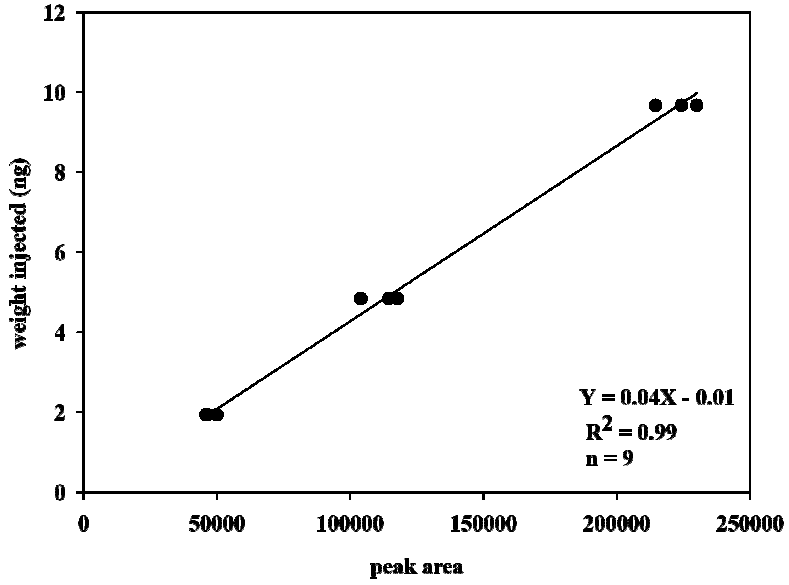


Figure 2.9: HPLC chlorophyll *a* calibration (January 2005).

Pigment concentrations (Pc) were calculated according to the following equation (Barlow *et al.*, 1993):

$$\mathbf{Pc\ (\mu g\ l^{-1} or\ mg\ m^{-3}) = (Pa\ v\ 1000\ /\ Pr\ Vi\ V\ 0.5)/1000} \qquad (3)$$

where *Pa* = Peak area, *v* = Volume of extracted acetone (ml), *Pr* = Pigment response factor, *Vi* = Volume injected in the column (100 µl), *V* = Volume of filtered sample (l) and 0.5 = the buffer dilution factor.

Internal consistency of the HPLC pigment data, and comparison of chlorophyll a determinations by HPLC and fluorescence

Within HPLC derived data sets for marine phytoplankton pigments, there is generally a consistent relationship between the quantities of chlorophyll *a* and total accessory pigments (Tac) from a wide range of environments (Trees *et al.*, 2000). The comparisons of chlorophyll *a* and total accessory pigments for the English Channel and Bay of Biscay show significant correlations for both 2003 (R= 0.97 and $p < 0.05$) and 2004 (R= 0.95 and $p < 0.05$) as shown in Figure 2.10. However, the slopes of the regression lines were different in the two years, perhaps due to differences in environmental conditions (e.g. light intensity and nutrients) or phytoplankton species composition (Trees *et al.*, 2000). On average chlorophyll *a* formed ~ 57 % of the total pigments which is consistent with values reported for a station in the English Channel by Aiken *et al*., (2004).

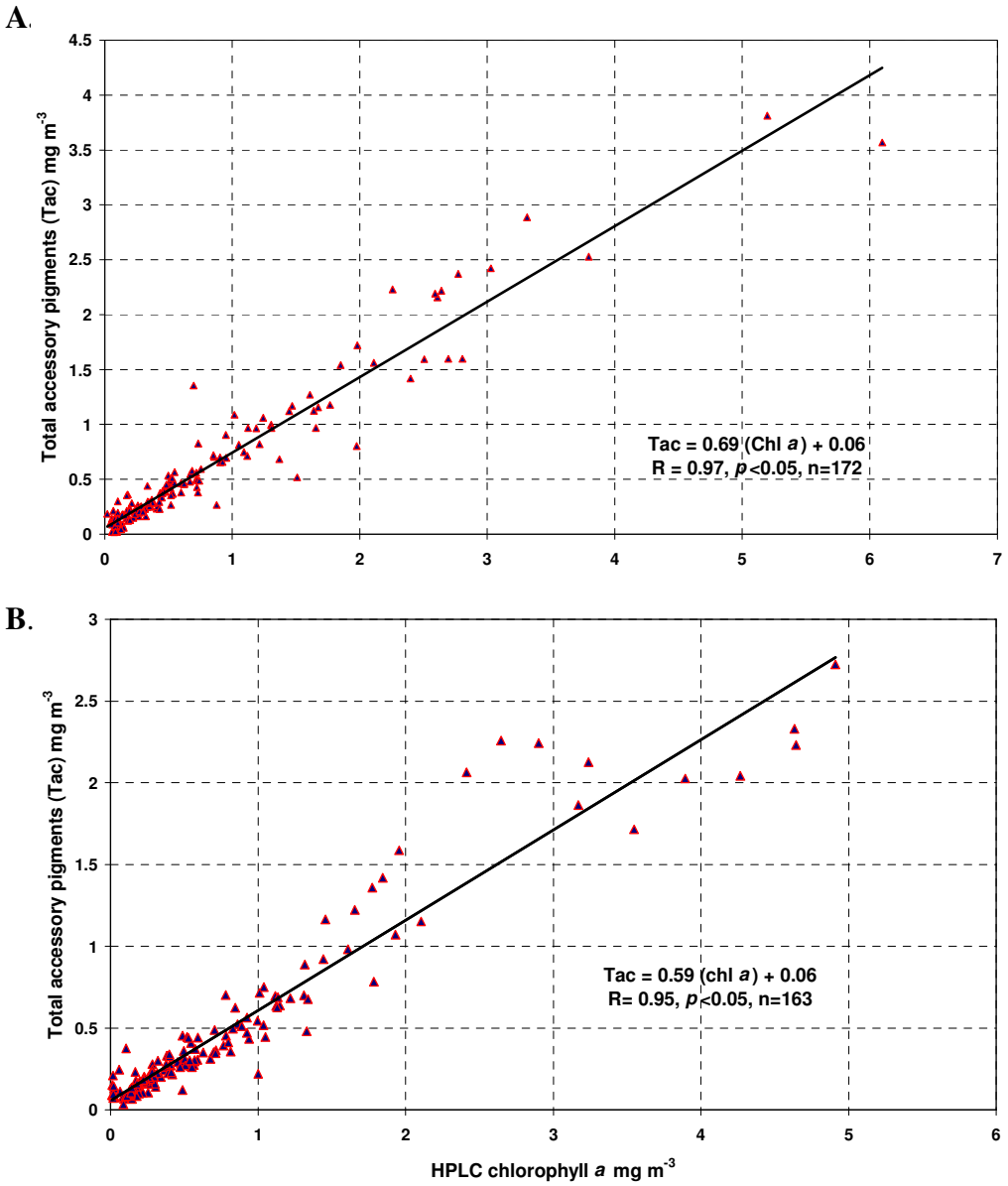


Figure 2.10: Relationships between HPLC chlorophyll *a* and total accessory pigments (Tac) measured by HPLC for A) 2003 and B) 2004.

The fluorometric technique can overestimate or underestimate chlorophyll *a* concentration compared to HPLC measurements of chlorophyll *a* largely due to interference by other chlorophylls or by chlorophyll degradation products (Cupp, 1943; Welschmeyer, 1994). Trees *et al*., (1985) reported that differences varied between – 68 % to +53 % when comparing the concentrations of chlorophyll *a* measured by fluorometer and by HPLC although typically they are at the upper end of this range (i.e. the fluorometric method overestimates chlorophyll *a*). Figure 2.11 shows the

comparisons of chlorophyll *a* measurements from the fluorometer (acetone extractions) and HPLC chlorophyll *a* for the English Channel and Bay of Biscay for 2003 and 2004.

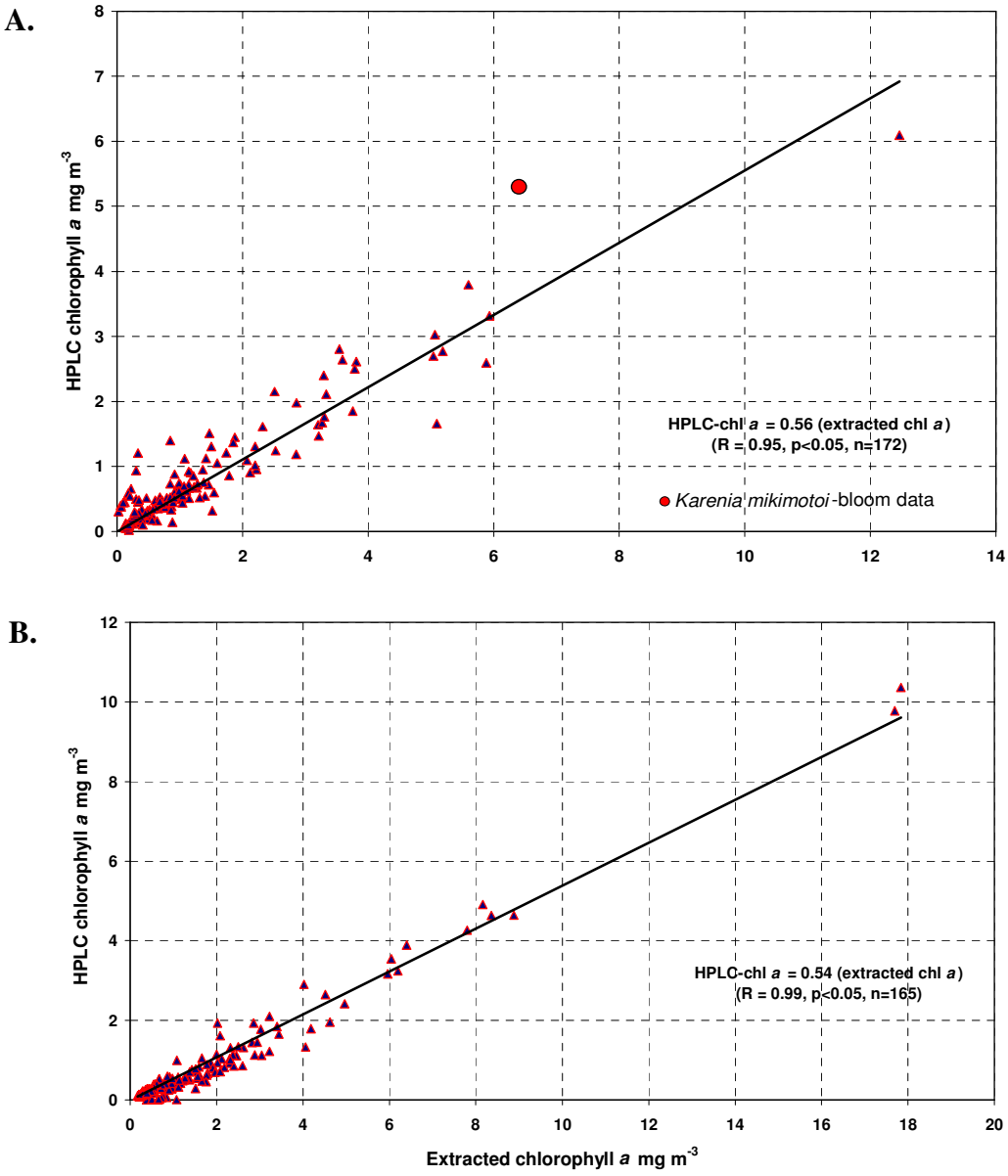


Figure 2.11: Comparison of chlorophyll *a* from HPLC and acetone extractions (mg m^{-3}) for A) 2003 and B) 2004. The red dot indicates *Karenia mikimotoi*-bloom data where the extracted and HPLC chlorophyll *a* are 64 and 53 mg m^{-3} respectively in 2003. The *Karenia mikimotoi*-bloom data are divided by 10 in order to be shown in the figure and they were not included in the trend line.

There were significant correlations between the two methods (R=0.95 and $p < 0.05$ for 2003, and R=0.99 and $p < 0.05$ for 2004) and the slopes of the lines were very similar when the 2003 samples from the bloom of the dinoflagellate, *Karenia mikimotoi*, were excluded from the analysis. Thus, chlorophyll *a* concentrations determined by HPLC

were ~55 % of those measured by fluorescence. However, a chi-squared test showed a significant difference (χ^2=36.7 $p < 0.05$) between the 2003 and 2004 correlations, reflecting the different R values, which may be related to one or more of the following factors: 1. differences between the two methods were not constant along the transect, 2. variations in the sensitivity of the HPLC system between 2003 and 2004, and 3. differences in fluorometer measurements between the two years due interference by degradation products.

2.5.4 *Calibration of the MiniPack fluorometer*

The relationships between fluorescence values and concentrations of extracted chlorophyll for the 10 crossings in 2003 for which both data sets were available are shown in Figure 2.12. Comparable data for 2004 are given in Appendix 2.

When data points are grouped by geographic region coherent relationships between in vivo fluorescence and extracted chlorophyll emerge as observed by Pingree *et al*., (1982). For example, the May 2003 fluorometer calibrations are plotted in Figure 2.13 and the relationships between the fluorescence and chlorophyll are described by the following regression equations:

Central Bay of Biscay: Fluorescence = 7.6 (chl*a*) - 1.16 (R^2 = 0.96, $p < 0.05$, n = 10) (4a)

North Bay of Biscay: Fluorescence = 3.3 (chl*a*) + 1.37 (R^2 = 0.94, $p < 0.05$, n = 6) (4b)

Ushant region: Fluorescence = 1.2 (chl*a*) - 0.31 (R^2 = 0.80, $p < 0.05$, n = 8) (4c)

Western English Channel: Fluorescence = 1.4 (chl*a*) + 1.14 (R^2 = 0.97, $p < 0.05$, n = 8) (4d)

Central English Channel: Fluorescence = 1.2 (chl*a*) + 1.92 (R^2 = 0.88, $p < 0.05$, n = 7) (4e)

A chi-squared test showed significant differences (χ^2=17.05 $p < 0.05$) between these regression lines. A similar analysis was carried out for each month as summarised in Table 2.5, enabling the MiniPack fluorometer to be calibrated for the full year.

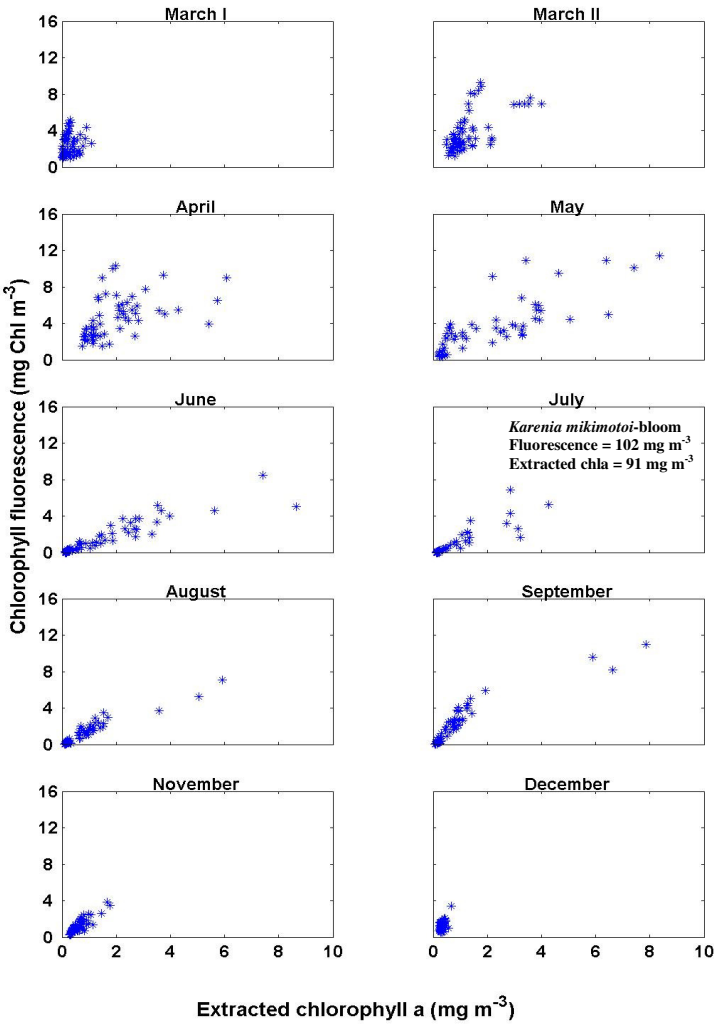


Figure 2.12: Plots of in vivo fluorescence against chlorophyll *a* measured by fluorescence for each calibration crossing in 2003. Data for the *Karenia mikimotoi* bloom in July are not included.

Table 2-5: The relationship between fluorescence and extracted chlorophyll for 2003 (B= slope of the regression line and R^2= coefficient of determination).

Hydrographic regions	March		April		May		June		July		August		September		November		December	
	B	R^2	B	R^2	B	R^2	B	R^2	B	R^2	B	R^2	B	R^2	B	R^2	B	R^2
coastal regions	2.4	0.90	1.1	0.88	0.8	0.95	0.5	0.95	0.9	0.98	1.0	0.97	1.6	0.99	3.3	0.98	4.6	0.49
central English Channel	3.4	0.60	1.1	0.75	1.2	0.88	0.9	0.95	1.1	0.98	2.1	0.91	2.1	0.79	1.3	0.77	5.5	0.60
western English Channel	3.3	0.75	1.8	0.87	1.4	0.97	1.3	0.79	0.7	0.99	1.9	0.82	2.7	0.83	0.8	0.11	4.7	0.47
Ushant region	3.1	0.32	2.5	0.98	1.2	0.80	1.1	0.71	1.4	0.97	1.6	0.85	5.2	0.94	4.1	0.87	5.7	0.51
North Bay of Biscay	2.1	0.30	2.2	0.73	3.3	0.94	0.9	0.88	1.4	0.77	3.9	0.80	3.9	0.96	1.9	0.82	1.2	0.10
central Bay of Biscay	5.2	0.95	6.7	0.93	7.6	0.96	2.2	0.70	1.6	0.62	3.3	0.88	1.5	0.80	5.7	0.92	1.4	0.14

The regional differences in fluorescence yields probably reflect variations in the species composition and/or physiological state of phytoplankton populations (Falkowski and Raven, 1997). For example, in the central Bay of Biscay levels of inorganic nutrients were already very low (see Chapter 3), suggesting that high fluorescence

yields were associated either with nutrient limitation of the phytoplankton or with a different type of phytoplankton community compared to shelf waters.

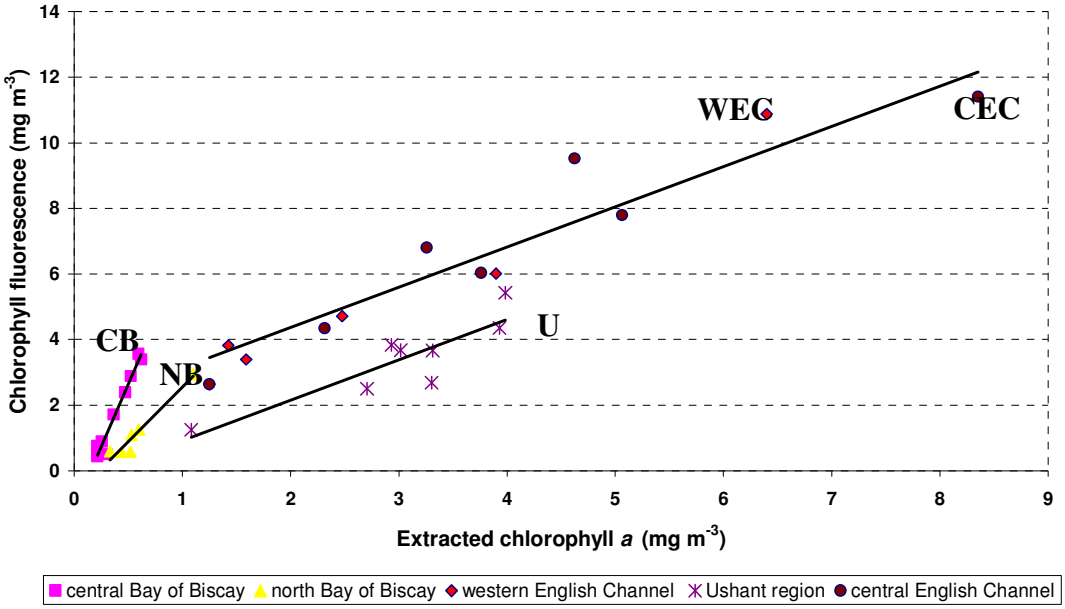


Figure 2.13: Surface fluorescence calibration curves for different hydrographic regimes: CB) central Bay of Biscay, NB) north Bay of Biscay, WEC) western English Channel, U) Ushant region, and CEW) central English Channel.

2.6 Phytoplankton cell counts

Duplicate 100 ml water samples were preserved in 100 ml dark glass bottles, one with 1ml of acidic Lugols solution and the other with 4 ml of 0.4 % buffered formalin. Phytoplankton cells were counted by the inverted light microscope technique of Hasle (1978) following settlement in 10 ml and 25 ml sedimentation chambers for about 24 hours. The larger chamber was used for samples with fluorometric chlorophyll *a* concentrations < 2.0 mg m^{-3}. Samples were examined with a Leica DMIRB inverted microscope. Lugols samples were enumerated for diatoms and autotrophic dinoflagellates, with cell counts from the whole of the chamber base at x100 magnification for large cells, two discrete transects at x200 for smaller more abundant cells and 10 fields of views (FOV) at x400 for dense (bloom) samples. Formaldehyde samples were enumerated for the coccolithophore, *Emiliania huxleyi*, on three discrete transects at x400 magnification. Cell concentrations were calculated using the following equations:

$$C = \frac{Nc \times AT}{Ac \times V} \quad (5a)$$

$$C = \frac{Nc \times AT}{Afov \times n \times V} \quad (5b)$$

where *N*c is the number of cells counted in the area examined, *Ac* is the area examined (equation 5a), *AT* is the area of the whole chamber, *Afov* is the area of one field of view, *n* is the number of fields of view (equation 5b) and *V* is the volume (ml) of sample settled. The value of *Ac* varied according to the magnification used. When examining the fields of view, the cells concentration was calculated from equation 5b. The number of transects or fields of view examined was determined by total cell numbers; the counts were continued until a total of > 200 cells had been counted.

Phytoplankton were identification using Tomas (1997), Horner, (2002) for diatoms; Dodge, (1982) for dinoflagellates, and Winter and Siesser, (1994) for coccolithophores. Autotrophic dinoflagellate species were distinguished from heterotrophic ones following the species lists of Lessard and Swift, (1986) and Tomas, (1997).

There are several potential sources of error associated with the counting of phytoplankton samples under light microscope including enumeration errors, classification errors, errors with estimating the abundance of large rare cells, and dependency on the experience of the observers (Venrick, 1978). As a measure of the precision of phytoplankton counts, and under the assumption of Poisson distribution, Venrick (1978), proposed that the standard error of the counts was proportional to the square-root of the total number of phytoplankton cells (> 5 µm) ($\sum x$). Applying this equation to the counts of phytoplankton for 2003 and 2004 gives a range of standard error between 0.5 and 5.2 % of the mean. The errors associated with counting decrease as the numbers of cells increase (Venrick, 1978). Besides the standard error, counts for replicate samples (n=5) from a *Karenia mikimotoi* bloom gave a standard error of 5.1 % around the mean.

2.7 Phytoplankton biomass estimation

Carbon biomass rather than cell numbers is considered a more appropriate estimate of phytoplankton population as cell volume varies between species by several

orders of magnitude. Cell abundances were converted into biovolume according to the different geometric formulae given by Hillebrand *et al*., (1999). The carbon content of each species was then calculated according to the carbon-to-volume relationships given by Menden-Deuer and Lessard, (2000) , using the following equations:

$$\mathbf{Pg\ C\ cell^{-1} = 0.216 x volume^{0.939}} \quad (7a)$$

$$\mathbf{Pg\ C\ cell^{-1} = 0.288 x volume^{0.811}} \quad (7b)$$

Equation (7a) is for taxonomically diverse protist plankton including dinoflagellates and equation (7b) is for diatoms. However, the calculation of cell biomass is complicated due to cell shrinkage during preservation and to intra-species variability in cell size. Therefore, the carbon biomass estimates for individual phytoplankton species can only be considered as semi-quantitative estimates.

2.8 Nutrient analyses

Water samples were collected every half hour in new disposable 30 ml plastic vials for the colometric determination of nutrients (nitrate, phosphate, and silicate). Each vial was rinsed with the sample twice before filling. Samples were stored in the dark in refrigerator (0-4.0° C) for later analysis. Analyses were performed on an automated analytical system as described by Hydes and Wright (1999). The system used was an autoanalyser from Skalar (UK) Ltd, model SAN++ Analyser, with an auto-sampler SA1000 connected to a computer. The volume of samples used for each analysis was 2ml and most samples were analysed in duplicate. The system was set up to measure nitrate, silicate and phosphate concentrations up to 10, 10, and 2 µM respectively.

The samples were pumped into the autoanlayser and the colorimetric reagents introduced into the sample line in the appropriate sequence. The concentration of nutrients present in the samples was determined by measuring the absorbance of light at the wavelength corresponding to the colour of the solution using appropriate filters in the photometer. Calibration standards covering the range of concentrations in the samples were run at the beginning of each analysis and drift standards every 20 samples. An artificial seawater solution made from 40 g l^{-1} sodium chloride was used as the wash, blank, and matrix for working standards.

The analysis of nitrate relies on the quantitative reduction of nitrate to nitrite because nitrate cannot be determined directly by colorimetric methods. This is done by passing the sea water through a column containing cadmium coated with copper, then the samples were mixed with an aromatic amine (sulphanilamide) and second aromatic amine (n-(1-naphthyl)-ethlenediamine dihydrochloride-NEDD) to produce a pink compound with a maximum extinction at 543 nm. No correction was made for nitrite which is generally below the detection limit in surface waters (Gentilhomme and Lizon, 1998). Phosphate was reacted with acidified ammonium molybdate and potassium antimonyl tartrate, then reduced using ascorbic acid to form a blue phosphoantimonyl molybdate complex with absorbance measured at 880 nm. To ensure completion of the reaction, the sample reagent mix was passed through a water bath with temperature of about 40.0° C. Dissolved silicate was reacted with ammonium molybdate to form a yellow silicomolybdate complex. Oxalic acid was added to the system to consume excess molybdate before the subsequent reduction step. Ascorbic acid was added to reduce the silicomolybdate complex to produce a strongly-coloured blue complex, with an extinction at 810 nm. These procedures are described in detail by Hansen and Koroleff, (1999).

Setup of the Skalar analyser was adjusted for all three analyses (nitrate, silicate and phosphate) to give a linear response over the calibration range (Grasshoff *et al.*, 1983; Kirkwood, 1996). To derive the calibration factor for each run, a linear least square regression was performed with the regression line forced through the origin. The consistency of the auto-analyser standard error is 1 % and the variation in calibration coefficients are shown in Table 2.6.

Table 2-6: The slope and calibration coefficients for series of nutrient analyses for 2003 and 2004.

Run No.	NO_3		$Si(OH)_4$		PO_4	
	Slope	R^2	Slope	R^2	Slope	R^2
March-03	267.5	0.99999	133.4	0.99997	342.0	1
March II 03	257.2	0.99997	140.5	1	338.1	0.99972
April-03	295.0	0.99999	192.9	1	342.2	0.9999
May-03	294.0	1	27.1	0.99998	352.7	1
June-03	304.7	1	180.6	0.99978	354.1	0.99996
July-03	219.5	1	203.1	0.99991	383.5	0.99996
August-03	269.3	0.99998	194.1	0.99974	352.6	0.99954
September-03	190.0	0.99998	208.8	0.99998	365.0	0.99999
November-03	224.7	0.99998	212.3	0.99988	341.3	0.99989
February-04	200.2	0.99966	170.2	1	326.6	0.99916
March-04	196.4	0.9995	170.8	0.99995	348.9	0.99751
April-04	203.2	0.99987	178.1	0.99994	343.9	0.99933
May-04	189.4	0.99998	173.1	0.99999	304.4	0.99685
June-04	187.5	0.99992	177.6	0.99999	343.6	0.99983
July-04	212.4	1	177.9	0.99999	348.7	0.99983
October-04	239.5	0.99985	177.0	0.99994	343.4	0.99965
November-04	229.7	0.99988	165.2	0.99999	342.2	0.99981

2.9 Salinity

Samples for salinity measurements were collected every two hours during the crossings (a total of about 36 samples). They were stored in 250-ml glass medicine bottle with plastic stoppers supplied by Ocean Scientific International (OSI). The bottles were rinsed twice before filling and stored at room temperature. On return to the laboratory, salinity was determined using a Guildline Salinometer in a temperature controlled laboratory. Salinity was calculated from measurements of conductivity and temperature made using a Chelsea Technologies Group MiniPack CTD-F. The manufacturer claims an accuracy and precision of 0.005 ± 0.001 mS/cm for conductivity. Calibration of the conductivity measurements has to be carried out because the mounting of the instrument on the Pride of Bilbao distorts the flow field round the conductivity head of the Minipack. The precision of calibration, expressed as the standard error, varied between 0.034 and 0.010. These data were then used to adjust the MiniPack output for changes through time. In 2003 the calibration factor varied between 1.063 and 1.067. In 2004 it drifted from 1.074 in March to 1.065 in December. This procedure is explained in detail by Kelly-Gerreyn *et al*., (2006).

2.10 Acquisition and processing of satellite images

The SeaWiFS and AVHRR satellite data were provided by the Remote Sensing Data Analysis Service (RSDAS), at the Plymouth Marine Laboratory. Weekly composite images are generated for specific areas and reprocessed to give average data for the cloud free areas.

CHAPTER 3

3.ENGLISH CHANNEL AND BAY OF BISCAY 2003

The aim of this chapter is to present information from 2003 on the surface biomass and species composition of phytoplankton in English Channel and Bay of Biscay within the context of measured environmental variables. Most of the figures in this chapter describe temporal and spatial changes in water properties by reference to day number (1st January = day 1, 31st December = day 365) and latitude (43.3^{o} to 50.8^{o} N). The different seasons are defined as follows: spring, days 80-172; summer, days 173-264; autumn, days 265-354; and winter, days 355-79.

3.1 Environmental data

The hydrographic environment in temperate seas effectively controls the availability of nutrients and light to phytoplankton communities, and is sensitive to climatic variables; in particular solar irradiance and wind strength and direction (see Chapter 1).

3.1.1 *Climatic data*

Light

Total solar radiation between Portsmouth and Bilbao was derived from the UK Meteorological Office NWP (Numerical Weather Prediction) database. Figure 3.1 shows the seasonal and latitudinal variability in the irradiance values between Portsmouth and Bilbao. The minimum mean daily irradiance values (22 W m^{-2}) were recorded in December (days 335-365) and the maximum mean values (243 W m^{-2}) in June (days 152-181) (see Table 3.1). Day-to-day variations in radiation were large especially in the north; solar radiation was almost as low during some days in June and July (between 30 and 70 W m^{-2}) as it was in December (Figure 3.1).

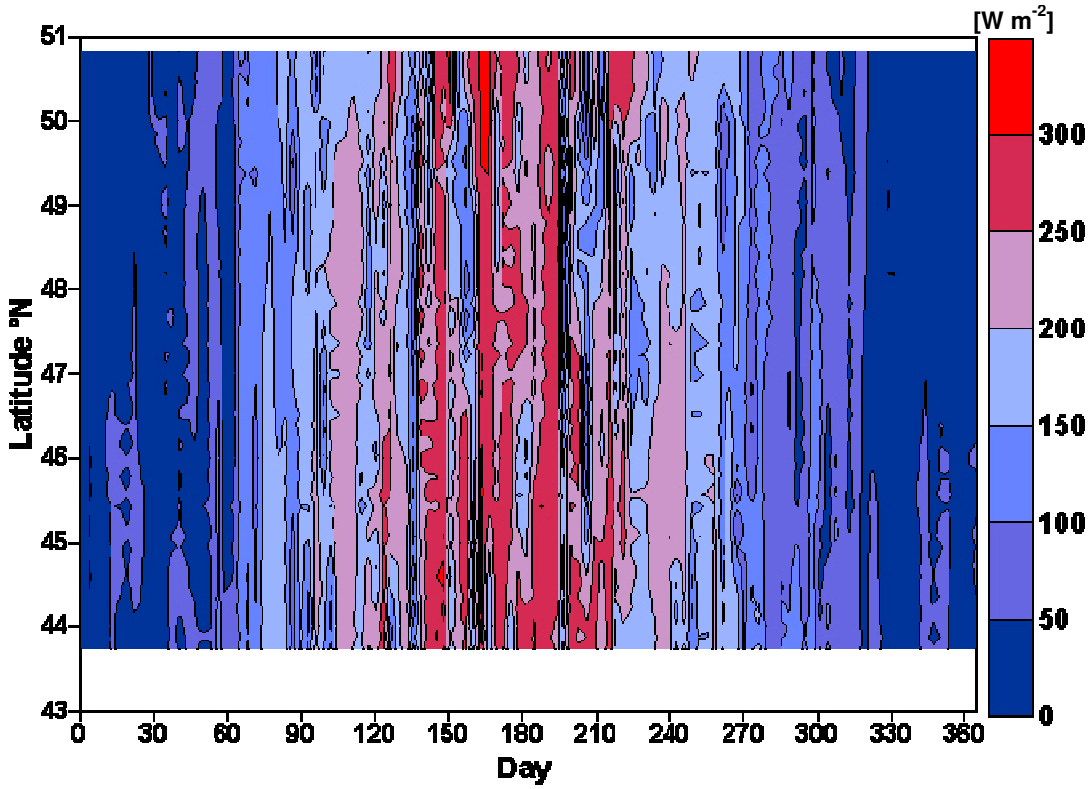


Figure 3.1: Distribution of daily surface solar radiation values for 2003 between Portsmouth and Bilbao derived from the UK Met Office NWP. Note that no data are available for coast of Spain (43.3°-43.6° N).

River discharge

Freshwater discharge from the Loire and Gironde Rivers between January and December 2003 are shown in Figure 3.2. The combined mean annual outflow of both rivers was 1554 $m^3 s^{-1}$. The maximum flows were observed in the winter between January and March (day 1 to 80) (mean=3368 $m^3 s^{-1}$) and the minimum values recorded between July and October (day 182 to 304) (mean = 389 $m^3 s^{-1}$). An increase in outflow occurred again in December (day 335 to 355) (mean =3005 $m^3 s^{-1}$) (Figure 3.2). The flow pattern observed in 2003 represents the typical pattern with a winter peak (up to 9000 $m^3 s^{-1}$) followed by a gradual decrease to a minimum (< 500 $m^3 s^{-1}$) in July and August (days 182-243) (Figure 3.2).

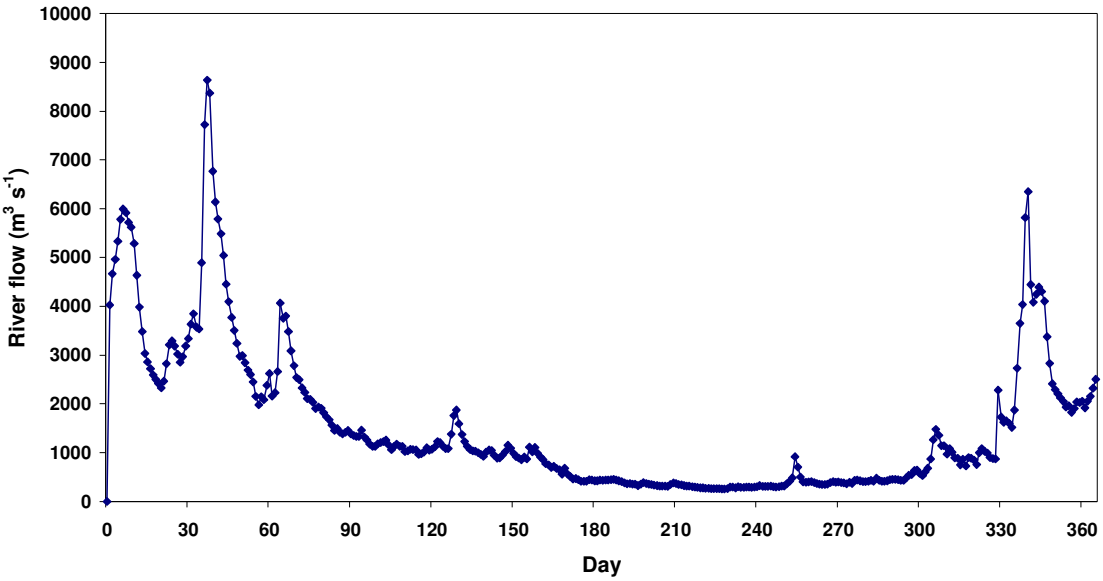


Figure 3.2: Daily-averaged river flow from Loire and Gironde Rivers for 2003, obtained by B. Kelly-Gerreyn from the Bordeaux Port Authority, France.

Wind

Figure 3.3 shows the daily means of wind velocities recorded at central points in English Channel (49.9° N 2.9° W) and Bay of Biscay (45.2° N 5.0° W). In both regions, there was a clear seasonal maximum in winter and early spring and minimum in late spring and summer. Winds were generally stronger towards the north.

Figure 3.4 a presents the annual and quarterly wind roses for the English Channel. On an annual basis, the main wind directions were west-southwest and east-northeast with minor components out of the northwest and southeast. During the first quarter of 2003, the winds were primarily from east-northeast and southwest with an average of wind speed 10.0 ± 0.3 m s^{-1} (Figure 3.3 and 3.4 a). However, between days 13 and 40, coincident with the main peak in river flow (Figure 3.2), the prevailing winds were northwesterly with mean speed of 11.3 ± 0.2 m s^{-1}. Between days 40 and 120 winds were more variable in direction (northeasterly, southeasterly and southwesterly) with a mean speed of 8.5 ± 0.1 m s^{-1}. This period coincided with the second peak in river flow (Figure 3.2). In spring, the dominant wind directions were west-southwest and east-northeast, with average wind speed 7.1 ± 0.3 m s^{-1}. Winds in the third quarter were mostly from the west and east-northeast with an average wind speed of 6.3 ± 0.2 m s^{-1} (Figure 3.4 a). Wind speeds increased in autumn and were mainly from the west and northwest (Figure 3.4 a).

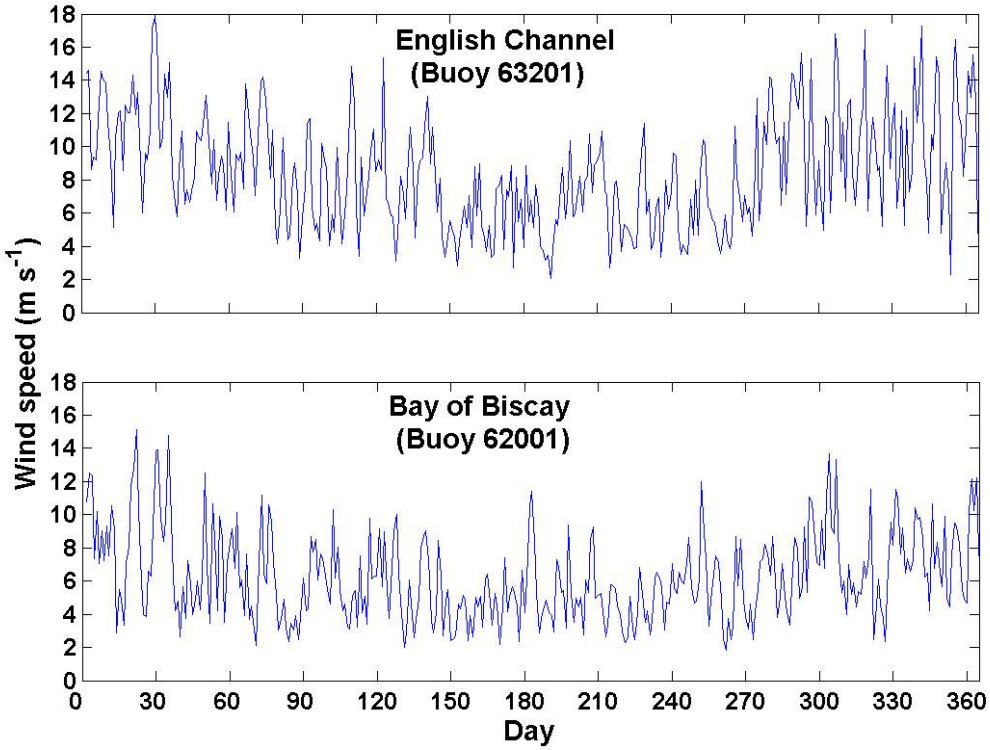


Figure 3.3: Daily-averaged wind speed (m s^{-1}) for the English Channel and Bay of Biscay in 2003. Data were provided by the UK Meteorological Office and are from two moored buoys: 63201 (English Channel at 49.9° N 2.9° W) and 62001 (Bay of Biscay at 45.2° N 5.0° W).

In comparison to the English Channel, the annual wind patterns for Bay of Biscay (Figure 3.4 b) showed somewhat weaker winds mostly from the west, east and west-southwest, with a relatively weak northeast component. In winter, the winds were variable in direction (mainly east-northeast, south-southeast and west) and the average wind speed was 7.0 ± 0.3 m s^{-1} (Figure 3.3). In the second quarter winds were relatively light, averaging 5.4 ± 0.2 m s^{-1}, and the main direction was west-southwest (Figure 3.4 b). In the summer, there was a greater frequency of winds from the northeast, northwest and west-southwest. In the autumn wind speed increased, averaging 7.3 ± 0.3 m s^{-1} and the main directions were from the east and west-southwest (Figure 3.4 b).

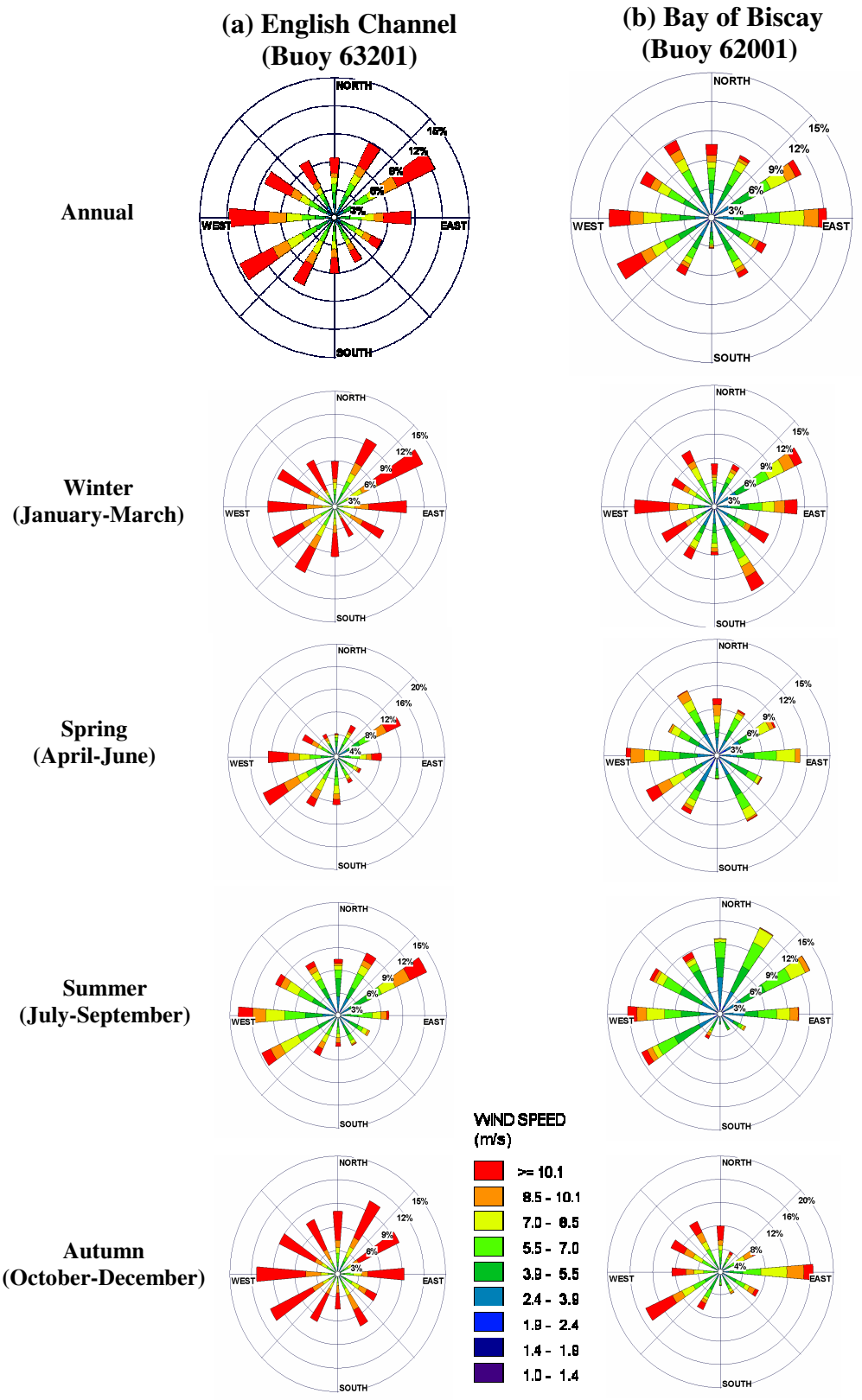


Figure 3.4: Annual and quarterly windroses (wind strength and wind direction) for (a) English Channel and (b) Bay of Biscay in 2003. Data were provided by UK Meteorological Office and are from two moored buoys: 63201 (English Channel at 49.9° N 2.9° W) and the 62001 (Bay of Biscay at 45.2° N 5.0° W).

3.1.2 *Temperature*

Sea surface temperatures (SST) between Portsmouth and Bilbao for 2003 (Figure 3.5) showed a clear seasonal cycle at all latitudes, and increased from north to south, with the difference in temperature between Portsmouth and Bilbao varying from about 5° C in winter to about 8° C in summer. Surface temperature increased in the early spring and decreased in autumn, following the changes in solar radiation (Figure 3.6). There was a greater lag between the maxima and minima of irradiance and temperature north of 47.0° N. In the autumn, the reduction in solar radiation and increase in the mean wind speed (Figures 3.1 and 3.3) caused the temperature to decrease (Figure 3.5).

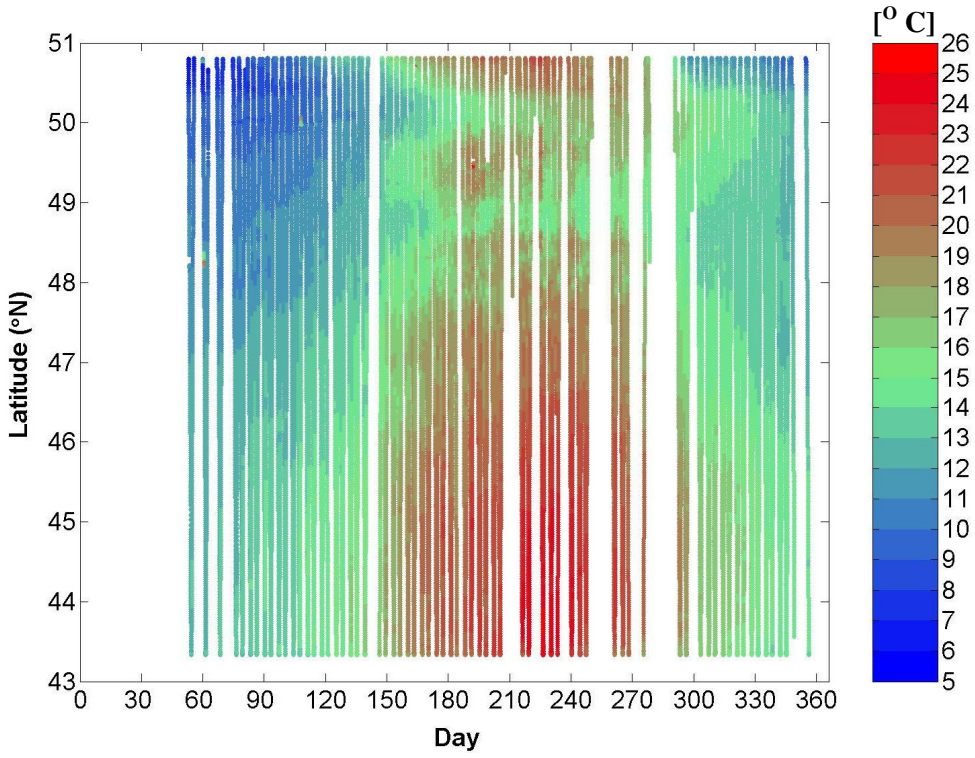


Figure 3.5: The distribution of sea surface temperature (° C, five-minute averaged values) for 2003 between Portsmouth (UK) and Bilbao (Spain) from the FerryBox MiniPack.

In the southern and central Bay of Biscay (43.6-45.0 and 45.0-46.4° N respectively), the surface water temperature gradually increased from ~13.0° C in March to ~18.0° C in May (days 60-151) as shown in Figure 3.5. Subsequently, continued solar heating (Figure 3.1) led to maximum temperatures in August (days 213-243) with averages of 23.8 and 22.1° C in the southern and central Bay of Biscay respectively (Table 3.1).

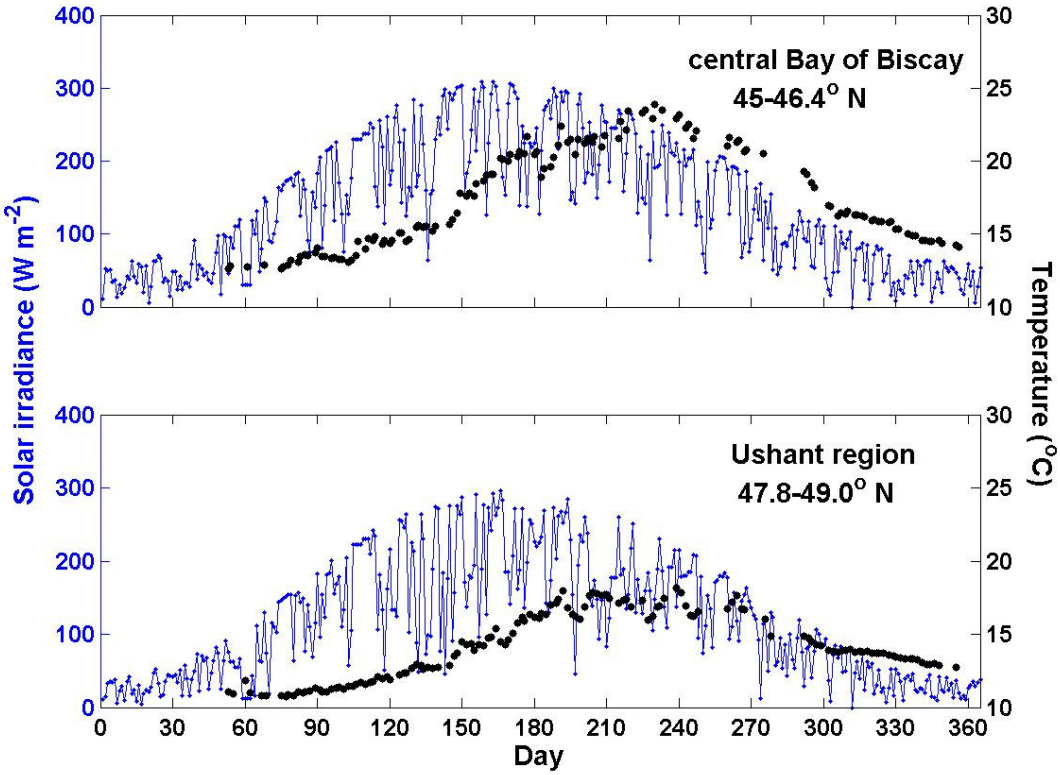


Figure 3.6: The relationship between daily-averaged surface solar irradiance (W m^{-2}) derived from the Met Office NWP and daily-averaged temperature (^{o} C) from the MiniPack for Bay of Biscay (45.0-46.4^{o} N) and Ushant region (47.8-49.0^{o} N) in 2003.

Table 3-1: Monthly averaged total daily solar irradiance (L) W m^{-2}, temperature (T)^{o} C, and salinity (S) for 2003 between Portsmouth and Bilbao. The irradiance data were derived from the Met Office NWP and the temperature and salinity data (five minute averages) from the MiniPack. Note that no data are available for the coast of Spain (43.3^{o}-43.6^{o} N).

Months (days)	(43.3-43.6° N)			(43.6-45.0°N)			(45.0-46.4°N)			(46.4-47.8°N)			(47.8-49.0°N)			(49.0-49.7°N)			(49.7-50.3°N)			(50.3-50.8°N)		
	L	T	S	L	T	S	L	T	S	L	T	S	L	T	S	L	T	S	L	T	S	L	T	S
March (60-90)	x	13.0	34.59	132	13.1	35.49	120	12.8	35.57	114	12.1	35.48	103	10.9	35.02	98	10.1	35.23	106	9.3	35.30	114	9.3	35.30
April (91-120)	x	13.8	34.75	190	13.9	35.55	186	13.6	35.61	180	12.8	35.60	174	11.5	34.89	174	10.6	34.91	118	9.9	34.96	177	9.9	34.96
May (121-151)	x	15.7	34.32	216	15.7	35.55	228	15.1	35.65	203	14.2	35.63	182	12.7	35.19	186	12.1	34.75	207	11.4	35.20	216	11.4	35.20
June (152-181)	x	18.9	34.47	243	19.7	35.52	237	19.0	35.61	224	17.6	35.43	217	14.7	35.28	221	15.0	34.98	226	13.5	35.00	228	13.5	35.00
July (182-212)	x	21.1	34.63	238	21.3	35.53	217	20.4	35.60	203	19.1	35.46	194	16.2	35.35	201	17.5	34.83	208	15.8	35.00	213	15.8	35.00
August (213-243)	x	23.0	34.53	198	23.8	35.42	205	22.1	35.60	188	20.1	35.49	176	15.7	35.41	175	17.1	35.04	192	17.0	34.90	202	17.0	34.90
September (244-273)	x	20.7	34.58	152	22.0	35.36	150	21.0	35.61	147	19.3	35.54	144	15.5	35.44	148	16.5	35.14	150	17.6	34.88	162	17.6	34.88
November (305-334)	x	15.6	34.62	61	16.1	35.53	54	15.6	35.53	47	14.3	35.50	45	13.7	35.46	42	14.1	35.35	39	14.2	35.00	36	14.2	35.00
December (335-365)	x	14.3	34.20	41	14.8	35.48	40	14.4	35.51	33	13.2	35.43	28	13.1	35.37	26	13.1	35.36	24	12.8	35.09	22	12.8	35.09

The northern Bay of Biscay region (46.4-47.8^{o} N) represented the limit of cold water (< 11.0^{o} C) on the shelf to the north in winter and relatively warm (> 21.0^{o} C) oceanic water to the south in summer (Figure 3.5). The minimum surface temperatures were recorded between days 60 and 151 (12.1-14.2^{o} C respectively) and the maximum between days 152 and 243 (17.6-20.1^{o} C respectively) (Table 3.1). During a period of prevailing northwesterly winds and reduced solar radiation between days 160 and 200

(Figures 3.1, 3.4 and 3.5), surface temperatures in the region of the shelf edge were somewhat lower than adjacent regions (Figure 3.7).

The average temperature values in the Ushant region and the western and central English Channel (47.8°-50.3° N) varied between 9.3° C in March and 17.6° C in September (Table 3.1). The minimum temperature of 6.5° C occurred in these regions before day 60 (Figure 3.5). During the early part of the year, the sea surface temperature was relatively uniform but, in summer, it was spatially variable due to the effects of interaction between tidal currents and bottom topography on water column stratification. At latitudes of approximately 47.5°-50.0° N along the ship's track, sharp changes in temperature were generally observed during July (days 182-212) (Figure 3.7) marking crossings of the boundary, known as the Ushant front, between the cold, well-mixed water off the coast of France and the central English Channel and the relatively warm, stratified water in the northern Bay of Biscay and the western English Channel.

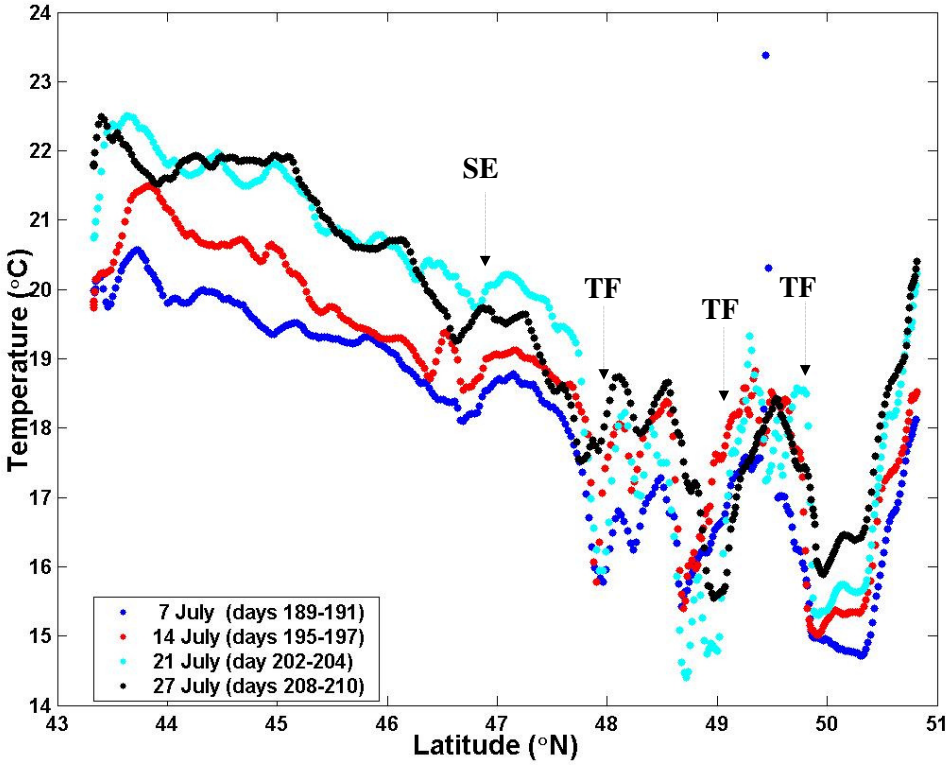


Figure 3.7: Transects of sea surface temperature (° C) for July 2003 between Portsmouth and Bilbao. Note anomalously high temperature values (up to 23.5° C) between 49.0 and 50.0° N corresponding to the bloom of *Karenia mikimotoi* (see Figure 3.14). SE and TF indicate respectively the shelf edge and tidal fronts (see Figure 3.8).

The Ushant front is also clearly apparent in the Advanced Very High Resolution Radiometer (AVHRR) image of sea-surface temperature (SST) for 6-12 July 2003

(Figure 3.8), marking the boundary between well-mixed (low SST) (47.8-49.0° N) (M1) and stratified (higher SST) (49.0-49.7° N) (S) waters (Figures 3.7 and 3.8). On the coastal mixed side of the front, surface temperatures were around 15.0° C (Figures 3.7 and 3.8).

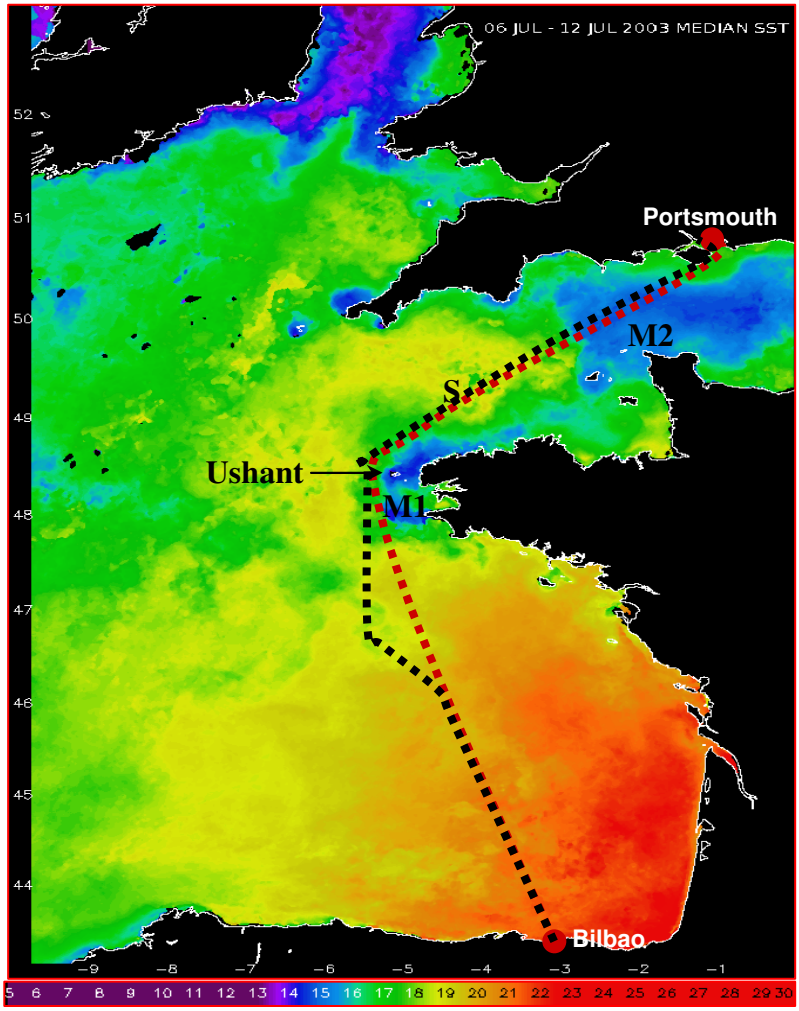


Figure 3.8: Sea surface temperature distribution in the Western English Channel and Bay of Biscay derived from Advanced Very High Resolution Radiometer (AVHRR) images for 6-12 July 2003 (days 188-194). The black and red dots represent the tracks of MV Pride of Bilbao (8-11 July 2003) from Portsmouth and from Bilbao respectively. M1 and M2 indicate mixed waters around Ushant and in the central English Channel, and S stratified waters in the western English Channel.

On the stratified side of the front the temperature of surface water increased to over 19.0° C between day 190 and 200 (Figures 3.7 and 3.8) under conditions of weak winds (ranging from 3.0 to 7.0 m s^{-1}) and high solar radiation (ranging from 170 to 290 W m^{-2}) (Figures 3.3 and 3.5). Superposition of the ship's track on the satellite image gives a clear indication of the source of variability in surface temperature that is illustrated in Figure 3.7.

Mixed water all the year was observed between 49.7 and 50.3° N (Figures 3.7 and 3.8) where the average temperature values varied between 9.3° C in March and 15.8° C in July (Table 3.1).

3.1.3 *Salinity*

Ferrybox data show that salinity varied between ~34.0 near the coasts of Spain and England and ~36.0 offshore (oceanic) in the Bay of Biscay (Figure 3.9). In general, salinity increased from north to south.

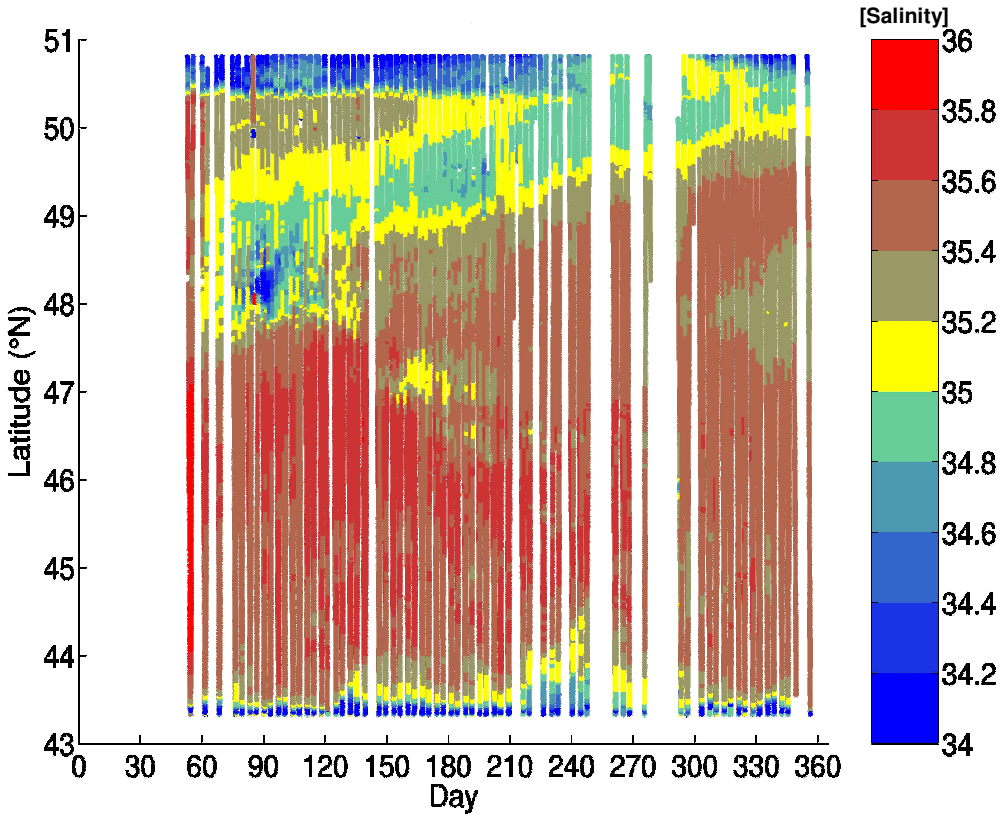


Figure 3.9: Distribution of salinity (five-minute averaged values) between Portsmouth (UK) and Bilbao (Spain) for 2003 from the FerryBox MiniPack.

In the Bay of Biscay (43.6- 47.8° N) surface salinity was relatively constant throughout the year (Figure 3.9). However, relatively low salinity water (~34.9) was detected in the southern Bay of Biscay between days 213 and 247 and appears to have originated from the coast of northern Spain due to advection from a coastal input of fresh water. In addition, salinity decreased to < 35.0 in the northern Bay of Biscay as indicated by the blue circles in Figure 3.10. A small peak in flows from the Loire and Gironde Rivers (1875 m^3s^{-1}) was recorded in end of April (Figure 3.2), and the

prevailing northwesterly winds in late spring and early summer (Figure 3.4) appear to have caused this fresher water to move offshore.

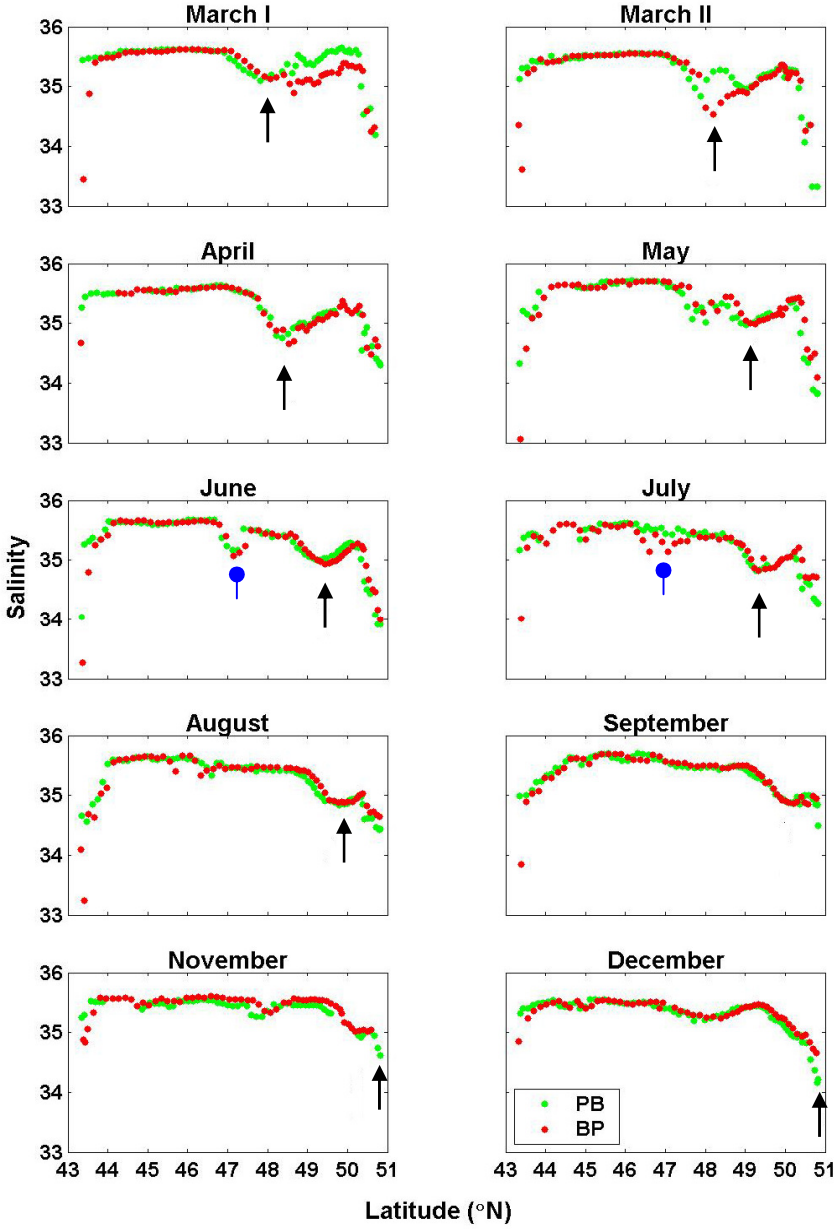


Figure 3.10: Plots of salinity (five-minute averaged values) from the FerryBox MiniPack on all the calibration crossings in 2003. The green and red dots represent the tracks from Portsmouth (P) and from Bilbao (B) respectively. The arrows show the low salinity water patch movement in the English Channel. The blue circle arrows show the low salinity water patch between May and July (days 159-210) in the northern Bay of Biscay.

In the English Channel, north of 47.8° N, salinity was more variable with high salinity (> 35.2) water penetrating from the west in late winter and early spring, and relatively low salinity (< 34.8) water close to the English coast throughout most of the year (Figure 3.9). The most marked feature, however, was the low salinity water

(defined as waters with salinities < 35.0) which became apparent in the vicinity of Ushant (48.4°N) in early March (day 60) and moved into the central English Channel by the autumn (Figures 3.9 and 3.10). It can be attributed to strong flows the French rivers in late winter (Figure 3.2) followed by prevailing winds from between south and west during spring (Figure 3.4), which forced the freshwater plume into the English Channel (Figure 3.10).

3.1.4 *Inorganic nutrients*

The surface distributions of inorganic nutrients (nitrate, phosphate and silicate) between Portsmouth and Bilbao are shown in Figure 3.11, and the monthly means presented in Table 3.2. More detailed information about nitrate and silicate is given in Appendices 3 and 4. In 2003, the highest concentrations of nutrients were recorded from coastal regions where salinity values (ranging from 34.0-35.5) were relatively low due to river runoff (compare Figures 3.9 and 3.11).

Nitrate

Close to the coast of Spain, south of 43.6° N, nitrate levels were relatively high throughout the year, with a maximum of 19.1 µM on day 261 (Figure 3.11 a). By contrast, in southern and central Bay of Biscay (43.6-46.4° N), mean concentrations of nitrate ranged from a maximum of 1.8 – 3.6 µM in March (days 60-80) to < 0.4 µM for the rest of the year (Figure 3.11 a, Table 3.2). In the northern Bay of Biscay (46.4-47.8° N), similar seasonal changes were observed, but nitrate ranged from 4.1 µM in March to ≤ 0.1 µM between May and September (days 133-262) (Table 3.2).

In the Ushant region and western and central English Channel (47.8-50.3° N), mean levels of nitrate decreased from 7.5 µM in April to 0.1 µM in July, and then increased again to 4.0- 6.1 µM late in the year (Table 3.2). The relatively high concentrations in spring were associated with fresh water inputs from the Loire and Gironde Rivers (see Figure 3.9) and it is noteworthy that, during May, the average concentrations of nitrate in central English Channel decreased faster than they did in western English Channel (Table 3.2).

When the nitrate data are plotted against salinity different trends were observed (Figure 3.12). Overall there was a negative correlation between nitrate and salinity during the late winter and early spring months (March -April) for nitrate values > 5.0

µM, suggesting that sources of freshwater on the continental shelf represent a source of nitrate (Figure 3.12). In late spring (May) nitrate decreases across the whole range of salinity and remained low during the summer except close to the coast. However, in March (and to a lesser extent April and December), some data indicate a positive correlation between nitrate and salinity as shown by the arrows in Figure 3.12. These appear to show trends close to the shelf break where phytoplankton growth starts earlier in the somewhat lower salinity water on the shelf than in the saltier oceanic water.

Phosphate

In the Bay of Biscay, the distribution of inorganic phosphate was similar to that of nitrate (Figure 3.11 b), with average concentrations ranging from 0.23 µM in March to 0.03 µM in July (Table 3.2).

In the Ushant region and western and central English Channel, phosphate concentrations ranged from 0.39 µM in March to 0.04-0.1 µM in June (Table 3.2). The anomalously high concentrations recorded in western English Channel in July (up to 0.88 µM between 49.0^{o} and 49.7^{o} N) were associated with the bloom of the dinoflagellate, *Karenia mikimotoi*. As the analyses were based on unfiltered water, it is possible that most of the phosphate in these samples was derived from *Karenia* cells.

Silicate

The distribution pattern of inorganic silicate was similar to that of nitrate and phosphate (Figure 3.11 c). In the southern and central Bay of Biscay, the mean concentrations of silicate were generally low throughout the year, ranging from 1.4 µM early in the year (March) to 0.4 µM in spring (May) (Table 3.2).

In the western and central English Channel, the mean concentrations of silicate ranged from 3.7 µM in March to 0.6 µM in July, with slightly higher values of 5.5 and 0.8 µM in December and June respectively for coastal waters north of 50.3^{o} N (Table 3.2). The times of both the spring decrease and the summer minimum for silicate were somewhat later in the English Channel than in the Bay of Biscay except for coastal water off England.

The plots of silicate concentration as a function of salinity (Figure 3.13) were also similar to the corresponding ones for nitrate (Figure 3.12), with lower salinity water having a higher silicate content. In general, the decrease in silicate due to biological

consumption occurred somewhat earlier than for nitrate especially in low salinity (coastal) waters. Also silicate started to increase again in July as opposed to September for nitrate. Also as for nitrate, one group of data for high salinity (> 35.2) water indicated a positive relationship between silicate and salinity (see March II in Figure 3.13) suggesting that the timing of silicate removal may be somewhat different between shelf and oceanic water.

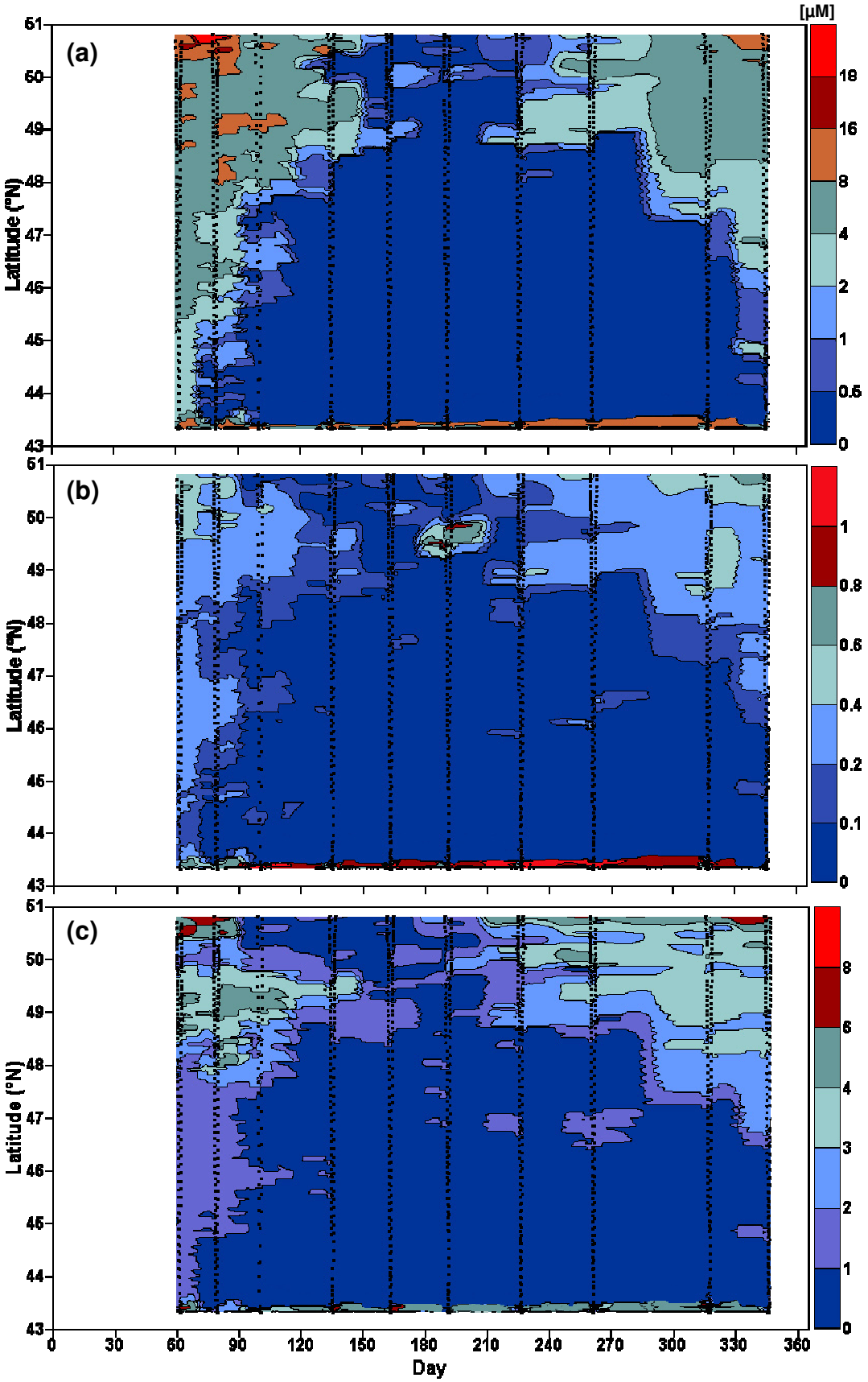


Figure 3.11: Distributions of (a) nitrate, NO_3, (b) inorganic phosphate, PO_4 and (c) silicate, Si (µM) between Portsmouth and Bilbao in 2003.

Table 3-2: The monthly mean concentrations of nitrate (NO_3) phosphate (PO_4) and silicate (Si) (µM) for 2003 between Portsmouth and Bilbao.

Month (days)	(43.3-43.6° N)			(43.6-45.0° N)			(45.0-46.4° N)			(46.4-47.8° N)			(47.8-49.0° N)			(49.0-49.7° N)			(49.7-50.3° N)			(50.3-50.8° N)		
	NO_3	Si	PO_4	NO_3	Si	PO_4	NO_3	Si	PO_4	NO_3	Si	PO_4	NO_3	Si	PO_4	NO_3	Si	PO_4	NO_3	Si	PO_4	NO_3	Si	PO_4
March (77-80)	8.2	3.2	0.59	1.8	1.0	0.13	3.6	1.4	0.23	4.1	1.5	0.22	6.4	3.1	0.24	7.1	3.7	0.33	6.6	2.1	0.39	13.7	5.0	0.44
April (98-101)	7.0	2.9	0.84	0.2	0.3	0.06	0.4	0.7	0.05	1.0	0.8	0.08	6.1	2.7	0.15	7.5	3.9	0.30	6.6	1.5	0.38	6.5	0.8	0.14
May (133-137)	7.2	4.1	0.70	<0.1	0.4	0.05	<0.1	0.7	0.05	0.1	0.5	0.04	1.6	0.8	0.11	5.1	2.5	0.18	0.8	0.7	0.08	3.7	0.7	0.08
June (161-164)	7.2	4.7	0.78	0.2	0.6	0.05	<0.1	0.6	0.05	<0.1	0.4	0.05	0.5	0.9	0.07	0.4	0.9	0.04	0.6	0.8	0.10	0.4	0.8	0.08
July (189-192)	6.3	1.2	0.71	<0.1	0.5	0.03	0.1	0.7	0.03	0.1	0.8	0.03	0.1	0.8	0.04	0.1	0.6	0.39	0.5	1.6	0.28	0.5	1.4	0.12
August (224-227)	10.0	3.4	1.11	0.1	0.5	0.06	0.1	0.7	0.07	<0.1	0.7	0.05	1.2	1.2	0.17	1.2	2.0	0.14	0.7	2.6	0.14	0.9	3.2	0.25
September (259-262)	10.4	2.6	0.95	<0.1	0.5	0.03	<0.1	0.8	0.05	<0.1	0.8	0.05	1.2	1.3	0.13	2.9	2.8	0.23	3.8	3.6	0.25	2.2	3.9	0.33
November (315-318)	8.7	4.7	0.81	<0.1	0.7	0.03	<0.1	0.5	0.04	1.1	1.0	0.11	4.5	3.0	0.34	5.4	3.2	0.40	6.1	3.4	0.38	6.1	3.6	0.44
December (343-346)	7.5	4.4	0.59	0.8	0.8	0.07	1.0	0.6	0.10	3.3	2.1	0.21	4.0	2.9	0.26	5.7	3.1	0.37	6.1	3.4	0.36	9.8	5.5	0.57

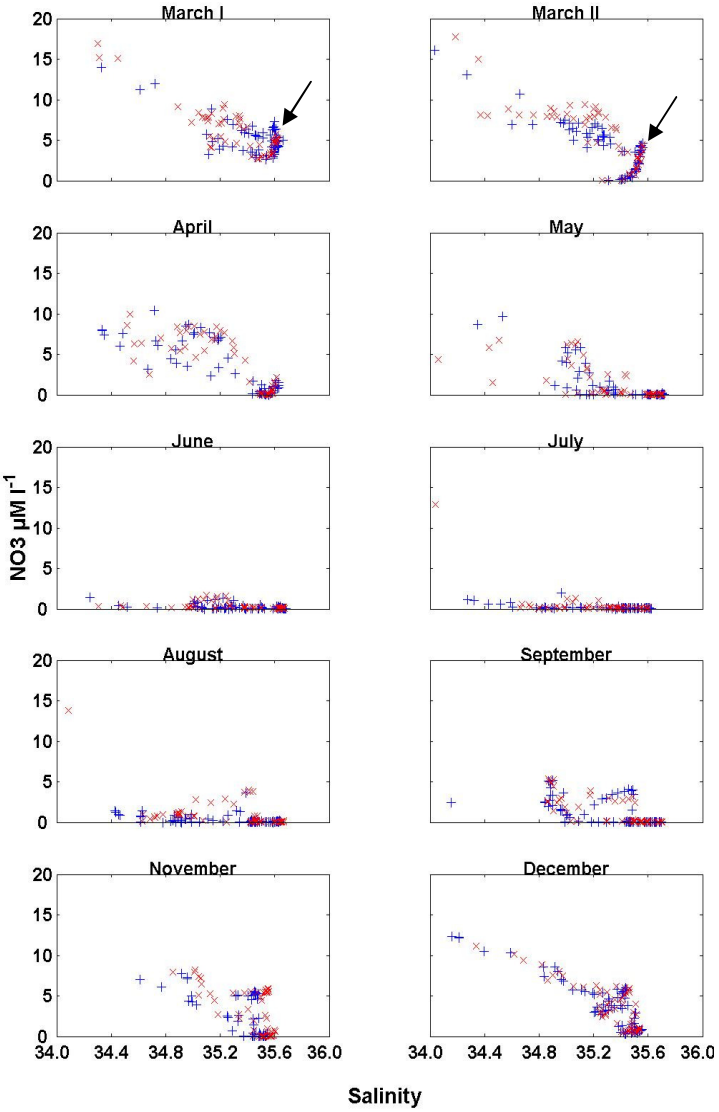


Figure 3.12: Nitrate versus salinity relationships for 2003. The red and blue dots represent data for the tracks from Portsmouth (P) and from Bilbao (B) respectively. The black arrows indicate the positive trend between nitrate and salinity in March for salinity values > 35.2.

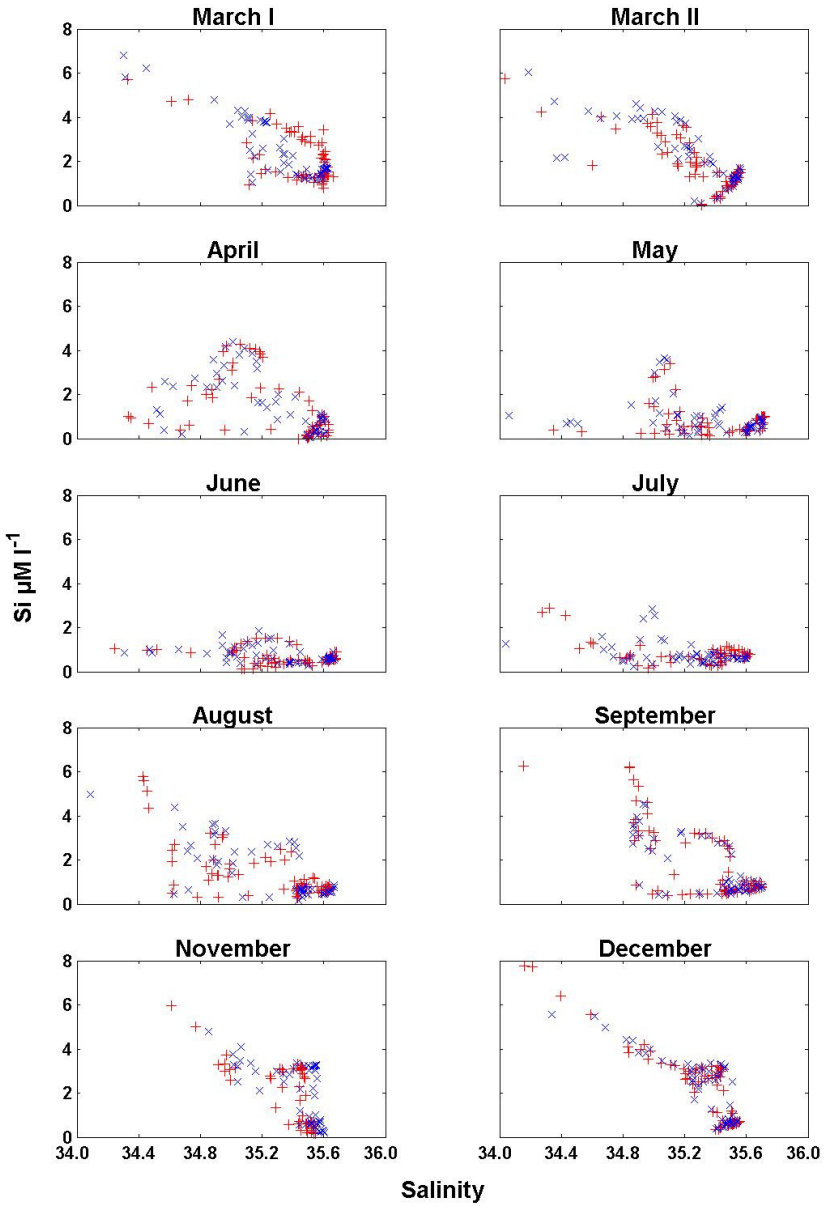


Figure 3.13: Silicate versus salinity relationships for 2003. The red and blue dots represent data for the tracks from Portsmouth (P) and from Bilbao (B) respectively.

N: P and Si: N ratios

Variations in the nitrate to phosphate and nitrate to silicate ratios are shown in Tables 3.3 and 3.4. The Redfield ratio for N/P by atoms is 16. In March, at the time of the maximum observed levels of nutrients, N/P values were greater than the Redfield ratio close to the coast of England and in the western English Channel, suggesting a relative excess of N compared to the normal N/P composition of phytoplankton. Unfortunately the lack of data for February when annual maximum nutrient concentrations occur (e.g. Pingree *et al.*, 1977) means that it is not known whether the

March ratio values are representative of winter conditions. It is possible that the excess of nitrate, compared to the Redfield ratio, reflects greater inputs of nitrate relative to phosphate at the land (i.e. riverine) and bottom sediment boundaries (Nedwell *et al.*, 2002).

During spring and early summer (March-June), the N/P ratio tended to fall as nitrate levels became very low, reaching minimum values in the southern Bay of Biscay in May and on the shelf (northern Bay of Biscay and English Channel) in about July (Table 3.3). A contributing factor is that the regeneration of phosphate within the water column is somewhat faster than the regeneration of nitrate. N/P ratios started to increase in the autumn (November and December), first in the English Channel and then in the Bay of Biscay. By December, however, they were still much lower than those measured in March. A notable exception to this general pattern is that the N/P ratio in English and French (Ushant) coastal waters showed a marked increase and was much higher than the Redfield value during April (continuing into May close to England). This anomaly reflects a relatively rapid fall in phosphate in these regions. Overall, it appears that nitrate rather than phosphate is likely to limit phytoplankton growth during the summer. The relatively low N/P ratio of 1.5 in the English Channel is linked to nutrient samples from the dinoflagellate bloom that contained anomalously high phosphate (see previous Section).

Ratios of nitrate to silicate (N/Si) were relatively high in late winter (March) and low in summer (June-September) again suggesting that nitrate becomes limiting for phytoplankton (Table 3.4). The tendency for the N/Si ratio to increase in April is indicative of a relatively high rate of removal of Si at this time of year as would be expected from the growth of diatoms in spring, especially in coastal waters. The proportionate decreases in nitrate to silicate at this time of year are approximately 2:1 by atoms, about double the N/Si assimilation ratio shown by cultures of diatoms (Brzezinski, 1985). The late occurrence of minimum N/Si values in the English Channel (July-August) and southern and central Bay of Biscay (November) reflects slight increases in Si (Figure 3.11 c) rather than continuing decreases in nitrate (Table 3.4).

Table 3-3: The monthly averages of surface nitrate to phosphate ratios for 2003 between Portsmouth and Bilbao. (Note that no data are available for October).

Latitude	March	April	May	June	July	August	September	November	December	
(50.3-50.8° N)	31.8	78.5	78.3	5.2	4.1	3.6	7.2	14.1	17.2	> 40
(49.7-50.3° N)	17.5	18.2	9.8	6.2	4.8	4.8	14.2	16.1	16.8	18-40
(49.0-49.7° N)	22.3	25.2	29.3	11.4	1.5	6.5	12.4	13.7	15.6	
(47.8-49.0° N)	27.8	56.5	13.8	5.7	5.1	5.1	5.4	13.0	15.6	14-18
(46.4-47.8° N)	21.1	12.2	3.7	2.4	5.5	1.0	1.4	8.5	15.4	
(45.0-46.4° N)	15.7	5.5	1.0	1.8	6.9	1.6	1.3	2.1	10.5	7-14
(43.6-45.0° N)	14.6	3.9	1.0	4.4	2.8	1.7	3.1	1.6	13.9	
(43.3-43.6° N)	13.5	7.9	9.4	8.8	8.1	7.9	11.4	11.4	13.4	< 7

Table 3-4: The monthly averages of surface nitrate to silicate ratios for 2003 between Portsmouth and Bilbao. (Note that no data are available for October).

Latitude	March	April	May	June	July	August	September	November	December	
(50.3-50.8° N)	2.8	9.3	7.1	0.5	0.3	0.3	0.6	1.8	1.8	> 7
(49.7-50.3° N)	3.1	5.5	1.7	0.7	0.4	0.3	1.1	1.8	1.8	3-7
(49.0-49.7° N)	1.9	1.9	2.1	0.5	0.3	0.5	1.0	1.7	1.8	
(47.8-49.0° N)	2.2	2.3	2.1	0.4	0.2	0.7	0.6	1.5	1.4	2-3
(46.4-47.8° N)	2.7	2.0	0.3	0.2	0.2	0.1	0.1	1.3	1.7	
(45.0-46.4° N)	2.5	0.5	0.1	0.1	0.2	0.1	0.1	0.3	1.6	1-2
(43.6-45.0° N)	1.6	2.4	0.2	0.4	0.1	0.2	0.2	0.1	1.1	<1
(43.3-43.6° N)	2.8	2.1	1.5	1.3	5.9	2.4	3.9	1.6	1.6	

3.2 Phytoplankton Data

Phytoplankton distributions along the FerryBox transect are considered first in terms of biomass (chlorophyll *a*) determined by three independent methods, and then in terms of the taxonomic composition of the populations assessed indirectly by HPLC analysis of marker pigments and directly by light microscopy. Particular attention is given to the larger cells i.e. microphytoplankton.

3.2.1 *Chlorophyll a by fluorescence*

Figure 3.14 shows the distribution of chlorophyll fluorescence in 2003 as detected by the MiniPack fluorometer. The nominal calibration factor given with the instrument has been used to derive chlorophyll concentrations. No attempt was made to apply region and/or time specific calibration factors as presented in Chapter 2 due to the difficulties in setting boundaries (or gradients) to the observed changes in fluorescence yield per unit chlorophyll.

There was a general south to north development of spring bloom, starting at the end of February (day 59) in the southern Bay of Biscay and persisting until May (day 150) in central English Channel. Once the surface nutrients were depleted (see Figure 3.11), the chlorophyll values decreased sharply after about day 145 in the southern and central Bay of Biscay (43.6-46.4° N). In northern Bay of Biscay (46.4-47.8° N),

phytoplankton biomass started to increase during March and remained high into May before decreasing to a summer minimum. A distinct autumn peak was recorded between 46.0° and 48.0°N during October and November (days 292 – 330) (Figure 3.14).

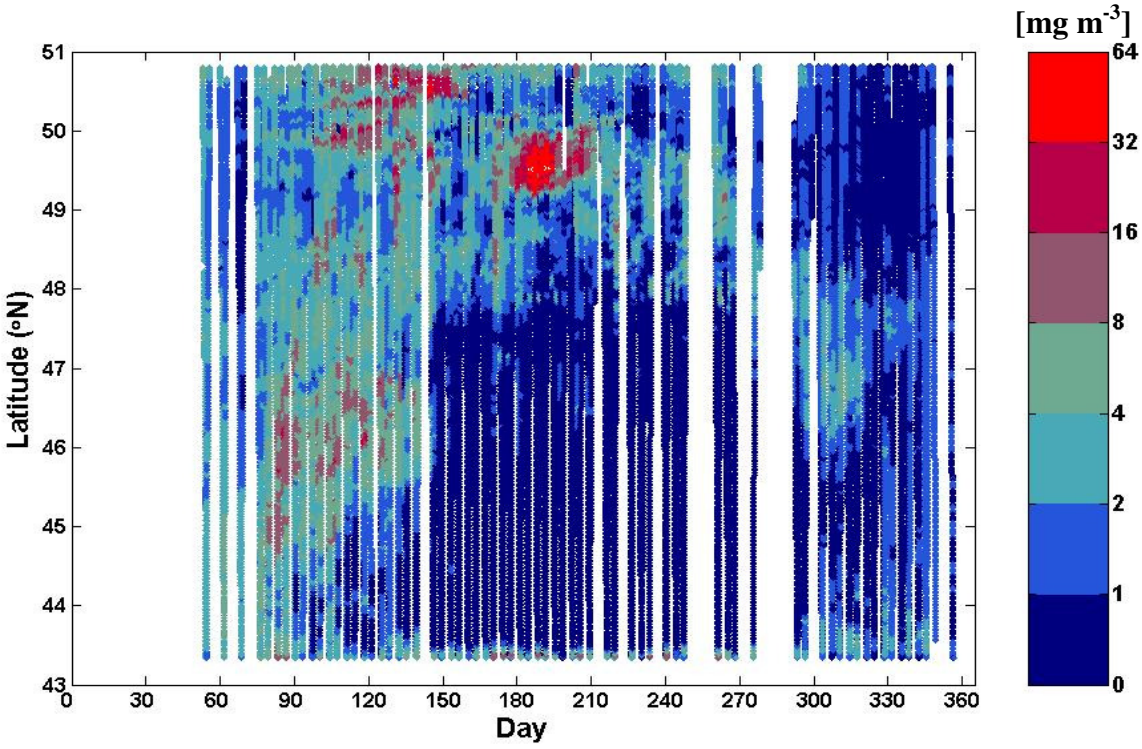


Figure 3.14: Distribution of surface chlorophyll *a* (mg m^{-3}, nominal calibration) for 2003 between Portsmouth (UK) and Bilbao (Spain). Values are 5-minute averages derived from the FerryBox MiniPack fluorescence sensor.

In the Ushant region, and western and central English Channel (47.8-50.3° N), the main increase in chlorophyll occurred at the beginning of April (day 92) (Figure 3.14) and was earliest around Ushant region and along the south coast of England. In summer, high chlorophyll levels persisted in the region of the position of the Ushant tidal front (Figure 3.5), and during July (days 182-204), an intense bloom of phytoplankton was recorded in the central part of the western English Channel (49.2-49.7° N) corresponding to a region of anomalously high sea surface temperature (Figures 3.5 and 3.7). In autumn, chlorophyll values decreased throughout the English Channel and were relatively low by about day 280.

Typical maximum chlorophyll values given by the MiniPack were about 8.0 mg m^{-3} during the spring bloom extending from northern Biscay to the coast of southern England, > 32.0 mg m^{-3} in the summer bloom in the English Channel and about 4.0 mg m^{-3} in the autumn bloom in northern Biscay. Only in the Bay of Biscay in late spring

and summer (days 150-290) and on the shelf in late autumn and early winter (day 320 onwards) did values appear to fall below 1 mg m^{-3} (Figure 3.14).

3.2.2 *Fluorometric chlorophyll a concentrations from acetone extractions*

The distributions of chlorophyll based on analysis of a relatively small number of discrete water samples shows similar trends (Figure 3.15) to those given by the MiniPack fluorometer records. The main differences are that small scale patchiness is not resolved (for example, the red colours shown in Figure 3.14 during the spring and early summer (days 80-170)). The measured chlorophyll values are uniformly lower than those given by the MiniPack fluorometer. Thus maximum values were typically 2.0-4.0 mg m^{-3} and 0.5-1.0 mg m^{-3} for the spring (days 80-135) and autumn (days 315-346) blooms respectively. Within the summer (189-192) bloom in the western English Channel, chlorophyll *a* values were as high as 70.0 mg m^{-3} (Figure 3.15) and it is likely that the output of the MiniPack fluorometer was non-linear under such extreme conditions. From May to December (days 133-346) concentrations were generally < 0.5 mg m^{-3} in the Bay of Biscay (Figure 3.15).

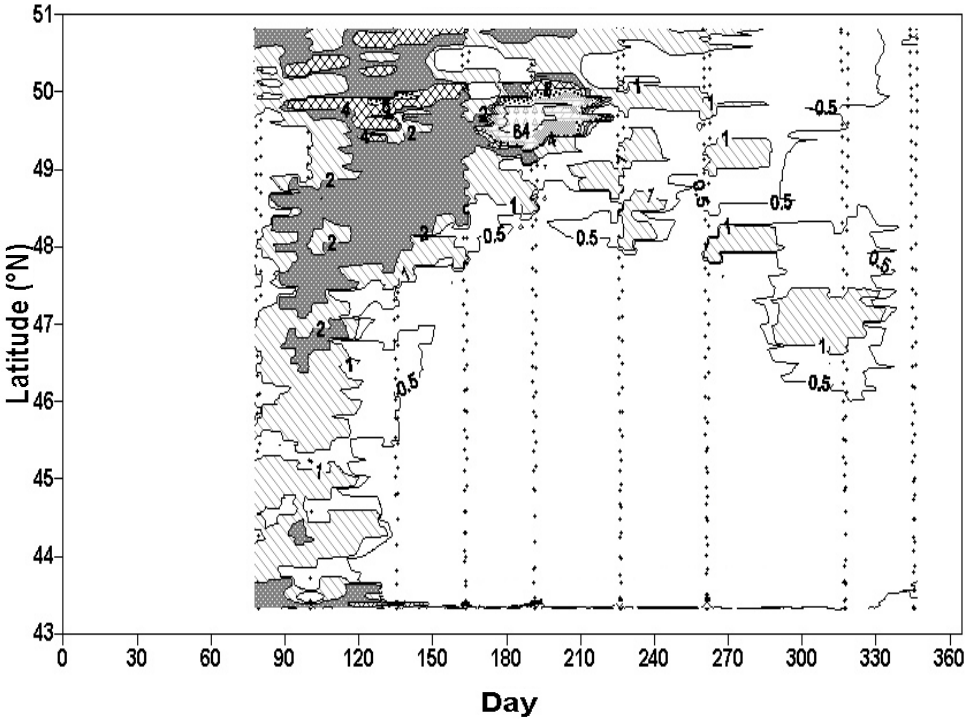


Figure 3.15: Distribution of extracted chlorophyll *a* (mg m^{-3}) for 2003 between Portsmouth (UK) and Bilbao (Spain). Maximum values of *Karenia* bloom in the English Channel in July were > 50 mg m^{-3}.

The monthly means of the extracted chlorophyll values for the different regions of the transect are given in Table 3.5. Values ranged from 0.2 mg m^{-3} in the summer

(July) waters of the Bay of Biscay to 37.6 mg m^{-3} in the western English Channel in July.

Table 3-5: The monthly means of extracted chlorophyll *a* (mg m^{-3}) for 2003 between Portsmouth and Bilbao.

Month (days)	(43.3-43.6° N)	(43.6-45.0° N)	(45.0-46.4° N)	(46.4-47.8° N)	(47.8-49.0° N)	(49.0-49.7° N)	(49.7-50.3° N)	(50.3-50.8° N)
March (77-80)	2.1	1.3	0.9	1.0	0.8	0.7	1.1	1.9
April (98-101)	3.2	1.3	1.4	2.0	2.2	1.2	3.5	2.8
May (133-137)	3.3	0.3	0.4	0.8	3.2	3.0	4.6	3.7
June (161-164)	2.4	0.2	0.2	0.2	1.6	2.8	2.2	2.0
July (189-192)	2.3	0.1	0.1	0.2	0.6	37.6	5.9	1.8
August (224-227)	1.7	0.2	0.2	0.2	0.9	0.8	0.9	1.2
September (259-262)	1.9	0.1	0.2	0.2	0.6	0.9	1.0	1.0
November (315-318)	0.8	0.4	0.4	1.0	0.5	0.4	0.6	0.8
December (343-346)	0.4	0.3	0.3	0.3	0.3	0.3	0.3	0.4

3.2.3 *Satellite estimates of chlorophyll*

The distribution of chlorophyll derived from weekly satellite (SeaWiFS) data along the ferry route during 2003 is shown in Figure 3.16 and corresponds well in time and space to the shipboard in vivo fluorescence measurements (Figure 3.14) and the discrete chlorophyll determinations (Figure 3.15). The values of satellite-determined chlorophyll are generally a little lower than the coincident

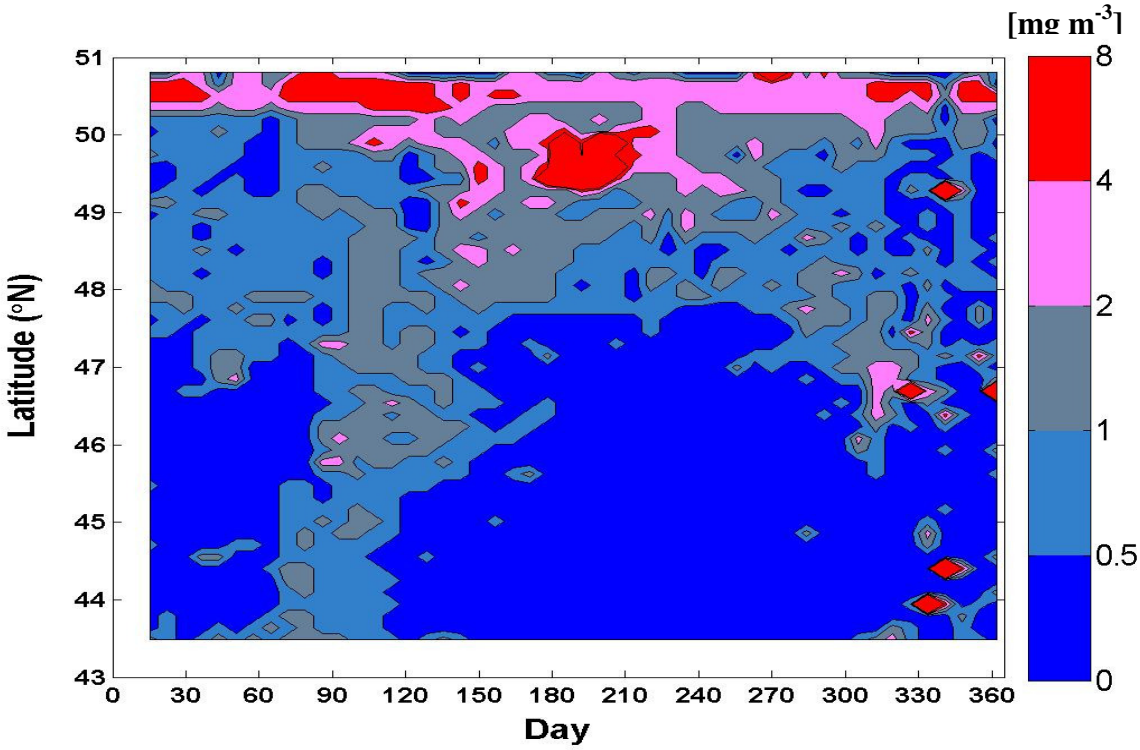


Figure 3.16: Distribution of chlorophyll *a* determined by satellite from weekly SeaWiFS composite images for 2003 using the NASA Case 1 waters algorithm. (Note that the anomalous red points in early winter south of 50.0° N are artefacts of the data processing.

extracted chlorophyll concentrations. However, for coastal waters at the northern end of the route the satellite overestimated chlorophyll almost certainly because of interference

from coloured dissolved organic matter and suspended matter with the retrieval algorithms (Moore *et al.*, 1999; Maritorena *et al.*, 2002; Morel and Bélanger, 2006). One important feature of Figure 3.16 is the clear distinction between shelf water north of 47.5^{o} N and oceanic water to south in winter as well as in summer. Thus the satellite indicates that chlorophyll *a* concentrations on the shelf typically remain > 0.5 mg m^{-3} all year.

3.2.4 *Pigment chemotaxonomy*

Accessory pigments determined by HPLC represent biomarkers for particular phytoplankton groups (see Table 2.4) and have been used by Vidussi *et al*., (2001) to classify the size structure of populations. Following the method of Vidussi *et al*., (2001) seven diagnostic pigments (DP) were selected: fucoxanthin, peridinin, 19'-hexanoyloxyfucoxanthin, 19'-butanoyloxyfucoxanthin, alloxanthin, chlorophyll *b* and zeaxanthin. They define the biomass proportions (BP) of pico- (< 2µm cell diameter), nano- (approximately 2-20 µm), and micro- (20-200 µm) according to the following equations:

$$\mathbf{BP_{pico\text{-}phytoplankton} = (Zea + Tchl\ b) / DP} \quad (1a)$$

$$\mathbf{BP_{nano\text{-}phytoplankton} = (Hex\text{-}fuco + But\text{-}fuco + Allo) / DP} \quad (1b)$$

$$\mathbf{BP_{micro\text{-}phytoplankton} = (Fuco + Perid) / DP} \quad (1c)$$

In addition, the proportion of chlorophyll *a* associated with each of the three size classes was estimated as the product of the BP of each class to total chlorophyll *a*:

$$\mathbf{Pico\text{-}phytoplankton\ chl\ \textit{a} = BP_{pico\text{-}phytoplankton} \times chl\ \textit{a}} \quad (2a)$$

$$\mathbf{Nano\text{-}phytoplankton\ chl\ \textit{a} = BP_{nano\text{-}phytoplankton} \times chl\ \textit{a}} \quad (2b)$$

$$\mathbf{Micro\text{-}phytoplankton\ chl\ \textit{a} = BP_{micro\text{-}phytoplankton} \times chl\ \textit{a}} \quad (2c).$$

Confidence in this approach is based on the consistent relationship between chlorophyll *a* and total accessory pigments (see Figure 2.10) the bulk of which is made up of the seven DPs. Thus total DPs (or total accessory pigment) is a good predictor of chlorophyll *a*. Furthermore, the distributions of the major DPs are consistent with knowledge of the ecology of taxonomic groups they represent (Vidussi *et al.*, 2001). For example, the distribution of 19'-hexanoylfucoxanthin (Figure 3.17) is displaced slightly in time (and space) from that of chlorophyll (Figure 3.18 a) as expected for a pigment that is characteristic of taxa that follow diatoms in the seasonal succession. The major

uncertainties in the method are that some dinoflagellates with peridinin are smaller than 20 μm (i.e. belong to the nano- rather than micro- phytoplankton), and that fucoxanthin is not confined to the diatoms but also found in various small flagellates. Thus, in both respects, the importance of the nano-phytoplankton is likely to be underestimated.

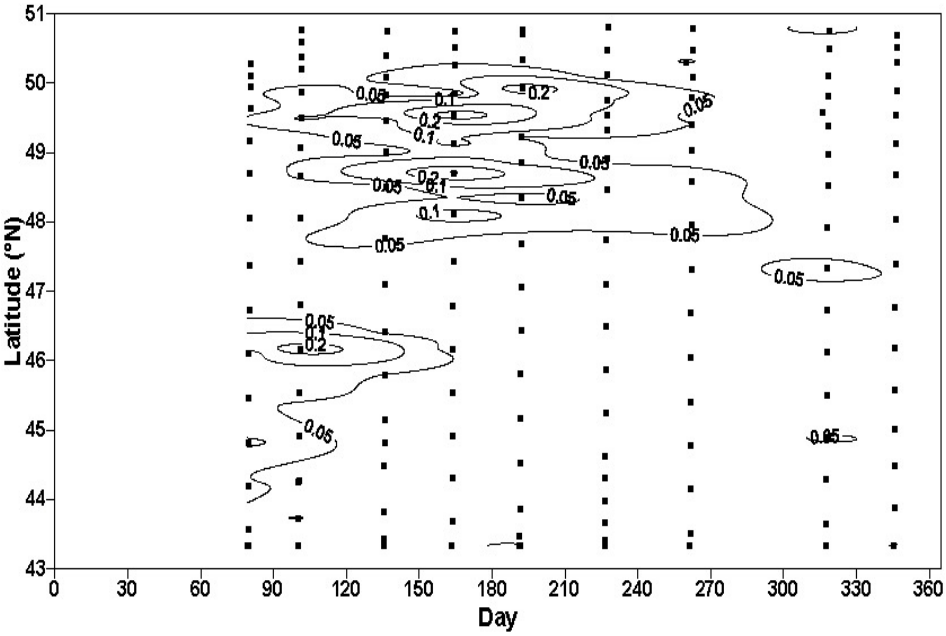


Figure 3.17: Distribution of Hex (19'-hexanoyloxyfucoxanthin, mg m^{-3}) for 2003 between Portsmouth (UK) and Bilbao (Spain).

Figure 3.18 shows the distributions of HPLC-chl *a*, and the estimated percentage contributions of the three phytoplankton size classes. Despite the relatively small number of samples, the distribution of HPLC- chl *a* (figure 3.18 a) is comparable to that shown in the previous section for chlorophyll *a* by the three different methods.

Based on HPLC pigment data, the micro-phytoplankton formed the major component (> 50 %) of phytoplankton in all regions during spring (days 77-135) and in the English Channel and southern Bay of Biscay during summer (days 189-262). The major DP was generally fucoxanthin, characteristic of diatoms, but dinoflagellate peridinin was important during summer in the English Channel. The estimated contribution of the micro-phytoplankton only fell below 30 % in the central and northern Bay of Biscay during summer (days 189-262) and somewhat more widely during the late autumn. In general micro-phytoplankton distribution followed that of chlorophyll *a* (compare Figures 3.18 a and d).

By contrast, nano-phytoplankton constituted > 50 % of phytoplankton biomass just in the central and northern Bay of Biscay (including the Ushant region) in June (days 161-164) and in the central Bay of Biscay in September (days 259-262) (Figure 3.18 c). The correspondence in the distributions of this group and of hexanoyloxyfucoxanthin (Figure 3.17) was not good, suggesting that the importance of 2-20 μm cells might have been underestimated from microscope counts. Pico-phytoplankton were the most important group in the low-chlorophyll waters of the Bay of Biscay in summer, autumn and early winter (Figure 3.18 b).

The method of Vidussi *et al*., (2001) for defining general size categories has clear limitations related to the occurrence of some DPs in taxa belonging to more than one size class. However, the development of the spring bloom is well illustrated by the distribution of micro-phytoplankton, as is the expected succession from micro- to nano-phytoplankton chl *a*. Reliability of the estimation of pico-phytoplankton is uncertain because the method does not account for the DPs of picoeukaryotes.

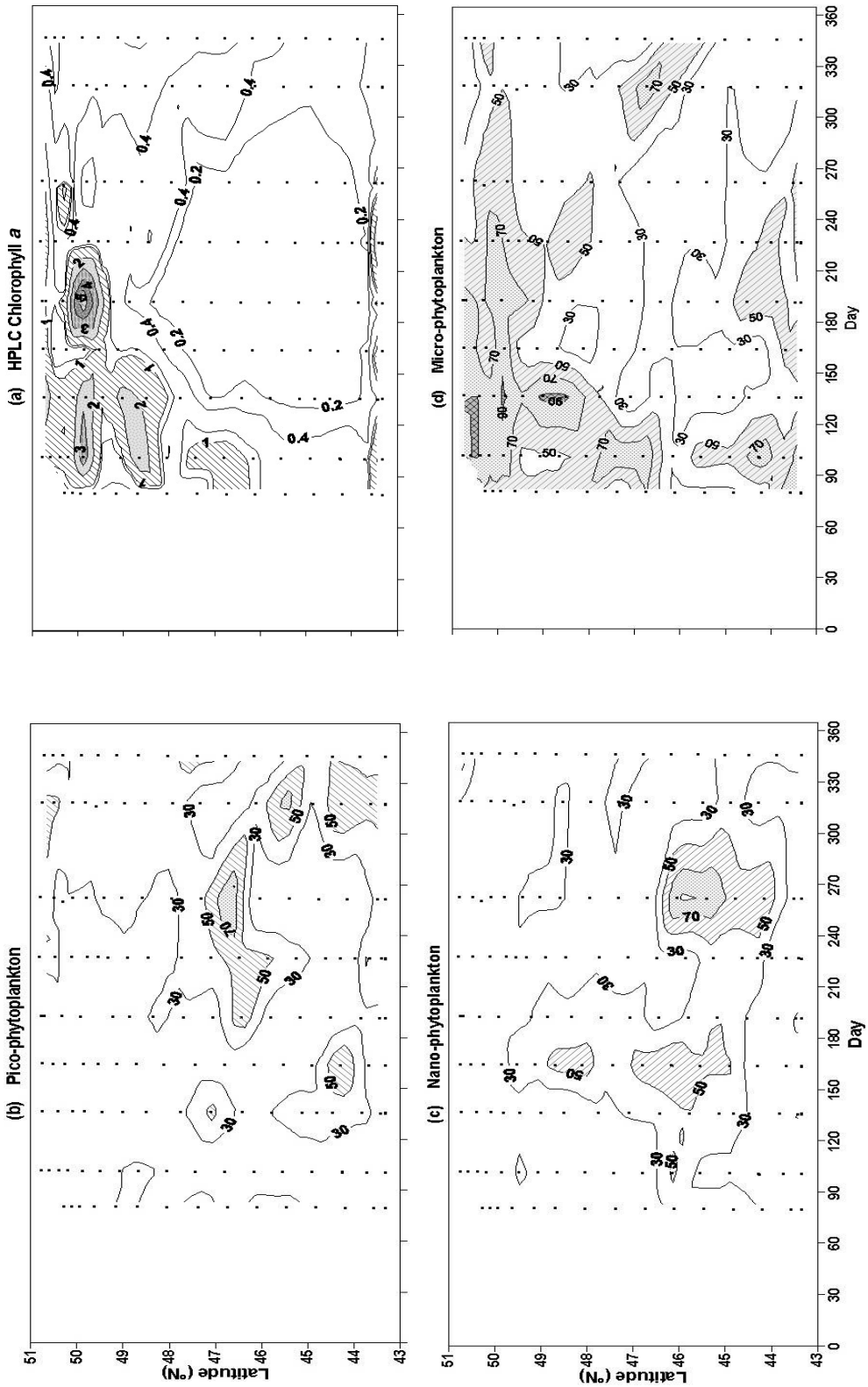


Figure 3.18: Distributions of (a) HPLC chlorophyll *a* (mg m^{-3}) and % contributions to chlorophyll *a* of (b) pico-phytoplankton (0.2-2µm), (c) nano-phytoplankton (2-20µm) and (d) micro-phytoplankton (> 20µm) for 2003 between Portsmouth and Bilbao.

3.2.5 *Phytoplankton species composition*

A total of 42 species were identified between Portsmouth and Bilbao, including 28 diatoms, 13 autotrophic dinoflagellates and 1 coccolithophore (*Emiliania huxleyi*). Table 3.6 summarizes the phytoplankton counts for the main hydrographic regions. The highest cell densities were recorded in the English Channel from the diatom populations in spring and a dinoflagellate bloom (*Karenia mikimotoi)*, and off Ushant in summer in association with a population of *Emiliania huxleyi.* In the Bay of Biscay, very few micro-phytoplankton were recorded in summer. The autumn increase in chlorophyll *a* was attributable to a mixed population of diatoms. There was no consistent relationship between total cell number and chlorophyll *a* as expected for populations with a very wide range in cell size.

In order to show the contributions of individual species or groups of species to phytoplankton biomass, cell volumes were calculated for each species and converted to carbon. The relationship between phytoplankton biomass (mg C m^{-3}), derived from the cell counts, and extracted chlorophyll *a* is shown in Figure 3.19.

The slope of the relationship gives a C/chl ratio of 19, and a positive intercept on the chl *a* (x) axis. Both the low C/chl ratio compared to values in the literature (Geider, 1987) and the inference that some component of chl *a* contains no carbon are consistent with the fact that only micro-phytoplankton were counted. Addition of pico- and nano-phytoplankton carbon would increase the C/chl *a* ratio across the whole range of chlorophyll values. When chlorophyll *a* is low, phytoplankton biomass tends to be dominated by small cells that would not have been counted.

In Figure 3.19, different symbols are used to distinguish samples from the English Channel, the Ushant region and the Bay of Biscay. The distribution of data points within each group is suggestive of regional (or taxonomic) differences in the C/chl *a* ratio. However, the groups are relatively small in size and cover a limited range of chlorophyll *a* values. The relatively high C/chl a ratio (89.0) for the *Karenia mikimotoi* sample is similar to the earlier estimates by Holligan *et al*., (1984a) for this species and not atypical for an autotrophic dinoflagellate.

Table 3-6: Averaged counts of phytoplankton species (cell ml^{-1}) for 2003 between Portsmouth and Bilbao for spring (Spr), summer (Sum), and autumn (Aut) samples. + indicates < 1 cell ml^{-1}. L and S indicate respectively large and small.

Genus and species	(43.6-45.0° N)			(45.0-46.4° N)			(46.4-47.8° N)			(47.8-49.0° N)			(49.0-49.7° N)			(49.7-50.3° N)		
	Spr	Sum	Aut	Spr	Sum	Aut	Spr	Sum	Aut	Spr	Sum	Aut	Spr	Sum	Aut	Spr	Sum	Aut
Diatoms																		
Bacillaria paxillifera																+		
Biddulphia aurita																+		
Cerataulina pelagica																		
Chaetoceros (S)							13		17				2	+			+	
*Chaetoceros (*L)							+									+		
Cosinodiscus oculis-iridis	+	+								+				+		+		
Cylindrotheca closterium				+			1		2	12			+	+		+		
Detonula pumila	2						+		1	+						+		
Ditylum brightwelli				+						+				+		+		
Eucampia sp.	1									+			2					
Guinardia delicatula	7			4		+	2		23	12	+		115	+		8	+	2
Guinardia flaccida	+													+			+	
Guinardia striata	+				+		+				+		5	+		+	+	+
Hemiaulus hauckii								2										
Licmophora sp.																		
Melosira sp.	+						+						2					
Meuniera membranacea									+	3	+		107	+		2	+	
Navicula sp.	+																	+
Odontella mobiliensis																+		
Paralia sulcata						2												2
Pleurosigma	+									+	+			+				+
Pseudo-nitzschia sp.	11	+		4			60	1	33	14	110			5		+	95	1
Rhizosolenia imbricata	+			1	+		1			4			3	+		1	+	
Rhizosolenia setigera									+		+							+
Skeletonema costatum																		
Thalassionema nitzschioides	39						5		24					2		12		4
Thalassiosira rotula														+		+		
Thalassiosira sp.	+			+					+							12		
Autotrophic/ Mixotrophic Dinoflagellates																		
Ceratium azoricum							+											
Ceratium furca	+	+		+			+		+	+				+				+
Ceratium fusus		+		+			+						+	+				
Ceratium lineatum										+	+			+				
Ceratium macroceros	+						+	+		+	+			+				
Ceratium trichoceros											+							
Ceratium tripos	+				+						+							
Dinophysis acuminata										+				+				
Gymnodinium							+		+	+				+				
Karenia mikimotoi	+	+			+		+			+	5			1131			154	
Prorocentrum gracile																		
Procentrum micans								+	+		+			+		+	1	
Scrippsiella trochoidea		+		+		34	3			2	7			+		+	+	2
Coccolithophores																		
Emiliania huxleyi	34			69			0			48	1380			115		11	76	
Sample number	4	5	0	5	3	2	4	4	2	4	4	0	3	8	0	4	3	2
Average chlorophyll *a* (mg m^{-3})	1.1	0.3		1.0	0.2	0.3	1.6	0.2	1.0	2.0	1.1		5.6	12.0		4.1	4.0	0.6
Total (cell ml^{-1})	95	1		77	0	36	88	2	100	99	1503		235	2568		51	328	12

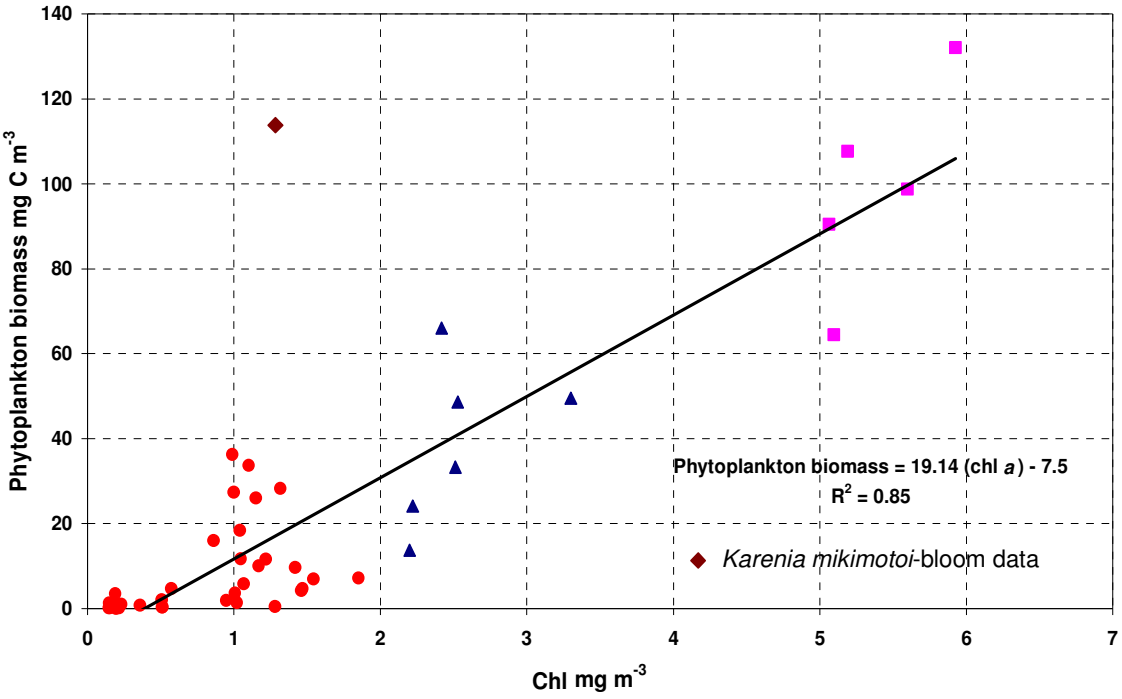


Figure 3.19: The relationship between the phytoplankton C biomass and extracted chlorophyll for 2003. The dark red diamond indicates *Karenia mikimotoi*-bloom for which both the chlorophyll and carbon values have been divided by 50 (this point is not included in the regression analysis). The three different groupings are 1. central English Channel in spring and summer, pink squares; 2. Ushant region in spring and summer, blue triangles; and 3. Bay of Biscay and western English Channel in spring and summer as well as the autumn data for all regions, red circles. Coastal samples are excluded (for more details see the text).

The estimates of phytoplankton species carbon for the main hydrographic regions are summarised in Table 3.7. Comparison of Tables 3.6 and 3.7 shows that small species, such as the diatom *Pseudo-nitzschia* sp. and coccolithophore *Emiliania huxleyi*, contribute relatively little to the total carbon compared to total cell counts whereas larger species such as *Rhizosolenia imbricata* were much more prominent in terms of carbon biomass. Consideration of the whole data set shows that only three species were both major contributors to biomass and widely distributed – they are the diatoms, *Guinardia delicatula* and *Rhizosolenia imbricata*, and the dinoflagellate, *Scrippsiella trochoidea*. An additional three species were locally abundant on the continental shelf – the diatom *Meuneria membranacea*, the dinoflagellate, *Karenia mikimotoi*, and the coccolithophore, *Emiliania huxleyi*.

Table 3-7: Averaged biomass of phytoplankton species (mg C m^{-3}) for 2003 between Portsmouth and Bilbao for spring (Spr), summer (Sum), and autumn (Aut) samples. + indicates < 0.1 mg C m^{-3}. L and S indicate respectively large and small.

	(43.6-45.0° N)			(45.0-46.4° N)			(46.4-47.8° N)			(47.8-49.0° N)			(49.0-49.7° N)			(49.7-50.3° N)		
Genus and species	Spr	Sum	Aut	Spr	Sum	Aut	Spr	Sum	Aut	Spr	Sum	Aut	Spr	Sum	Aut	Spr	Sum	Aut
Diatoms																		
Bacillaria paxillifera																+		
Biddulphia aurita																+		
Cerataulina pelagica																		
Chaetoceros (s)							2.6		3.4				0.2	+			+	
*Chaetoceros (*L)							+									0.2		
Cosinodiscus oculis-iridis	+	+								+				0.1		0.2		
Cylindrotheca closterium	+			+			+		+	0.3			+	+		+		
Detonula pumila	0.7						0.5		0.4	0.3						0.6		
Ditylum brightwelli	+			+						+				+		0.1		
Eucampia sp.	0.2									+			0.3					
Guinardia delicatula	3.9			2.0		0.5	1.3		12.5	6.7	0.2		31.2	0.2		4.4	0.3	0.8
Guinardia flaccida	0.2													0.3			1.8	
Guinardia striata	0.2				+		1.5				0.6		6.1	0.4		0.5	1.5	0.6
Hemialus hauckii								1.5										
Licmophora sp.																		
Melosira sp.	+						0.1						0.5					
Meuniera membranacea									+	3.2	+		52.7	0.2		2.2	+	
Navicula sp.	+																	+
Odontella mobiliensis																0.1		
Paralia sulcata	+					0.3											+	0.4
Pleurosigma	+									0.5	+			+			+	0.2
Pseudo-nitzschia sp.	0.5	+		0.2			2.1	+	1.2	0.5	3.9			0.2		+	3.3	+
Rhizosolenia imbricata	0.2			2.9	+		3.1			10.6			3.6	+		3.4		
Rhizosolenia setigera									0.2		0.1						1.2	0.1
Skeletonema costatum																		
Thalassionema nitzschioides	4.1						0.5		2.5					0.2		1.2		0.5
Thalassiosira rotula														0.1		0.4		
Thalassiosira sp.	0.2			+					0.1							8.7		
Autotrophic/ Mixotrophic Dinoflagellates																		
Ceratium azoricum							0.2											
Ceratium furca	+	0.3		0.2			0.5		+	0.2				+				0.2
Ceratium fusus		+		+			+						+	+				
Ceratium lineatum										0.9	+			+				
Ceratium macroceros	0.2						0.2	0.2		0.2	0.1			+				
Ceratium trichoceros											0.1							
Ceratium tripos	0.2				0.6						0.2							
Dinophysis acuminata										0.2				+				
Gymnodinium sp.							0.3		0.4	1.7				0.4				
Karenia mikimotoi	+	+		+	+		+			0.1	3.1			714.6			96.9	
Prorocentrum gracile																		
Prorocentrum micans	+	+						+	+	+	0.2			0.3		+	2.0	
Scrippsiella trochoidea	0.2	+				37.9	4.4			2.2	8.1			0.4		+	0.5	1.8
Coccolithophores																		
Emiliania huxleyi	0.1			0.7			+			0.5	13.8			1.2		0.1	0.8	
Sample number	4	5	0	5	3	2	4	4	2	4	4	0	3	8	0	4	3	2
Averages chlorophyll *a* (mg m^{-3})	1.1	0.3		1.0	0.2	0.3	1.6	0.2	1.0	2.0	1.1		5.6	12.0		4.1	4.0	0.6
Total (mg C m^{-3})	11.2	1.0	0	5.8	0.7	38.7	17.3	3.9	21.0	28.0	30.4	0	94.6	719.0	0.0	22.3	108.5	9.8

The biomass distributions for diatoms, dinoflagellates and coccolithophores (*E. huxleyi*) are shown in Figure 3.20 b-d. Diatoms were most widespread and abundant in the spring (days 80-135), with localised population in autumn (days 315-346) on the continental shelf and in Spanish coastal waters. In contrast, the main dinoflagellate population was the summer (days 189-192) bloom of *Karenia mikimotoi* in the English Channel although this species was also relatively abundant in spring (days 80-135) in the northern Bay of Biscay and in December (day 346) and at one station in the southern Bay of Biscay. The maximum abundance of *E. huxleyi* occurred in early summer in the northern Bay of Biscay and western English Channel. Comparison of these group distributions to that of chlorophyll *a* (Figure 3.20 a), indicates that phytoplankton biomass along the ferry transect over an annual cycle was dominated by spring and autumn diatoms and the summer bloom of the dinoflagellate, *Karenia mikimotoi*. The general relationship between micro-phytoplankton biomass and chlorophyll also indicates that the combined biomass of pico- and nano-phytoplankton was relatively low and uniform during the year, as suggested by Figure 3.19, with small cells dominating total phytoplankton biomass only at chlorophyll concentrations ≤ 0.5 mg m^{-3}.

A closer look at species biomass distributions (Table 3.7) shows that all of the more abundant diatoms (except *Meuneria membranacea*) were widespread in both oceanic and shelf waters and that those occurring in the autumn were also found in the spring. The highest biomass of *Pseudo-nitzschia* sp. was recorded in summer in the English Channel although to the south, in the Bay of Biscay, it reached a maximum in the spring. A notable feature of the dinoflagellate distribution was that in the northern Bay of Biscay, including the Ushant region, this group was most abundant and diverse in the spring. The scarcity of dinoflagellates in the summer probably reflects the extremely low nutrients in surface waters of the Bay of Biscay at this time of year. The maximum abundance of *Scrippsiella trochoidea* was recorded in early winter in one sample from the southern Bay of Biscay (see Figure 3.20 c) but was not linked to a local increase in chlorophyll *a*. The coccolithophore, *E. huxleyi*, was first recorded in the Bay of Biscay in spring before reaching a maximum biomass on the shelf in early summer.

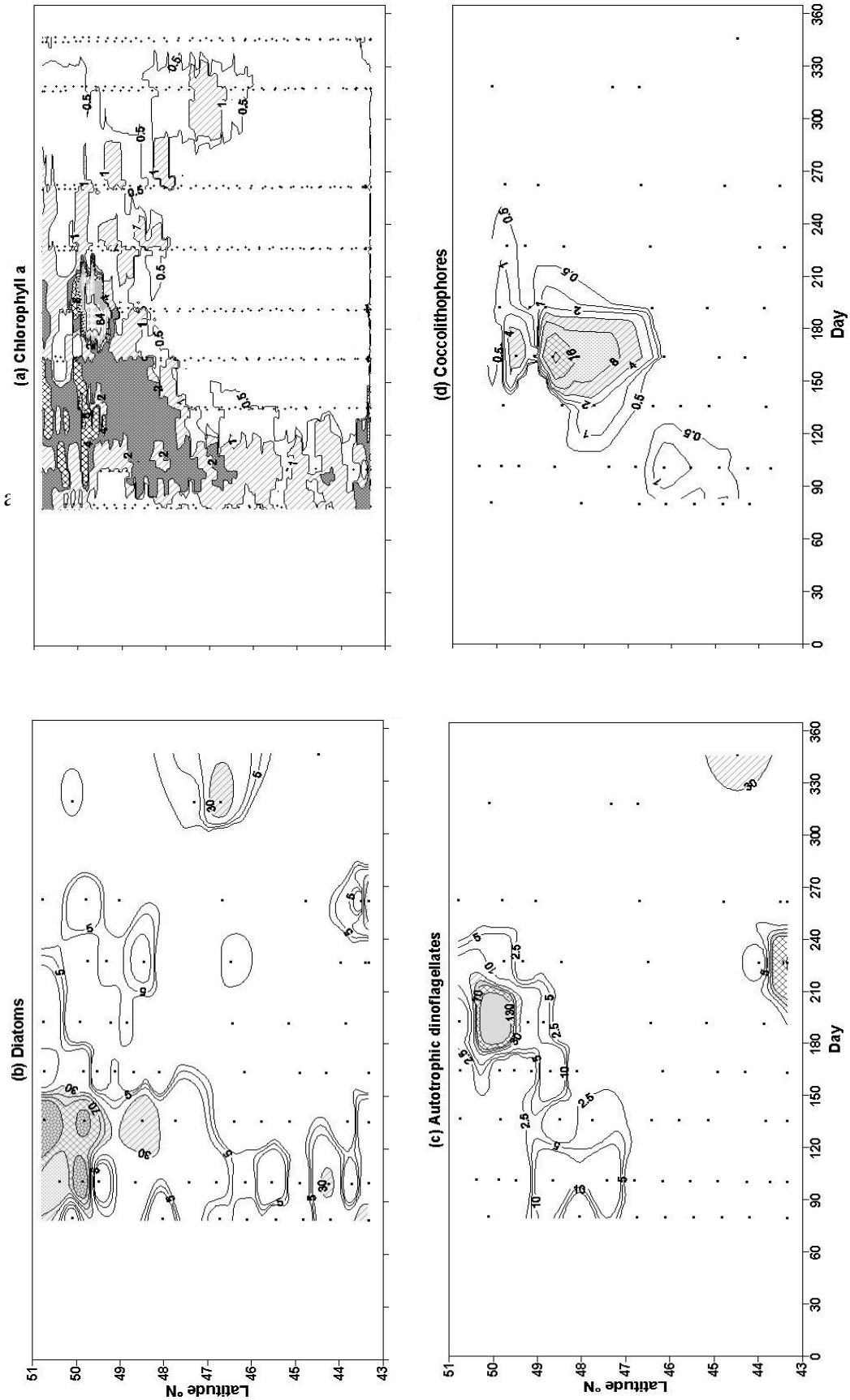


Figure 3.20: Distribution of (a) extracted chlorophyll *a* (mg m^{-3}) and the biomass (mg m^{-3}) of the main phytoplankton groups: (b) Diatoms, (c) Dinoflagellates and (d) Coccolithophores for 2003.

3.3 Zooplankton Data

3.3.1 *Regional abundance*

The zooplankton abundance data were obtained from the Continuous Plankton Recorder (CPR) survey which is operated by the Sir Alister Hardy Foundation for Ocean Science (SAHFOS) as described by Warner and Hays (1994) and Richardson *et al*., (2006). Zooplankton data were selected for the Ferrybox route between Portsmouth and Bilbao for 2003. However, there was no sampling in the Bay of Biscay (43.0-48.0^{o} N) east of 6.0^{o} W from October to December so that, for this region, data from a different route between 7.0^{o} and 10.0^{o} W were used instead.

The abundance of herbivorous copepods was investigated as they prey directly on phytoplankton. Their biomass (B) was calculated according to Peters (1983) and Richardson et al. (2006):

$$\mathbf{W = (0.08L^{2.1})} \qquad (3a)$$

$$\mathbf{B = \sum_{i=1}^{N}(W_i \times X_i)} \qquad (3b)$$

where W is the mass (mg wet weight) estimated from body length L (mm) for each species i (obtained from the literature - see Richardson *et al*., 2006), X is the abundance of a species and N is number of all species.

Figure 3.21 shows the average biomass of herbivorous copepods for day and night samples combined. There was no significant difference ($P > 0.05$) between day and night samples, suggesting that the general distributional patterns were not biased by diel vertical migration. The mean biomass of herbivorous copepods was found to differ significantly ($p < 0.05$) among the three regions (western and central English Channel and central Bay of Biscay), with higher copepod biomass ($P < 0.05$) in western English Channel waters than in the other two regions (Figure 3.21).

3.3.2 *Seasonal abundance*

Figure 3.22 shows the distribution of herbivorous copepods for 2003 between Portsmouth and Bilbao. In the central Bay of Biscay, increases of herbivorous copepod biomass were observed in March and April (days 75-105) around 45.0^{o} N where *Paracalanus* sp., *Pseudocalanus* sp., *Clausocalanus* sp. and *Calanus helgolandicus* (Claus,1863) were the dominant species. The biomass of most of the copepod was

relatively low in summer (days 165-195) but increased in the autumn with *Temora stylifera* (Dana, 1849), *Pseudocalanus elongates* (Boeck, 1872), *Paracalanus* sp., *Pseudocalanus* sp. and *Clausocalanus* sp. the most abundant species.

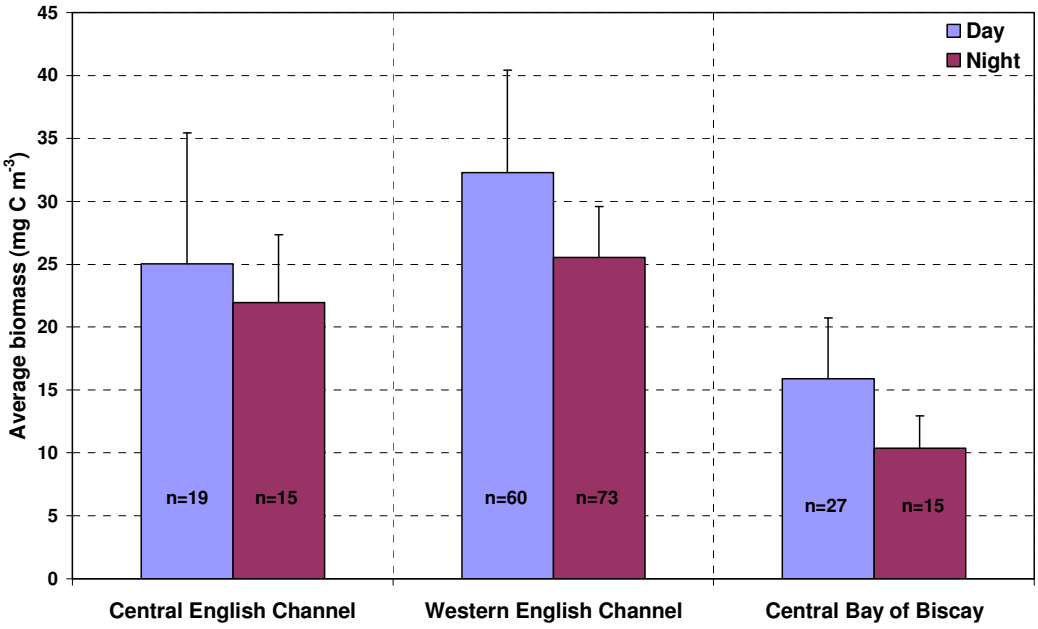


Figure 3.21: Day and night surface distributions of average biomass (mg m^{-3}) of herbivorous copepods in the central and western English Channel, and in the central Bay of Biscay in 2003. N indicates the number of samples, bars show standard errors.

Compared to the Bay of Biscay, the herbivore biomass in western and central English Channel (49.0-50.3° N) reached a maximum somewhat later in spring and remained high through the summer before declining in late autumn (Figure 3.22). In the western English Channel, the dominant species were *Calanus helgolandicus*, *Para-pseudocalanus* sp. and *Pseudocalanus elongates* whereas in the central English Channel the most abundant copepods were *Clausocalanus* sp., *Pseudocalanus elongates*, *Calanus* sp. and *Calanus helgolandicus* in spring (days 100-160), and *Calanus helgolandicus* and *Calanus* sp. in summer (days 195-260).

The main increases in herbivore abundance in the spring appeared to occur at about the same time or after the main increases in chlorophyll *a* (compare Figure 3.22 with Figures 3.14, 3.15 and 3.16). A possible exception was the Ushant region (48.0° N) where the biomass of herbivorous copepods exceeded 50 mg m^{-3} as early as day 50 but the main increase in chlorophyll did not occur until after day 90.

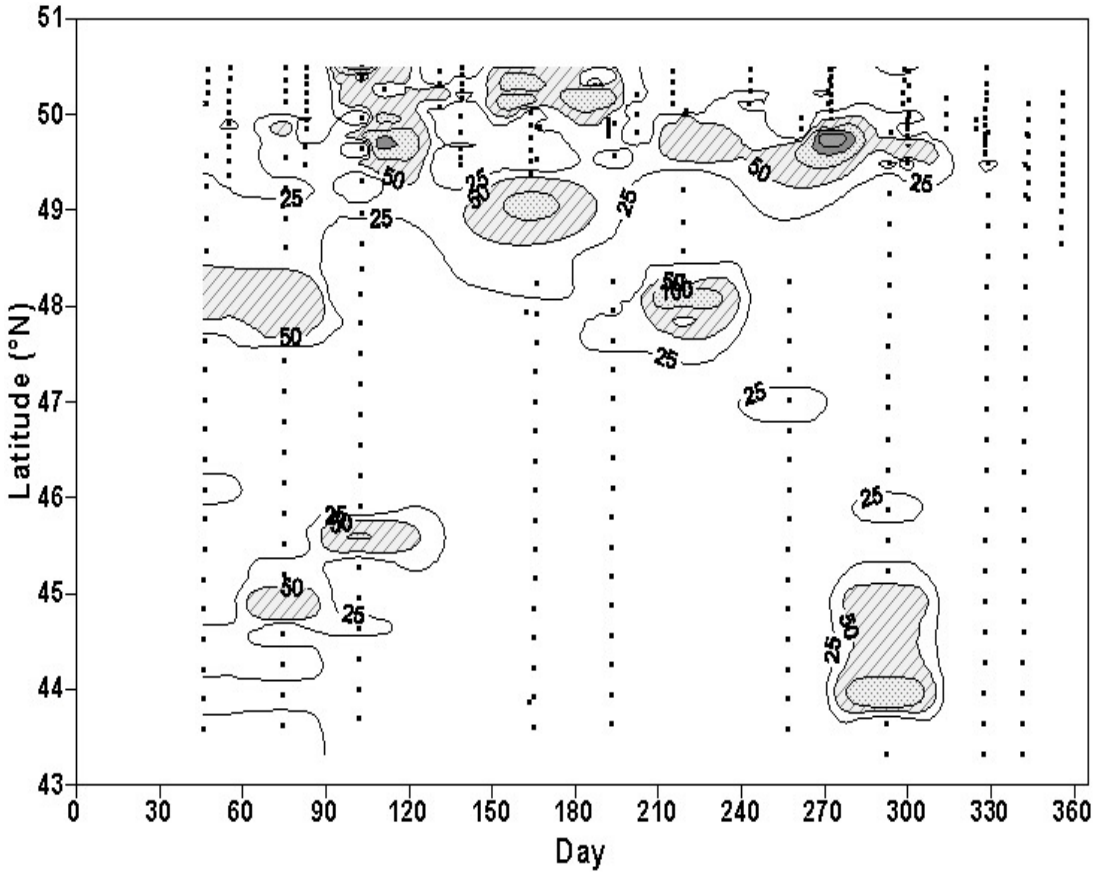


Figure 3.22: Surface distribution of the biomass (mg m^{-3}) of herbivorous copepods between Portsmouth and Bilbao in 2003.

3.4 Summary

The climatic and hydrographic data obtained for 2003 were typical of the oceanic and shelf sea environments of the NE Atlantic Ocean (Waniek, 2003; Puillat *et al.*, 2004; Edwards *et al.*, 2006). In response to the increasing irradiance and decreasing wind strength in the spring and summer surface water temperatures reached a maximum in late July / early August. This warming was strongest in the south of the study area and in regions of weak tidal mixing on the continental shelf. Shelf sea tidal fronts were marked by strong gradients in temperature between warm, seasonally-stratified waters and cold, well mixed waters. Surface salinity distributions reflected the influence of small rivers flowing into coastal waters off Spain and England, and of the relatively large Gironde and Loire Rivers feeding into the Bay of Biscay. A well-defined low salinity anomaly, which formed in the northern Bay of Biscay in late winter after the peak of river outflow was advected into the English Channel during the summer.

The three different methods (fluorescence, acetone extractions and satellite estimates) used for estimating surface chlorophyll *a* concentrations provide consistent and complementary (in time and space) information about the development of phytoplankton populations over the annual cycle. Chlorophyll *a* values were generally higher in shelf waters compared to oceanic waters. The spring phytoplankton bloom reached its peak during March in the southern part of the transect and during April on the continental shelf to the north, with maximum chlorophyll *a* values typically 2.0-4.0 mg m^{-3}. An intense summer bloom was detected in the tidal frontal region of the English Channel, giving chlorophyll *a* concentrations up to 70.0 mg m^{-3}. A distinct autumn increase in chlorophyll *a* was observed in the northern Bay of Biscay (Figures 3.14, 3.15 and 3.16). The timing of depletion of surface nutrients during the spring corresponded well with chlorophyll *a* distribution at this time of year.

Investigation of the composition of phytoplankton populations by a combination of light microscopy and HPLC pigment analysis showed that diatoms dominated the spring bloom to be replaced in summer by low numbers of dinoflagellates. During early summer the coccolithophore, *Emiliania huxlyei*, was widespread in oceanic and stratified shelf waters; bloom proportions were reached in terms of cell density (> 1000 cells ml^{-1}) in stratified shelf although maximum levels of chlorophyll *a* were generally only ~1.0 mg m^{-3}. The summer frontal bloom in the English Channel, which was associated with the advected low salinity water, was composed of an almost monospecific population of the dinoflagellate, *Karenia mikimotoi*, giving cell densities up to 8000 cells ml^{-1}.

The information on the distributions of herbivorous zooplankton (copepods) obtained from the CPR survey was relatively sparse compared to that for phytoplankton. The most notable features were the high abundance of herbivores in shelf waters compared to off shelf waters, and in contrast, the scarcity of herbivores within the bloom of *K. mikimotoi* on shelf waters.

In comparison to earlier data (Pingree *et al.*, 1982; Holligan *et al.*, 1984a; Fernandez *et al.*, 1993; Varela, 1996; Moore *et al.*, 2003) for the Bay of Biscay and English Channel, the data reported here for 2003 appear to be typical.

CHAPTER 4

4.ENGLISH CHANNEL AND BAY OF BISCAY 2004

Data for 2003 on surface hydrography and plankton distributions along the Portsmouth – Bilbao ferry track have been described in Chapter 3. In this chapter, the corresponding results for 2004 are presented.

4.1 Environmental data

4.1.1 *Climatic data*

Light

Figure 4.1 shows the spatial and temporal variability of total solar radiation values between Portsmouth and Bilbao during 2004. The monthly mean total solar radiation varied

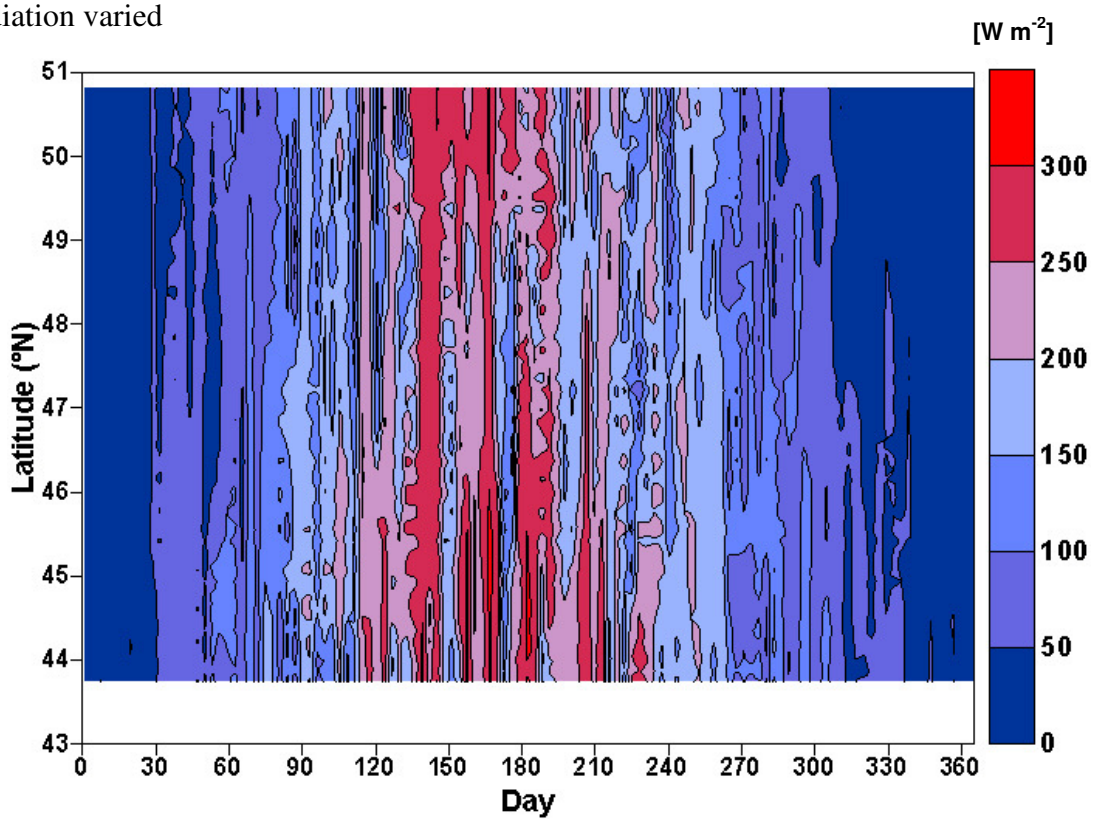


Figure 4.1: Distribution of daily surface solar radiation values for 2004 between Portsmouth and Bilbao derived from the UK Met Office NWP. (*X*-axis: day 1=1st of January). Note that no data are available for the coast of Spain (43.3°-43.6° N).

between 22 W m^{-2} in December (days 335 - 365) and 252 W m^{-2} in June (days 152 - 181) (see Table 4.1). Values fluctuated more in 2004 compared to 2003 (Tables 3.1 and 4.1, and Figures 3.1 and 4.1), and there were statistical differences (t-test unequal variances) between the two years ($p < 0.05$). In general the shelf north of 49.0° N received more light in 2004 than in 2003 for the period April to June (days 91-181). For example, the solar radiation value in April for central English Channel (49.7-50.3° N) was 171 W m^{-2} in 2004 compared to 118 W m^{-2} in 2003, and in May and June solar irradiance for the English Channel north of 49.0° N was 5-10 % higher than in 2003.

River discharge

Discharge rates from the Loire and Gironde Rivers between January and July (days 1-212) are shown in Figure 4.2. In 2004, the combined outflow was significantly higher (Mann-Whitney test $p < 0.05$) than in 2003 both during the period of peak flow at the beginning of the year and during the spring and early summer (compare Figures 3.2 and 4.2). In 2004 the flow exceeded 5000 m^3 s^{-1} for over three weeks in late January to early February (days 19-33). It then remained at or above 2000 m^3 s^{-1} until mid-May (day 137) with a secondary peak (average 3397 m^3 s^{-1}) between days 122 and 137 (Figure 4.2). By comparison, the flow rates in 2003 (Figure 3.2) fell to < 2000 m^3 s^{-1} by mid-March, and were about half those of 2004 during May.

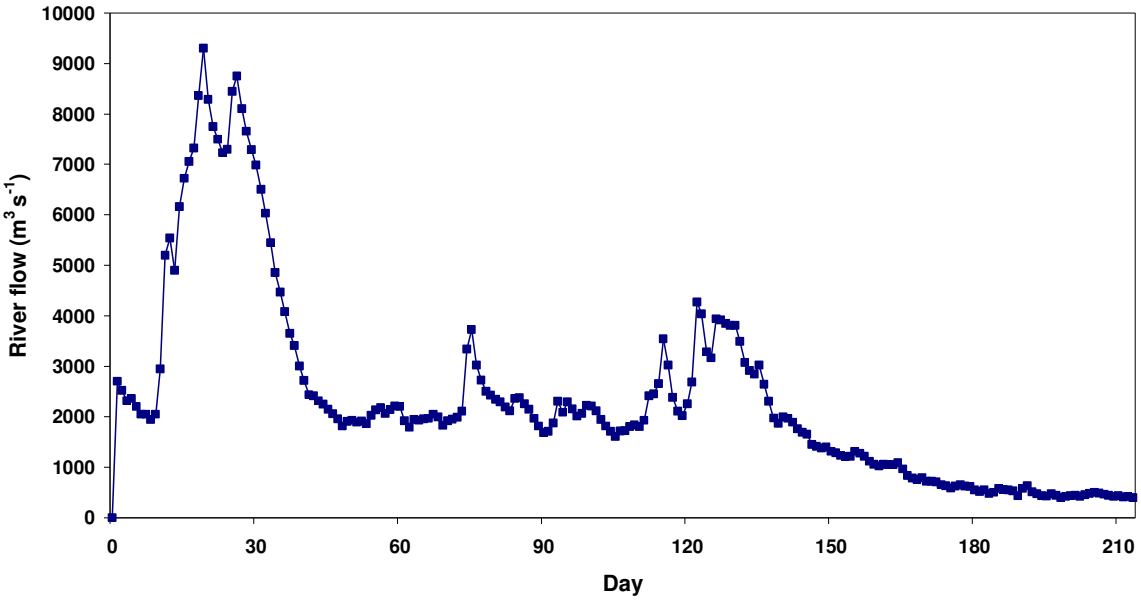


Figure 4.2: Daily-averaged river flow from the Loire and Gironde Rivers for January to July 2004, obtained by B. Kelly-Gerreyn from the Bordeaux Port Authority, France.

Wind

Figure 4.3 shows the daily-averaged wind speeds for the English Channel and the Bay of Biscay in 2004. As in 2003, the frequency of high wind speeds was greater in the English Channel than in the Bay of Biscay. A notable feature of 2004 record was high wind speeds (> 10 m s^{-1}) in the English Channel recorded in mid-summer between days 175-190 (Figure 4.3).

The annual and quarterly wind roses for English Channel and Bay of Biscay in 2004 are shown in Figure 4.4. A comparison of the quarterly wind roses for 2003 (Figure 3.4) and 2004 shows that southwest winds were more frequent and stronger during the winter of 2004 in both regions. Also spring 2004 was characterised by strong northwest winds in the English Channel, and by less strong northeast winds in the Bay of Biscay, whereas in 2003 southwest winds had been relatively frequent in both regions. Northwest winds continued to be a feature of the 2004 summer in the English Channel with an almost complete absence of easterly winds.

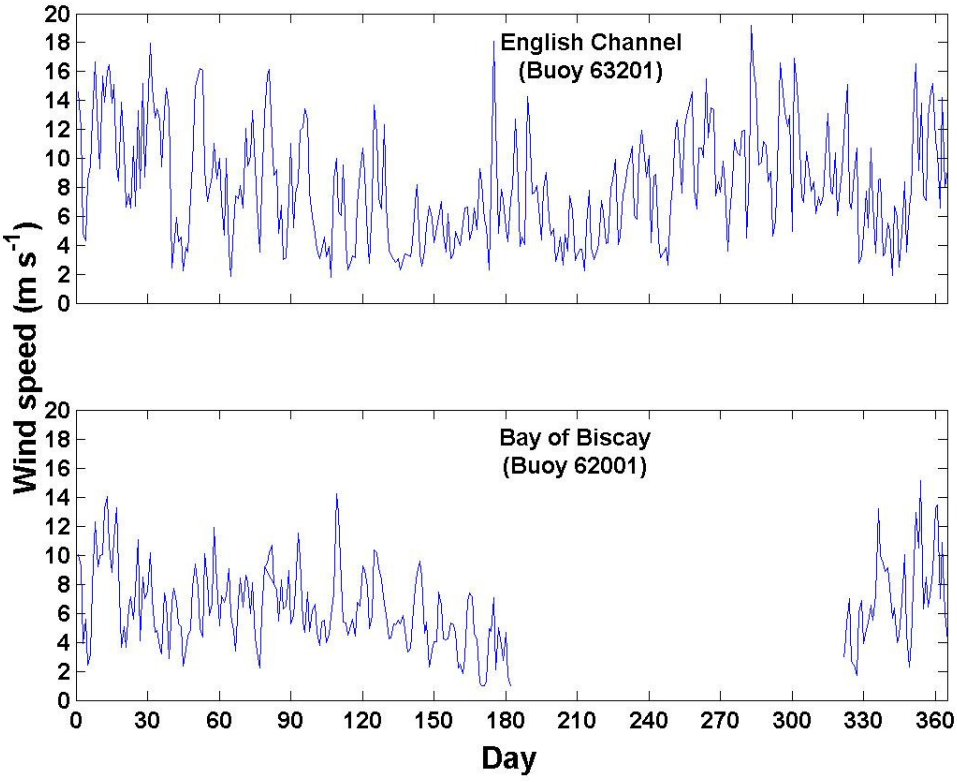


Figure 4.3: Daily-averaged wind speed (m s^{-1}) for the English Channel and Bay of Biscay for 2004. Data were provided by UK Meteorological Office from two moored buoys: 63201 (English Channel at 49.9° N 2.9° W) and 62001 (Bay of Biscay at 45.2° N 5.0° W). Note that no data were recorded in the summer by the Bay of Biscay buoy.

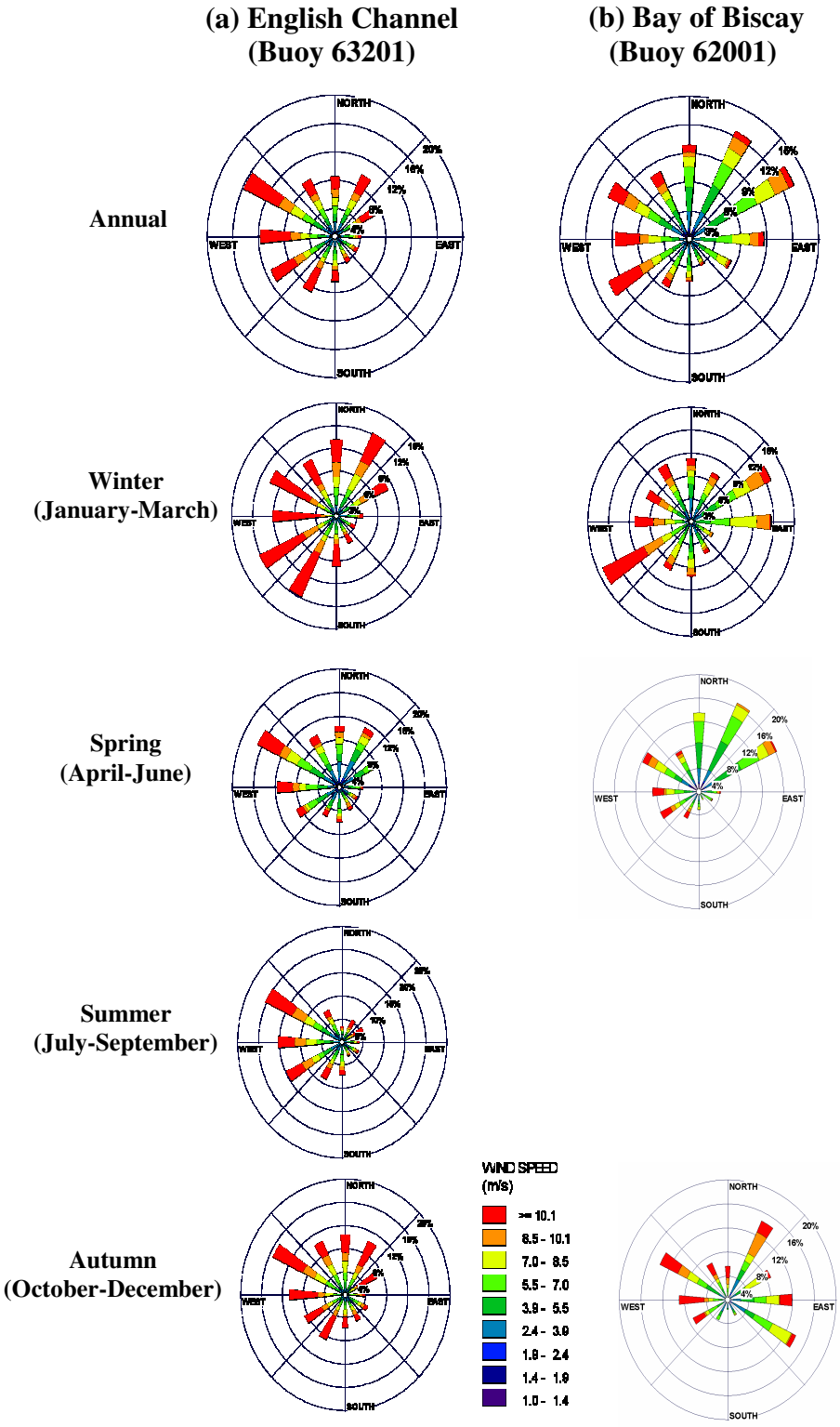


Figure 4.4: Annual and quarterly windroses (wind strength and wind direction) for (a) English Channel and (b) Bay of Biscay in 2004. Data were provided by UK Meteorological Office from two moored buoys: 63201 (English Channel at 49.9° N 2.9° W) and 62001 (Bay of Biscay at 45.2° N 5.0° W). Note that no data were recorded in the summer by the Bay of Biscay buoy.

4.1.2 *Temperature*

Sea surface temperatures (SST) for 2004 are shown in Figure 4.5 and summarised in Table 4.1. They increased from north to south as in 2003, but compared to 2003 were cooler in the southern Bay of Biscay early in the year, in the Ushant region and western English Channel in early July (days 182-200), and in the central English Channel throughout July (Tables 3.1 and 4.1). By contrast, water temperatures were warmer in 2004 in coastal waters of the English Channel (50.3-50.8^{o} N) between April and July (days 90-212), probably as a result of relatively high solar irradiance during spring and early summer (see Tables 3.1 and 4.1), and along the whole transect except English coastal waters late in the year. The difference between the two years in early July was as much as 2^{o} C as clearly shown by the AVHRR images of sea surface temperature for 6-12 July in 2003 (see Figure 3.8) and for the corresponding period in 2004 (Figure 4.6) which followed a period of relatively unsettled weather (see Figure 4.3). The July difference for the central English Channel appears to be related to the development of the dinoflagellate bloom in 2003 which was associated with anomalously warm surface temperatures (see Chapter 3).

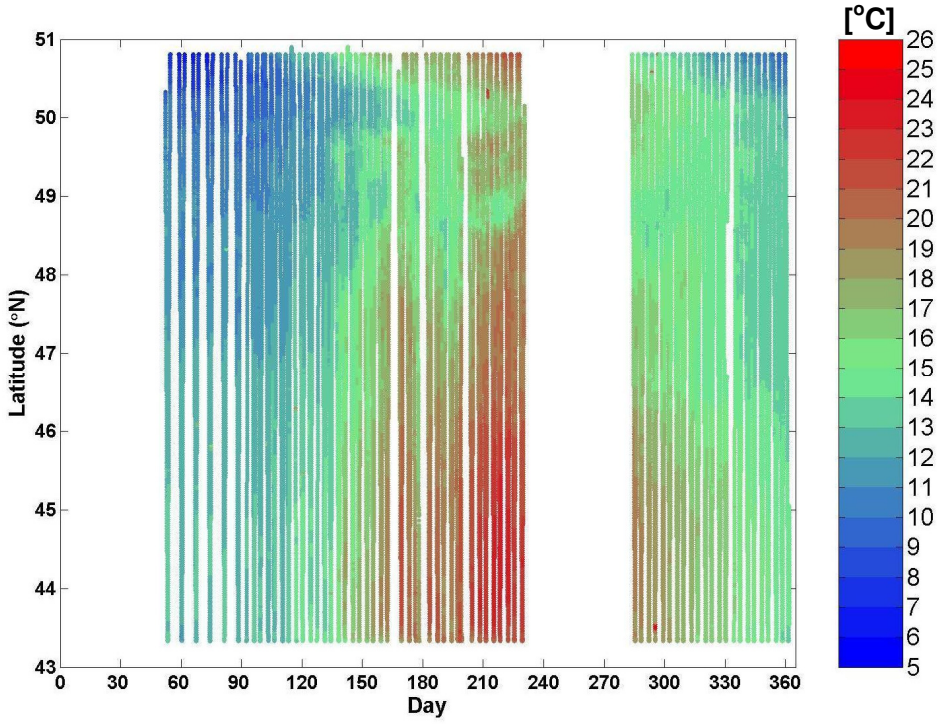


Figure 4.5: Distribution of sea surface temperature (^{o} C, five-minute averaged values) for 2004 between Portsmouth (UK) and Bilbao (Spain) from the FerryBox MiniPack.

Table 4-1: Monthly averaged total daily solar irradiance (L) W m^{-2}, temperature (T) ^{o}C, and salinity (S) for 2004 between Portsmouth and Bilbao. The irradiance data were derived from the Met Office NWP, and temperature and salinity data (five minute averages) from the FerryBox MiniPack. Note that no data are available for the coast of Spain (43.3^{o}-43.6^{o} N).

Month (days)	(43.3-43.6° N)			(43.6-45.0° N)			(45.0-46.4° N)			(46.4-47.8° N)			(47.8-49.0° N)			(49.0-49.7° N)			(49.7-50.3° N)			(50.3-50.8° N)		
	L	T	S	L	T	S	L	T	S	L	T	S	L	T	S	L	T	S	L	T	S	L	T	S
February (53-60)	x	12.8	34.22	93	13.0	34.87	85	12.9	35.08	78	12.2	35.02	72	11.4	34.76	80	10.8	34.89	88	10.1	34.73	93	7.8	34.02
March (61-90)	x	12.7	34.12	123	12.9	35.00	119	12.8	35.25	113	11.9	35.12	95	11.0	34.55	90	10.3	35.00	93	9.7	34.94	96	7.9	34.17
April (91-120)	x	13.3	34.44	180	13.4	35.45	187	13.2	35.62	165	12.4	35.28	154	11.5	35.10	161	10.9	35.20	171	10.3	35.31	177	10.2	34.52
May (121-151)	x	15.0	34.79	219	15.1	35.31	219	14.8	35.60	215	14.0	35.06	203	12.9	35.10	219	12.7	35.16	218	11.8	35.28	223	13.0	34.62
June (152-181)	x	17.9	34.69	236	19.0	35.73	232	18.4	35.89	212	17.4	35.15	208	15.7	35.09	226	15.1	35.43	246	13.5	35.51	252	15.6	34.92
July (182-212)	x	20.1	34.60	230	20.9	35.82	214	20.2	35.93	204	18.3	35.37	187	15.9	35.27	194	16.1	35.56	201	15.3	35.57	206	17.2	35.00
October (274-304)	x	18.5	34.89	106	18.8	35.77	100	18.2	35.74	90	16.3	35.60	81	14.8	35.70	75	15.3	35.73	69	15.9	35.58	74	15.1	35.40
November (305-334)	x	16.7	34.60	58	16.7	35.80	56	16.4	35.79	48	15.0	35.70	40	14.8	35.50	41	14.6	35.73	39	14.7	35.60	36	13.3	35.37
December (335-365)	x	14.8	34.73	33	15.1	35.75	33	14.8	35.90	26	13.8	35.70	23	13.6	35.70	22	13.7	35.70	25	13.4	35.61	25	11.1	35.39

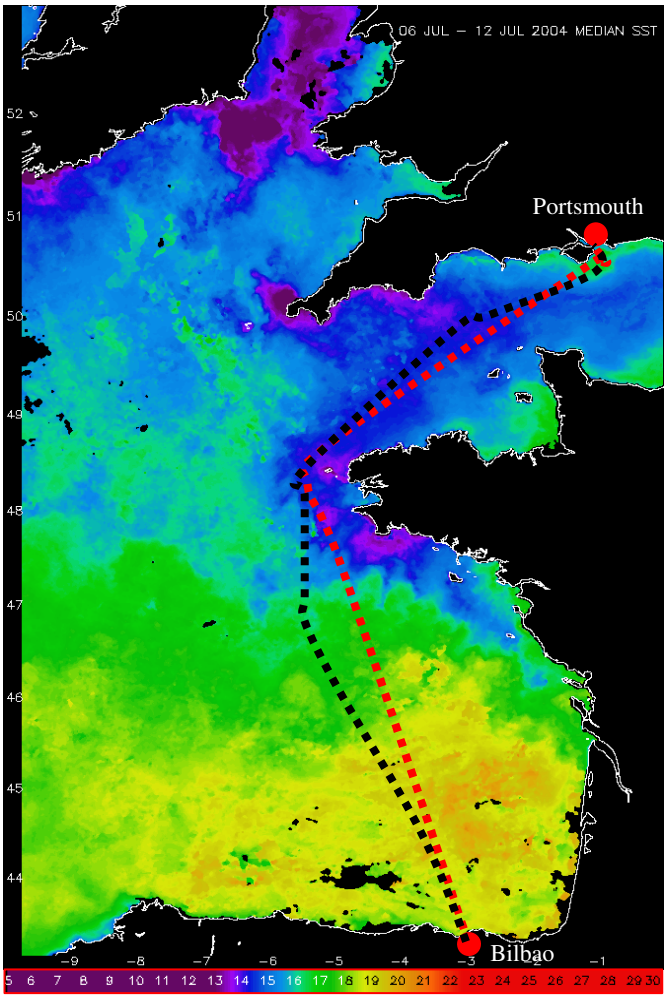


Figure 4.6: Sea surface temperature distribution in the Western English Channel and Bay of Biscay derived from Advanced Very High Resolution Radiometer (AVHRR) images for 6-12 July 2004. The black and red dots represent the tracks of R V Pride of Bilbao (8-11 July 2004) from Portsmouth and from Bilbao respectively.

The relationship between irradiance and sea surface temperature for the Ushant region and central Bay of Biscay (Figure 4.7) followed a similar pattern to that observed in 2003 (see Figure 3.6). In late June and early July 2004 (days 175- 190), the combination of relatively low solar radiation values and strong winds (see Figure 4.3) for the time of year, especially in the English Channel, was associated with a marked fall in surface temperature in the Ushant region as indicated by the red arrow in Figure 4.7.

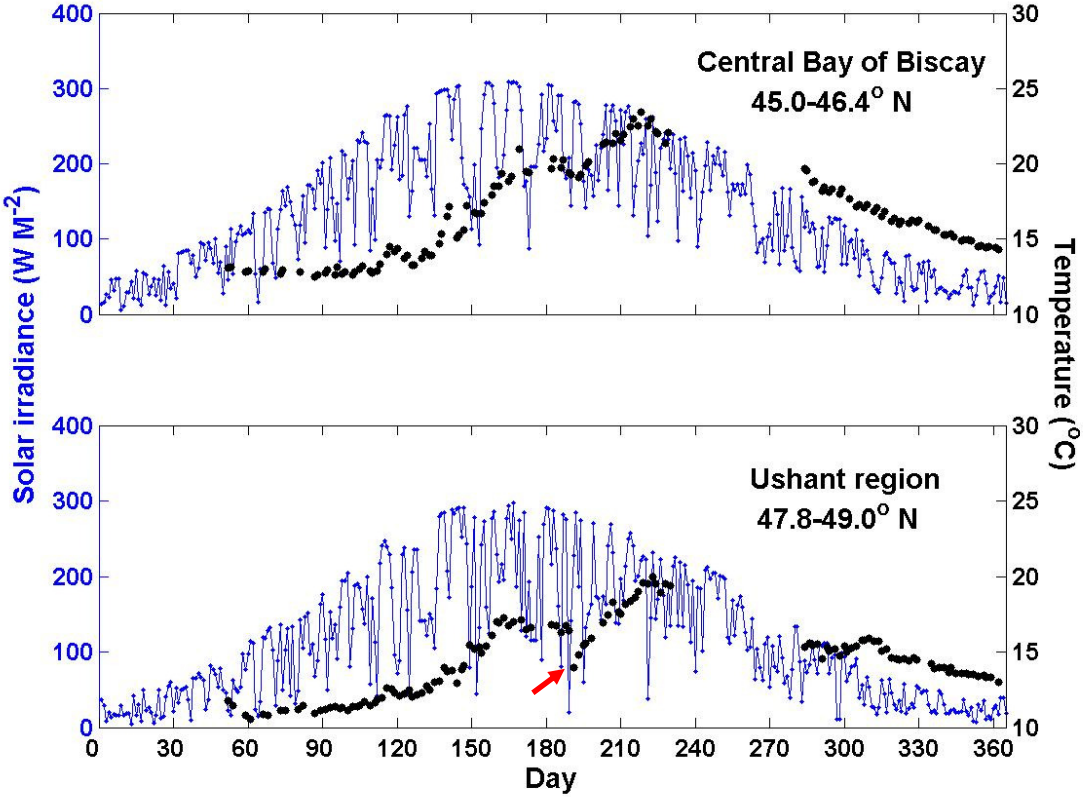


Figure 4.7: The relationship between daily-averaged surface solar irradiance (W m^{-2}) derived from the Met Office NWP and daily-averaged surface temperature (^{o} C) from the FerryBox MiniPack for Bay of Biscay (45.0-46.4^{o} N) and Ushant region (47.8-49.0^{o} N) in 2004. The red arrow shows low solar irradiance and temperature in the Ushant region in early July.

Transects of surface temperature between Bilbao and Portsmouth for July 2004 are shown in Figure 4.8. Rapid warming occurred during mid-month especially in the southern Bay of Biscay where temperature values approached or even slightly exceeded those of 2003 by the end of the month. The shelf region between 46.4-50.3^{o} N was again characterised by wide fluctuations of temperature associated with the frontal boundaries, but these were generally somewhat less coherent over time than observed in 2003 (compare Figures 3.7 and 4.8). The reasons for this difference are likely to be

associated with spring and neap cycle and the consequent variation in the position and structure of the frontal boundary between mixed and stratified waters.

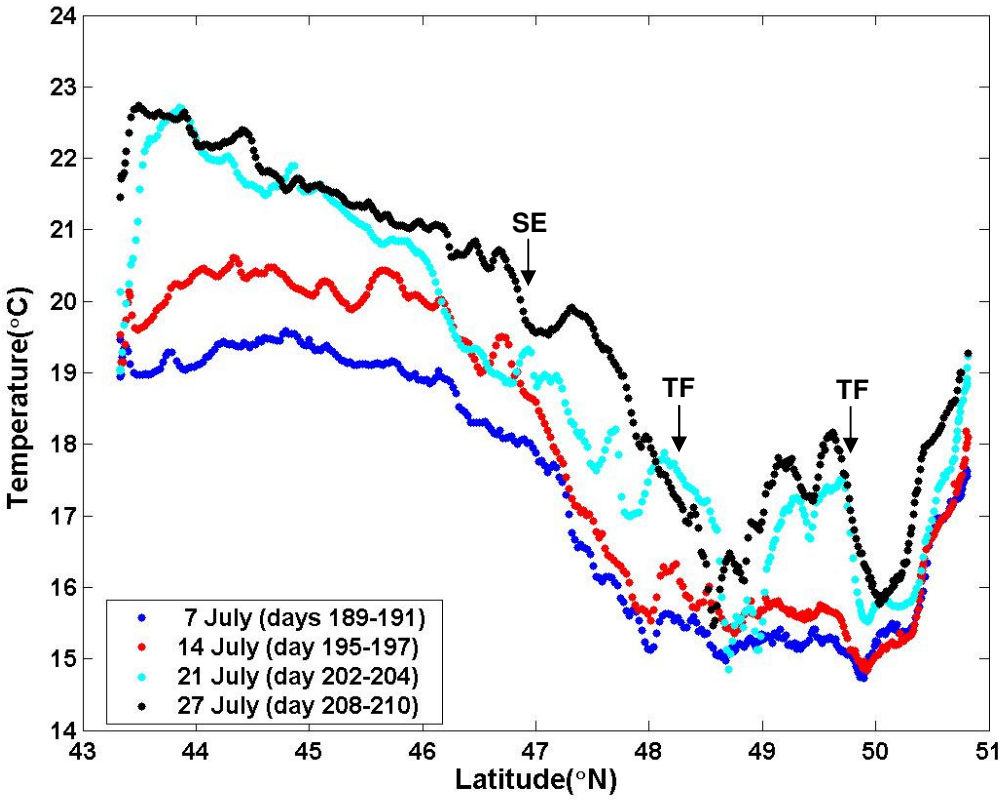


Figure 4.8: Transects of sea surface temperature (^{o} C) for July 2004 between Portsmouth (P) and Bilbao (B). SE and TF indicate respectively the shelf edge and tidal fronts.

A more detailed view of the western English Channel is shown by the composite AVHRR image of sea surface temperature for late July 2004 (days 25-31) (Figure 4.9). The contrast along the ship's track between the Ushant region (cold, mixed water) (48.5- 49.0^{o} N), the western English Channel (warm stratified water) (49.0 - 49.7^{o} N), and the central English Channel (cold, well mixed water) (49.7-50.3^{o} N) compares well with the ship observations for the second half of July (Figures 4.8 and 4.9).

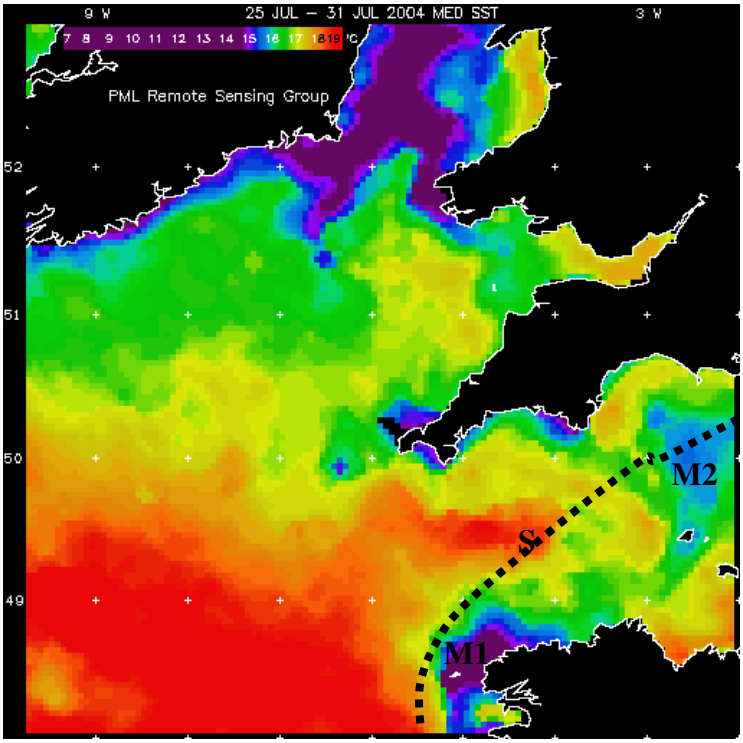


Figure 4.9: Sea surface temperature distribution in the western English Channel derived from Advanced Very High Resolution (AVHRR) images for 25-31 July 2004. The black dots represent the track of the R V Pride of Bilbao (27 July 2004) from Portsmouth. M1 and M2 indicate mixed waters around Ushant and in the central English Channel, and S stratified waters in the western English Channel.

4.1.3 *Salinity*

Figure 4.10 shows the changes in surface salinity for 2004. As in 2003 (Figure 3.9), salinity was generally lower in the northern region compared to southern regions, and low salinities (generally < 34.8) were observed close to the coasts of Spain and England.

At the end of February, salinity was lower in 2004 along the whole transect compared to 2003 probably as a result high flows from the French rivers early in the year (Figure 4.2). Subsequently a salinity anomaly (35.0-35.2) extended northwards (and eastwards) into the English Channel (Figure 4.10) but this feature was considerably less pronounced than the corresponding one in 2003 (see Figure 3.9) despite the lower input of fresh water that year. In contrast, south of 48.0^{o} N, an extensive patch of relatively low salinity (< 34.6) water developed during May, extending to the outer shelf around 47.0^{o} N (see the black arrows in Figure 4.11). The coincided with high

outflows from the Gironde and Loire rivers that persisted until mid-May (Figure 4.2). A small patch of low salinity (< 35.4) water was also observed in 2004, south of 45.0° N around day 215 but no information is available to determine the likely origin of this water.

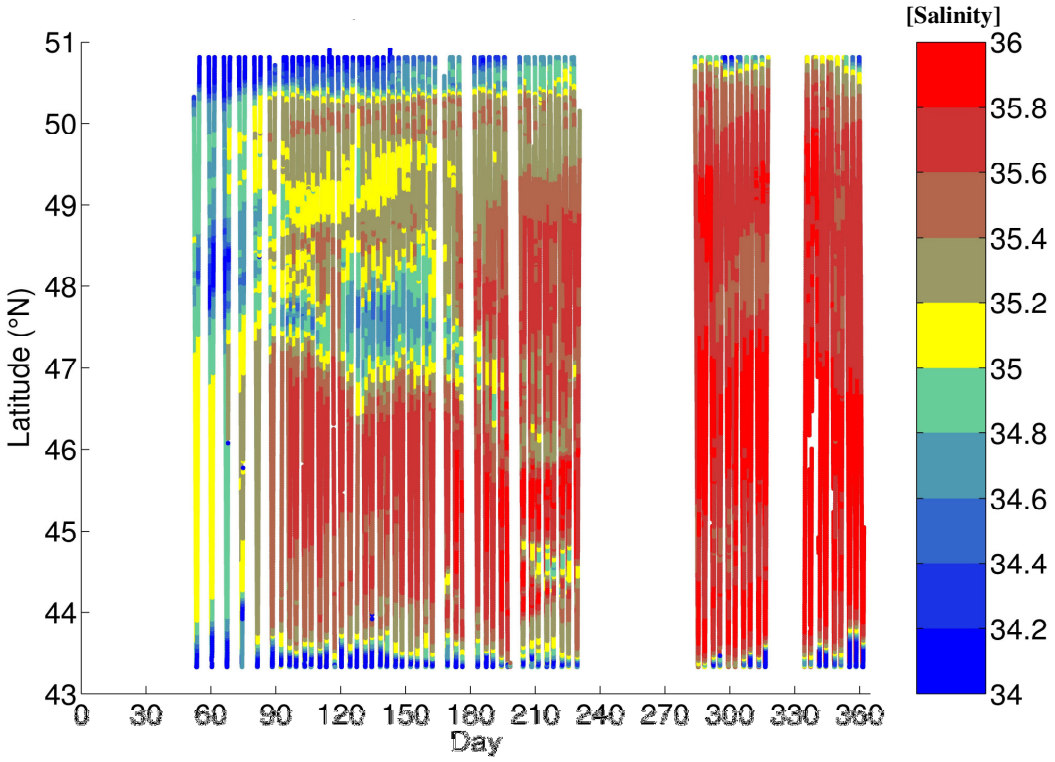


Figure 4.10: Distribution of salinity (five-minute averaged values) between Portsmouth (UK) and Bilbao (Spain) for 2004 from the FerryBox MiniPack.

The different patterns of salinity distributions for 2003 and 2004 reflect differences in river flows from France and in prevailing winds during the first half of the year. It appears that in 2004 relatively little fresh water penetrated the English Channel despite persistently high river flows. This may be because of stronger winds from between west and north during the spring months (Figure 4.4) which would have driven the fresher water southwards into the Bay of Biscay rather than northwards into the English Channel. It also seems that relatively low surface water temperatures over the outer shelf south of 48.0° N during spring and early summer (Table 4.1; Figure 4.5) were linked to the presence of the relatively low salinity water in this region (Figure 4.11).

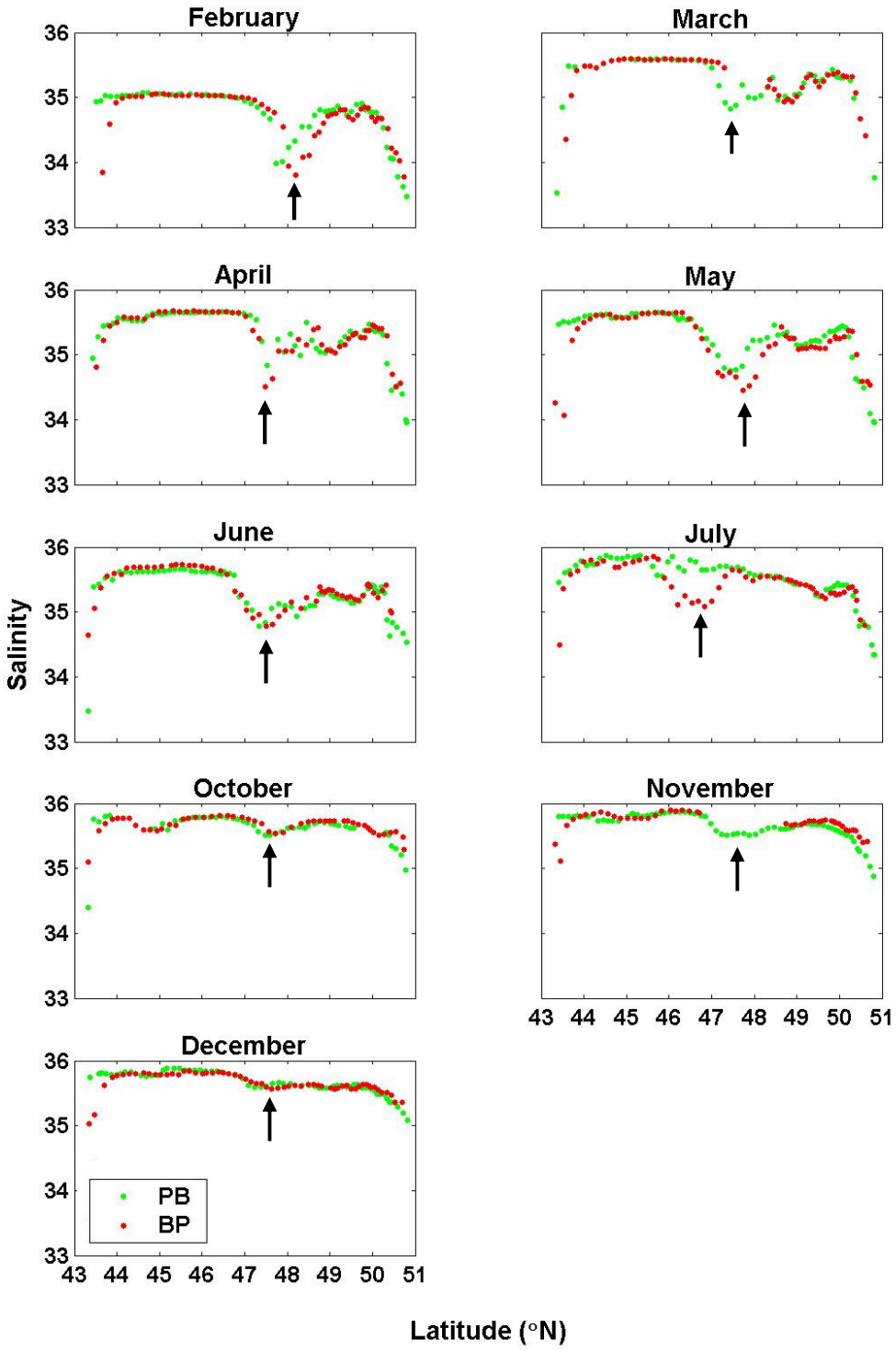


Figure 4.11: Plots of salinity (five-minute averaged values) from FerryBox MiniPack on all the calibration crossings in 2004. The green and red dots represent the tracks from Portsmouth (P) and from Bilbao (B) respectively. The arrows show the low salinity water patch that persisted during summer in the northern Bay of Biscay (see Figure 4.10). Note that no data are available for August and September.

4.1.4 *Inorganic nutrients*

Figure 4.12 shows the spatial and temporal distributions of nutrients (nitrate, phosphate and silicate) between Portsmouth and Bilbao in 2004. The monthly means of nutrients for different segments of the transect are presented in Table 4.2.

Nitrate (also see Appendix 5)

The highest nitrate concentrations were observed across all regions in February (days 59-60) with means that ranged from 23.1 and 16.1 µM in the coastal waters of Spain and English Channel respectively and to 5.2 µM in central Bay of Biscay (Table 4.2). The lowest concentrations were recorded in June and July (days 160–198), and ranged from < 0.1 µM in the central and northern Bay of Biscay to 0.3 µM in the central English Channel (Table 4.2).

There were significant differences between the year with respect to the timing of nitrate depletion associated with phytoplankton growth in spring. Comparison of Figures 3.11a and 4.12a shows that nitrate was removed in 2004 relatively late in the Bay of Biscay and relatively early in the English Channel. For example, in 2004 in parts of the western English Channel (49.0-49.7^{o} N), nitrate levels were between 2.0 and 4.0 µM by day 100 (early April), whereas the corresponding figures for 2003 were 4.0-8.0 µM. Conversely, in the southern, central and northern Bay of Biscay (south of 47.0^{o} N) around day 80 (mid-March) nitrate concentrations were 0.5-4.0 µM in 2004 compared to < 0.1-2.0 µM in 2003 (Figures 3.11a and 4.12a). Possible reasons for these differences are the effects on phytoplankton growth of relatively high irradiance in the English Channel (Table 4.1) and relatively high winds (surface mixing) in the Bay of Biscay (Figure 4.3) in 2004.

Unfortunately, a similar comparison for the timing of the autumn increase in nitrate is not possible due to a lack of suitable observations between days 200 and 290 during 2004 although, in the southern Bay of Biscay, very low concentrations persisted through November in 2004 but not in 2003.

The relationships between nitrate and salinity are illustrated in Figure 4.13. As for 2003, the inverse linear trend between these variables during the winter and early spring months (February- May II) suggests that river water carries significant additional nitrate into the ocean. However, the relatively small range of salinity away from the

coast suggest that annual differences in fresh water inputs are unlikely to have a large effect on nitrate concentrations over the region as a whole. There was no relationship between nitrate and salinity in summer (days 160-198), which indicates that freshwater sources of nitrate become fully utilised within the marine environment (Figure 4.13). In June, the persistence of nitrate concentrations $\geq$ 2.0 µM at salinities between 35.0 and 35.5 (Figure 4.13 and Appendix 5) reflects relatively slow biological utilisation in the deep, tidally well-mixed waters around Ushant.

Phosphate

Maximum average phosphate concentrations in winter and early spring (days 59-89) ranged from 0.63 µM in coastal water of Spain to 0.17 µM in the southern Bay of Biscay, and minimum average concentrations in summer (days 160-198) ranged from 0.05 µM in the western and central English Channel to 0.02 µM in the central Bay of Biscay (Table 4.2 and Figure 4.12b). Similar ranges were observed in 2003 (Table 3.2) although the summer minima were generally not quite as low. Also as for nitrate, high values (up to 1.1 µM) were measured off coastal waters of Spain in the summer months of 2004 (Table 4.2).

The removal of phosphate in spring and early summer (days 87-163) of 2004 followed a similar pattern to that of nitrate, being earlier than 2003 in the English Channel and later than 2003 in the Bay of Biscay (Figures 3.11b and 4.12b). Another difference between the two years was that in 2004 anomalously high phosphate values were not detected in the English Channel in summer as had occurred as in 2003 in association with a dinoflagellate bloom (Figures 3.11b and 4.12b).

Silicate

The highest average silicate concentrations in winter ranged from 15.0 µM in the coastal water of Spain to 1.9 µM in the central Bay of Biscay, and the lowest values in July (days 195-198) ranged from 0.9 µM in the central English Channel and 0.1 µm in Ushant region (Table 4.2 and Figure 4.12 c). Similar data were obtained for 2003 (Table 3.2).

Depletion of silica occurred earlier than in 2003 in the English Channel where concentrations were widely < 0.5 µM in Ushant region and western English Channel (47.8-49.7^{o} N) as early as April, but later than in 2003 in the Bay of Biscay where levels

up to 3 µM persisted until the end of March (Figures 3.11c and 4.12c). Figure 4.14 shows the relationship between silicate and salinity between Portsmouth and Bilbao. The relatively high Si concentrations in Ushant region in February (days 59-60) were associated with relatively low salinity water (high discharge from French rivers in January and February) (Figures 4.2 and 4.14). Silicate concentrations > 2.0 µM, associated with salinity > 35.2 in May II and June occurred in the Ushant region and the western English Channel (Figures 4.11 and 4.12, 4.14 and Appendix 6).

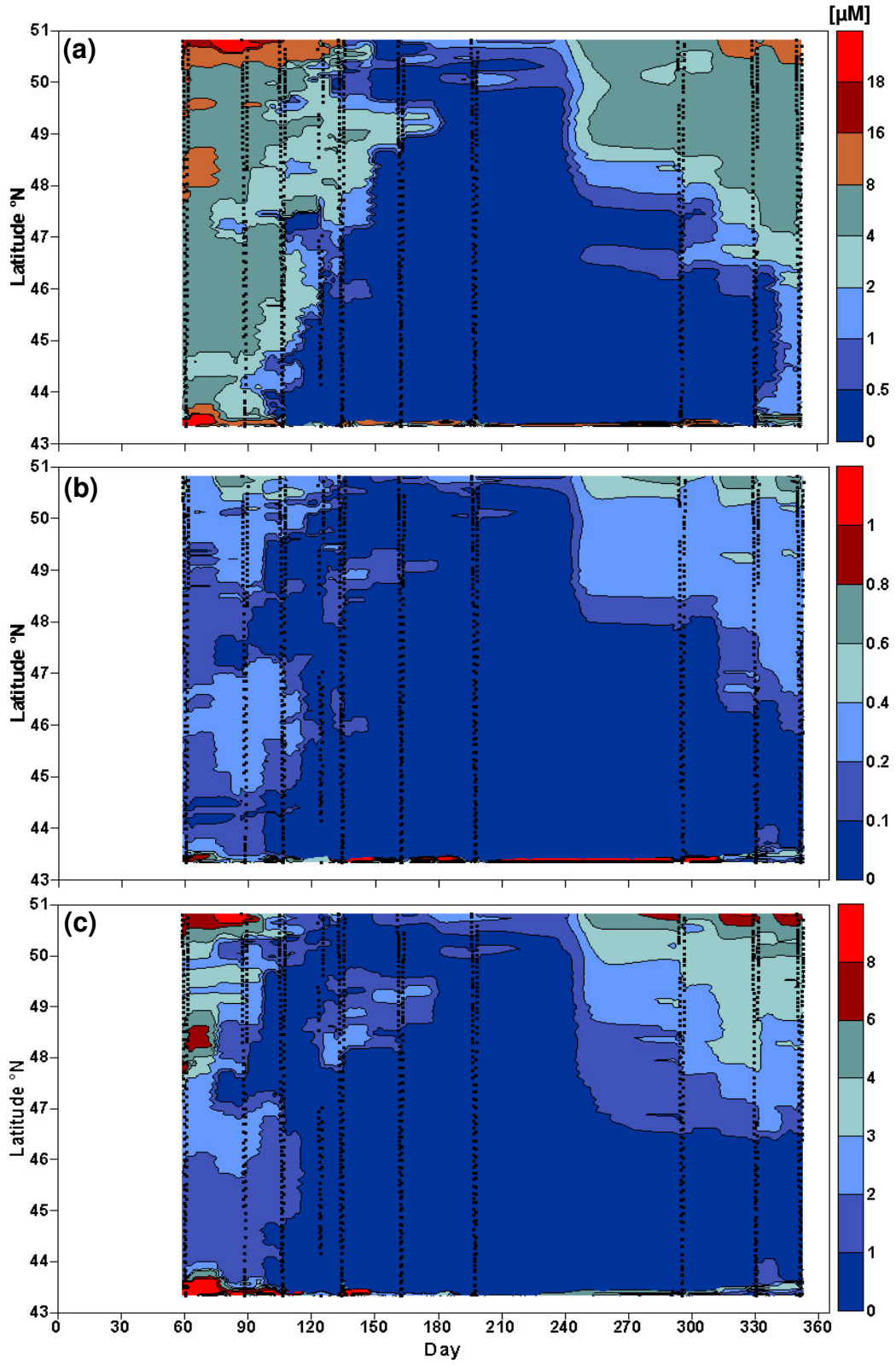


Figure 4.12: Contour plots for the distributions of (a) Nitrate NO_4 (b) inorganic phosphate PO_4 and (c) silicate Si, (µM) data collected along the route of the Pride of Bilbao in 2004, during FerryBox calibration crossings.

Table 4-2: The monthly means of nitrate (NO_3), phosphate (PO_4) and silicate (Si) µM for 2004 between Portsmouth and Bilbao.

Month (days)	(43.3-43.6° N)			(43.6-45.0° N)			(45.0-46.4° N)			(46.4-47.8° N)			(47.8-49.0° N)			(49.0-49.7° N)			(49.7-50.3° N)			(50.3-50.8° N)		
	NO_3	Si	PO_4	NO_3	Si	PO_4	NO_3	Si	PO_4	NO_3	Si	PO_4	NO_3	Si	PO_4	NO_3	Si	PO_4	NO_3	Si	PO_4	NO_3	Si	PO_4
February (59 - 60)	23.1	15.0	0.63	7.6	4.0	0.24	5.2	1.9	0.21	5.3	2.4	0.19	7.4	4.3	0.16	6.7	3.1	0.21	8.2	4.1	0.28	16.1	7.5	0.46
March (87- 89)	9.2	6.9	0.41	3.6	2.1	0.17	5.4	2.0	0.30	4.6	1.6	0.24	7.1	3.0	0.18	6.6	3.0	0.28	5.9	2.0	0.28	18.6	7.2	0.59
April (104 -107)	11.1	8.4	0.66	1.6	1.2	0.11	3.4	1.5	0.20	3.6	1.0	0.18	3.2	<0.1	0.07	3.4	0.5	0.11	5.2	1.5	0.23	14.4	2.8	0.40
May (122 -135)	14.0	7.1	1.08	0.9	0.5	0.09	0.6	0.2	0.08	1.1	0.4	0.07	3.5	1.7	0.12	2.6	0.8	0.08	1.8	0.4	0.07	7.4	1.2	0.20
June (160 -163)	6.3	1.0	0.65	0.1	0.2	0.04	<0.1	0.3	0.02	<0.1	0.6	0.03	0.9	1.1	0.07	1.3	1.3	0.05	0.3	0.5	0.05	0.6	0.9	0.07
July (195 -198)	16.7	2.7	1.10	0.5	0.5	0.05	<0.1	0.5	0.02	<0.1	0.4	0.03	0.0	0.1	0.04	0.1	0.2	0.06	0.5	0.9	0.08	1.2	1.9	0.17
October (293 - 296)	9.9	2.9	0.84	0.2	0.6	0.04	0.1	0.6	0.02	0.6	1.1	0.05	3.5	2.4	0.26	4.5	3.0	0.31	4.1	3.3	0.30	5.4	4.5	0.46
November (328 - 331)	5.1	3.0	0.37	0.9	1.0	0.09	0.3	0.8	0.06	1.9	1.8	0.15	4.5	3.4	0.30	5.4	3.6	0.37	5.6	3.9	0.38	8.5	5.8	0.58
December (349 - 352)	5.9	2.6	0.32	1.6	0.9	0.09	1.4	0.7	0.09	2.9	1.6	0.18	5.1	3.0	0.31	5.8	3.6	0.35	6.8	4.1	0.40	8.8	5.6	0.54

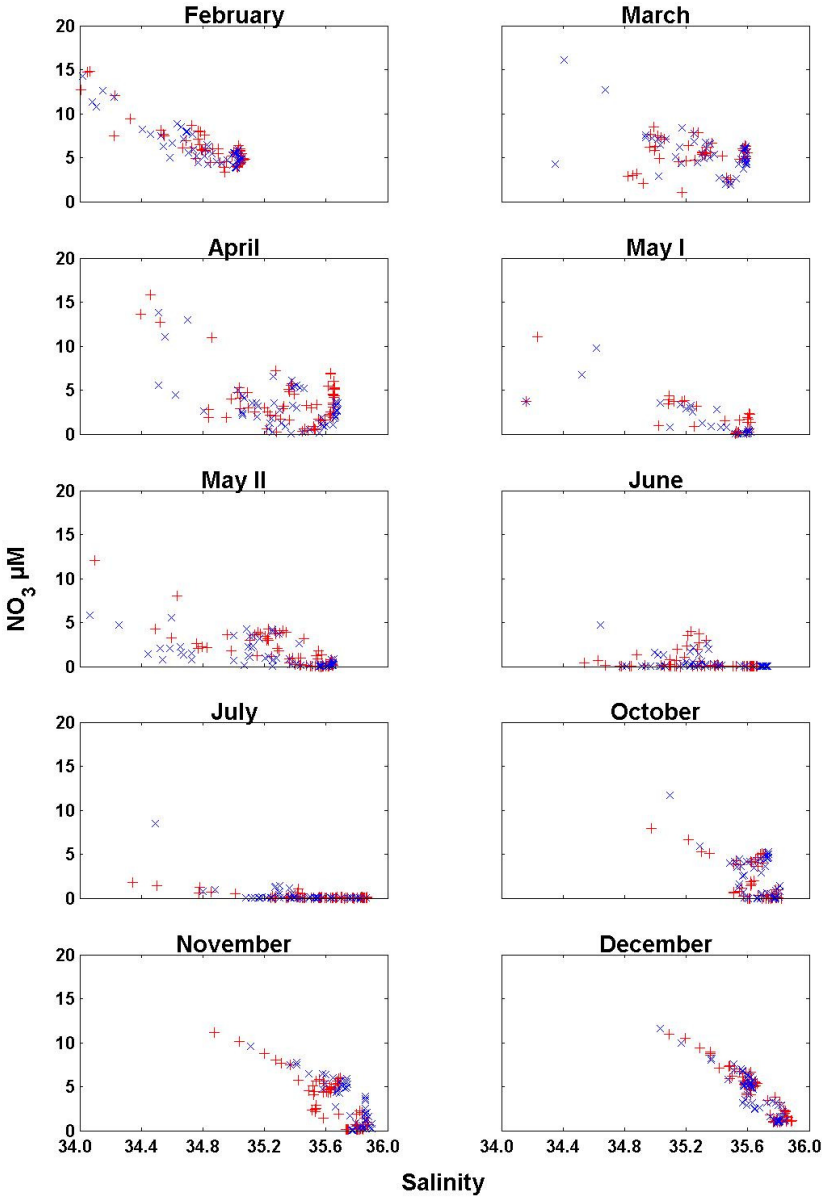


Figure 4.13: Nitrate versus salinity relationships for 2004. The red and blue crosses represent data for the tracks from Portsmouth (P) and from Bilbao (B) respectively.

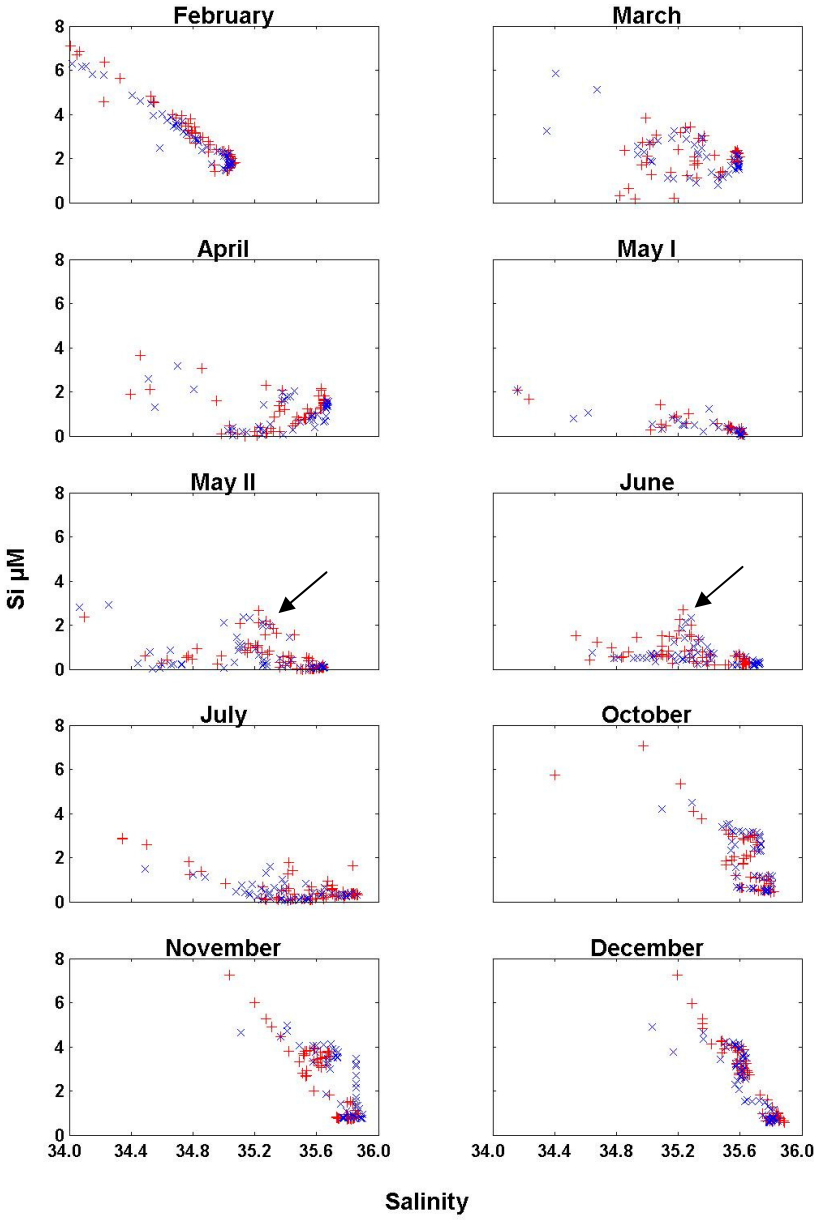


Figure 4.14: Silicate versus salinity relationships for 2004. The red and blue dots represent data for the tracks from Portsmouth (P) and from Bilbao (B) respectively. The black arrows indicate the increase of silicate at salinities between 35 and 35.6 (see text for more details).

N:P and Si:N ratios

In 2004, the mean nitrate to phosphate ratios (Table 4.3) were significantly greater than the Redfield ratio (16:1) along the whole transect in late winter and spring (February-May) and were highest (> 40) in Ushant region (47.8-49.0^{o} N) where salinity was relatively low due to the strong influence of the French freshwater input. This pattern is very similar to that observed in 2003. One exception is that, during April and May in the Bay of Biscay, ratios were somewhat higher in 2004 than 2003, perhaps

associated with the later removal of nutrients in this region in 2004. The low N:P ratios in summer (except in coastal waters) are again indicative of potential nitrate rather than phosphate limitation of phytoplankton growth.

The mean ratio between nitrate and silicate was also similar in the two years, reaching a maximum in spring and a minimum in early summer (Tables 3.4 and 4.4). In 2004 values were relatively high compared to 2003 across the whole transect in spring. High N:Si ratios found in northern Bay of Biscay, Ushant region and western English Channel in April, were possibly due to silicate depletion by phytoplankton populations with a high proportion of diatoms although, as in 2003, the mean N:Si removal rate during the main period of Si assimilation was ~2. In summer (days 160-198) generally and in the autumn in the Bay of Biscay N:Si ratios were very low (< 1) mainly due to low levels of nitrate.

Table 4-3: The monthly averages of surface nitrate to phosphate ratios for 2004 between Portsmouth and Bilbao. (Note that no data are available for August and September.)

Latitude	February	March	April	May	June	July	October	November	December	
(50.3-50.8° N)	39.5	32.0	37.2	38.9	14.6	8.5	11.7	14.7	16.7	> 40
(49.7-50.3° N)	31.0	22.4	23.2	21.5	6.7	6.4	14.4	14.9	17.4	18-40
(49.0-49.7° N)	33.9	24.1	33.0	35.1	20.4	1.9	14.7	14.7	16.9	
(47.8-49.0° N)	51.5	43.2	104.5	44.9	8.4	1.1	13.8	15.0	16.7	14-18
(46.4-47.8° N)	34.3	26.2	34.5	34.2	1.3	1.6	12.9	12.5	16.9	
(45.0-46.4° N)	26.8	18.1	15.9	5.5	1.4	2.8	2.3	4.1	18.2	7-14
(43.6-45.0° N)	35.0	19.2	11.9	3.4	2.4	4.1	6.7	7.0	18.6	< 7
(43.3-43.6° N)	35.0	22.7	14.1	10.3	8.0	9.2	18.4	12.7	18.4	

Table 4-4: The monthly averages of surface nitrate to silicate ratios for 2004 between Portsmouth and Bilbao. (Note that no data are available for August and September.)

Latitude	February	March	April	May	June	July	October	November	December	
(50.3-50.8° N)	2.1	2.4	5.6	14.0	0.9	0.6	1.2	1.5	1.6	> 7
(49.7-50.3° N)	2.0	3.3	3.7	5.0	0.5	0.6	1.3	1.4	1.6	3-7
(49.0-49.7° N)	2.2	2.2	15.7	3.6	0.7	0.7	1.5	1.5	1.6	
(47.8-49.0° N)	1.7	3.2	49.2	2.5	0.6	0.4	1.3	1.3	1.7	2-3
(46.4-47.8° N)	2.3	3.9	19.7	3.6	0.1	0.2	0.5	1.0	2.0	
(45.0-46.4° N)	2.7	2.8	2.3	4.9	0.1	0.1	0.2	0.4	1.9	1-2
(43.6-45.0° N)	2.4	1.9	1.2	2.8	0.4	0.5	0.2	0.5	1.7	<1
(43.3-43.6° N)	1.7	1.3	1.3	10.8	4.7	3.1	2.4	1.5	2.1	

4.2 Phytoplankton data

4.2.1 *Chlorophyll a by fluorescence*

The changes in chlorophyll *a* for 2004 between Portsmouth and Bilbao, estimated from in-situ fluorescence values, are shown in Figure 4.15 and followed a

similar seasonal pattern to that observed in 2003 (Figure 3.14). However, there were some significant differences between the two years. In the central and northern Bay of Biscay, the spring bloom was later (starting just before day 120) and more intense in 2004. By contrast, in the offshore waters of the English Channel the initial increase in chlorophyll *a* was earlier (~day 75) than in 2003 although maximum spring values occurred at about the same time (~day 120) in the two years. The chlorophyll maximum in midsummer (days 182-212) associated with the tidal front in the western and central English Channel was much less pronounced in 2004 relative to 2003 both in terms of the maximum concentrations and persistence in time (Figure 4.15). In the autumn and early winter (days 285-79), chlorophyll levels appeared to be relatively high across much of the Bay of Biscay compared to 2003 (Figure 4.15).

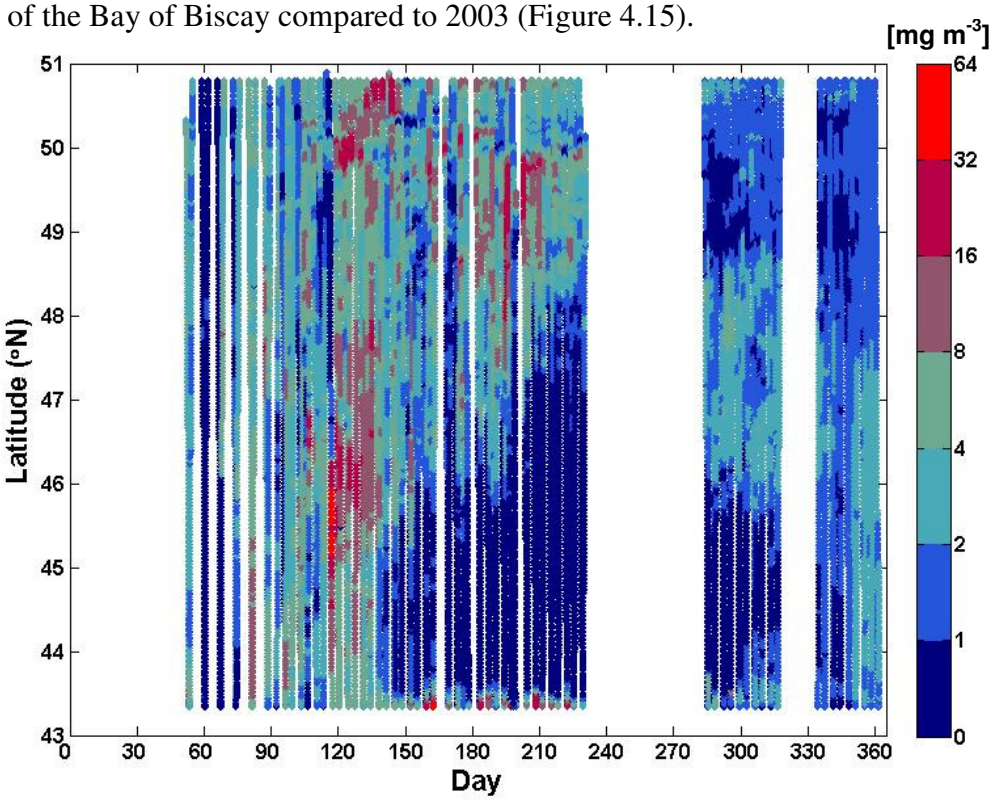


Figure 4.15: Distribution of surface fluorescence (mg m^{-3}, nominal calibration) for 2004 between Portsmouth (UK) and Bilbao (Spain). Values are five-minute averages derived from the FerryBox MiniPack fluorescence sensor.

4.2.2 *Fluorometric chlorophyll a concentrations from acetone extractions*

Measurements of chlorophyll *a* from filtered water samples (Figure 4.16) confirmed the general pattern of phytoplankton distribution given by the FerryBox fluorescence data (Figure 4.15) and, as in 2003, showed that the fluorometer calibration overestimated chlorophyll *a*. The main features of early increases in chlorophyll *a*

during March north of 47.0° N, the late (April/May) spring bloom in north Biscay, and the relatively weak (compared to 2003) summer frontal bloom in the English Channel are clearly defined. However, compared to the FerryBox fluorescence measurements (Figure 4.15), there was no evidence of enhanced phytoplankton abundance in the Bay of Biscay late in the year.

The 2004 chlorophyll *a* measurements are summarised in Table 4.5. Comparison with equivalent data for 2003 (see Table 3.5) shows that May chlorophyll *a* levels in the Biscay region ranged from 1.3 to 1.7 mg m^{-3} in 2004 compared to < 0.8 mg m^{-3} in 2003, and that for March in the central and western English Channel the equivalent figures were 1.4 and 1.0 mg m^{-3} in 2004 and 1.1 and 0.7 mg m^{-3} in 2003. Another notable feature of 2004 is the persistence of relatively mean chlorophyll *a* levels > 1.0 mg m-3 in the shelf waters of northern Bay of Biscay until July whereas, in 2003, they were < 1.0 mg m-3 by May. Finally, in July, the western English Channel showed a mean chlorophyll *a* level of 4.9 mg m-3 in 2004 compared to 37.6 mg m-3 in 2003.

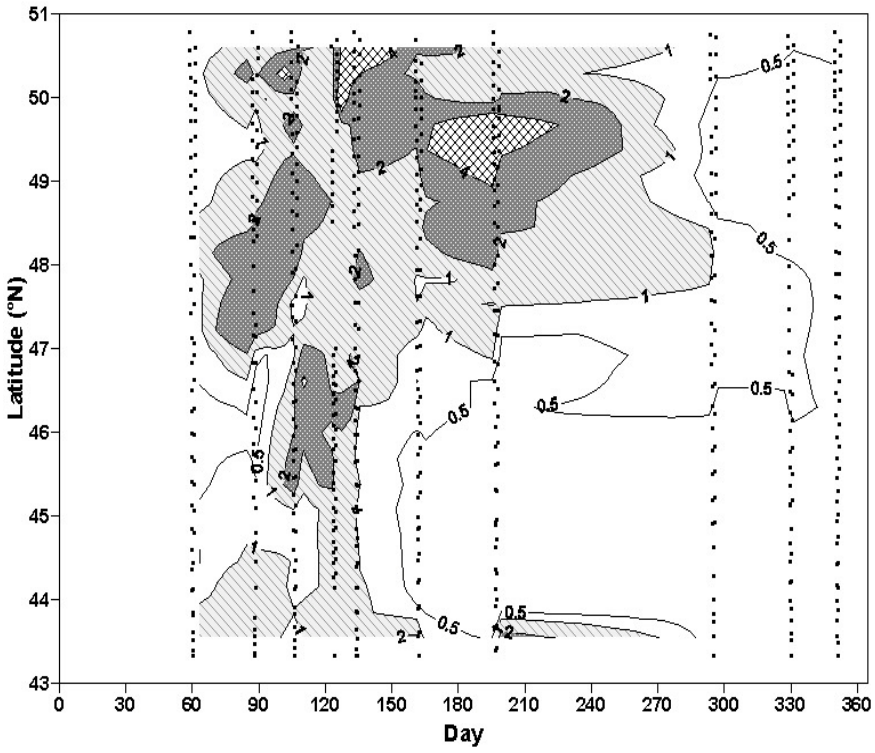


Figure 4.16: Distribution of extracted chlorophyll *a* (mg m^{-3}) for 2004 between Portsmouth (UK) and Bilbao (Spain).

Table 4-5: The monthly means of extracted chlorophyll a (mg m^{-3}) for 2004 between Portsmouth and Bilbao.

Month (days)	(43.3-43.6° N)	(43.6-45.0° N)	(45.0-46.4° N)	(46.4-47.8° N)	(47.8-49.0° N)	(49.0-49.7° N)	(49.7-50.3° N)	(50.3-50.8° N)
February (59-60)	1.6	0.7	0.4	0.6	0.8	0.6	0.8	0.8
March (87-89)	1.1	1.2	0.5	2.1	2.6	1.0	1.4	0.9
April (104-107)	0.5	0.8	2.1	1.5	3.0	2.2	2.4	1.9
May (122-135)	1.4	1.3	1.6	1.7	1.6	1.9	4.2	6.2
June (160-163)	2.0	0.4	0.5	1.1	1.5	2.7	2.9	1.9
July (195-198)	1.3	0.3	0.3	1.0	2.7	4.9	2.4	1.6
October (293-296)	0.3	0.3	0.3	0.6	0.7	0.3	0.5	0.7
November (328-331)	0.5	0.4	0.4	0.6	0.4	0.3	0.3	0.5
December (349-352)	0.5	0.4	0.4	0.4	0.3	0.3	0.3	0.5

4.2.3 *Satellite colour estimates of chlorophyll*

The distribution of surface chlorophyll along the ferry route for 2004 estimated from weekly composite images from the Sea-viewing Wide Field-of-View Sensor (SeaWiFS) is presented in Figure 4.17. As in 2003, chlorophyll levels in English coastal waters appeared high throughout the year due to interference from suspended sediment and dissolved organic matter with the Case II chlorophyll algorithm (Moore *et al.*, 1999; Maritorena *et al.*, 2002; Morel and Bélanger, 2006).

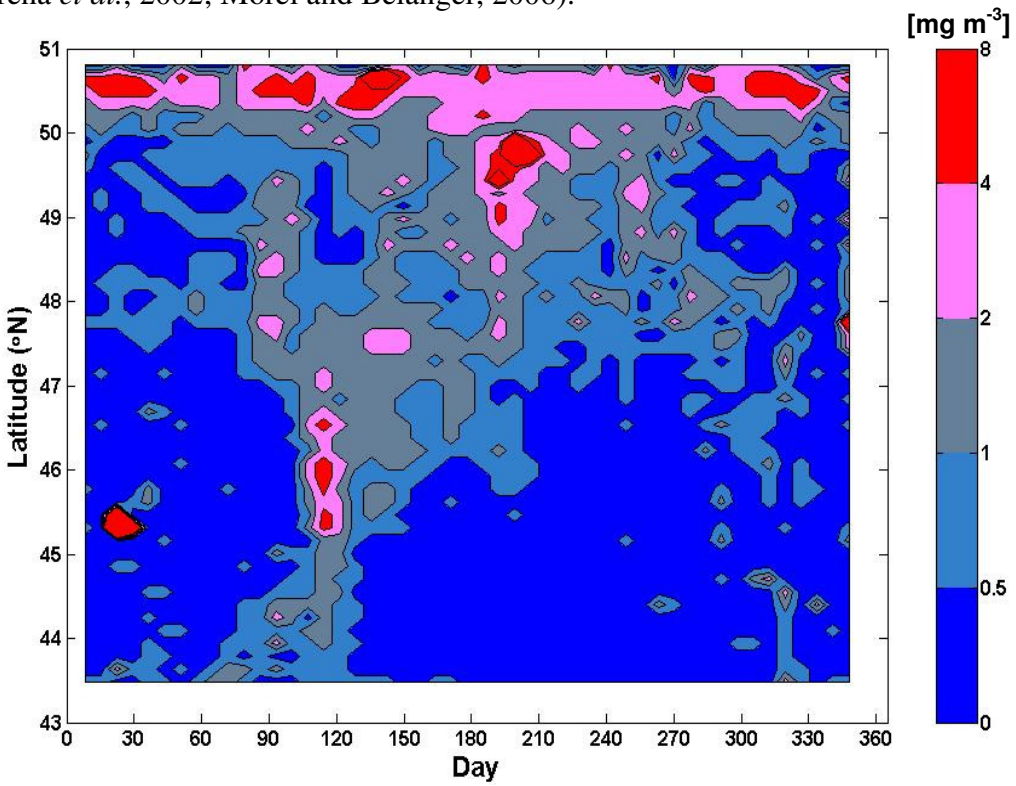


Figure 4.17: Distribution of chlorophyll determined by satellite from weekly composite SeaWiFS satellite images for 2004 using the NASA Case I waters algorithm. (Note that the anomalous red point in January in the central Bay of Biscay is an artefact of the data processing).

The main features of chlorophyll distribution described by the FerryBox and extracted chlorophyll measurements are well resolved, in particular the late March (day

85) spring bloom north of 47.5° N and the late April (day 110) spring bloom in the central and northern Bay of Biscay (45.0-47.8° N). Also it is noticeable that, in the western English Channel and Ushant region, the early increase of chlorophyll was followed by a period in late April to early May (days 110-130) of relatively low values before chlorophyll increased again in mid-May. Comparison with the satellite data for 2003 (Figure 3.16) shows that the extent of high (> 4.0 mg m^{-3}) chlorophyll levels in the central English Channel in summer was much more restricted in 2004. On the other hand, in the northern Biscay shelf between 46.0 and 48.0° N chlorophyll levels were considerably higher in 2004 for an extended period during the early summer (days 150-205) (Figure 4.17).

4.2.4 *Pigment chemotaxonomy*

Following the procedures described in Chapter 3, based on the method of Vidussi *et al*., (2001), measurements of the seven diagnostic phytoplankton pigments (DP) (see Section 3.2.4) for 2004 were used to describe the distributions of pico- nano- and micro-phytoplankton. A strong positive correlation between total accessory pigments (dominated by DP) and chlorophyll *a* was again found (see Chapter 2), and the major accessory pigment, hexanoyloxyfucoxanthin, showed a similar distribution (Figure 4.18) to that observed in 2003 with main centre in stratified shelf waters in early summer.

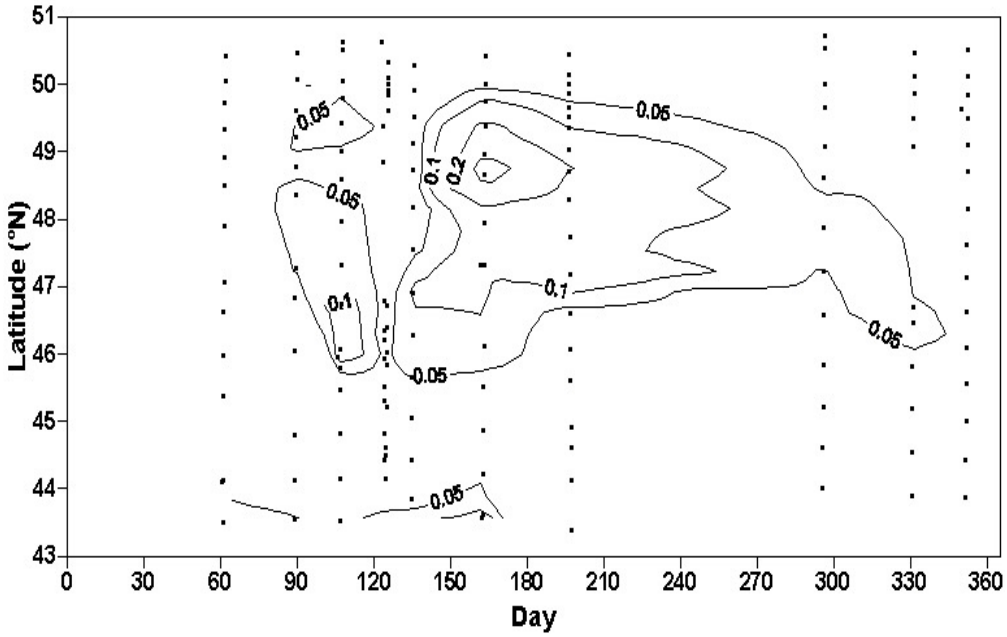


Figure 4.18: Distribution of Hex (19'-hexanoyloxyfucoxanthin, mg m^{-3}) for 2004 between Portsmouth (UK) and Bilbao (Spain).

The 2004 distributions of HPLC-chl *a* and the three size classes of phytoplankton, estimated from the diagnostic pigments, are shown in Figure 4.19. The HPLC chlorophyll *a* data is consistent with the other 2004 measurements of chlorophyll that have already been described, and the distributional patterns for the three phytoplankton groups are broadly consistent with those described for 2003 (Figure 3.18). Pico-phytoplankton were relatively most important in oceanic waters of the Bay of Biscay in early spring (day 89), nano-phytoplankton in the Bay of Biscay in early summer (day 160), and micro-phytoplankton along the whole transect in spring and in the central English Channel in summer. The main distinction between the two years, given the differences in chlorophyll *a* distributions, is the greater dominance in 2004 of micro-phytoplankton in the central and southern Bay of Biscay in spring. This signal reflects the higher chlorophyll values in this region in 2004 but, even for samples with HPLC chl*a* < 1 mg m^{-3}, large cells appear to have been particular abundant. The apparent scarcity in 2004 of nano-phytoplankton in autumn reflects the lack of samples for this period of time.

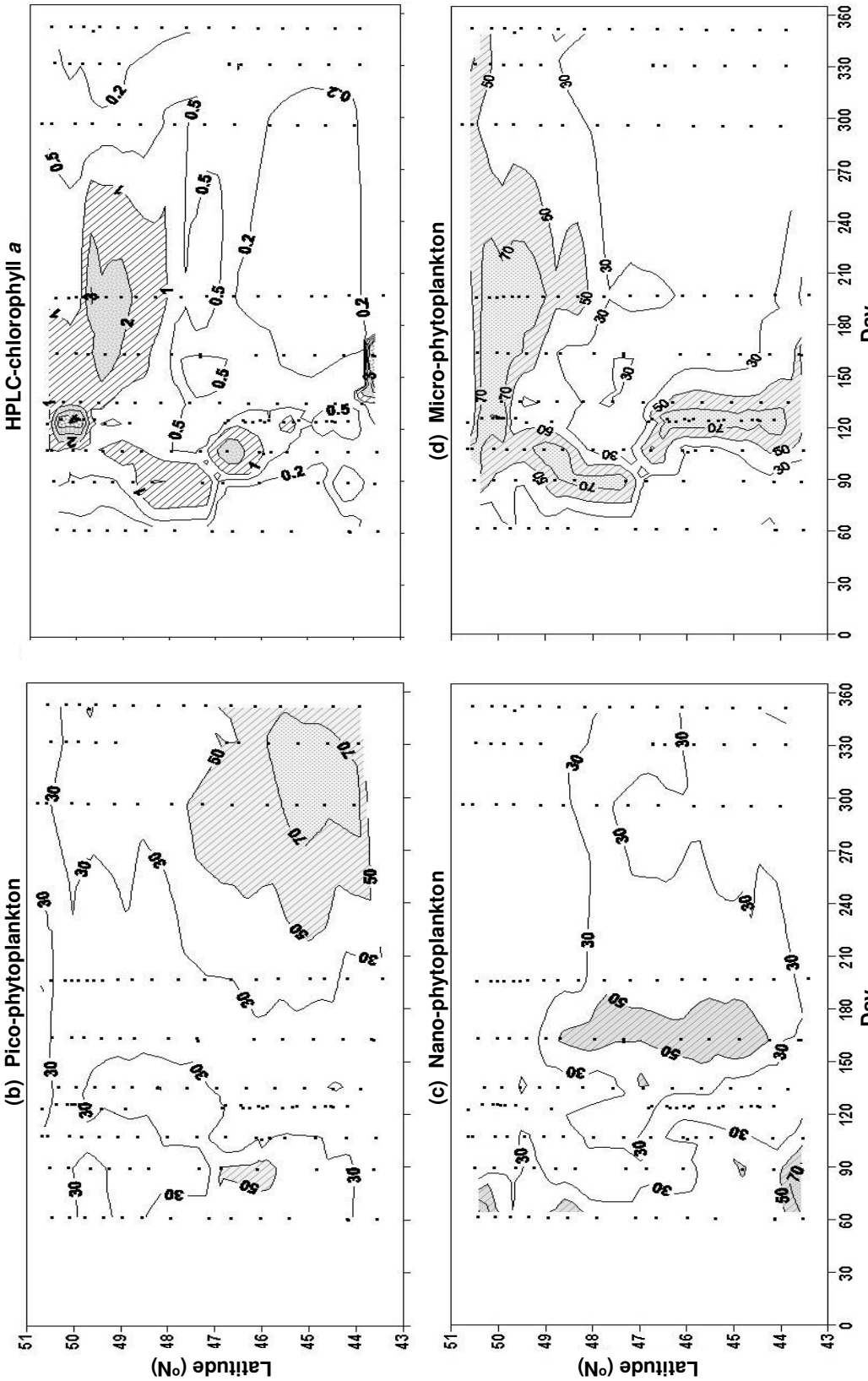


Figure 4.19: Distributions of (a) HPLC chlorophyll *a* (mg m^{-3}) and % contribution to chlorophyll *a* from (b) pico-phytoplankton (0.2-2 µm), (c) nano-phytoplankton (2-20 µm) and (d) micro-phytoplankton (> 20 µm) for 2004 between Portsmouth and Bilbao.

4.2.5 *Phytoplankton species composition*

The phytoplankton cell counts for 2004 are summarised in Table 4.6. The species list was remarkably similar to that of 2003 (see Table 3.6), the only difference being two diatom species that were recorded only on one year – *Odontella sinensis* in a single sample in 2004 and *Hemiaulus hauckii* in a single sample in 2003. In general in 2004, diatoms were rather more abundant in spring samples from the Bay of Biscay and in summer samples from the English Channel, counts for the bloom dinoflagellate, *Karenia mikimotoi*, were relatively low in the English Channel, and the coccolithophore, *Emiliania huxleyi*, was more widespread along the transect. The very high count for the diatom, *Guinardia delicatula*, in southern Bay of Biscay in summer (Table 4.6) was associated with high chlorophyll *a* values in coastal waters.

Phytoplankton carbon biomass was calculated from cell volumes for each species and the slope of the relationship ($p < 0.05$, $R^2 = 0.82$, n= 70) between chlorophyll *a* (chl *a*) and the estimated phytoplankton carbon (C) (Figure 4.20) gave an average C/chl ratio of 27.3, somewhat higher than the value obtained from the 2003 data (Figure 3.19). Once again, low C values were obtained for the low chlorophyll samples, reflecting the dominance of small cells in these samples that could not be counted with the light microscope. Also samples from different regions and/or seasons appear to be grouped, but there was insufficient data for C/chl ratios to be calculated for each group.

The phytoplankton carbon biomass estimates for 2004 are given in Table 4.7. Diatom C values were higher than in 2003 (see Table 3.7) in the spring in the central and northern Bay of Biscay and in summer in the English Channel. On both years, *Guinardia delicatula* and *Rhizosolenia imbricata* were abundant and widespread, with *Detonula pumila* in southern Bay of Biscay in 2004 and *Guinardia striata*, *G. flaccida* and *Rhizosolenia setigera* in the English Channel being more abundant in 2004. The distribution of *Scrippsiella trochoidea* in 2004 was similar to that in 2003 except that an autumn population in Biscay was not found. As previously noted, no bloom of *Karenia mikimotoi*, was detected in the English Channel in 2004, and *Emiliania huxleyi* was more widespread but the maximum cell count lower than in 2003 (Tables 3.7 and 4.7).

Table 4-6: Averaged counts of phytoplankton species (cell ml^{-1}) for 2004 between Portsmouth and Bilbao for spring (Spr), summer (Sum), and autumn (Aut) samples. + indicates < 1 cell ml^{-1}. L and S indicate respectively large and small.

	(43.6-45.0° N)			(45.0-46.4° N)			(46.4-47.8° N)			(47.8-49.0° N)			(49.0-49.7° N)			(49.7-50.3° N)		
Genus and species	Spr	Sum	Aut	Spr	Sum	Aut	Spr	Sum	Aut	Spr	Sum	Aut	Spr	Sum	Aut	Spr	Sum	Aut
Diatoms																		
Bacillaria paxillifera				+												+		
Biddulphia aurita																		
Cerataulina pelagica							1											
Chaetoceros (S)	+		+				20			4			+	+				
*Chaetoceros (*L)	+			3			27							+				
Chaetoceros danicus													+					
Cosinodiscus oculis-iridis	+															+		
Cylindrotheca closterium	+					+					+				+	+		+
Detonula pumila	12			12		+	2			2			2			4	+	
Ditylum brightwelli	+						+			+						+		+
Eucampia sp.							+				+		+	+		+		
Guinardia delicatula	15	1187		9			39			3			13	33		83	+	
Guinardia flaccida	+												+	1		+	1	+
Guinardia striata				1					+				+	8		6	13	
Licmophora sp.																		
Melosira sp.																		
Meuniera membranacea	+									+			6	+		5		
Navicula sp.															+	+		+
Odontella mobiliensis																		
Odontella sinensis										+								
Paralia sulcata						+			+			+			+	2		1
Pleurosigma						+				+		+	2		+	+		+
Pseudo-nitzschia sp.	62		1	18		1	40		+	4	1	+	+	38	+	+	13	+
Rhizosolenia imbricata	+	+			+	+		10			8		6	24		3	6	
Rhizosolenia setigera										4			8			+		
Skeletonema costatum																		
Thalassionema nitzschioides	+			8		+	6		+					5	+	+		+
Thalassiosira rotula																		
Thalassiosira sp.	+			+		+	7		+	+		+	+			2		+
Autotrophic/ Mixtrophy Dinoflagellates																		
Ceratium azoricum																		
Ceratium furca	+	+		+	+		+			+	+		+			+		
Ceratium fusus	+			+			+			+	+			+			+	
Ceratium lineatum				+														
Ceratium macroceros	+			+			+	+						+				
Ceratium trichoceros																		
Ceratium tripos																		
Dinophysis acuminata	+	+		+						+	+		+					
Gymnodinium sp.								+	+		+			2				
Karenia mikimotoi		+			+			10			+			22			+	
Prorocentrum gracile																		
Prorocentrum micans	+	+							+	+	+		+	+		+	+	
Scrippsiella trochoidea	1	+		+			+	4		+	+		+	15		+		
Coccolithophores																		
Emiliania huxleyi	27			148			67	30			337		356	12		141		
Sample number	7	2	2	11	2	4	5	2	3	5	4	2	3	6	2	6	3	4
Average chlorophyll *a* (mg m^{-3})	1.4	9.0	0.5	1.4	0.2	0.3	2.0	1.1	0.5	2.0	1.8	0.7	3.5	3.8	0.3	4.3	2.1	0.3
Total (cell ml^{-1})	118	1188	2	198	1	2	209	52	2	41	348	0	396	160	2	249	33	3

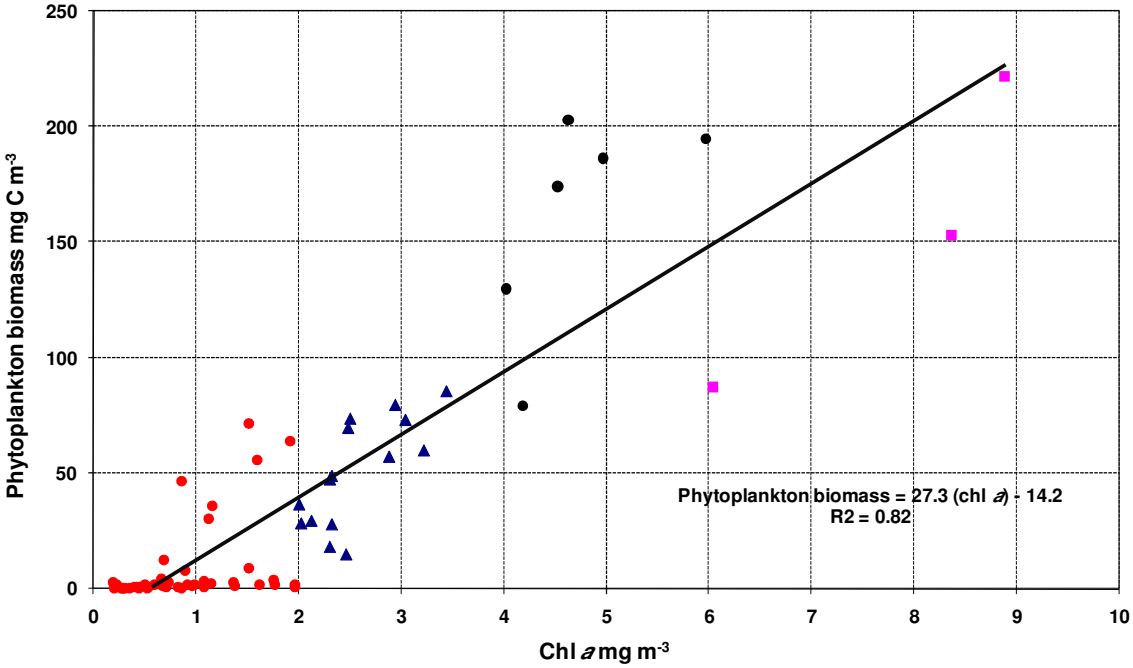


Figure 4.20: The relationship between phytoplankton C biomass and chlorophyll *a* for 2004. The coastal data are excluded (for more details see the text). The four different groupings are 1. central English Channel in spring, pink squares; 2. western English Channel in spring and summer, black circles; 3. Ushant region and western English Channel in spring and summer, blue triangles; and 4. Bay of Biscay plus autumn data for all regions, red circles.

The overall distributions of chlorophyll *a* and the main phytoplankton groups, diatoms, dinoflagellates and coccolithophores, are shown in Figure 4.21. The main features are a generally good correspondence between chlorophyll *a* and diatom abundance, spring and early summer peaks in coccolithophores in Biscay and on the shelf, and summer peaks in dinoflagellates on the shelf. Perhaps the most notable feature of the 2004 data compared to that of 2003 (see Figure 3.20) is the high abundance of diatoms in shelf waters in midsummer.

Table 4-7: Averaged biomass of phytoplankton species (mg C m^{-3}) for 2004 between Portsmouth and Bilbao for spring (Spr), summer (Sum), and autumn (Aut) samples. + indicates < 0.1 mg C m^{-3}. L and S indicate respectively large and small.

	(43.6-45.0° N)			(45.0-46.4° N)			(46.4-47.8° N)			(47.8-49.0° N)			(49.0-49.7° N)			(49.7-50.3° N)		
Genus and species	Spr	Sum	Aut	Spr	Sum	Aut	Spr	Sum	Aut	Spr	Sum	Aut	Spr	Sum	Aut	Spr	Sum	Aut
Diatoms																		
Bacillaria paxillifera				+												0.1		
Biddulphia aurita																		
Cerataulina pelagica							1.4											
Chaetoceros (S)	0.2		+	+			3.9			0.8			+	+				
*Chaetoceros (*L)	0.2			2.0			16.1							+				
Chaetoceros danicus													0.3					
Cosinodiscus oculis-iridis	+															+		
Cylindrotheca closterium	+								+		+				+	+		+
Detonula pumila	5.5			5.5		+	1.1			0.9			1.0			2.1	+	
Ditylum brightwelli	+						+			0.4						+		+
Eucampia sp.							+				+		+	+		+		
Guinardia delicatula	8.3	647.5		4.9			21.2			1.6			7.0	17.9		45.3	0.1	
Guinardia flaccida	0.6												1.9	5.7		3.3	5.0	+
Guinardia striata				2.2					+				1.9	18.1		12.6	29.6	
Licmophora sp.																		
Melosira sp.																		
Meuniera membranacea	0.2									0.6			5.6	0.4		5.0		
Navicula sp.															+	+		+
Odontella mobiliensis																		
Odontella sinensis										+								
Paralia sulcata						+			0.1			+			0.2	0.5		+
Pleurosigma						+				+		+	1.5		+	0.2		+
Pseudo-nitzschia sp.	2.2		+	0.6		+	1.4		+	0.2	+	+	+	1.3	+	+	0.4	+
Rhizosolenia imbricata	1.2	0.2		+	1.4	+		25.9			21.3		15.6	65.9		7.0	15.0	
Rhizosolenia setigera										12.2			22.5			+		
Skeletonema costatum																		
Thalassionema nitzschioides	+			0.8		+	0.6		+					0.5	+	+		+
Thalassiosira rotula																		
Thalassiosira sp.	+			+		+	4.7		+	0.5		0.1	+			1.1		0.2
Autotrophic/ Mixotrophic Dinoflagellates																		
Ceratium azoricum																		
Ceratium furca	0.6	0.5		0.3	1.0		+			0.3	0.2		0.8			+		
Ceratium fusus	0.1			+			+			+	+			+			0.2	
Ceratium lineatum				+														
Ceratium macroceros	0.3			0.3			+	0.2						+				
Ceratium trichoceros																		
Ceratium tripos																		
Dinophysis acuminata	+	0.1		+						+	+		+					
Gymnodinium sp.								0.1	0.3		0.6			2.7				
Karenia mikimotoi		0.1			0.2			6.0			0.4			13.6			+	
Prorocentrum gracile																		
Procentrum micans	+	0.2							+	+	0.8		0.5	+		+	0.2	
Scrippsiella trochoidea	1.1	0.1		+			0.3	3.9		1.0	0.8		0.8	16.9		+		
Coccolithophores																		
Emiliania huxleyi	0.3			1.9			0.9	0.3			3.4		3.6	0.1		1.4		
Sample number	7	2	2	11	2	4	5	2	3	5	4	2	3	6	2	6	3	4
Averages chlorophyll *a* (mg m^{-3})	1.4	9.0	0.5	1.4	0.2	0.3	2.0	1.1	0.5	2.0	1.8	0.7	3.5	3.8	0.3	4.3	2.1	0.3
Total (mg C m^{-3})	20.8	648.8	0.1	18.3	2.5	0.3	51.6	36.3	1.4	18.7	27.6	0.2	63.3	143.4	0.3	78.8	50.7	0.7

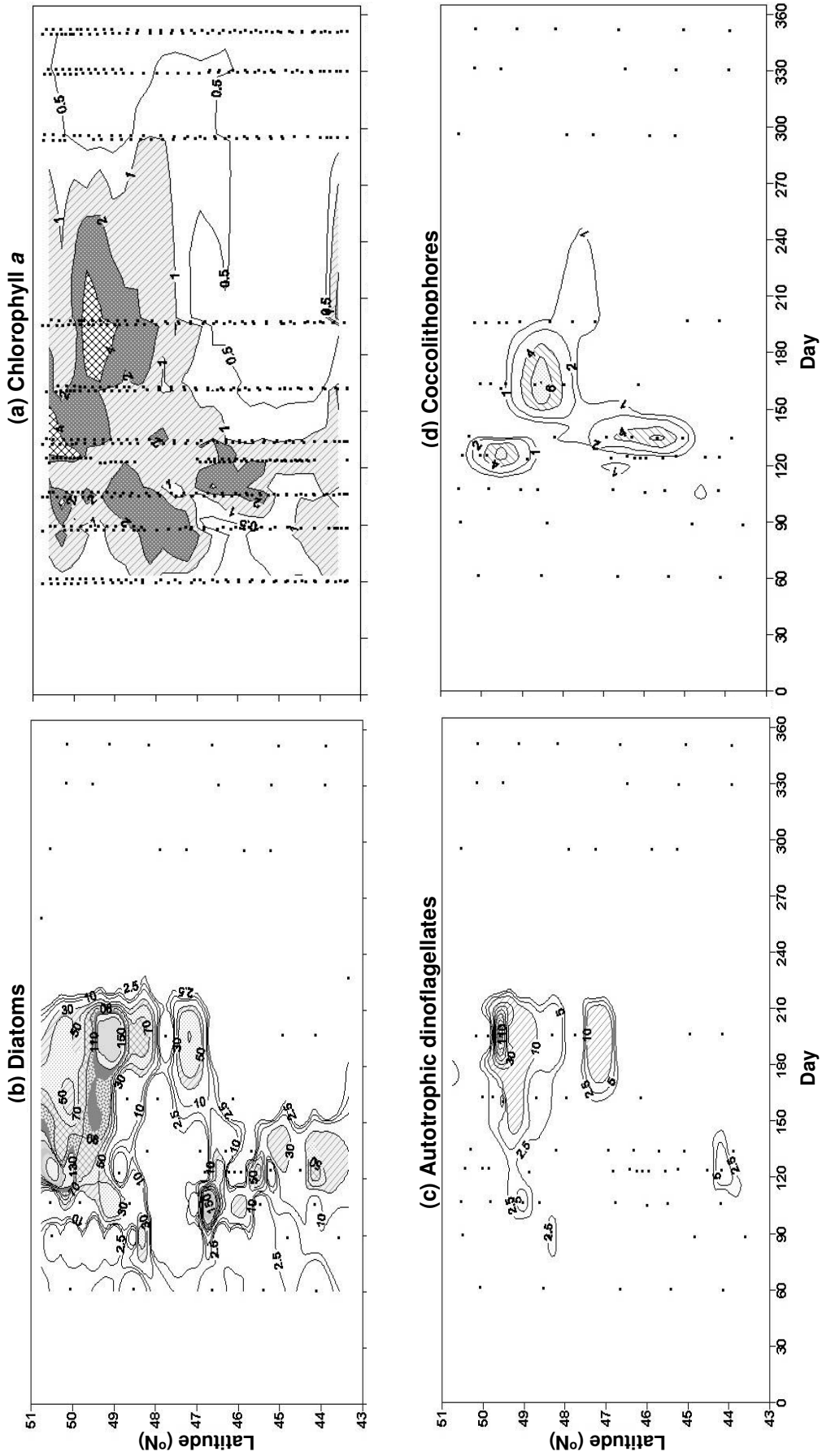


Figure 4.21: Distribution of (a) extracted chlorophyll *a* (mg m^{-3}) and the biomass (mg m^{-3}) of the main phytoplankton groups: (b) Diatoms, (c) Dinoflagellates and (d) Coccolithophores for 2004.

4.3 Zooplankton Data

4.3.1 *Regional Abundance*

Figure 4.22 shows the estimated average carbon biomass for herbivorous copepods in day and night samples from the central and western English Channel and the central Bay of Biscay for 2004. There was a significant difference ($P < 0.05$) between day and night for the central English Channel, with night samples showing about a 3-fold higher biomass of herbivores. The day-night differences for the western English Channel and central Bay of Biscay were not significant ($p > 0.05$). A Duncan's multiple comparison test showed that the biomass of herbivorous copepods were significantly higher ($P < 0.05$) in central English Channel than in the other regions.

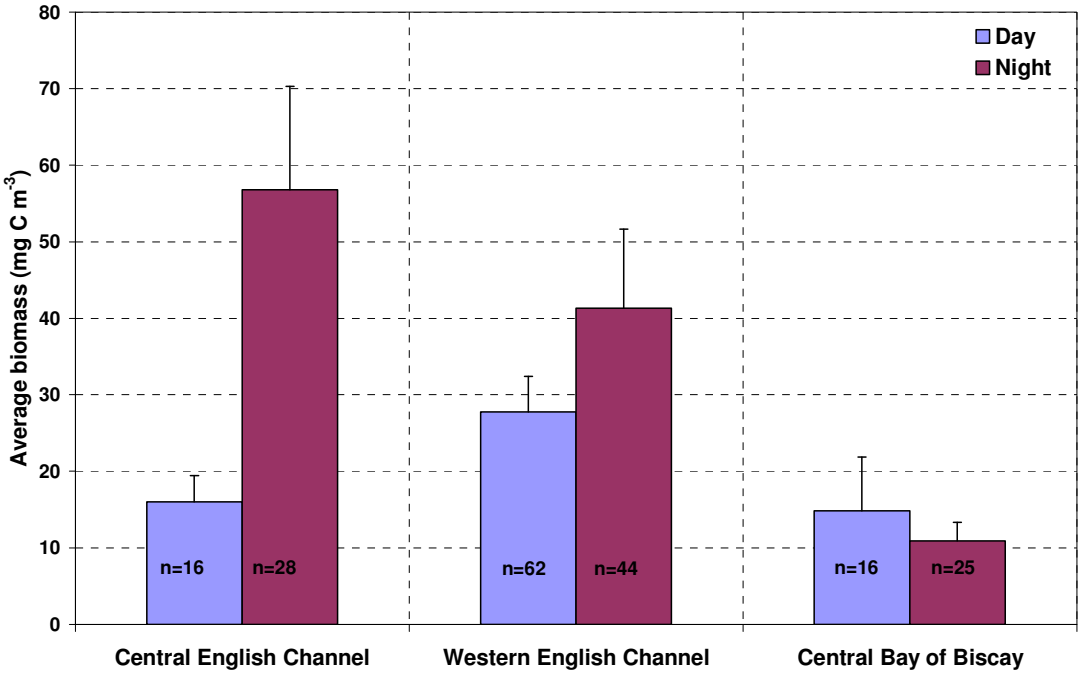


Figure 4.22: Day and night surface distributions of average biomass (mg m^{-3}) of herbivorous copepods in the central and western English Channel and in the central Bay of Biscay in 2004. N indicates the number of samples, bars show standard errors.

Comparison of the data for 2004 (Figure 4.22) with those of 2003 (Figure 3.21) shows that herbivore biomasses in the western English Channel and central Bay of Biscay were similar on the two years. In central English Channel, herbivores were more abundant in 2004 due to the high biomass values for the night samples. This difference may have resulted from a higher proportion of summer samples in 2004 (compare Figures 3.22 and 4.23).

4.3.2 *Seasonal Abundance*

Figure 4.23 shows the spatial and temporal distributions of herbivorous copepod biomass along the FerryBox transect in 2004. In central Bay of Biscay, few data were available in the spring. The highest biomasses were recorded in mid-summer, with *Calanus helgolandicus* and *Calanus* sp. the dominant species. Thereafter biomass values were low for the remainder of the year.

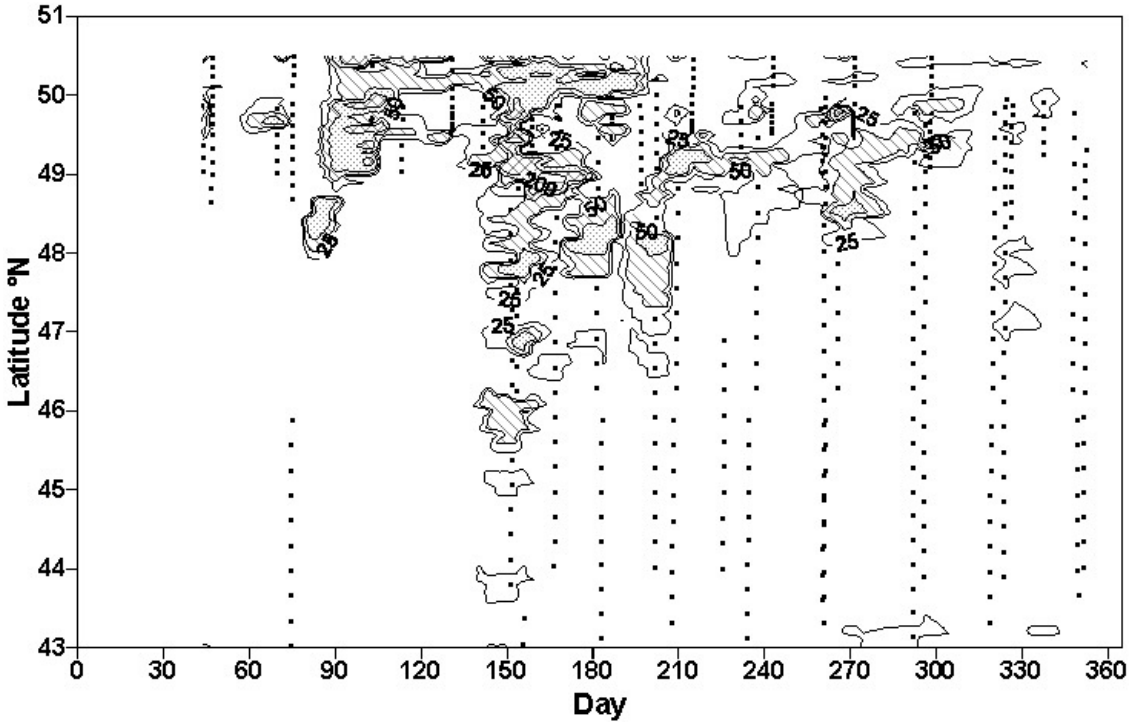


Figure 4.23: Surface distribution of the biomass (mg m^{-3}) of total herbivorous copepod for 2004.

In western English Channel, the biomass of herbivorous copepods increased in spring and the main taxa were *Calanus helgolandicus*, *Calanus* sp. and *Pseudocalanus elongates*. The same species occurred in the summer, together with *Paracalanus* sp., *pseudocalanus* sp. The central English Channel waters were showed a rapid increase in the biomass of herbivorous copepods (mainly *Temora longicornis* and *Calanus* sp.) in spring at the time of the diatom bloom. Relatively high biomass values were maintained through most of the summer except in the frontal region (around 49.0° N) between days 160 and 200 even though *Karenia mikimotoi* was relatively scarce.

The patchiness in herbivore biomass apparent in shelf waters during the summer of 2004, when sampling was more frequent than in the previous year, suggests that there is considerable short term variability in herbivore populations at this time of year. The

processes controlling such variability are likely to include food (phytoplankton) availability which itself is dependent on dynamic climatic and hydrographic factors.

4.4 Summary

The distributions of hydrographic properties and of phytoplankton in 2004 followed the expected trend for temperate latitude waters; however, when the details were considered, differences with respect to 2003 were apparent. There were differences between the two years in the timing of seasonal changes and in the abundance of particular phytoplankton species, both of which were reflected in the nutrient data.

In 2004, the spring phytoplankton bloom was relatively late in the Bay of Biscay and early in the English Channel compared to 2003. The relatively strong and persistent SW winds in Biscay between January and March in 2004 (Figure 4.4) could inhibit the seasonal development of stratification and may delay the phytoplankton growth in this region. In contrast, conditions in the English Channel were characterised by relatively low salinity water off western France in March and high solar irradiance in the north in April. Both are likely to have promoted earlier growth of phytoplankton in 2004 than in 2003, with the light environment linked to the salinity anomaly through stratification of the water column.

With respect to the species and distributions of phytoplankton in 2004, the recorded cell densities of both *Emiliania huxleyi* in early summer in the Bay of Biscay and *Karenia mikimotoi* in mid-summer in the English Channel were low compared to 2003. The reasons for these differences are not obvious although mid-summer conditions in the English Channel were characterised in 2004 by a period of relatively strong winds and the absence of any low salinity signal originating from the French rivers. Diatoms were more abundant in 2004 compared to 2003.

The herbivorous zooplankton populations were better sampled in 2004 than in 2003. Higher abundance at night compared to day for the shelf waters probably reflects the effects of diel vertical migration, especially in stratified waters in the summer. Also the increase of herbivore biomass was shown to be rapid but patchy in the early summer in response to the spring bloom (Cushing, 1983; Banse, 1995).

CHAPTER 5

5. DISCUSSION OF DIFFERENCES BETWEEN YEARS AND REGIONS

5.1 Introduction

In the previous two chapters the distributions of physical, chemical and biological variables along the ferry track (Figure 2.3) between Portsmouth (UK) and Bilbao (Spain) were investigated. In both years, relatively few samples were collected from the UK and Spanish coastal waters, from the Ushant region or from the southern Bay of Biscay. Therefore, the observations from the previous chapters are combined in this chapter to consider the relationship between oceanographic conditions and the seasonal cycle of phytoplankton in 2003 and 2004 only in four different regions: the central Bay of Biscay (oceanic waters), the northern Bay of Biscay (southern stratified shelf), the western English Channel (northern stratified shelf), and the central English Channel (well mixed shelf) (Figure 5.1).

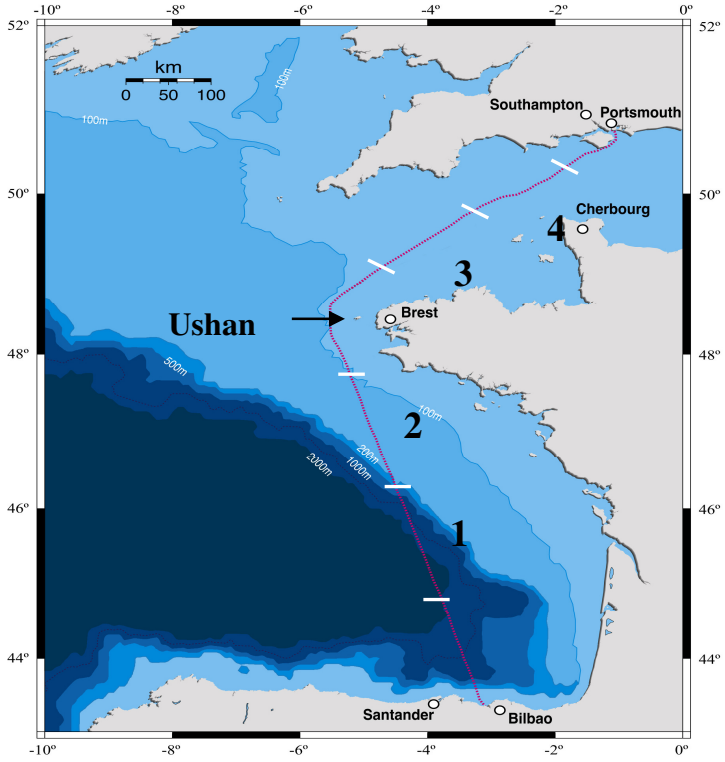


Figure 5.1: The standard track of RV Pride of Bilbao from Portsmouth to Bilbao is marked to indicate the regional subdivisions: (1) central Bay of Biscay (oceanic region), (2) northern Bay of Biscay (southern stratified shelf), (3) western English Channel (northern stratified shelf), and (4) central English Channel (well-mixed shelf).

This Chapter investigates the regional and seasonal variability in physical and chemical variables in the surface waters of these four regions and the effects of such environmental variability on phytoplankton abundance and community composition in the context of topographic (oceanic vs shelf), climatic (south vs north) and hydrographic (seasonally stratified vs well mixed shelf waters) differences along the transect. Some information from Chapters 3 and 4 needs to be repeated in order to compare both years and regions. The herbivorous copepod data, obtained from CPR tows were available for three regions (ocean region, northern stratified and well-mixed shelves), but there were no enough data for the southern stratified shelf in both years.

5.2 Interannual differences in climatic and physical variables in 2003 and 2004

Surface irradiance:

The distributions of weekly-averaged surface irradiance within the four regions are compared in Figure 5.2 for 2003 and 2004. In general, the annual cycles are similar, but with considerable week-to-week variability during the spring and summer months when periods of high irradiance were also characterised by relatively weak winds (Chapter 3 and 4, also Figure 5.10). The periods of greatest difference (see arrows in Figure 5.2) between the two years were:

- Days 55-85 (March) for the northern stratified and well mixed shelf waters when irradiance was relatively strong during the early part of the month in 2004 (days 55-70) and during the later part of the month in 2003 (days 70-85),
- Days 125-145 (May) for the northern stratified region (and to a lesser extent the southern stratified and well-mixed regions) when irradiance was relatively strong in 2004, and
- Days 175-195 (late June / early July) for the oceanic, southern stratified, northern stratified and well-mixed regions when irradiance was relatively strong in 2003.

The implications of these differences for stratification of the water column are discussed at the end of this Section, and for phytoplankton growth at the end of Section 5.4.

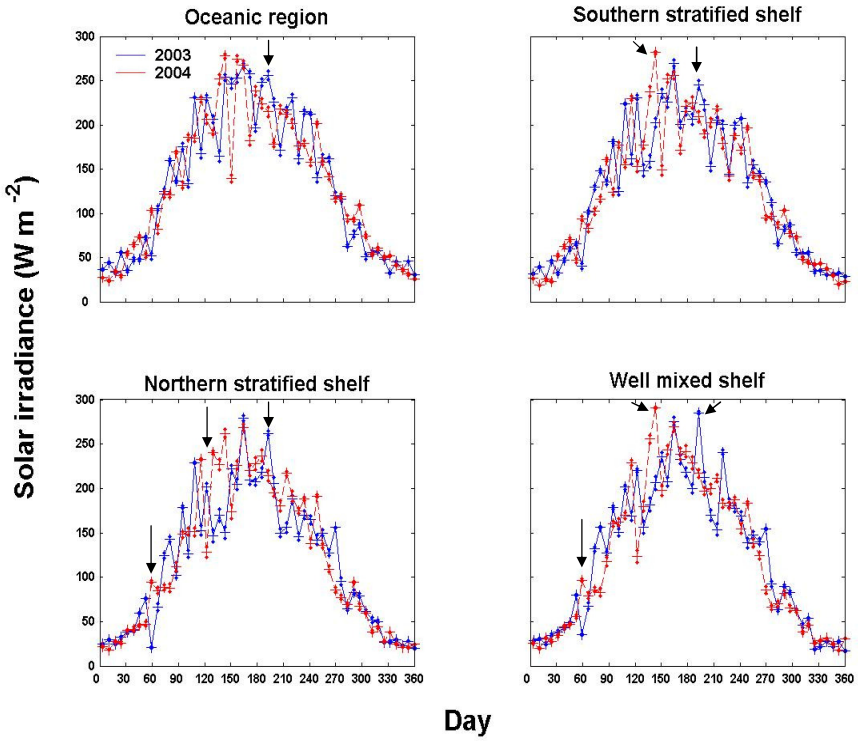


Figure 5.2: Weekly-averaged values of surface solar irradiance (W m-2) for 2003 (blue line) and 2004 (red line) for the four regions (oceanic region, southern and northern stratified shelf and well-mixed shelf).

Temperature

Figure 5.3 shows the monthly-averaged surface sea temperature in 2003 and 2004 for the four regions. The temperature varied significantly between years and regions (F-approximation to Friedman' test, $p < 0.05$) and a significant interaction (testing the effect of the two years on the four regions) occurred between years and regions ($p < 0.05$). The full seasonal cycle could only be described for 2003 as data were lacking for August and September (days 212-273) 2004. The minimum annual temperatures appeared to be reached during March (days 59-90) in 2003 and 2004 in all regions and the maximum temperatures during August (day 225) 2003 for oceanic and southern stratified shelf waters and during September (day 262) 2003 for well-mixed shelf waters. The observed maximum in July (day 192) 2003 for the northern stratified shelf appears anomalous (an increase of ~4.0^{o} C from June to July).

Interannual variability is evident in Figure 5.3, with surface temperatures in all regions cooler (1.0-3.0^{o} C) in July (day 195) 2004 and relatively warm (~ 0.5^{o} C) in November / December (days 328 / 352) 2004. The July anomaly is associated with unusually high wind speeds (~18 m s^{-1}) and low solar radiation occurring in late June /

early July (days 175-190) 2004. This may have resulted in strong mixing and the introduction of colder deeper water into the surface, weakening stratification (Pingree and Griffiths, 1978) and creating cold anomalies (Figures 4.1 and 4.3).

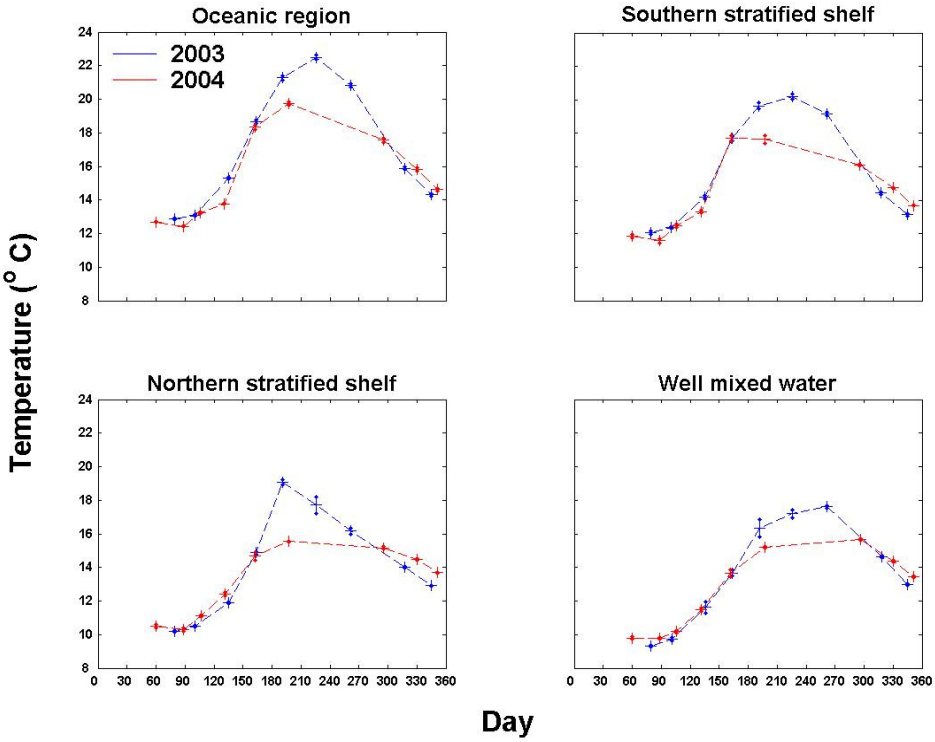


Figure 5.3: Monthly-averaged values of surface temperature (° C) for 2003 (blue line) and 2004 (red line) for the four regions. Note that no data are available for October in 2003 and for August and September in 2004.

Sea surface temperature distributions in 2003 and 2004 are consistent with those given in the literature (Pingree *et al.*, 1982; Holligan *et al.*, 1984a; Koutsikopoulos and Le-Cann, 1996; Koutsikopoulos *et al.*, 1998; Puillat *et al.*, 2004). Considerable variations from year to year are known to occur (Maddock and Swann, 1977; Reid *et al.*, 1993; Koutsikopoulos *et al.*, 1998; Puillat *et al.*, 2003).

Salinity

The monthly-averaged salinities for 2003 and 2004 are shown in Figure 5.4. No clear seasonal cycle is apparent although, when the influence of salinity anomalies (see below) is taken into account, there may be a tendency for a general slight increase in salinity during the summer and autumn months. However, the salinity was significantly different between years and regions (F-approximation to Friedman' test $p < 0.05$).

As expected, salinity was more variable in shelf regions than in the oceanic region. In both 2003 and 2004, relatively low salinity water appeared at the southern

entrance of the western English Channel, close to the Ushant region (Figures 5.1, 3.9 and 4.10). The source of this water, as suggested by Lazure and Jegou, (1998), and Puillat *et al*. (2004) is the northward transport of outflow from the Loire and Gironde Rivers. However, the fate of the low salinity lenses off the Ushant region was different in 2003 and 2004 (Figure 5.4). In 2003, a low salinity lens developed on the northern stratified and well-mixed shelves during June (day 150 onwards) and persisted in the well-mixed shelf waters until after the end of September (day 265), whereas in 2004 the low salinity lens was clearly seen on the southern stratified shelf between days 90-165 but was not advected into the English Channel (Figure 5.4).

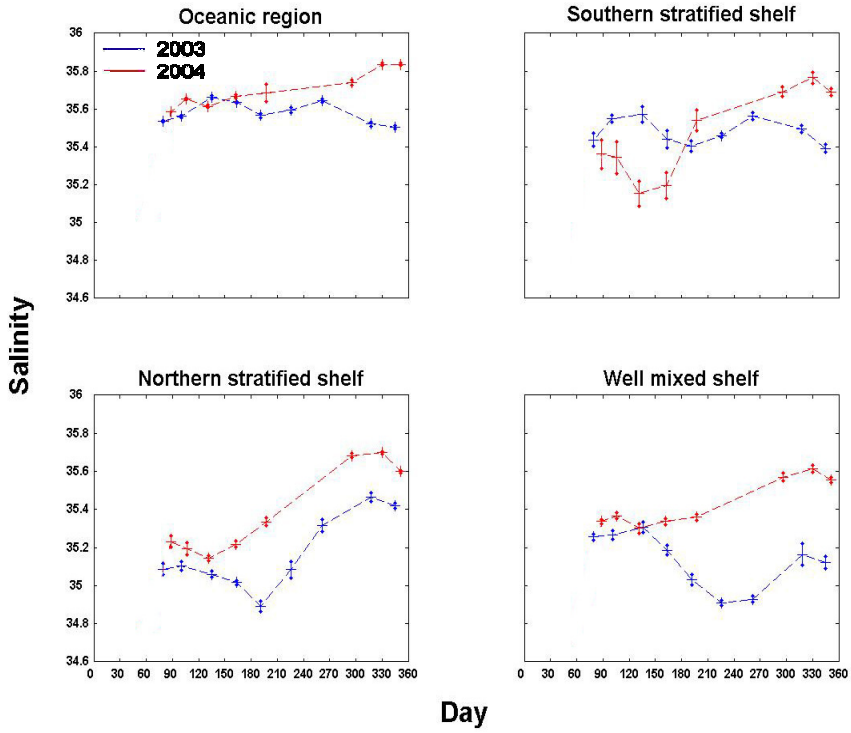


Figure 5.4: Monthly-averaged values of salinity for 2003 (blue line) and 2004 (red line) for the four regions. Note that no data are available for October in 2003 and for August and September in 2004.

Tidal currents, wind direction and river discharge need to be considered in order to understand the variations and distributions of salinity. The magnitude of river discharge determines the minimum salinity value in late winter (February) in the Ushant region. In this study, the combined outflows from the Loire and Gironde Rivers for the winter periods were higher in 2004 than in 2003 (Figures 3.2 and 4.2). However, the pattern of tidal currents (spring and neap) forming the Ushant front are the key factor in determining the transport regime further north of the Ushant region extending to the

western English Channel. In 2003, the low salinity surface water near Ushant became part of the residual flow through the English Channel, when low salinity water occurred near Ushant on a stronger (spring) tide, as discussed in more detail in Kelly-Gerreyn *et al*., (2006). The interannual variability in the prevailing wind conditions also plays an important role in the interannual variability of the low salinity plume transport. In the present study, the prevailing wind in 2003 was southeasterly and southwesterly, which influenced the residual flow into the northern stratified shelf. In contrast, in 2004, low salinity water occurred near the Ushant region during weaker (neap) tides (Kelly-Gerreyn *et al.*, 2006) and the prevailing wind direction was north and northwesterly. Consequently, the low salinity waters travelled into the southern stratified shelf (Figure 5.4).

Stratification

The vertical stability of oceanic waters is determined largely by seasonal changes in solar irradiance and wind strength whereas, for the continental shelf, tidal mixing and freshwater inputs also have to be taken into account (Pingree and Griffiths, 1978).

No direct observations were made during this study on variations in the depth of the surface mixed layer (SML) or the vertical distribution of temperature and salinity. However, some inferences can be drawn from annual differences in irradiance levels and wind strength, noting that increases in irradiance are generally accompanied by decreases in wind strength and vice versa (Figures 3.3, 4.3 and 5.2). The main climatic and hydrographic differences between 2003 and 2004 that were likely to have affected water column stability and, therefore, conditions for phytoplankton growth were:

- March (days 59-90) – relatively strong irradiance north of 49.0^{o} N early in the month in 2004, promoting thermal stratification, although this would have been offset by the period of relatively low irradiance which immediately followed.
- April/May (days 105-135) – relatively low surface salinity in the southern stratified shelf region in 2004, aiding the development of early stratification.

- May (days 124-135) – relatively strong irradiance across the northern part of the transect in 2004, especially in the northern stratified region, promoting early thermal stratification.
- June to September (days 161 to 262) – relatively low salinity in the English Channel in 2003, reinforcing established thermal stratification.
- Late June / early July (days 175-190) – relatively low irradiance and occasional strong winds in 2004 for oceanic and shelf stratified regions, weakening thermal stratification and reducing the length of the productive season.

Comparison of the surface temperature data (Figure 5.3) shows that differences up to the end of June were small and inconsistent between the two years, suggesting that the onset of stratification cannot be inferred from spatial and temporal variations in surface water temperature. However, in 2003, the surface water by July was much warmer in all regions due to a combination of stronger midsummer irradiance and (probably) lower salinity in the English Channel and hence stratification may have been stronger.

5.3 Interannual differences in chemical variables in 2003 and 2004

Figures 5.5, 5.6 and 5.7 show the interannual variability in inorganic nutrient (nitrate, phosphate and silicate) concentrations for 2003 and 2004 for the four regions. Nutrient dynamics follow a marked seasonal pattern, especially in the transition from winter to spring, due to nutrients removed by phytoplankton activity. The general seasonal cycle of the nutrients shows nutrient concentrations decreasing in the oceanic and southern stratified shelf regions in March and April, followed by decreasing concentrations in April and May on the northern stratified and well-mixed shelves.

If it is assumed that the end of February / early March (day 59-80) nutrient concentrations were representative of maximum winter values (i.e. pre spring bloom), these values were not constant between the two years and between the four regions (Figures 5.5, 5.6 and 5.7). For example, in February and early March, nutrient concentrations were considerably higher in 2004 (Friedman's test $p < 0.05$) compared to 2003 in the oceanic waters and southern stratified shelf, but less so on the northern and well mixed shelves. The sampling series in the current study allows analysis of the

changes for example in nitrate concentrations from high values in late winter to low values after the spring bloom for all the regions.

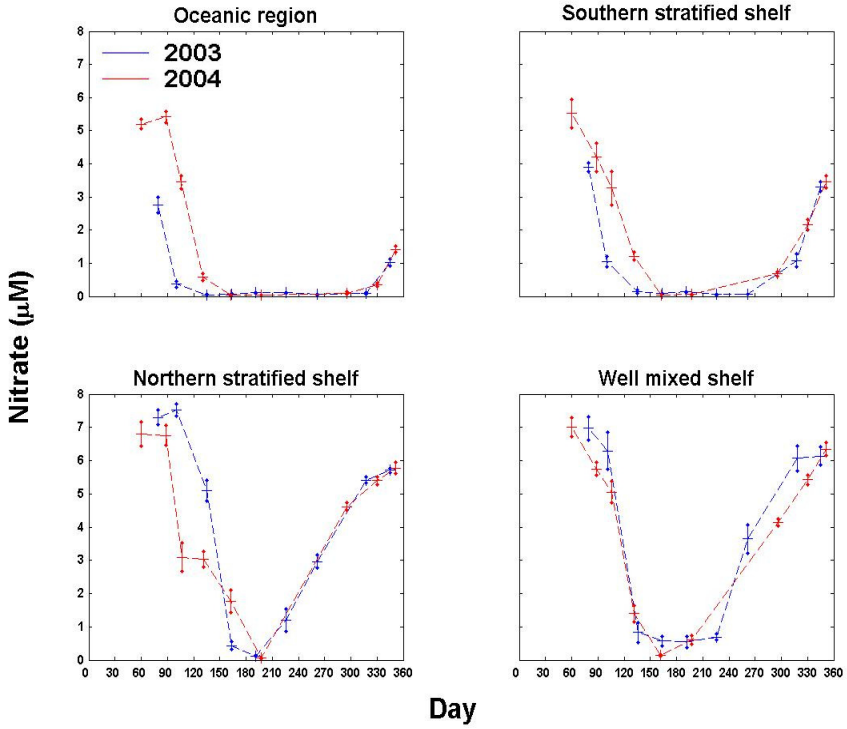


Figure 5.5: Monthly-averaged values of nitrate (µM) for 2003 (blue line) and 2004 (red line) for the four regions. Note that no data are available for October in 2003 and for August and September in 2004.

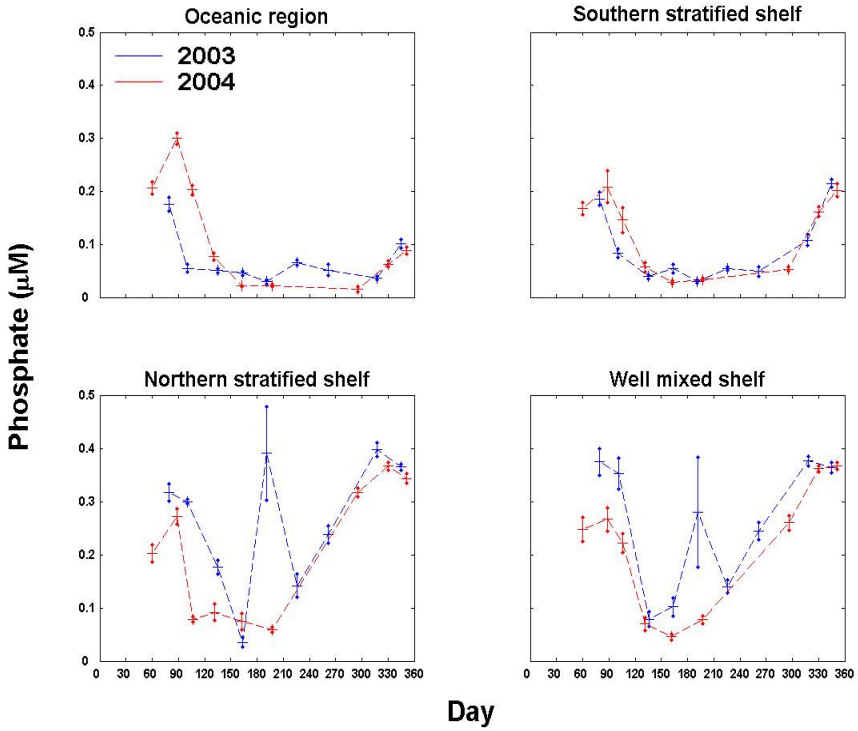


Figure 5.6: Monthly-averaged values of phosphate (µM) for 2003 (blue line) and 2004 (red line) for the four regions. Note that no data are available for October in 2003 and for August and September in 2004.

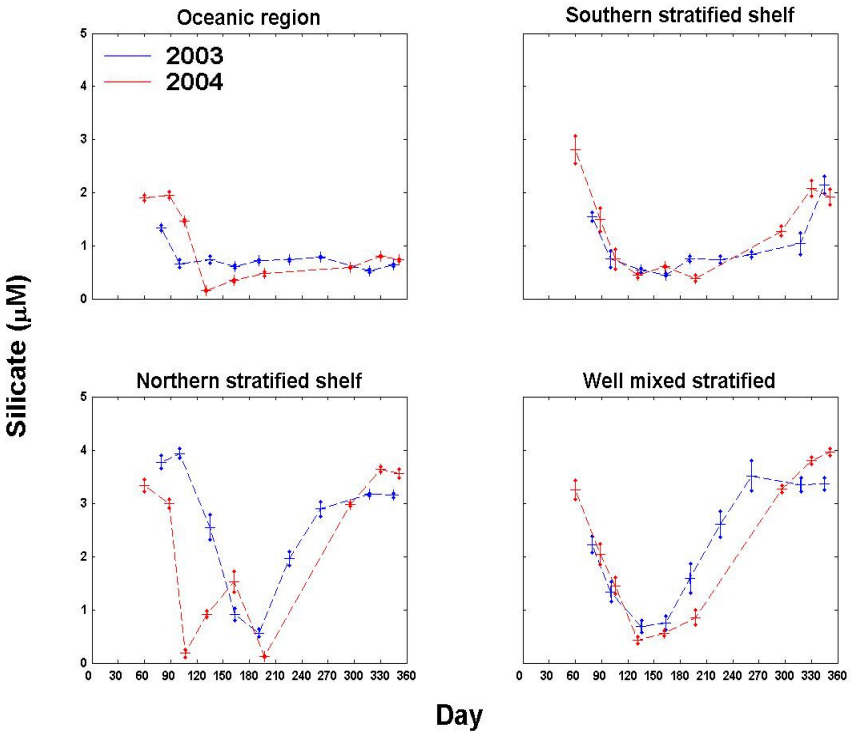


Figure 5.7: Monthly-averaged values of silicate (µM) for 2003 (blue line) and 2004 (red line) for the four regions. Note that no data are available for October in 2003 and for August and September in 2004.

This study shows that there were interannual differences in the timing of spring (March to May (days 90-150)) nutrient depletion between the regions (Figures 5.5 to 5.7). In 2003, the spring depletion of nutrients occurred earlier than in 2004 in the oceanic region and southern stratified shelf (regions of weak tidal streams, see Pingree *et al*., 1982), but in 2004 it occurred earlier than in 2003 in the northern stratified shelf waters. The spring draw down of nutrients in well-mixed shelf waters was similar in both years.

The noteworthy feature in the interannual differences of the monthly mean values of nutrient concentrations (NO_3, Si and PO_4) between the regions is the duration of the summer (June to September) minimum. Minimum nutrient values lasted throughout the late spring until the end of summer (days 135-265) for both years in the oceanic region and southern stratified shelf (Figure 5.5 to 5.7). In contrast, nutrient concentrations increased in the northern stratified and well-mixed shelf waters in August and September 2003 (days 210-265). The possible reasons for this increase are different in the two regions. This increase in the northern stratified shelf waters may be related to episodic mixing events (high wind and spring tide) in August. The increases

in nutrients in the well-mixed shelf waters at the same period suggests that the low salinity intrusion may influence this region where the concentrations of nitrate and silicate increased at salinities < 35.0 (Figures 3.10, 5.4, 5.5 and 5.7).

Any interannual differences in the timing of the autumn regeneration of nutrients are not obvious due to a lack of observations in October 2003 and in late July to September (days 200-295) in 2004. However, some features of the nutrient regeneration in autumn can be seen from the November and December observations. For example, in the southern stratified shelf waters, lower concentrations of nutrients through November were observed in 2003 but not in 2004 and this correspond with the phytoplankton biomass in November 2003 relative to 2004 (Figure 5.5 to 5.7). The increase of nutrients in November (days 315-331) occurred in 2003 before 2004 in the well-mixed shelf waters. In contrast, the autumn increase of nutrients in northern stratified shelf waters was similar in both years.

An anomalous increase of silicate concentration (up to1.8 µM) occurred in May and June (days 135 and 160 respectively) in 2004 in the northern stratified shelf waters. This is difficult to explain because there is no evidence to link this to cooling, mixing, or advection events. Interestingly, in April and July 2004 (days 107 and 198, respectively) in the latter region, the silicate concentrations were extremely low, whereas in 2003 the silicate was not fully depleted (Figure 5.7).

The plot of silicate concentrations as a function of salinity in both years (Figures 3.13 and 4.14) shows an interesting distribution. For example, in August 2003, samples with silicate concentrations between 2.1 and 4.0 µM and salinity less than 35.0 indicate a direct river water influence in well-mixed shelf waters. The second group (salinity 35.0-35.3) had concentrations < 2.1 µM and shows no gradient with salinity, but these waters were increased in comparison to measurements in July by about 1.5 µM and probably reflect regeneration of silicate into the northern stratified shelf. The third group (salinity > 35.3) is the oceanic water and southern stratified shelf. Here values remained low, as summer stratification limited any resupply from deeper waters. These groupings of silicate concentrations with salinity continue to be seen and intensify in the data throughout the rest of the year. Looking at the March data, a positive gradient with

salinity associated with the high salinity samples (Figure 3.13), reflecting the supply of silicate to surface waters by deep winter mixing (Hydes *et al.*, 2001).

The range of nutrient values measured in this study is comparable to those reported by a number of authors (Table 1.1) and follow similar seasonal patterns. (Treguer *et al.*, 1979; Tappin *et al.*, 1993; Loyer *et al.*, 2006). For example, in the oceanic region, Treguer *et al*., (1979) measured winter nitrate levels of 4.0 µM and Loyer *et al*., (2006) reported a winter nitrate level of 7.0 µM for the southern stratified shelf.

5.4 Interannual differences in phytoplankton biomass (chlorophyll *a*) in 2003 and 2004

Figure 5.8 shows the interannual variability in chlorophyll *a* concentration from acetone extractions for 2003 and 2004 within the four regions. There is a significant difference (F-approximation to Friedman' test $p < 0.05$) in chlorophyll *a* concentrations between the two years. The average chlorophyll *a* concentrations for 2003 was 2.6 mg m^{-3} and for 2004 was 1.5 mg m^{-3}.

The general seasonal pattern shows chlorophyll *a* concentrations increasing in the oceanic and southern stratified shelf regions in March and April (days 60-110), followed by a rapid increase in April and May (110-135) on the northern stratified and well-mixed shelf waters (Figure 5.8). Spring chlorophyll *a* values were similar in both years in well-mixed shelf waters (Figure 5.8). Following the spring bloom, chlorophyll *a* fell to below 0.75 mg m^{-3} and remained at that level in the oceanic region and southern stratified shelf through the summer months (June-September). In contrast, on the northern stratified and well-mixed shelves, chlorophyll *a* concentrations remained high in mid summer (July) due to blooms of *Karenia mikimotoi* in 2003 or to populations of diatoms events in 2004. The effects of increasing wind mixing in late June and July (days 175-190) of 2004 are also apparent in the southern stratified shelf region where surface chlorophyll concentrations in June and July were about three times the levels for the corresponding months in 2003 (Figure 5.8). Variations in surface wind stress episodically weakens the thermocline allowing nutrient inputs to the photic zone from below in shelf regions (Behrenfeld *et al.*, 2008).

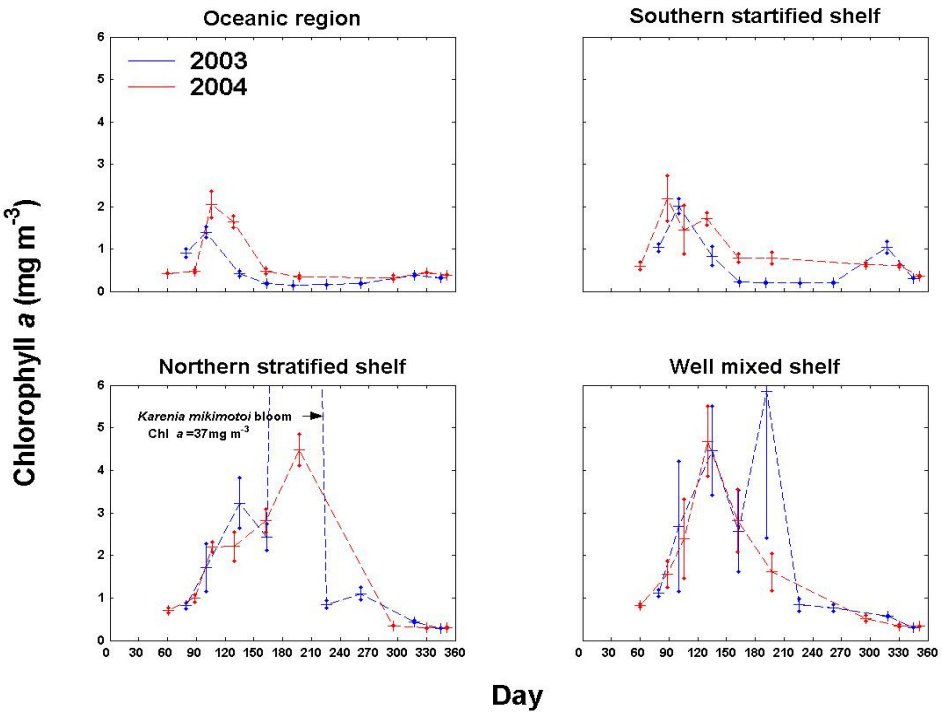


Figure 5.8: **Monthly-averaged values for extracted chlorophyll *a* (mg m^{-3}) for 2003 (blue line) and 2004 (red line) for the four regions. Note that no data are available for August and September in 2004. Black arrow indicates the chlorophyll value observed during the bloom of the dinoflagellate, *Karenia mikimotoi,* in the northern stratified shelf region.**

The start of the phytoplankton spring bloom, primarily diatoms, is associated with variations in surface irradiance and wind mixing (Henson *et al.*, 2006). Here the relationship between the depth of the column mixing and the availability of irradiance controls the onset of the spring bloom. The progress of the spring bloom is predominantly dependant on intermittent turbulence, following short periods of stratification which allows the resuspension of species from the bottom mixing layer (Henson *et al.*, 2006). However, with increasing frequency of wind mixing events, the spring stratification is delayed, with the consequence that a reduction in the spring bloom occurs (Van-Haren *et al.*, 1998; Henson *et al.*, 2006). In this study, the monthly changes in chlorophyll *a* levels shown in Figure 5.8 do not show a clear correspondence with annual differences in the timing of nutrient removal during spring that were described in the previous section.

To get a precise determination of the onset the spring bloom, weekly-averaged chlorophyll values can be extracted from satellite data (Figures 3.16 and 4.17), which is less noisy than the data available from fluorescence. These are given in Figure 5.9 for the oceanic region and the northern stratified shelf (days 60-200) for 2003 and 2004.

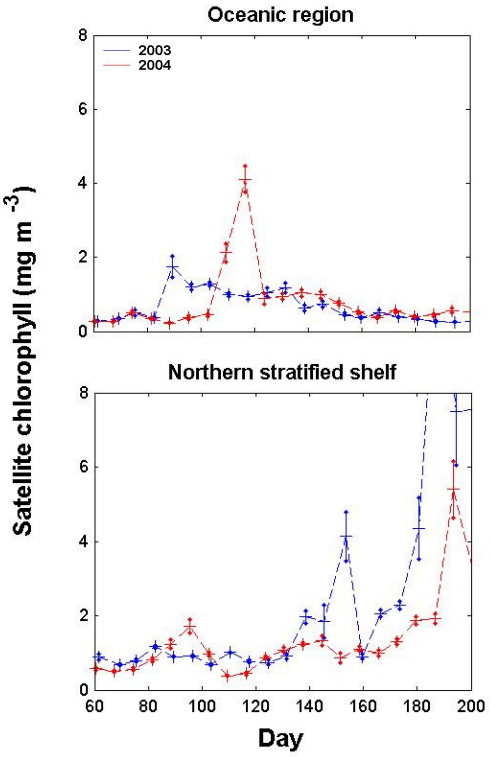


Figure 5.9: Weekly-averaged values of satellite chlorophyll (mg m^{-3}) in spring and summer 2003 (blue line) and 2004 (red line) for the oceanic and northern stratified shelf regions.

Corresponding information on weekly changes in solar irradiance and wind speed is provided in Figure 5.10. In the oceanic region, during 2003, maximum satellite chlorophyll values of ~2.0 mg m^{-3} (Figure 5.9) were related to low winds ~4.0 m s^{-1} around day 80-90 in 2003 (Figure 5.10). Whereas, in 2004 maximum satellite chlorophyll values (~ 4.0 mg m^{-3}) were related to a combination of decreasing wind speed from 12.0 to 8.0 m s^{-1} and increasing irradiance (~225 W m^{-2}) around day 115. In the northern stratified shelf region during 2003, maximum satellite chlorophyll values (4.2 mg m^{-3}) were related to a decrease in wind speed (~4.0 m s^{-1}) and increase in irradiance (~ 225 W m^{-2}) around day 150 (Figure 5.10). Note there were persistently strong winds (> 8.0 m s^{-1}) prior to this date. In 2004 in the northern stratified shelf waters, maximum chlorophyll values were related to weak winds (~4.0 m s^{-1}) around days 95-120, and increasing irradiance (> 150 W m^{-2}) (Figures 5.9 and 5.10), corresponding to a removal of 50 % of winter nutrients (Figures 5.5 to 5.7). A second chlorophyll *a* peak around day 140 was also related to weak winds (~5.0 m s^{-1}) and increasing irradiance (~ 250 W m^{-2}).

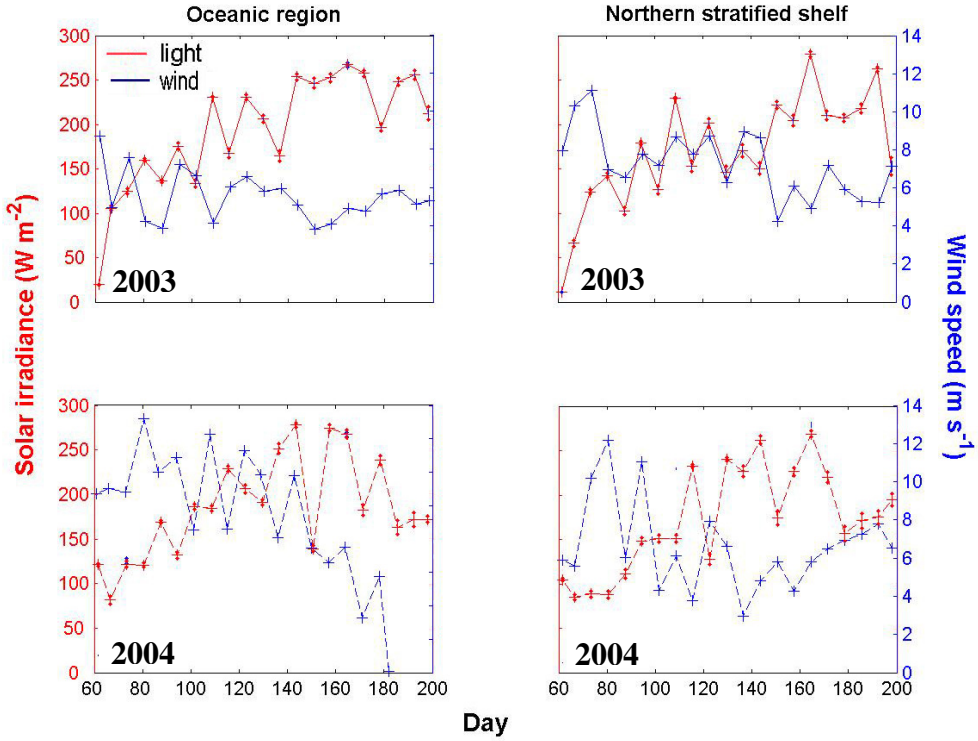


Figure 5.10: Comparison of the weekly-averaged surface solar irradiance (W m^{-2}) (red line) and the weekly-averaged wind speed (m s^{-1}) (blue line) for the oceanic and northern stratified shelf regions in spring and summer 2003 and 2004.

From the above analyses, the greater temporal resolution shows clear differences in the timing of the spring bloom between the two years for each region (oceanic and shelf regions). In 2003, the spring bloom started earlier in oceanic waters compared to the shelf region, while in 2004 the bloom started earlier in the shelf region. Likely conditions for the start of the spring bloom can be identified as a combination of the variability of surface irradiance and wind speed, hence the depth of mixed layer (Figure 5.9). The evidence from these data set is that the start of the spring bloom occurs when irradiance is > 150 W m^{-2} and wind speeds are less than 5.0 m s^{-1} (Figures 5.9 and 5.10). There is a significant difference in the surface irradiance and wind speed (F-approximation to Friedman' test $p < 0.05$) between the two years and two regions. This might suggest that the bloom that started late had missed the optimum bloom condition and low surface irradiance and increasing wind have contributed in the delay of the bloom. The timing of increases in chlorophyll matches closely with the periods of nutrient removal (Figures 5.5 to 5.7). For example, the nutrient removal started earlier in 2004, which matches the spring bloom increase (Figures 5.5 to 5.7 and 5.9).

However, the interannual variability in the timing of the spring bloom was not reflected in the magnitude of the spring bloom.

5.5 The distribution of phytoplankton biomass in relation to environmental data

The interannual and regional variability in the climatic, physical and chemical variables were shown in the previous sections in this Chapter and this section investigates the existence of statistically distinct seasonal and regional groups through multivariate analysis of environmental variables. Additionally, this section also investigates the relationship between phytoplankton biomass and environmental data.

5.5.1 *Environmental data groups*

Cluster and non-metric Multidimensional Scaling (MDS) analysis, based on a normalised Euclidean distance with log (1+x) transformation of these data (Clarke and Warwick, 1994), was carried using irradiance, salinity, sea surface temperature, nitrate, phosphate and silicate for 2003 and 2004. One-way analysis of similarity (ANOSIM) tests demonstrated the variables were statistically different between 2003 and 2004, with a global $R > 0.95$ at a significance level of $p < 0.05$.

According to the similarity profile analysis (SIMPROF) results ($p < 0.05$), the cluster dendrogram and MDS ordination for the 2003 data showed separation at a normalised Euclidean distance of 2.2 into 12 major groups (A-M) (Figures 5.11 and 5.12). The MDS stress is low (0.1) indicating good two dimensional representation of these data. A seasonal pattern in the grouping can be distinguished from the MDS plot (Table 5.1). Groups (m) and (d) represent late winter and early spring, and spring respectively in the oceanic region and southern stratified shelf, groups (j) and (i) represent the spring at the northern stratified and well-mixed shelve regions. Group (c) represents summer in the oceanic region and southern stratified shelf, groups (b and a), and (h and g) represent summer in northern stratified and well-mixed shelve regions respectively. Group (k), (f) and (e) represents the autumn at the northern stratified, southern stratified and well-mixed shelve and oceanic regions respectively.

Table 5-1: Distribution of the environmental variables (solar irradiance, temperature, salinity, nitrate, phosphate and silicate) groups for 2003.

Regions/ seasons (days)	Late winter and early spring (60-90)	Spring (90-150)	Summer (173-264)	Autumn (315-354)
Oceanic region	m	d	c	e
Southern stratified shelf	m	d	c	f
Northern stratified shelf	j	j	b and a	k
Well mixed shelf	j	j and i	h and g	f

In 2004, according to SIMPROF ($p < 0.05$), the cluster dendrogram and MDS analysis of the environmental data showed separation at a normalised Euclidean distance of 1.2 into nine groups (A-I) (Figures 5.13 and 5.14). The low MDS stress in 2004 of 0.04 indicates a good two-dimensional representation of these data. As summarised in Table 5.2, group (c) represents the late winter and early spring in the oceanic region and southern and northern stratified and well-mixed shelves; Group (a) was separated from the late winter and early spring group for the southern stratified shelf, because of a low salinity intrusion. Group (f) represents spring for the oceanic region and southern and northern stratified shelves; group (g) represents spring at well-mixed shelf. Group (e) represents the summer for the four regions and there is a tendency for in significant subgroup to be seen within group (e), representing the four regions (Figure 5.14). Group (d) represents the early autumn in the oceanic region and southern stratified shelf; and group (h) and (i) represent the autumn in the oceanic region and southern stratified shelf respectively. Group (b) represents autumn conditions at the northern stratified and well-mixed shelve regions.

Spatial variability of hydrographic conditions was not restricted to regional differences, as there were also significant seasonal and annual differences. The similarity percentage analysis (SIMPER) on the environmental data for 2003 and 2004 suggested the distribution of the environmental variables in the four regions (Tables 5.1 and 5.2 and Figures 5.12 and 5.14). A high similarity (90) was noted between the oceanic region and southern stratified shelf. Environmental variables (as bubble plots) have been superimposed on the MDS ordination, in order to demonstrate the distribution of each variable between the groups (Figures 5.15 and 5.16).

Table 5-2: Distribution of the environmental variables (solar irradiance, temperature, salinity, nitrate, phosphate and silicate) groups for 2004.

Regions/ seasons (days)	Late winter and early spring (59-90)	Spring (90-150)	Summer (173-212)	Early autumn (295-315)	Autumn (315-354)
Oceanic region	c	f	e	d	h
Southern stratified shelf	c and a	f	e	d	i
Northern stratified shelf	c	f	e	b	b
Well mixed shelf	c	g	e	b	i

Late winter and early spring groups (days 59-90) in the oceanic region and southern stratified shelf were characterised by low irradiance and high nutrients in both years, but intermediate salinity in 2004. However, one group (a) (only one sample) in 2004 was separated from the early spring group at the southern stratified shelf due to its relatively low salinity. Spring groups in both years were also similar (Figures 5.12 and 5.14), with increased irradiance, salinity and temperature values, but showed lower nitrate and higher silicate in 2003 than in 2004 (Figures 5.15 and 5.16). The summer groups were similar in the two years, with high irradiance, temperature and salinity, depleted nitrate and low phosphate and silicate (Figures 5.15 and 5.16).

The variation in environmental data in the northern stratified and well-mixed shelve regions was more complex than in the two southern regions. There was one group (j) representing the late winter and spring in 2003 for the latter regions due to a high similarity (96 %) between them, with decreasing salinity and intermediate irradiance and high nutrients (Table 5.1 and Figures 5.11 and 5.15). Whereas, in 2004, late winter and early spring (group c) in both regions was characterised by high salinity, intermediate irradiance, low temperature and high nutrients (Figure 5.16). Furthermore, the spring groups in 2004 for both regions were separated into two groups (f and g), with group (f) from the northern stratified shelf distinguished by increasing irradiance, salinity and temperature and decreasing nutrients; interestingly, group (g) was separated from the spring groups by the following characteristics: very low irradiance and temperature, high salinity, and decreasing nutrients especially silicate.

The main difference between summer groups (h and b for well-mixed and northern stratified shelves respectively) in 2003 was lower nutrient levels at the northern stratified shelf (Figure 5.15). Group (a) was separated from group (b) (the

summer group in northern stratified shelf), because of the occurrence of a *Karenia mikimotoi* bloom in 2003. This group was distinguished by high irradiance, low salinity, high phosphate (see Chapter 3), low nitrate, and silicate. Whereas, Group (g) was separated from group (h) (the summer group in well-mixed shelf) by increased nitrate. On the other hand, the summer groups in 2004 in both regions were characterised by intermediate irradiance level, depletion of nitrate and an unusual decrease in silicate, perhaps due to different phytoplankton communities, compared to 2003 (Figures 5.15 and 5.16).

The autumn groups (days 295-354) in both years and in all regions were characterised by low irradiance values, high salinity, and decreasing temperature. In addition, nutrient concentrations increased from the oceanic region to the southern and northern stratified and well-mixed shelves.

In general, the main differences between 2003 and 2004 were: 1. northern and southern regions were more distinct in 2003 than 2004 (see Tables 5.1 and 5.2); 2. the spring groups in 2004 separated into two groups (f and g) (Figures 5.12 and 5.14); 3. there was a similarity of the summer group for all regions in 2004; 4. a separation of environmental group (group a) which was related to *Karenia* bloom was clearly seen (Figure 5.12).

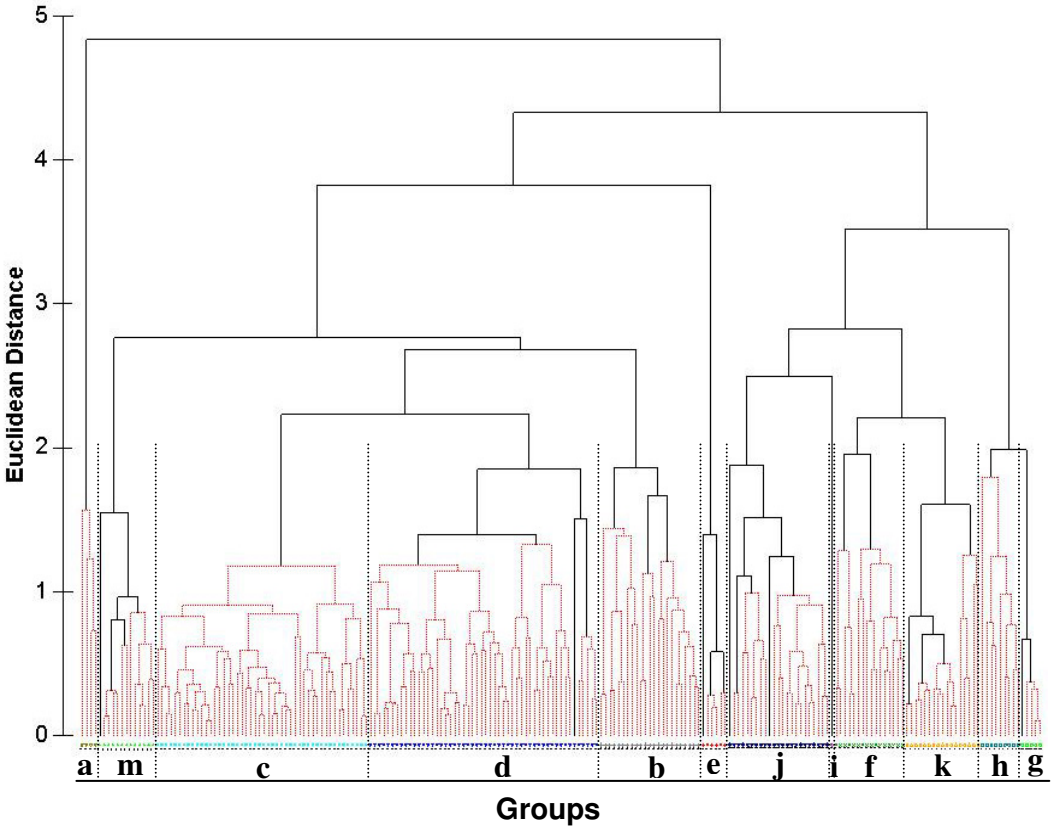


Figure 5.11: Dendrogram for hierarchical cluster analysis of environmental variables (solar irradiance, temperature, salinity, nitrate, phosphate and silicate) for 2003. Note that samples connected by red line cannot be significantly differentiated ($p > 0.05$).

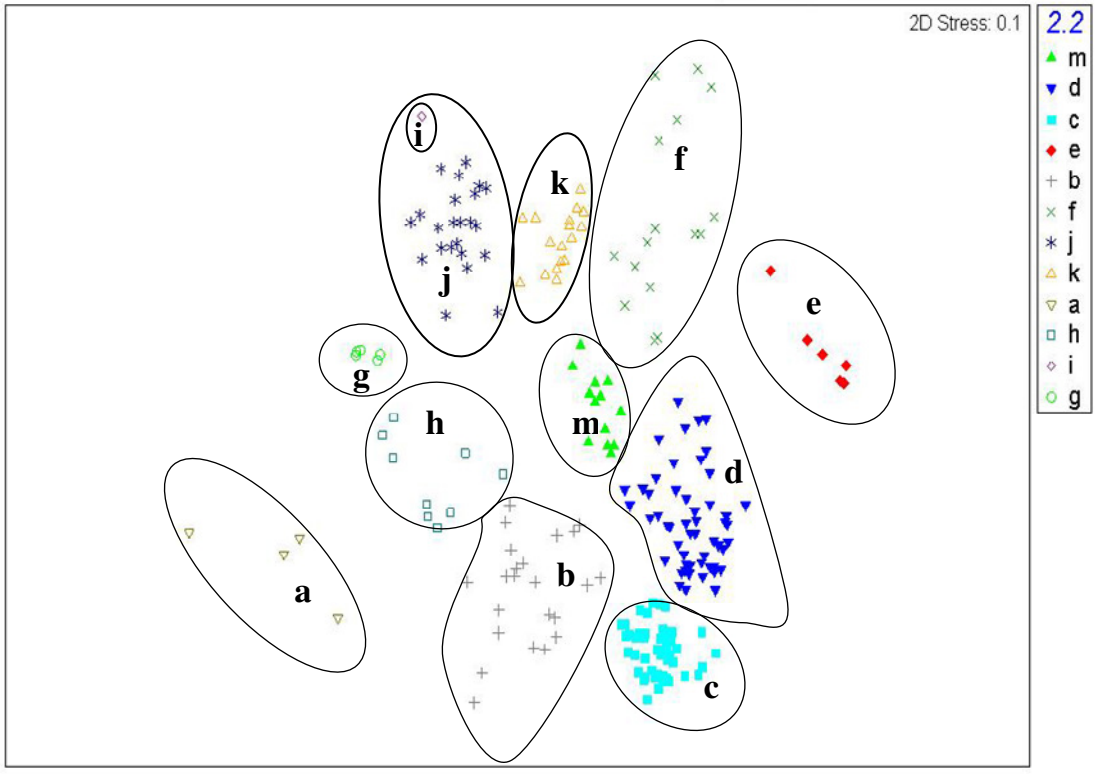


Figure 5.12: MDS plot of environmental variable (solar irradiance, temperature, salinity, nitrate, phosphate and silicate) groups for 2003.

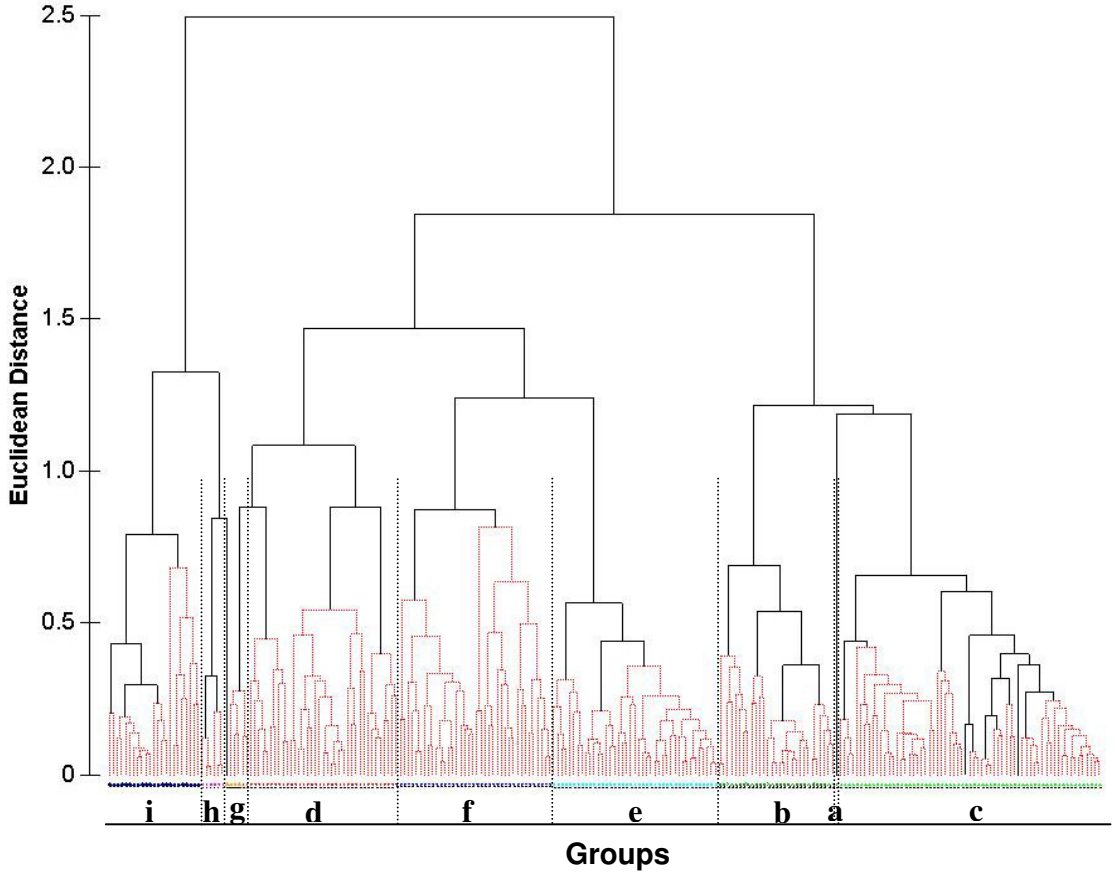


Figure 5.13: Dendrogram for hierarchical cluster analysis of environmental variables (solar irradiance, temperature, salinity, nitrate, phosphate and silicate) for 2004. Note that samples connected by red line cannot be significantly differentiated ($p > 0.05$).

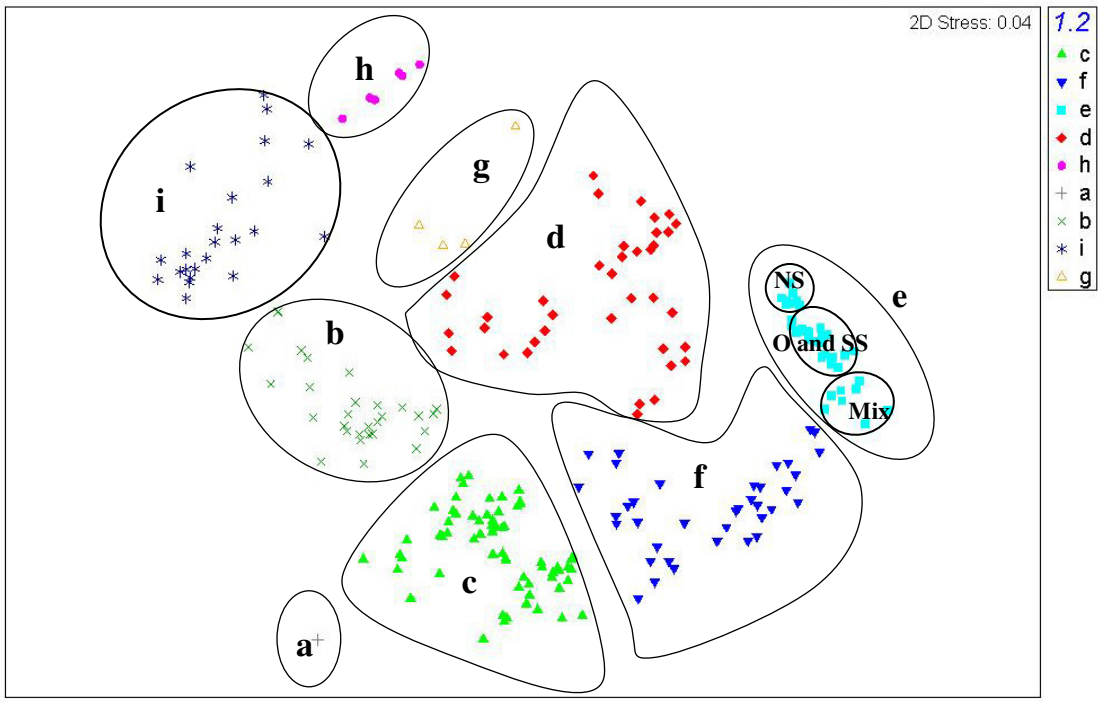


Figure 5.14: MDS plot of environmental variable (solar irradiance, temperature, salinity, nitrate, phosphate and silicate) groups for 2004.

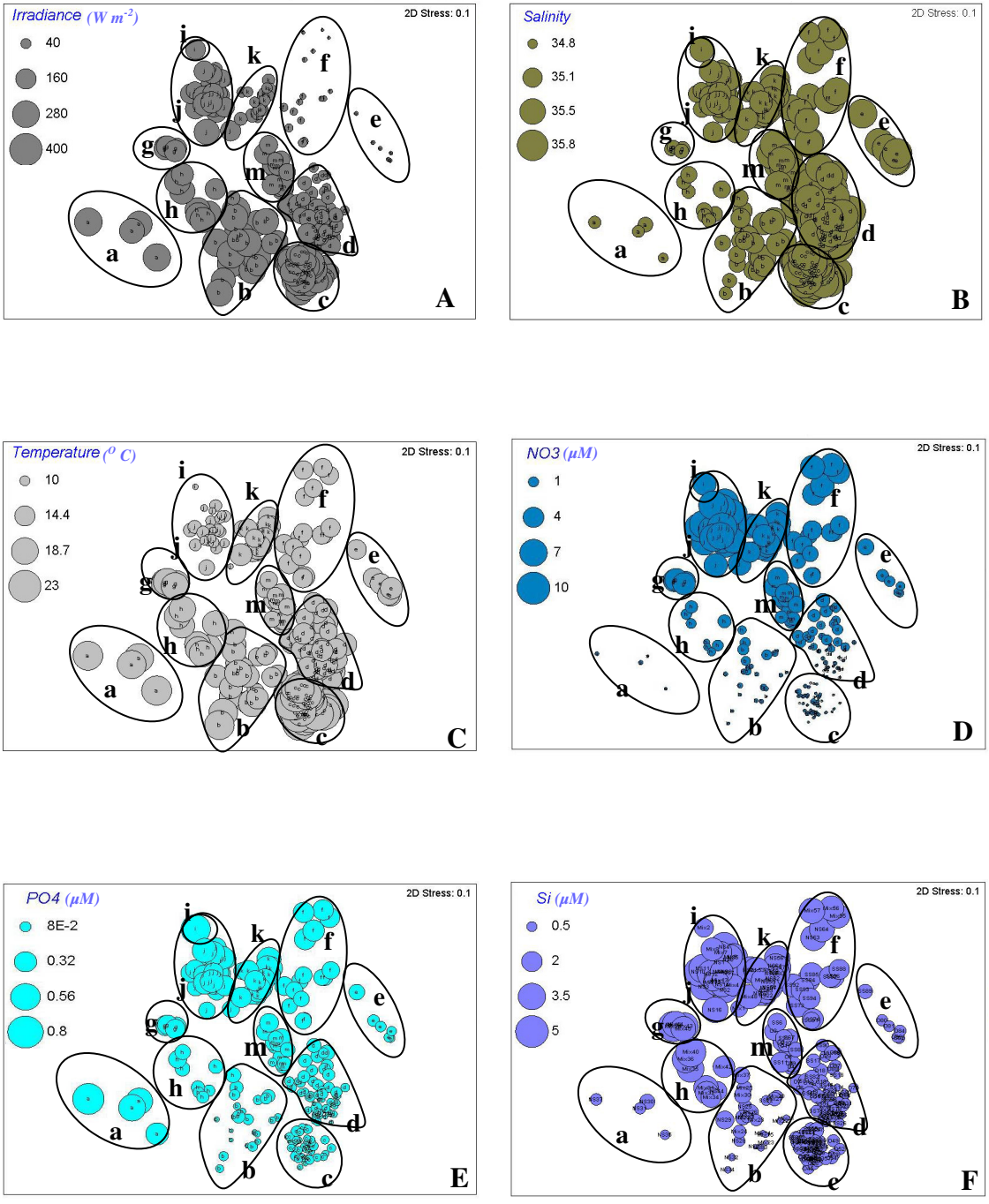


Figure 5.15: MDS ordination plot showing the 2-dimensional representation of similarity of environmental variables for 2003 in the four regions. The overlying bubble plots indicate: (A) solar irradiance (B) salinity, (C) temperature (D) nitrate, (E) phosphate, and (F) silicate.

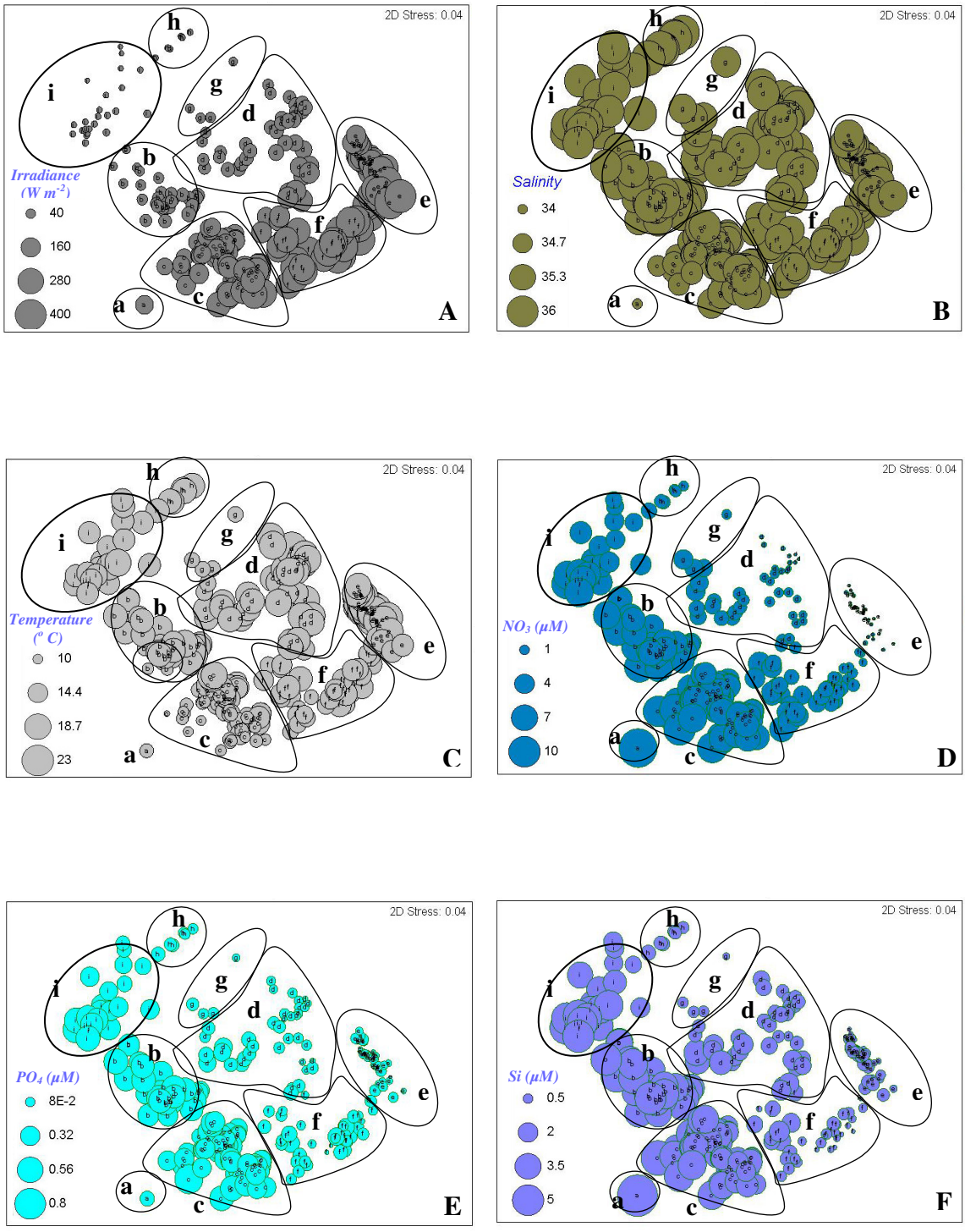


Figure 5.16: MDS ordination plot showing the 2-dimensional representation of similarity of environmental variables for 2004 in the three regions. The overlying bubble plots indicate: (A) solar irradiance (B) salinity, (C) temperature (D) nitrate, (E) phosphate, and (F) silicate.

5.5.2 *The relationship between environmental data and phytoplankton biomass (chlorophyll a)*

The MDS plots of the environmental variables were superimposed with bubble plots of chlorophyll *a*, in order to indicate how environmental conditions affect changes in phytoplankton biomass (chlorophyll *a*) (Figures 5.17 and 5.18).

Seasonal and regional differences in chlorophyll *a* can be largely explained by the various factors that control the availability of light and nutrients to phytoplankton (Pingree *et al.*, 1976). Accordingly, the chlorophyll *a* spring increase can be attributed to increased irradiance when nutrient levels were still high. However, as explained above (Section 5.2), there were differences in the duration of the chlorophyll *a* spring peaks from oceanic deep water to shallow water in both years. For the oceanic region and southern stratified shelf waters early spring and spring groups (days 60 to 150) in both years showed increasing chlorophyll *a* values, with different levels of irradiance (see groups (m and d) and (c and f) in Figures 5.15 and 5.16 respectively) and with high nutrient concentrations, which were quickly utilised and remained low for a great part of the year (days 173-264) (Figures 5.15 and 5.16). In the summer (days 173-264), even though the irradiance levels were high (> 250 W m^{-2}), the low chlorophyll *a* values (groups c and e in Figures 5.17 and 5.18 respectively) corresponded with low nutrient concentrations, especially nitrate depletion (groups c and e in Figures 5.15 and 5.16 respectively).

Comparison of the relationship between chlorophyll *a* and environmental data in 2003 and 2004 in the northern stratified and well-mixed shelf waters show some significant differences. In the spring groups (days 90-150), more chlorophyll *a* was measured in 2004 than 2003 (Figures 5.17 and 5.18) and the spring groups in 2004 were separated into two groups f and g for the northern stratified and well-mixed shelf respectively (see Figure 5.18). These differences are attributed to the differences in the irradiance levels and nutrient availability (see groups (j and i) and (f and g) in Figures 5.15 and 5.16 respectively). For example, chlorophyll *a* increased (~4.5 mg m^{-3}) in spring 2004 (group g) in the well-mixed shelf waters, where the irradiance level and SST were low (< 40 W m^{-2} and <14.0^{o} C respectively) (group g in Figure 5.16). Additionally, nitrate and phosphate decreased and silicate concentrations depleted in the surface water subsequent to spring biomass and reached a low concentration (< 0.5 µM)

before either nitrate or phosphate had reached their minimum values (group g in Figure 5.16).

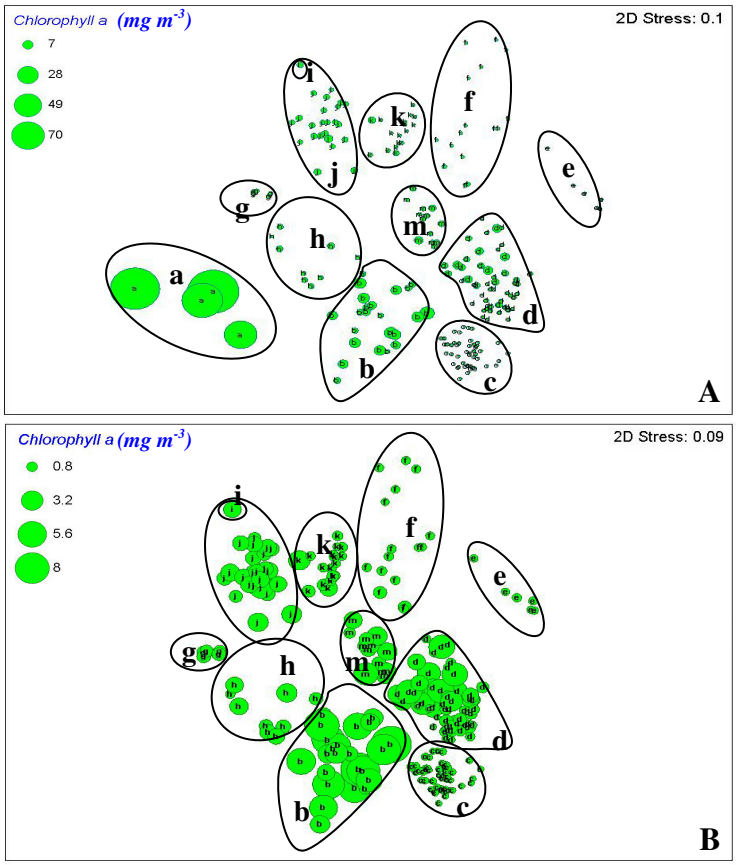


Figure 5.17: MDS ordination plot showing the 2-dimensional representation of similarity of environmental variables and phytoplankton biomass for 2003 in the four regions. The overlying bubble plots indicate chlorophyll *a* A) with *Karenia mikimotoi* bloom samples and B) without the bloom samples.

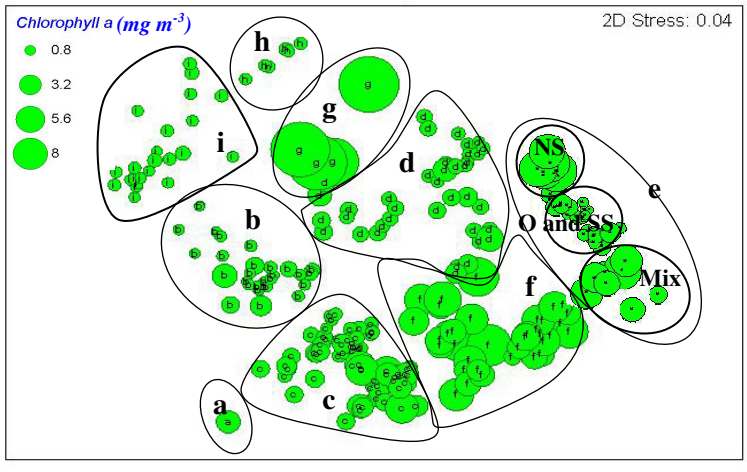


Figure 5.18: MDS ordination plot showing the 2-dimensional representation of similarity of environmental variables and phytoplankton biomass for 2004 in the four regions. The overlying bubble plot indicates chlorophyll *a*.

High chlorophyll *a* (> 70.0 mg m^{-3}) occurred in the summer 2003 in the northern stratified shelf region where there was high irradiance. The high temperature and low salinity in this time suggests the water column was stable (group (a) in Figures 5.15 and 5.17a). Additionally, nitrate concentration was low, suggesting limiting nutrient conditions in summer 2003 in northern stratified shelf waters (Figure 5.15). In contrast, chlorophyll *a* levels in summer group (e) in 2004 in northern stratified and well-mixed shelf waters increased and this group was distinguished by a surface irradiance of > 160 W m^{-2}, nitrate depletion, and low phosphate and silicate (Figures 5.16 and 5.18). It is noticeable that the decrease in silicate was greater in 2004 than in 2003 especially in well-mixed shelf waters (Figures 5.15 and 5.16).

The chlorophyll *a* values in autumn groups (days 295-354) were relatively low (< 1.0 mg m^{-3}) despite the corresponding enrichment of nutrients to the surface water, so that factors other than nutrient concentrations must influence the chlorophyll *a* values during the rest of the year. Surface irradiance values were < 40 W m^{-2} (Figures 5.15 and 5.16). Irradiance levels are likely to be the limiting factors in the autumn (Figure 5.15, 5.16, 5.17 and 5.18).

5.6 Distributions of phytoplankton species in 2003 and 2004

The data on phytoplankton species biomass were subjected to cluster and MDS analyses, with rare species eliminated from the dataset. Also a presence and absence transformation of the phytoplankton carbon biomass data was used. Groupings of phytoplankton species biomass could be distinguished for 2004 but not 2003. The results of a hierarchical clustered analysis for 2004 are illustrated as a dendrogram in Figure 5.19, and identify three phytoplankton groups (A-C) at a similarity level range of 71-76 %. The two-dimensional MDS plot (Figure 5.20) with stress 0.13 indicates a good two dimensional representation of the data. One-way ANOSIM (analysis of similarities) tests on a Bray-Curtis Similarity for the phytoplankton species biomass (transformed to presence/ absence) demonstrated that the differences between the groups were statistically significant, with a global R > 0.82 at a significance level of $p <$ 0.05. The groups follow a seasonal pattern extending across all regions, with A, B and C representing spring, summer and autumn respectively. The results of SIMPER analysis showed the dominant species in each group (Table 5.3). Diatoms were a major contributor to each group, with dinoflagellates occurring only in the summer group.

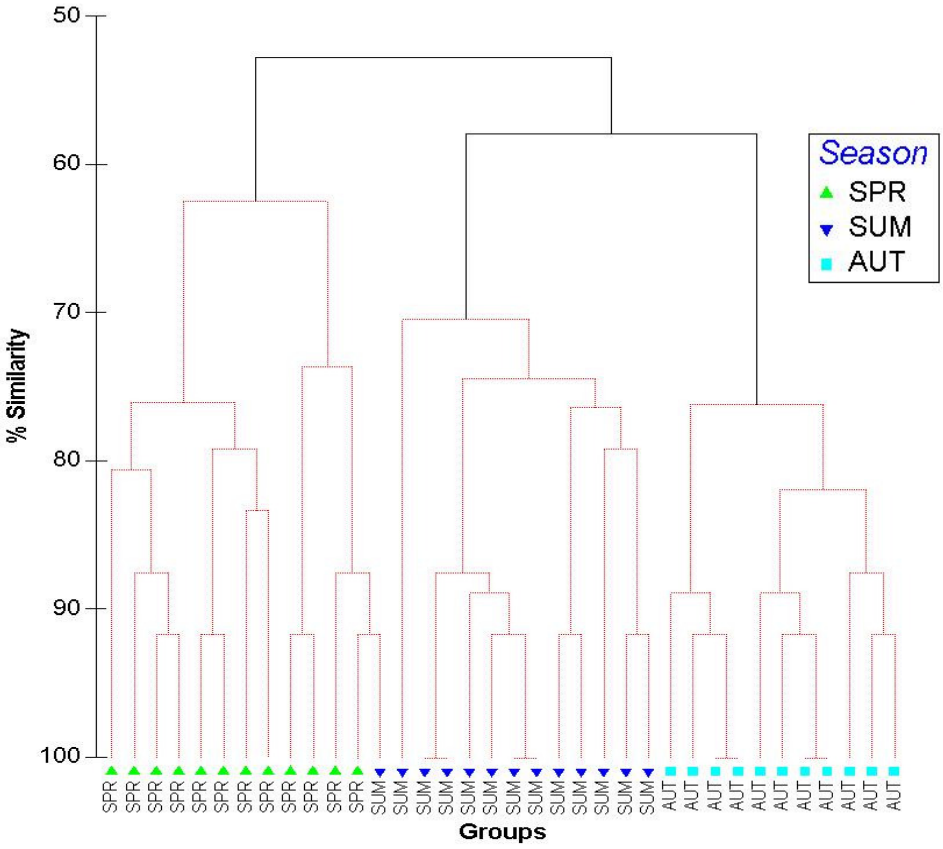


Figure 5.19: Dendrogram for hierarchical cluster analysis of dominant species of diatoms and dinoflagellates in 2004. Note that samples connected by red line cannot be significantly differentiated ($p > 0.05$).

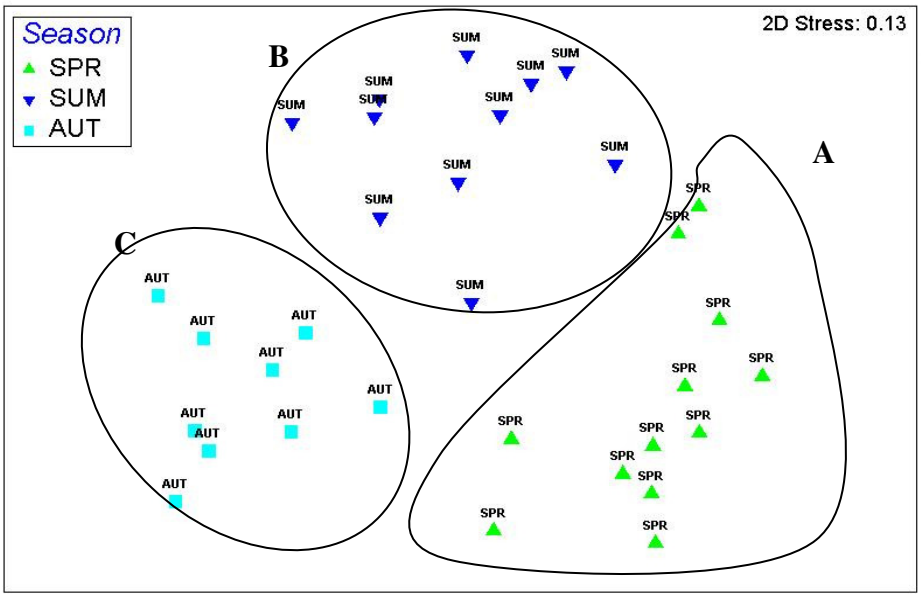


Figure 5.20: MDS plot of groups of dominant diatoms and dinoflagellates species (C biomass) in 2004.

Table 5-3: The main sample groups defined by phytoplankton species biomass in 2004 for the oceanic, southern and northern stratified and well-mixed shelf regions.

Spring (days 90-150) Average similarity: 75	Summer (days 173-212) Average similarity: 71	Autumn (days 265-354) Average similarity: 76
Guinardia delicatula	*Rhizosolenia imbricata*	*Pseudo -nitzschia* sp.
Guinardia striata	*Scrippsiella trochoidea*	*Thalassiosira* sp.
Guinardia flaccida	*Karenia mikimotoi*	
Thalassiosira sp.	*Pseudo -nitzschia* sp.	
Detonula pumila	*Guinardia delicatula*	
Rhizosolenia imbricata	*Guinardia striata*	
Meuniera membranacea		
Pseudo -nitzschia sp.		
Chaetoceros sp.		
Thalassionema nitzschioides		

Data on diatom, coccolithophore (*E. huxleyi*) and dinoflagellate biomass are summarised in Figure 5.21. Diatoms were generally the dominant taxonomic group except within the northern and mixed shelf regions, which were affected by the *K. mikimotoi* bloom in summer 2003. *E. huxleyi* occurred in northern stratified shelf waters mainly during late spring and early summer (day 150-190). A spring peak in diatom abundance was observed in all regions although in 2004 this extended into the summer period (July) for the southern and northern stratified and well-mixed shelf regions. More details regarding the phytoplankton groups (diatoms, coccolithophore (*E. huxleyi*) and dinoflagellate) are shown in the next section.

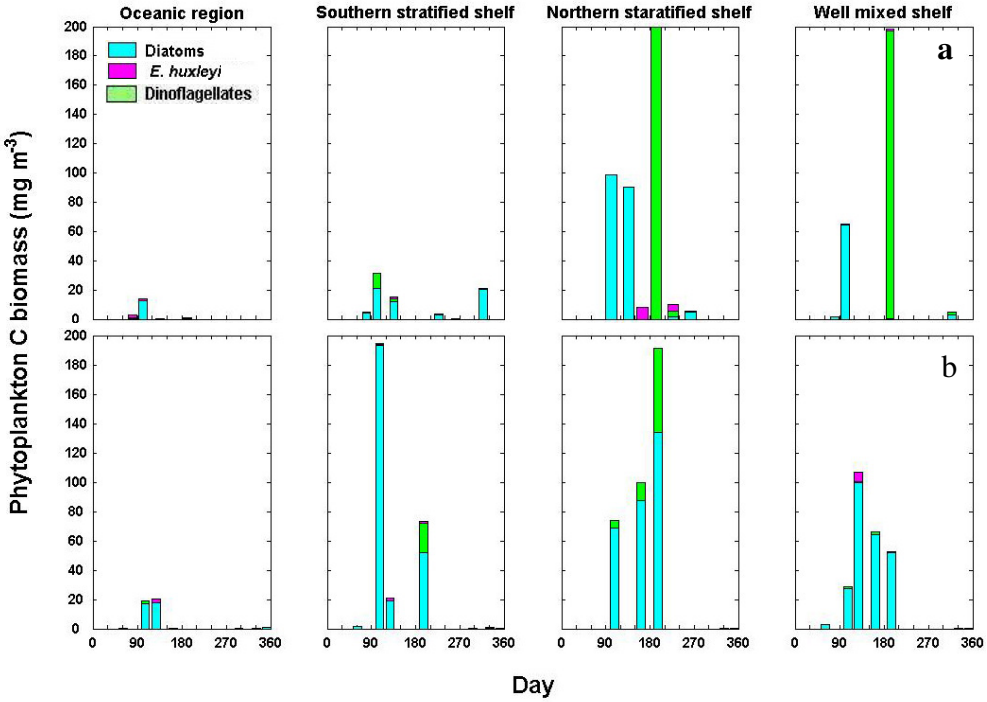


Figure 5.21: Average values of phytoplankton biomass (mg C m^{-3}) in 2003 (a) and 2004 (b) for the four regions.

5.6.1 *Distribution of diatoms*

Figure 5.22 shows the diatom distributions in 2003 and 2004. When comparing the two years, the occurrence, persistence and biomass of diatoms in spring and summer 2003 were lower than 2004 (Figure 5.22), except in northern stratified shelf waters in spring 2003 where a high diatom biomass occurred (Figure 5.22). It is noticeable that most of the diatom species found in 2003 were present in 2004 but in lower biomass. The pennate diatom *Meuniera membranacea*, and the centric diatoms *Guinardia delicatula*, *Guinardia striata*, *Rhizosolenia imbricata*, *Chaetoceros* sp. and *Thalassiosira* sp. formed the bulk of the diatom community (in terms of cell biomass) in both years (Figure 5.22).

In both years, the oceanic region and southern stratified shelf showed low diatom biomass compared to the other two regions, although a higher number of species was recorded in spring 2004 in the southern stratified shelf waters (Figure 5.22). In the northern stratified and well-mixed shelf waters, *G. delicatula*, *G. striata*, *R. imbricata* (group A, see Table 5.3) and *Rhizosolenia setigera* formed a high biomass of diatoms in spring 2004 (Figure 5.22). Interestingly, in the northern stratified shelf, silicate was completely depleted in early spring (day 107) while the nitrate and phosphate were still measurable (Figure 5.5 to 5.7).

A clear change in the species composition was observed during 2003, when the diatoms rapidly declined in summer (June and July) especially in the northern stratified shelf regions and were replaced by other groups (coccolithophores (*E. huxleyi*) and dinoflagellates) (Figure 5.21). In contrast, in 2004 across all the shelf regions, mixed diatoms occurred in mid summer (July) 2004, especially in northern stratified shelf waters. *G. delicatula*, *G. striata*, *R. imbricata* (Group B) were the dominant species (Table 5.3 and Figure 5.22) and may have been related to the increasing concentrations of silicate in May and June 2004 (Figures 5.7 and 5.16 (group e)).

Figure 5.22: Distributions of the most abundant diatom species (mg C m^{-3}) in (A) 2003 and (B) 2004.

5.6.2 *Distribution of the coccolithophore, Emiliania huxleyi*

Considerable work has been done to validate the identification of coccolithophore (*Emiliania huxleyi*) blooms in the surface waters. They can be mapped by classifying pixels of weekly global composites of available ocean colour data, such as those from SeaWiFS and Modis into bloom and non-bloom classes based on their mean normalized water-leaving radiances (Holligan *et al.*, 1983; Brown and Yoder, 1994a, 1994b). The monthly sampling of species from the ferry failed to sample and to cover most of the *E. huxleyi* blooms in both years. Therefore, several satellite images of coccolithophore (*E. huxleyi*) blooms in the Bay of Biscay and English Channel in 2003 and 2004 were obtained from Remote Sensing Data Analysis Service (RSDAS) at the Plymouth Marine Laboratory and are shown in Figure 5.23. These images still contain both strong signals from both coccolithophore (*E. huxleyi*) and sediments, so careful decisions have to be made in their interpretations (Brown, 1995; Tyrrell and Merico, 2004). In this study, strong signals (red colour) caused by suspended sediment are found in the central English Channel and coastal waters of western France (Figure 5.23). Similarly, a patch of relatively high reflectance close to the Ushant region in April 2003 (see the black arrow in Figure 5.23) was probably caused by suspended sediment in the low salinity intrusion.

With respect to *E. huxleyi*, the time series of the visible satellite images indicated early initiation (April) of *E. huxleyi* growth in the northern Bay of Biscay (southern stratified shelf) in 2003 and the southern Bay of Biscay in 2004. The bloom of *E. huxleyi* had increased by May in both years, covering the southern stratified shelf along the shelf break in 2003 and the oceanic region and the Celtic Sea in 2004. The *E. huxleyi* bloom in June 2003 intensified in the Ushant region and the northern stratified shelf, whereas the bloom recorded in May 2004 in the oceanic region ended in June. On the other hand, the *E. huxleyi* bloom in the Celtic Sea increased and stretched to the northwest of the Celtic Sea. The blooms had ended by July in both years. This raises a question as to what were the factors that affected the occurrence and distribution of the *E. huxleyi* bloom in both years.

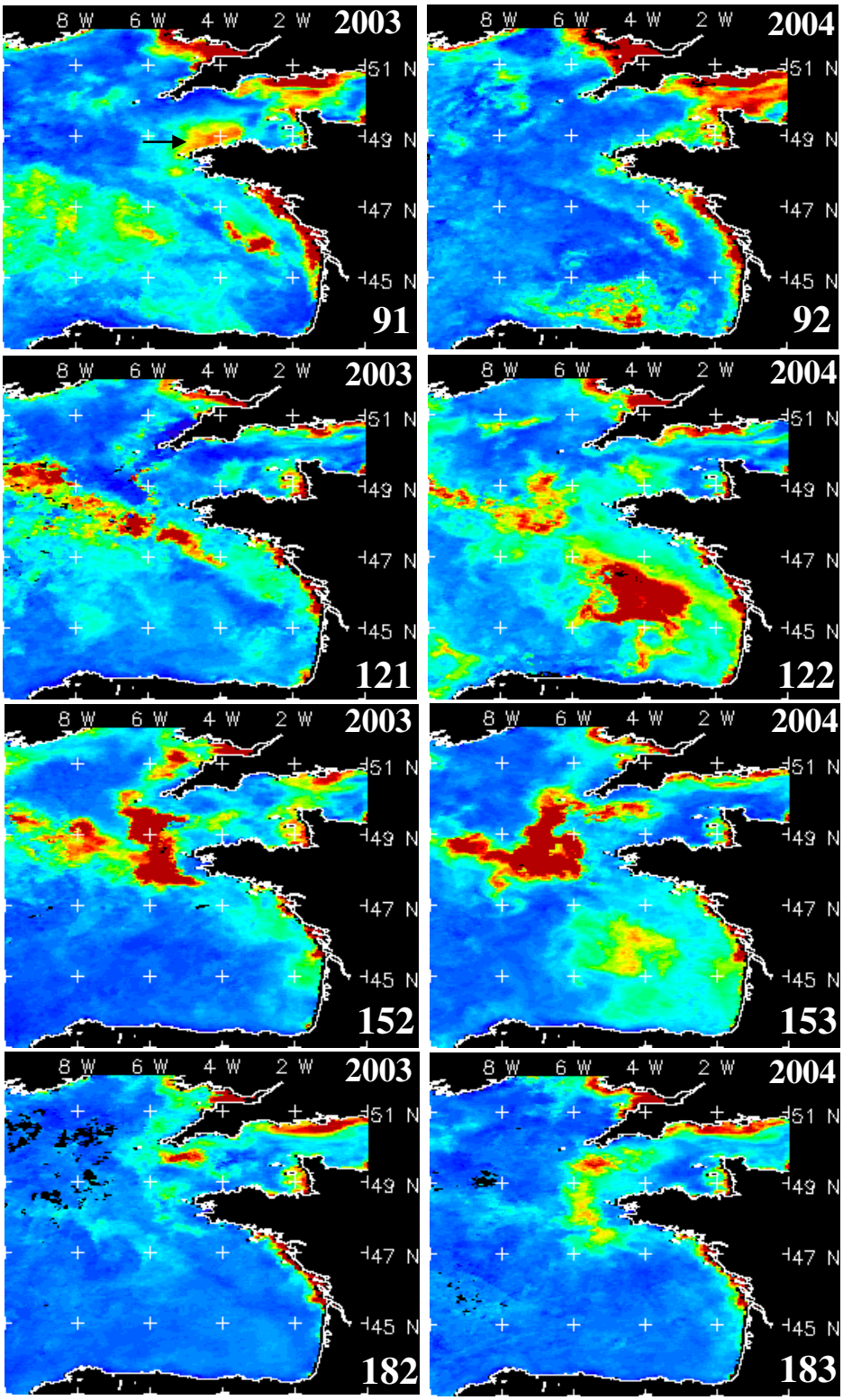


Figure 5.23: Monthly colour composites of MODIS-derived normalized water-leaving radiance (nl_w) at 551 nm with 4 km resolution for April, May, June and July 2003 and 2004. Strong signals (red colour) are caused by suspended sediment in the Bristol Channel, central English Channel and coastal waters of western France, and by *Emiliania huxleyi* elsewhere (for more details see the text). Black arrow indicates the low salinity water entering the English Channel in April 2003.

The *E. huxleyi* blooms usually occur in highly stratified water where the mixed layer depth is ~10–20 m, and tidal currents are weak (Nanninga and Tyrrell, 1996; Tyrrell and Merico, 2004). Accordingly, in this study, the bloom in June 2003 in the western English Channel was accompanied by a rapid increase in temperature, reduced salinity, low wind and high surface irradiance, together increased the water stability (Figures 5.3, 5.4 and 5.10). The bloom can be strongly influenced by meteorological conditions, such as wind (Garcia-Soto *et al.*, 1995). In this study, the strength and direction of the wind (Figure 4.3) might have reduced the stability of the stratified water in June and July 2004, as a result, the western English Channel did not provide suitable ecohydrodynamic conditions for the bloom.

5.6.3 *Distribution of dinoflagellates*

Figure 5.24 shows the distribution of the most common dinoflagellate in 2003 and 2004. Several species of dinoflagellates were common to the both years. The most abundant was *Karenia mikimotoi*. *Scrippsiella trochoidea* was found in 2003 in spring and summer with low biomass (< 1.0 mg m^{-3} – see Figure 5.24 A), and this species was also present with low biomass in spring 2004, but increased in the summer (Table 5.3 and Figure 5.24 B). This fits in with Smayda and Reynolds, (2001) suggestion that this species is found in habitats where nutrient concentrations are low and can become important in the summer. *Prorocentrum micans* was present at low biomass (< 1.0 mg m^{-3}) in the shelf regions, but was not recorded in the oceanic region in either year. This species is cosmopolitan in temperate waters and is more common in coastal and shelf than oceanic waters (Steidinger and Tangen, 1996).

The main difference in the dinoflagellate distributions of 2003 and 2004 was the occurrence of the *K. mikimotoi* bloom. This species is well adapted to frontal regions (Holligan, 1979; Le Corre *et al*., 1993), and the previous studies have reported that *K. mikimotoi* (formerly named as *Gyrodinium aureolum*) was the dominant species in the western English Channel (northern stratified shelf) (Pingree *et al.*, 1975; Holligan, 1979; Holligan *et al.*, 1984a). The data from the present study showed that an almost monospecific population of *K. mikimotoi* occurred in summer 2003 on the northern stratified shelf and extended into well mixed waters (see Chapter 3). In contrast, summer populations in 2004 were less dense and contained a mix of dinoflagellate and diatom species as explained in the section on diatom distribution.

This species is well adapted to seasonally stratified side of the frontal region in the western English Cannel (Holligan, 1979; Holligan *et al.*, 1984a; Nielsen and Tonseth, 1991). These authors suggested that temperature is an important factor in the initiation of blooms in northern European waters, and that the growth of this species in situ is associated with high temperatures (between 16.0 and 18.0^{o} C) which also increase the water stability. In the present study, the bloom occurred in summer 2003 in northern stratified shelf with a sea surface temperature of 19.6^{o} C (Figure 5.3).

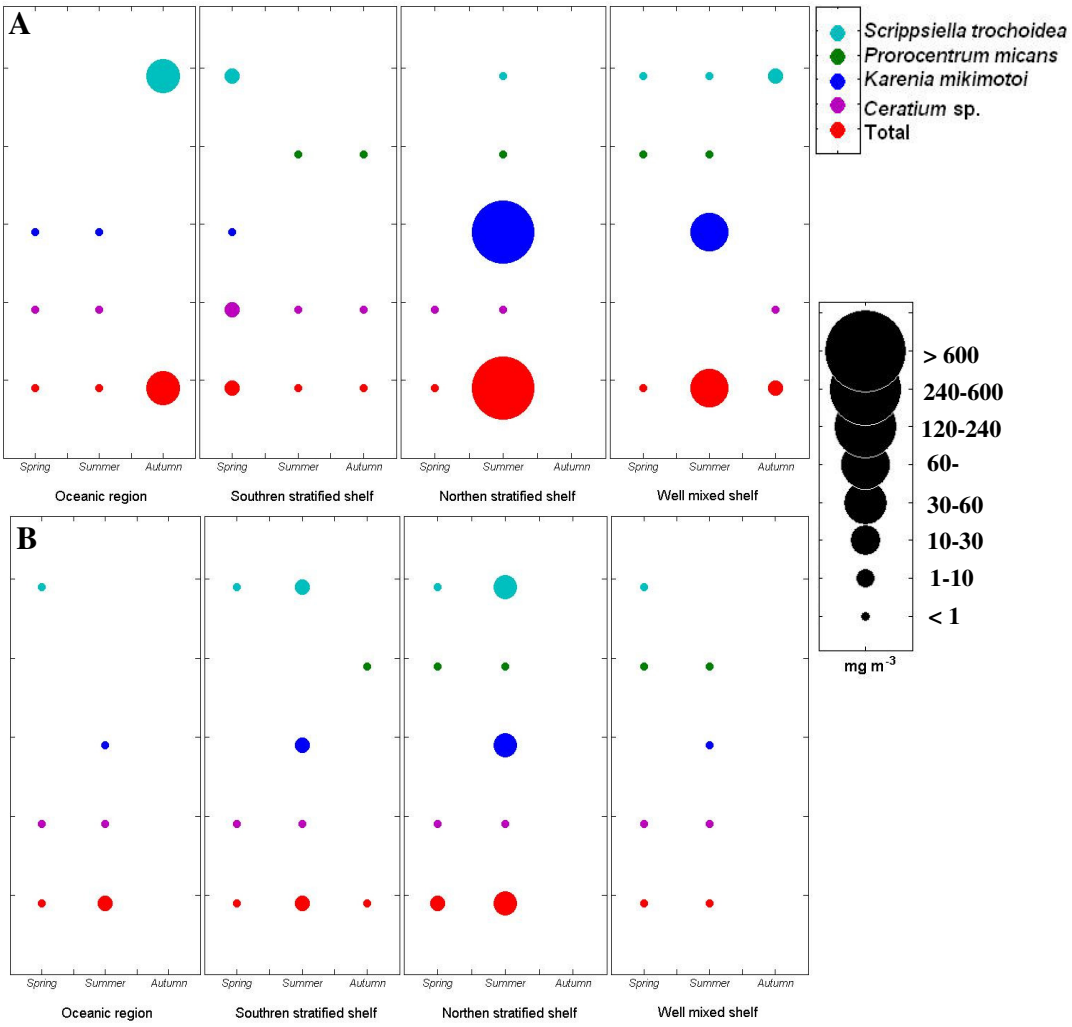


Figure 5.24: Distributions of the most abundant dinoflagellate species (mg C m^{-3}) in (A) 2003 and (B) 2004.

K. mikimotoi blooms follow the spring bloom and develop when ambient inorganic N (nitrate) is low. In this study, the concentrations of nitrate in early summer and mid summer were low (< 0.5 µM) (Figure 5.5). Vertical diffusion of nitrate from below the thermocline and the ability of this species to migrate to a layer with high

nitrate levels are important to maintaining the bloom (Pingree *et al.*, 1977b; Holligan *et al.*, 1984b). Le-Corre *et al*., (1993) and Blasco *et al*., (1996) concluded that the *K. mikimotoi* bloom tended to be found in ammonium-rich waters, thus seeming to favour high nutrient recycling activity.

The blooms of *K. mikimotoi* may also have originated from the low salinity water off the French river as a source of seed population into the northern stratified shelf in 2003. In contrast to other bloom-forming dinoflagellate species, vegetative cells of *K. mikimotoi* are capable of overwintering, as seen in Japanese waters by Honjo *et al*., (1990). They do not appear to form cysts (Ouchi *et al.*, 1994) and have been found in water temperatures as low as 4^{o} C (Blasco *et al.*, 1996). Blooms of *K. mikimotoi* are regularly recorded in the Bay of Brest (Le-Corre *et al*., 1993) and low cell numbers were found in winter, suggesting that the population of *K. mikimotoi* could have originated from southern Brittany (Gentien, 1998). In the current study, *K. mikimotoi* was recorded in early spring (March) in the Ushant region (see Chapter 3) but was not recorded in spring 2003 at the northern stratified and well-mixed shelve region (Figure 5.24). It is possible that low salinity intrusion may be a source of seed populations of *K. mikimotoi* for later blooms on the northern stratified shelf when environmental conditions were suitable.

K. mikimotoi is often identified as a member of the phytoplankton community in various parts of North West Europe. For example, blooms of *K. mikimotoi* were reported in the eastern Irish Sea during the autumn of 1971 (Helm *et al.*, 1974), at the Islay front on the Malin Shelf in August 1996 (Gowen *et al.*, 1998), and off the southern coast of Ireland in August 1998 (Raine *et al.*, 2001). In July to August 2005, an enormous bloom of *K. mikimotoi* (> 3,000,000 cell l^{-1}) occurred in the west coast of Ireland (Silke *et al.*, 2005). Raine *et al.,* (1993) investigated the link between surface wind stress and upwelling in the promotion of *K. mikimotoi* blooms in southwest Irish coast. In Scottish waters, an extensive *K. mikimotoi* bloom occurred along the west coast of Scotland during August 2006 (Davidson *et al.*, 2009). They linked the bloom to the unusually warm summer and resultant elevated sea temperatures and favourable winds may then have provided suitable conditions for bloom development and subsequent advection to the Scottish coast. In this study, the larger database available enables the suggestion that the annual differences in the intensity of the bloom between

2003 and 2004 may have been related to the following factors in 2003: (1) the unusually warm summer and resultant elevated sea temperatures (> 19.0^{o} C) (Figure 5.2) and favourable winds (Figure 3.4), and (2) an intrusion of low-salinity water from the French rivers into the English Channel by increasing the buoyancy of the upper water column (Figures 3.9 and 5.4).

To summarize the distribution of phytoplankton in both years, the distribution of the main species groups (diatoms in spring, coccolithophore (*E. huxleyi*) in early summer and dinoflagellate in mid summer) was seen in 2003. Contrastingly, in 2004, more diatoms and a mixed assemblage of diatoms and dinoflagellates occurred in the summer especially in the northern stratified shelf waters.

5.7 Distribution of herbivorous copepods in 2003 and 2004

Figure 5.25 shows the average biomass of herbivorous copepod distributions for 2003 and 2004 in three regions. There was a significant difference in copepod abundances between 2003 and 2004 in all three areas (F-approximation to Friedman' test $p < 0.01$) with higher values in 2004. The dominant copepod species in this study, *Temora longicornis, Pseudocalanus elongates* and *Calanus helgolandicus* were generally similar to previous studies carried out in the same area (Holligan *et al.*, 1984a; Villate *et al.*, 1997; Valdes *et al.*, 2001; Valdes *et al.*, 2007; Morales *et al.*, 1991). Unfortunately, there were insufficient data on herbivore distribution in the spring in oceanic region to be able to make a detailed comparison of the two years.

Peaks in copepod biomass were observed from February to April (days 50-110) in the northern stratified and well-mixed shelf regions. These peaks increased with the early spring increase of phytoplankton biomass. It is noticeable that the distribution of herbivorous copepods follows a similar pattern to that of phytoplankton biomass in spring and summer in both years (Figures 5.8 and 5.25). However, there was a lag between maximum spring phytoplankton biomass (chlorophyll *a*) and copepod biomass. Cushing, (1989) and Heinrich, (1962) discussed the time delay between the spring bloom of phytoplankton and the copepod population increase and showed that the delay in temperate waters was longer than tropical waters. In the current study, for example, the spring blooms (chl *a*) that occurred in May 2003 and 2004 in the well-mixed shelf region were followed by increased copepod biomass (Figures 5.8 and 5.24). However,

this increase was higher in 2004 than in 2003. Interestingly, the peaks of copepod biomass in spring 2003 and 2004 (day 110) at the northern stratified and well-mixed shelves were similar.

The well-mixed shelf region had a planktonic system dominated by the smaller copepods such as *Temora longicornis* and *Pseudocalanus elongates*. Many of these small species have adapted to feeding in shallow turbid water (Poulet, 1976; Roman, 1984), producing eggs and overwintering in the sediment to be released the next year (Lindley, 1990). Conversely, larger herbivorous copepods, such as *Calanus, Clausocalanus*, and *Paracalanus* sp. dominated the oceanic and northern stratified shelf region. The highest concentrations of herbivorous copepods occurred on the shelf in spring and summer but with great variability between regions (Figure 5.25).

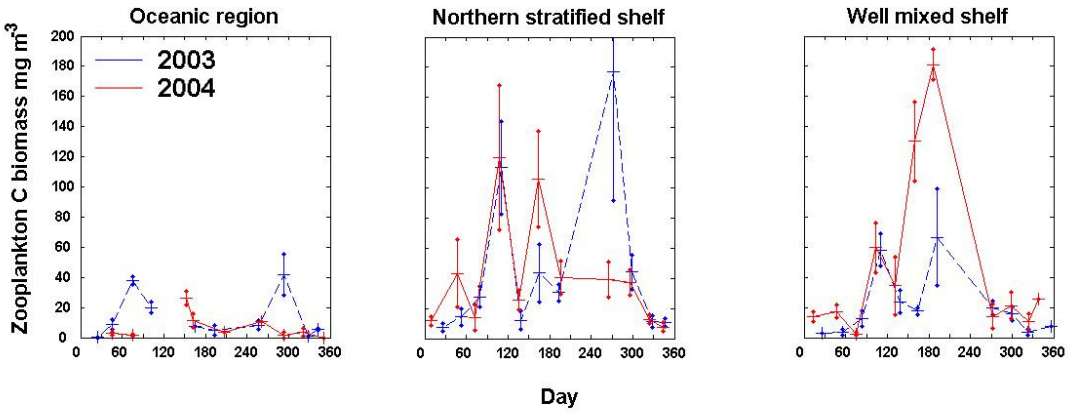


Figure 5.25: Monthly-averaged values of the biomass of herbivorous copepods (mg C m^{-3}) in 2003 (blue line) and 2004 (red line) for the oceanic, northern stratified and well-mixed shelf regions.

In July 2003, at the time of the *Karenia* bloom, the biomass of herbivores in the northern stratified shelf region was low, whereas it was higher in July 2004. Smayda, (1997) concluded that some dinoflagellates exhibit an allelopathic defence against copepod predation. However, it is not well established if the *K. mikimotoi* bloom area is avoided by zooplankton or if *K. mikimotoi* is toxic to its potential predators (Gentien, 1998). Holligan *et al*., (1984a) found no increase in copepod nauplii concentrations at the thermal front in the western English Channel in 1981 during the *K. mikimotoi* bloom. They suggested that the presence of *K. mikimotoi* in surface waters near the front might explain their failure to observe large numbers of nauplii in the frontal region. Some copepods reject *K. mikimotoi* as food (Uye and Takamatsu, 1990).

CHAPTER 6

6. SYNTHESIS AND CONCLUSION

The main objectives of this thesis were: 1) to study the distribution and succession of phytoplankton over two annual cycles (2003 and 2004) in the Bay of Biscay and English Channel by using the NOC FerryBox system, 2) to study the variations in phytoplankton biomass and species abundance in relation to the availability of light and nutrients and to zooplankton distributions, and 3) to link the annual differences in phytoplankton community structure to differences in weather and hydrographic conditions. In this Chapter, the success of achieving the stated aims and answering stated questions of the research are assessed.

6.1 Seasonal and geographic variations in phytoplankton biomass and species compositions

Figure 6.1 shows a summary synopsis of the phytoplankton biomass and abundance for the oceanic and shelf regions, in relation to the climatic (dominant wind directions and fresh water input), chemical (inorganic nutrients (NO_3 and Si)) and biological (herbivorous zooplankton) variables for 2003 and 2004.

The general seasonal cycle of distributions of phytoplankton biomass (chlorophyll *a*) and major species groups (diatoms, coccolithophores and dinoflagellates) was consistent across the regions studied in 2003 and 2004. However, there were year-to-year differences in the size, timing, and duration of seasonal-scale fluctuations of phytoplankton population (Figure 6.1). In 2003 especially in the western English Channel, the phytoplankton succession was from a diatom-dominated community in spring to coccolithophorid (*E. huxleyi*)-dominated early summer and then to the dinoflagellate *K. mikimotoi* in mid summer (Figure 5.21). This pattern is in agreement with previous results in the western English Channel (Holligan and Harbour 1977, Maddock *et al.,* 1981) and with the classical model of phytoplankton seasonal succession in temperate waters (Margalef, 1978; Smayda, 1980). In contrast, in 2004, a mixed assemblage of diatoms and dinoflagellates occurred in midsummer in the western English Channel and diatoms were generally more abundant in 2004 compared to 2003.

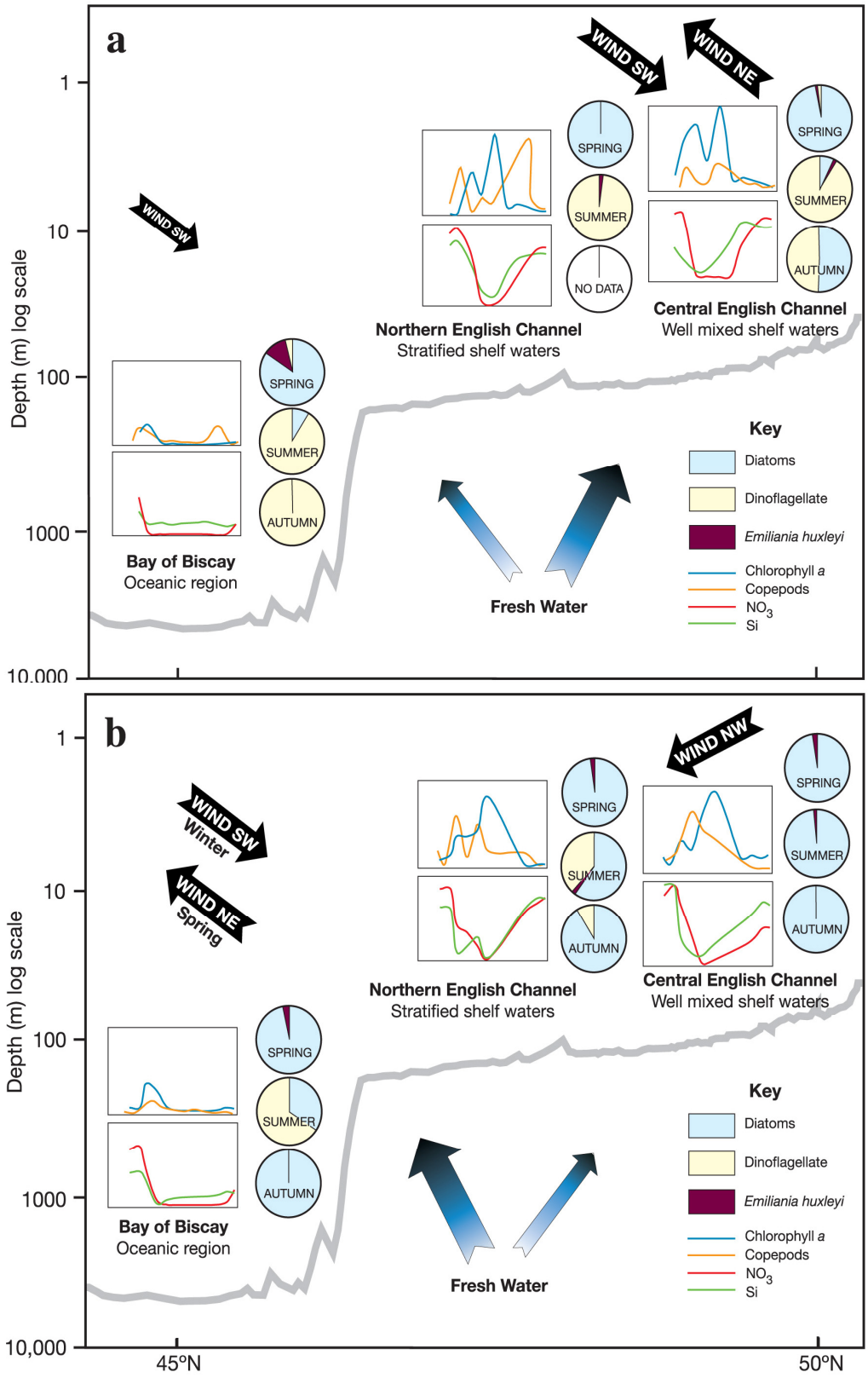


Figure 6.1: Summary of the phytoplankton biomass and abundance in a) 2003 and b) 2004 in relation to climatic, chemical and biological factors between oceanic and shelf regions. Pie charts represent the seasonal variation of phytoplankton. In the line graphs, the y-axes represent the relative distribution of chlorophyll *a*, copepods and nutrients (NO_3 and Si), and the x-axes are days from 0 to 365.

6.1.1 *Regional differences in phytoplankton biomass and species composition*

There were significant regional differences in the phytoplankton biomass and compositions in (oceanic vs. shelf), (south vs. north) and (seasonally stratified vs. well-mixed shelf waters) (Figure 6.1). The range was from those in the south (oceanic region) with a single peak of the phytoplankton biomass (chlorophyll) in spring, mainly diatoms, to the north (shelf) with a different pattern of seasonal changes of phytoplankton biomass (with three peaks) varying from early spring, mid summer and to autumn (Figure 6.1), as a function of variations in tidal strength, and river influence. The phytoplankton biomass (chlorophyll) declined sharply in the summer in the oceanic region. The distribution of accessory pigments (HPLC pigment analysis) showed that as the micro-phytoplankton (diatoms and dinoflagellates) declined an increase in nano- and pico-phytoplankton occurred in this region (Figures 3.18 and 4.19). Pico-phytoplankton and nano-phytoplankton dominate the oceanic waters (Zubkov *et al.*, 1998; Lavin *et al.*, 2006) because they are more dependant on regenerated sources of nitrogen rather than nitrate (Rees *et al.*, 1999). These results are in agreement with previous studies, which demonstrated that the phytoplankton biomass in the Bay of Biscay has one peak of biomass in spring and is influenced by low nutrient conditions in the summer (Fernandez *et al.*, 1993; Varela, 1996).

The differences in phytoplankton biomass and abundance between the seasonally stratified and well-mixed shelf waters such as the western and central English Channel respectively are in agreement with the earlier observations (Pingree *et al.*, 1978; Pingree *et al.*, 1982; Holligan *et al.*, 1984a). During summer, the maximum chlorophyll levels (> 70.0 mg m^{-3}) found during this study were in the western English Channel (tidal frontal region) in 2003 and largely attributable to the presence of the dinoflagellate, *K. mikimotoi*, which was associated with the advected low salinity (<35.0) water and higher surface temperatures (> 19.0^{o} C). In contrast, in the well-mixed shelf water, diatoms were the dominant species in 2004, with chlorophyll levels in the range of 1.0 - 3.0 mg m^{-3}, similar to levels found by Holligan *et al.,* (1984a).

6.1.2 *Seasonal changes in phytoplankton biomass and species composition*

The abundance and species composition of phytoplankton populations reflects previous environmental conditions and changes in environmental forcing leading to

restructuring of populations (Smayda, 1998). In spring, stabilisation of the nutrient-rich surface mixed layer combined with increasing irradiance and reduced wind speed gives sufficient stability for the spring bloom of diatoms to develop (Pingree, 1975; Legendre, 1990). The major uncertainties relate to the precise nature of physical processes that control the timing and rate of development of the spring bloom (van-Haren *et al*., 1998). In this study, surface irradiance and wind were shown to play an essential role in the spring bloom development for both years (Section 5.4). The timing of surface nutrient draw-down during the spring corresponded well with chlorophyll distribution at that time of year (Figure 6.1). However, variability in the timing, duration and magnitude of the bloom between years clearly occurs in all regions.

The decline of phytoplankton biomass (chlorophyll *a*) during the summer was attributed to nutrient limitation especially nitrate. However, on the continental shelf, at the frontal boundaries between tidally well mixed and seasonally stratified waters, there is a special case for the nutrient supply to the *K. mikimotoi* and mixed diatom and dinoflagellate bloom which occurred in summer 2003 and 2004 respectively. Here phytoplankton take advantage of the continuing availability of both light and nutrients through behavioural (e.g. motility) and/or physiological adaptations. The vertical migration of *K. mikimotoi* sustains the bloom populations through the uptake of nutrients at the seasonal pycnocline (Pingree *et al*., 1977b; Holligan *et al*, 1984b). Whereas, the diatoms present in summer 2004 were able to grow due to continued availability of nutrients. Silicate and nitrate ($> 2.0\ \mu M$) concentrations were well above the detection limits of the methods between May and June 2004 (Figure 6.1 and Appendix 6).

In this study, phytoplankton growth in the late summer and autumn was variable (Figure 6.1). However, an autumn bloom can be clearly seen in northern Bay of Biscay waters (Figures 3.14 and 4.15 show an increase in fluorescence between 46.0 and 48.0^{o} N). Phytoplankton biomass decreased in late autumn, when phytoplankton growth was restricted by low irradiance after day 320 (Figures 3.14 and 4.15) and nutrient regeneration exceeds assimilation (Figures 3.11 and 4.12).

Statistical analysis (PRIMER) of the environmental observations in relation to phytoplankton biomass (chlorophyll *a*) indicated that surface irradiance was the primary

driver of the spring bloom with nutrients (N and to some extent Si) of secondary importance (Figures 5.15 and 5.16). In contrast, nutrients especially nitrate were the primary driver of the summer biomass (Figures 5.15 and 5.16). Low salinity and high temperature values in the western English Channel were the major factors in determining the *K. mikimotoi* bloom.

6.2 The annual differences of the phytoplankton biomass and composition in relation to the environmental factors

Year-to-year variations in phytoplankton biomass reflect changes in climatic related variables- surface irradiance, wind, and freshwater, chemical (nutrient availability) and biological (herbivorous zooplankton) factors (Verity and Smetacek, 1996; Behrenfeld *et al.*, 2008). Phytoplankton biomass in temperate latitudes, has been considered to be either 'bottom-up' (light and nutrients) or 'top-down' (herbivores) (Smith and Lancelot, 2004). The annual differences in the phytoplankton biomass in the NE Atlantic Ocean based on CPR data are well documented (Beaugrand *et al.*, 2000; Leterme *et al.*, 2005; McQuatters-Gollop *et al.*, 2007). The nature of such differences influences the timing of seasonal changes in biomass or the maxima and duration of peaks in chlorophyll during bloom development. The former tends to be driven by variations in surface irradiance and the latter by variations of nutrient conditions, especially in the summer. In this section, the main questions of this thesis (section 1.8) are discussed and related to the annual differences in phytoplankton biomass and abundance.

This study demonstrates the annual variability in the timing of the spring bloom in the oceanic and shelf regions. The spring phytoplankton bloom started earlier in 2003 than 2004 in the Bay of Biscay (oceanic region), but started earlier in 2004 in the shelf regions (western English Channel) compared to 2003 (see Figures 5.8 and 5.9). Nutrients cannot be the cause of these differences, since they are not limiting in this period for both years (Figures 5.5 to 5.7 and 6.1). Instead, the depth of the mixed layer, is likely the main factor affecting the timing of the spring bloom (Townsend *et al.*, 1994; Brickley and Thomas, 2004). In this study, by comparing the wind speed and surface irradiance intensity, in relation to satellite chlorophyll (Figure 5.9 and 5.10), it was shown that a reduced surface irradiance and increasing wind-induced mixing might have been the reason for the delay in the spring bloom in 2003 and 2004 in the oceanic

and shelf regions respectively. The data showed that the surface irradiance (> 150 W m^{-2}) and wind speed (< 5.0 s m^{-1}) correspond to the occurrence of the earlier spring blooms.

During the summer, despite greater solar radiation levels, phytoplankton biomass in the Bay of Biscay and English Channel decreased rapidly (for example, < 1.0 mg m^{-3} chlorophyll in the Bay of Biscay). This decrease was a consequence of the depletion of nutrients especially nitrate in both regions (Figure 6.1). The N/P ratio fell in summer to values much lower than the Redfield ratio (Tables 3.3 and 4.3). A contributing factor is that the regeneration of phosphate within the water column is somewhat faster than the regeneration of nitrate (Loyer *et al*., 2006). Overall, this means that nitrate rather than phosphate was likely to have been the nutrient limiting phytoplankton growth during the summer. These results are in agreement with previous studies of the Bay of Biscay (Lunven *et al.*, 2005; Loyer *et al.*, 2006) and of English Channel (Pingree *et al.*, 1977a; Jordan and Joint, 1998).

The timing and duration of nutrient (NO_3 and Si) removal by the phytoplankton in the summer was variable in both years and between shelf and oceanic waters (Figure 6.1). The results of this study show that the regeneration of silicate in the shelf areas occurred earlier than nitrate (June to September) (Figure 6.1) as observed by Loyer *et al*., (2006). Furthermore, higher N:Si ratios found in the shelf in late spring and early summer 2004 compared to 2003, were possibly due to silicate depletion by phytoplankton populations with a high proportion of diatoms. In addition, silicate limitation occurring at the end of the spring and causing the collapse of the spring bloom resulted in a shift in the species composition to dinoflagellates, such as *K. mikimotoi* in summer 2003 in the western English Channel (Margalef, 1978; Smayda, 1997).

There was a greater abundance of herbivores in shelf waters compared to oceanic waters in both years, except for an apparent scarcity within the bloom of *K. mikimotoi* in 2003 (Section 5.7). There is a possibility of grazing control of phytoplankton in shelf waters (especially in well-mixed shelf) in early summer 2004 where a peak of herbivores biomass occurred (Figure 6.1 b).

The climatic factors of irradiance, and wind speed and direction are probably one of the main causes, directly or indirectly, of annual variability in phytoplankton abundance. As explained in the beginning of this section, a key indicator of the

interannual variability in the phytoplankton spring bloom is the timing of the start of the bloom, which depends largely on the surface irradiance and wind speed (Henson, *et al*., 2006). Variability in winds during spring is an important influence of interannual variability in the timing of the spring bloom in shelf seas (Sharples *et al.*, 2006) and in the open ocean (Waniek, 2003). This study showed interannual variability in the timing, intensity and duration of the spring phytoplankton bloom (for example the western English Channel) (Figure 6.1).

The occasional strong winds (~18.0 m s^{-1}) and relatively low irradiance levels that occurred in late June and early July 2004 in the shelf regions is likely to have weakened thermal stratification and could be the reason for the high abundance of diatoms in these waters in midsummer in 2004 (Figure 6.1). Margalef, (1978) concluded that turbulence augments nutrient concentrations and leads to an increase in the diatom population in the water column. Diatoms, in contrast to dinoflagellates, are less sensitive to turbulence, and can grow rapidly under relatively low irradiance levels (Smayda, 1997).

From the variability in salinity detected in this study, discussed in Section 5.2, an influence on the annual variability in phytoplankton abundance has been shown. The presence of low salinity water in the western English Channel from June to September 2003, and in the southern stratified shelf region in 2004 affected the water stability and acted as a transport pathway for nutrients as suggested by Kelly-Gerreyn *et al*., (2004 and 2006).

6.3 Recommendation for future research

The NOC FerryBox has been in operation since 2003, so there are now 6 years of measurements. Utilising these data sets, it may be possible to begin to quantify the interannual variability in the timing, strength and structure of the spring bloom, and summer depletion of nutrients, and relate them to patterns of wind, irradiance and river runoff. For example, some controlling factors and features could not be definitively clarified from the data collected in 2003 and 2004. For example, the process that allowed *E. huxleyi* to bloom in late spring in 2004 and not in 2003 in the Bay of Biscay (Section 5.6.2 and Figure 5.23) and the *K. mikimotoi* bloom in the western English Channel which was relatively low in 2004 compared to 2003 (Section 5.6.3 and Figure 5.24). The reason for this difference is not obvious. In the 2003 and 2004 data, a period

of relatively strong winds and the absence of any low salinity signal influencing the water column stability in early and mid summer may have led to unfavourable conditions for *K. mikimotoi* to bloom in 2004. An analysis of the data from later years may be able to confirm if water stability as being a major prerequisite for *K. mikimotoi* blooms.

In future, better linkage between the occurrence of blooms and underlying ecohydrodynamic conditions could be achieved through the use of data from devices and sensors such as:- (1) the automated in line nutrient sensors that are used in the FerryBox system operated by GKSS in Germany (Petersen *et al.*, 2008), (2) the autonomous measurements of oxygen. Oxygen measurements are being made on the Pride of Bilbao using an Aanderaa Oxygen Optode and can be used to derive estimates of net photosynthetic production. Bargeron *et al*., (2006) considered that measurements of oxygen concentrations would be useful in establishing the magnitude of the contribution to the carbon cycle in the hydrodynamically and biogeochemically different regions along the Portsmouth to Bilbao route and (3) the FRRF (Fast-Repetition-Rate-Fluorometry) measuring variable fluorescence. The FRRF would enable photosynthetic rate and physiological state of phytoplankton to be measured and related to environmental conditions (Moore *et al.*, 2003).

Associating measurements by the NOC FerryBox and biological observations of phytoplankton composition and herbivorous and other zooplankton abundance by the Continuous Plankton Recorder (CPR) survey from the Pride of Bilbao will provide data to better interpret the relationship between zooplankton and phytoplankton biomass. Currently, CPR sampling has only been maintained on a monthly basis. During the spring / summer period there would be advantage in carrying out more frequent tows to improve the precision of information on the relationship between zooplankton and phytoplankton biomass. However, the processing of CPR data is labour intensive and time consuming, consideration needs to be given to the development of continuous autonomous sampling system for phytoplankton and zooplankton that can reduce or eliminate the need for manual processing of samples.

Observations from FerryBox are limited to the near surface and low temporal resolution. Satellite images, however, show the distribution of chlorophyll over wider

spatial scales. The use of satellite data can overcome some of the limitations of the FerryBox approach. For example, the monthly sampling of species from the ferry failed to sample the *E. huxley* blooms in 2004, which were observed in the Bay of Biscay by satellite images (Figure 5.23). Further work needs to be done to compare the comparative effectiveness of the FerryBox type sampling and satellite imagery in detecting phytoplankton population over basin scale regimes. The strength of the FerryBox system is that it allows the actual species present to be identified when water samples can be collected and preserved. Use of automated sampling could in future make it possible to collect samples in response to information from satellite images.

REFERENCES

Aiken, J., Fishwick, J., Moore, G. and Pemberton, K. (2004). Annual cycle of phytoplankton photosynthetic quantum efficiency, pigment composition and optical properties in the western English Channel. *Journal of the Marine Biological Association of the UK,* 84**,** 301-303.

Albaina, A. and Irigoien, X. (2004). Relationships between frontal structures and zooplankton communities along a cross-shelf transect in the Bay of Biscay (1995-2003). *Marine Ecology Progress Series,* 284**,** 65-75.

Albaina, A. and Irigoien, X. (2007). Fine scale zooplankton distribution in the Bay of Biscay in spring 2004. *Journal of Plankton Research,* 29**, (**10), 851-870.

Alexander, R. M. (1990). Size, speed and buoyancy adaptation in aquatic animals. *American Zoologist,* 30**,** 189.

Anderson, T. R. (2005). Plankton functional type modelling: running before we can walk? *Journal of Plankton Research* 27**, (**11), 1073-1081.

Arar, E. J. (1994). Evaluation of a new fluorometric technique that uses highly selective interference filters for measuring chlorophyll *a* in the presence of chlorophyll *b* and pheopigments. *In Book Evaluation of a new fluorometric technique that uses highly selective interference filters for measuring chlorophyll a in the presence of chlorophyll b and pheopigments*. Cincinnati, Ohio.

Armstrong, F., Butler, E. and Boalch, G. T. (1974). Hydrographic and nutrient chemistry surveys in the western English Channel during 1965 and 1966. *Journal of the Marine Biological Association of the UK,* 54**,** 225-235.

Arrigo, K. R. (2005). Marine microorganisms and global nutrient cycles. *Nature,* 437**,** 349-355.

Azam, F., Fenchel, T., Field, J. G., Gray, J. S., Meyer-Reil, L. A. and Thingstad, F. (1983). The ecological role of water-column microbes in the sea. *Marine Ecology Progress Series,* 10**,** 257-263.

Banse, K. (1995). Zooplankton: pivotal role in the control of ocean production. *ICES Journal of Marine Science,* 52**,** 265-277.

Barlow, R. G., Mantoura, R. F. C., Gough, M. A. and Fileman, T. W. (1993). Pigment signatures of the phytoplankton composition in the north-eastern Atlantic during the 1990 spring bloom. *Deep Sea Research,* 40**, (**2), 495-477.

Barquero, S., Cabal, J. A., Anadon, R., Fernandez, E., Varela, M. and Bode, A. (1998). Ingestion rates of phytoplankton by copepod size fractions on a bloom associated with an off-shelf front off NW Spain. *Journal of Plankton Research,* 20**,** (5), 957-972.

Batten, S. D., Clarke, R. A., Flinkman, J., Hays, G. C., John, E. H., John, A. W., Jonas, T. D., Lindley, J. A., Stevens, D. P. and Walne, A. W. (2003). CPR sampling - the technical background, materials and methods, consistency and comparability. *Progress in Oceanography,* 58**,** 193-215.

Beaugrand, G., Ibanez, F. and Reid, P. C. (2000). Spatial, seasonal and long-term fluctuations of plankton in relation to hydroclimatic features in the English Channel, Celtic Sea and Bay of Biscay. *Marine Ecology Progress Series,* 200**,** 93-102.

Beaugrand, G., Reid, P. C., Ibanéz, F., Lindley, J. A. and Edwards, M. (2002). Reorganization of North Atlantic marine copepod biodiversity and climate. *Science,* 296**,** 1692-1694.

Becker, G. A., Frohse, A. and Damm, P. (1997). The northwest European shelf temperature and salinity variability. *German Journal of Hydrography,* 49**,** (2/3), 135-151.

Behrenfeld, M. J., Halsey, K. H. and Milligan, A. J. (2008). Evolved physiological responses of phytoplankton to their integrated growth environment. *Philosophical Transactions of the Royal Society B: Biological Sciences,* 363**,** 2687-2703.

Billett, D. S. M., Lampitt, R. S., Rice, A. L. and Mantoura, R. F. C. (1983). Seasonal sedimentation of phytoplankotn to the deep-sea benthos. *Nature,* 302**,** 520-522.

Blasco, D., Berard-Therriault, L., Levasseur, M. and Vrieling, E. G. (1996). Temporal and spatial distribution of the ichthyotoxic dinoflagellate *Gyrodinium aureolum* Hulburt in the St Lawrence, Canada. *Journal of Plankton Research,* 18**,** (10), 1917-1930.

Bode, A. and Fernandez, E. (1992). Influence of water-column stability on phytoplankton size and biomass succession patterns in the central Cantabrian Sea (Bay of Biscay). *Journal of Plankton Research,* 14**,** (6), 885-902.

Borges, A. V. and Frankignoulle, M. (2003). Distribution of surface carbon dioxide and air-sea exchange in the English Channel and adjacent areas. *Journal of Geophysical Research,* 108 (C5)**,** 3140-3154.

Brickley, P. and Thomas, A. C. (2004). Satellite-measured seasonal and inter-annual chlorophyll variability in the northeast Pacific and coastal Gulf of Alaska. *Deep Sea Research II,* 51**,** 229-245.

Brown, C. W. (1995). Global distribution of coccolithophore blooms. *Oceanography,* 8**,** (2), 59-60.

Brown, C. W. and Yoder, J. A. (1994a). Coccolithophorid blooms in the global ocean. *Journal of Geophysical Research,* 99**,** 7467-7482.

Brown, C. W. and Yoder, J. A. (1994b). Distribution pattern of coccolithophorid blooms in the western North Atlantic. *Continental Shelf Research,* 14**,** 175-197.

Brzezinski, M. A. (1985). The Si:C:N ratio of marine diatoms: interspecific variability and the effect of some environmental variables. *Journal of Phycology,* 21**,** 347-357.

Cabanas, J. M., Lavin, A., Garcia, M. J., Gonzalez-Pola, C. and Perez, E. T. (2003). Oceanographic variability in the northern shelf of the Iberian Peninsula 1990-1999. *ICES Marine Science Symposia,* 219**,** 71-79.

Calbet, A. (2001). Mesozooplankton grazing impact on primary production: a global comparative analysis in marine ecosystems. *Limnology and Oceanography,* 46**,** 1824-1830.

Castaing, P., Froidefond, J. M., Lazure, P., Weber, O., Prudhomme, R. and Jouanneau, J. M. (1999). Relationship between hydrology and seasonal distribution of suspended sediments on the continental shelf of the Bay of Biscay. *Deep Sea Research,* 46**,** (10), 1979-2001.

Cermeno, P. and Figueiras, F. G. (2008). Species richness and cell-size distribution:size structure of phytoplankton communities. *Marine Ecology Progress Series,* 357**,** 79-85.

Chisholm, S. (1992). Phytoplankton size *In*: *Primary productivity and biogeochemical cycle in the sea* (P. Falkowski and A. Woodhead, Eds.). Pittsburgh, Plenum Press, pp.213-237.

Clarke, K. and Gorley, R. N. (2006). PRIMER v6: User manual/ tutorial*,* Plymouth, PRIMER-E Ltd, pp.190.

Clarke, K. and Warwick, R. (2001). Change in Marine Communities: An Approach to Statistical Analysis and Interpretation*,* Plymouth, PRIMER-E, pp.174.

Cupp, E. E. (1943). Marine plankton diatoms of the west coast of North America. *Bulletin, Scripps Institution of Oceanography* 5**,** (1), 1-238.

Cushing, D. H. (1983). Sources of variability in the North Sea ecosystem. *In*: *North Sea dynamics* (J. Sündermann and W. Lenz, Eds.). Berlin, Springer, pp.499-516.

Cushing, D. H. (1989). A difference in structure between ecosystems in strongly stratified waters and in those that are only weakly stratified. *Journal of Plankton Research,* 11**,** 1-13.

Davidson, K., Miller, P., Wilding, T. A., Shutler, J., Bresnan, E., Kennington, K. and Swan, S. (2009). A large and prolonged bloom of *Karenia mikimotoi* in Scottish waters in 2006. *Harmful Algae,* 8**,** (2), 349-361.

Demaster, D. J. (2001). Marine silica cycle. *In*: *Encyclopedia of Ocean Sciences* (J. H. Steele, K. Turekian and S. A. Thorpe, Eds.). London, Academic Press, pp.1659-1667.

Dietrich, G. (1962). Mean monthly temperature and salinity of the surface layer of the North Sea and adjacent waters from 1905 to 1954 pp.293.

Dodge, J. D. (1982). Marine dinoflagellates of the British Isles*,* London, Her Majesty's Stationery Press, pp.301.

Dubinsky, Z. (1992). The functional and optical absorption cross-section of phytoplankton photosynthesis. *In*: *Primary produtivity and biogeochemical cycles in the sea* (P. G. Falkowski and A. D. Woodhead, Eds.). New York, Plenum Press, pp.31-46.

Dugdale, R. C. and Goering, J. J. (1967). Uptake of new and regenerated forms of nitrogen in primary productivity. *Limnology and Oceanography,* 12**,** 196-206.

Edler, L. (1979). Recommendations for marine biological studies in the Baltic Sea. Phytoplankton and chlorophyll. *Baltic Marine Biologist Publication***,** (5), 1-38.

Edwards, M., Johns, D. G., Leterme, S. C., Svendsen, E. and Richardson, A. J. (2006). Regional climate change and harmful algal blooms in the Northeast Atlantic. *Limnology and Oceanography* 51**,** 820-829.

Falkowsk, P. G. (1994). The role of phytoplankton photosynthesis in global biogeochemical cycles. *Photosynthesis Research,* 39**,** 235-258.

Falkowski, P. G., Barber, R. T. and Smetacek, V. (1998). Biogeochemical controls and feedbacks on ocean primary production. *Science,* 281**,** 200-206.

Falkowski, P. G. and Raven, J. A. (1997). Aquatic photosynthesis*,* London, Blackwell Science.

Fenchel, T. (1988). Marine plankton food chains. *Annual Reviews Eology Systems,* 19**,** 19-38.

Fernandez, E. and Bode, A. (1991). Seasonal patterns of primary production in the central Cantabrian Sea (Bay of Biscay). *Scientia Marina,* 55**, (**4), 629-636.

Fernandez, E., Cabal, J., Acuna, J. L., Bode, A., Botas, A. and Garca-Soto, C. (1993). Plankton distribution across a slope current-induced front in the southern Bay of Biscay. *Journal of Plankton Research,* 15**, (**6), 619-641.

Field, C. B., Behrenfeld, M. J., Randerson, J. T. and Falkowski, P. (1998). Primary production of the biosphere: integrating terrestrial and oceanic components *Science,* 281**,** 237-240.

Frouin, R. A., Fiuza, F., Ambar, I. and Boyd, T. J. (1990). Observation of a poleward surface current off the coast of Portugal and Spain during winter. *Journal of Geophysical Research,* 95**,** 679-691.

Garcia-Soto, C., Fernández, E., Pingree, R. D. and Harbour, D. S. (1995). Evolution and structure of a shelf coccolithophore bloom in the western English Channel. *Journal of Plankton Research,* 17**, (**11), 2011-2036.

Geider, R. J. (1987). Light and temperature dependence of the carbon to chlorophyll *a* ratio in microalgae and cyanobacteria: implications for physiology and growth of phytoplankton. *New Phytologist,* 106**,** 1-34.

Geider, R. J., Maclntyre, H. L. and Kana, T. M. (1997). Dynamic model of phytoplankton growth and acclimation: responses of the balanced growth rate and the chlorophyll *a*: carbon ratio to light, nutrient-limitation and temperature. *Marine Ecology Progress Series,* 148**,** 187-200.

Geider, R. J. and Roche, J. L. (2002). Redfield revisited: variability of C:N:P in marine microalgae and its biochemical basis. *Journal of Phycology,* 37**,** 1-17.

Gentien, P. (1998). Bloom dynamics and ecophysiology of the *Gymnodinium mikimotoi* species complex. *In*: *Physiological Ecology of Harmful Algal Blooms* (D. M. Anderson, A. D. Cembella and G. M. Hallegraef, Eds.). Berlin, Springer, pp.155-173.

Gentilhomme, V. and Lizon, F. (1998). Seasonal cycle of nitrogen and phytoplankton biomass in a well-mixed coastal system (eastern English Channel). *Hydrobiologia,* 361**,** 191-199.

Gil, J., Valdes, L., Moral, M., Sanchez, R. and Garcia-Soto, C. (2002). Mesoscale variability in a high-resolution grid in the Cantabrian Sea (southern Bay of Biscay), May 1995. *Deep Sea Research part I: Oceanographic Research Papers,* 49**,** 1591-1607.

Gohin, F., Lampert, L., Guillaud, J. F., Herbland, A. and Nezan, E. (2003). Satellite and in situ observations of a late winter phytoplankton bloom in the northern Bay of Biscay. *Continental Shelf Research,* 23**,** 1117-1141.

Gowen, R. J., Raine, R., Dickey-Collas, M. and White, M. (1998). Plankton Distributions in relation to physical oceanographic features on the southern Malin Shelf. *ICES Journal of Marine Science,* 55**,** 1095- 1111.

Gowen, R. J., Stewart, B. M., Mills, D. K. and Elliott, P. (1995). Regional differences in stratification and its effect on phytoplankton production and biomass in the northwestern Irish Sea. *Journal of Plankton Research,* 17**,** 753-769.

Grasshoff, K., Ehrhardt, M. and Kremling, K. (1983). Methods of seawater analysis*,* Weinheim, Verlag Chemie, pp.491.

Hansen, H. and Koroleff, F. (1999). Determination of nutrients. *In*: *Methods of Seawater Analysis* (K. Grasshoff, M. Ehrhardt and K. Kremling, Eds.), 3rd ed. Toronto, Wiley-VCH, pp.600.

Hasle, G. (1978). The inverted microscope method. *In*: *Phytoplankton Manual* (A. Sournia, Ed). Paris, UNESCO, pp.88-96.

Haynes, R. E. and Barton, R. E. D. (1990). A poleward flow along the Atlantic coast of the Iberian Peninsula. *Journal of Geophysical Research,* 95**,** 11425-11441.

Heinrich, A. K. (1962). The life history of plankton animals and seasonal cycles of plankton communities in the oceans. *J. Cons. int. Explor. Mer,* 27**,** 15-24.

Helm, M. M., Hepper, B. T., Spencer, B. E. and Walne, P. R. (1974). Lugworm mortalities and a bloom of *Gyrodinium aureolum* Hulbert in the eastern Irish Sea, Autumn 1971. *Journal of the Marine Biological Association of the UK,* 54**,** 857-869.

Henson, S. A., Robinson, I., Allen, J. T. and Waniek, J. J. (2006). Effect of meteorological conditions on interannual variability in timing and magnitude of

the spring bloom in the Irminger Basin, North Atlantic. *Deep sea research I,* 53**,** 1601-1615.

Hillebrand, H., Dürselen, C. D., Kirschtel, D., Pollingher, D. and Zohary, T. (1999). Biovolume calculation for pelagic and benthic microalgae. *Journal of Phycology,* 35**,** 403-424.

Hoch, T. and Garreau, P. (1996). Phytoplankton dynamics in the English Channel: A simplified three-dimensional approach. *Journal of Marine Research,* 16**, (**102), 133-150.

Holligan, P. (1979). Dinoflagellate blooms associated with tidal fronts around the British Isles. *In*: *Toxic dinoflagellate bloom: Developments in marine biology* (F. Taylor and H. Seliger, Eds.). New York, Elsevier Notrh, Holland Inc., pp.249-256.

Holligan, P. (1981). Biological implications of fronts on the northwest European continental shelf. *Philosophical Transactions of the Royal Society: Mathematical, Physical and Engineering Sciences,* 302**,** 547-562.

Holligan, P. M. (1989). Primary productivity in the shelf seas of north-west Europe *Advances in Botanical Research Incorporating Advances in Plant Pathology* 16**,** 194–252.

Holligan, P. M. (1992). Do marine phytoplankton influance global climate? *In*: *Primary productivity and biogeochemical cycles in the sea* (P. G. Falkowski and A. D. Woodhead, Eds.). New York, Plenuk Press, pp.487-501.

Holligan, P. M. and Harbour, D. S. (1977). The vertical distribution and succession of phytoplankton in the western English Channel in 1975 and 1976. *Journal of the Marine Biological Association of the UK,* 57**,** 1075-1093.

Holligan, P. M., Harris, R. P., Newell, R. C., Harbour, D. S., Head, R. N., Linley, E. A. S., Lucas, M. I., Tranter, P. R. G. and Weekley, C. M. (1984a). Vertical distribution and partitioning of organic carbon in mixed, frontal and stratified waters of the English Channel. *Marine Ecology Progress Series,* 14**,** 111-27.

Holligan, P. M., Viollier, M., Harbour, D., Camus, P. and Champagne-Philippe, M. (1983). Satellite and ship studies of coccolithophore production along a continental shelf edge. *Nature,* 304**,** 339-342.

Holligan, P. M., Williams, P. J. I., Purdie, D. and Harris, R. P. (1984b). Photosynthesis, respiration and nitrogen supply of plankton populations in stratified, frontal and tidally mixed shelf waters. *Marine Ecology Progress Series,* 17**,** 201-213.

Honjo, T., Yamamoto, S., Nakamura, O. and Yamaguchi, M. (1990). Annual cycle of motile cells of *Gymnodinium nagasakiense* and ecological features during the period of red tide development. *In*: *Toxic Marine Phytoplankton* (E. Graneli, B. Sundstrom, L. Edler and D. M. Anderson, Eds.). New York, Elsevier, pp.165-170.

Horner, R. A. (2002). A Taxonomic guide to some common marine phytoplankton, United Kingdom, Biopress Limited, pp.195.

Huntley, D. (1980). Tides on the north-west European continental shelf. *In*: *The North-West European shelf seas: the sea bed and sea in motion. II. physical and chemical oceanography, and physical resources* (F. Banner, M. Collins and K. Massie, Eds.). Amsterdam, Elsevier Scientific Publishing Company, pp.638.

Hureta, M., Gohina, F., Delmasb, D., Lunvena, M. and Garçonc, V. (2007). Use of SeaWiFS data for light availability and parameter estimation of a phytoplankton production model of the Bay of Biscay *Journal of Marine Systems,* Volume 65 (1-4), 509-531

Hydes, D. J., Gall, A. C. L., Miller, A. E. J., Brockmann, U., Raabe, T., Holley, S., Alvarez-Salgado, X., Antia, A., Balzer, W., Chou, L., Elskens, M., Helder, W., Joint, I. and Orren, M. (2001). Supply and demand of nutrients and organic matter at and across the NW European shelf break in relation to hydrography and biogeochemical activity. *Deep Sea Research,* 48**,** 3023-3047.

Hydes, D. J., Gowen, R. J., Holliday, N. P., Shammon, T. and Mills, D. (2004). External and internal control of winter concentration of nutrients (N, P, Si) in north-west European shelf seas. *Estuarine, Coastal and Shelf Science,* 59**,** 151-161.

Hydes, D. J. and Wright, P. N. (1999). SONUS: the Southern Nutrients Study 1995-1997, Southampton Oceanography Centre, pp.130.

Irigoien, X., Harris, R. P., Head, R. N. and Harbour, D. (2000). North Atlantic Oscillation and spring bloom phytoplankton composition in the English Channel. *Journal of Plankton Research,* 22**,** 2367-2371.

James, F. C. and Mcculloch, C. E. (1990). Multivariate analysis in ecology and systematic: panacea or pandora's box? *Annual review of ecological systems,* 21**,** 129-166.

Jeffrey, S. W. and Vesk, M. (1997). Introduction to marine phytoplankton and thier pigment and signature. *In*: *Phytoplankton pigments in oceanography guidelines*

to modern methods (S. W. Jeffrey, R. F. Mantoura and S. W. Wright, Eds.). Paris, UNESCO, pp.37-84.

Jeffrey, W. S. and Humphrey, G. F. (1975). New spectrophotometric equation for determining chlorophylls *a*, *b*, c_1 and c_2 in higher plants, algae and natural phytoplakton. *Biochem. Physiol. Pflanz,* BPP 167**,** 191-194.

Joint, I. (1991). The allometric determination of pelagic production rates. *Journal of Plankton Research,* 13**,** (supplement), 69-81.

Joint, I. and Groom, S. (2000). Estimation of phytoplankton production from space: current status and future potential of satellite remote sensing. *Journal of Experimental Marine Biology and Ecology,* 250**,** 233-255.

Joint, I., Owens, N. J. P. and Pomroy, A. J. (1986). Seasonal production of photosynthetic picoplankton and nanoplankton in the Celtic Sea. *Marine Ecology Progress Series,* 28**,** 251-258.

Jordan, M. B. and Joint, I. (1998). Seasonal variation in nitrate:phosphate ratios in the English Channel 1923-1987. *Estuarine, Coastal and Shelf Science,* 46**,** 157-164.

Kelly-Gerreyn, B., Hyde, D., Jegou, A., Lazure, P., Fernand, L., Puillat, I. and Garcia-Soto, C. (2006). Low salinity intrusions in the western English Channel. *Continental Shelf Research,* 26**,** (11), 1241-1257.

Kirchman, D. L. (2000). Microbial ecology of the oceans*,* New York, Wiley-liss, pp.542.

Kirk, J. T. (1994). Light & photosynthesis in aquatic ecosystems*.,* Cambridge, Cambridge university press, pp.509.

Kirkwood, D. S. (1996). Nutrients: Practical notes on their determination in sea water*,* Copenhagen, ICES, pp.83.

Koutsikopoulos, C., Beillois, P., Leroy, C. and Taillefer, F. (1998). Temporal trends and spatial structures of the sea surface temperature in the Bay of Biscay. *Oceanologica Acta,* 21**,** (2), 335-344.

Koutsikopoulos, C. and Le-Cann, B. (1996). Physical processes and hydrological structures related to the Bay of Biscay Anchovys. *Scientia Marina,* 60**,** 9-19.

Labry, C., Herbland, A., Delmas, D., Laborde, P., Lazure, P., Froidefond, J. M., Jegou, A. M. and Sautour, B. (2001). Initiation of winter phytoplankton blooms within the Gironde plume waters in the Bay of Biscay. *Marine Ecology Progress Series,* 212**,** 117-130.

Lalli, C. M. and Parsons, T. R. (2001). Biological oceanography an introduction*,* Oxford, Butterworth-Heinemann, pp.406.

Langdon, C. (1988). On the causes of interspecific in the growth-irradiance relationship for phytoplankton. II A general review. *Journal of Plankton Research,* 10**,** (6), 1291-1312.

Laroche, J. and Breitbarth, E. (2005). Importance of the diazotrophs as a source of new nitrogen in the ocean. *Journal of Sea Research,* 53**,** 67-91.

Lavin, A., Valdes, L., Sanchez, F., Abaunza, P., Forest, A., Boucher, J., Lazure, P. and Jegou, A. (2006). The Bay of Biscay: the encountering of the ocean and the shelf (18b,E). *In*: *The Sea, the global coastal ocean, interdisciplinary regional studies and syntheses* (A. Robinson and K. H. Brink, Eds.). Combridge, MA, Harvard University Press, pp.935-1002.

Lazure, P. and Jegou, A. M. (1998). 3D modelling of seasonal evolution of Loire and Gironde plumes on Biscay Bay continental shelf. *Oceanologica Acta,* 21**,** (2), 165-177.

Lecorre, P., Helguen, S. and Wafar, M. (1993). Nitrogen source for uptake by *Gyrodinium* cf. *aureolum* in a tidal front. *Limnology and Oceanography,* 38**,** (2), 446-451.

Lefèvre, J. (1986). Aspects of the biology of frontal systems. *Advances in Marine Biology,* 23**,** 163-299.

Legendre, L. (1990). The significance of microalgal blooms for fisheries and the export of particulate organic carbon in ocean. *Journal of Plankton Research,* 12**,** (4), 681-699.

Legendre, L. and Rassoulzadegan, F. (1995). Plankton and nutrient dynamics in marine waters. *Ophelia,* 41**,** 153-172.

Lessard, R. J. and Swift, E. (1986). Dinoflagellates from the North Atlantic classified as phototrophic or heterotrophic by epifluorescence microscopy. *Journal of Plankton Research,* 8**,** 1209-1215.

Leterme, S., Edwards, M., Seuront, L., Attrill, M. J., Reid, P. C. and John, A. W. G. (2005). Decadal basin-scale changes in diatoms, dinoflagellates, and phytoplankton color across the North Atlantic. *Limnology and Oceanography,* 50**,** (4), 1244-1253.

Leterme, S., L. Seuront, L. and Edwards, M. (2006). Differential contribution of diatoms and dinoflagellates to phytoplankton biomass in the NE Atlantic ocean and the North Sea. *Marine Ecology Progress Series,* 312**,** 57-65.

Lindley, J. A. (1990). Distribution of overwintering calanoid copepod eggs in sea-bed sediments around southern Britain. *Marine Biology,* 104**,** 209-217.

Llope, M., Anadón, R., Sostres, J. Á. and Viesca, L. (2007). Nutrients dynamics in the southern Bay of Biscay (1993–2003): winter supply, stoichiometry, long-term trends, and their effects on the phytoplankton community. *Journal of Geophysical Research,* 112**,** C07029.

Loyer, S., Lampert, L., Menesguen, A., Cann, P. and Labasque, T. (2006). Seasonal evolution of the nutrient pattern on Biscay Bay continental shelf over the years 1999-2000. *Scientia Marina,* 70**,** (1), 31-46.

Lunven, M., Guillaud, J. F., A.Youénou, Crassous, M. P., Berric, R., Gall, E. L., Kérouel, R., Labry, C. and Aminot, A. (2005). Nutrient and phytoplankton distribution in the Loire river plume (Bay of Biscay, France) resolved by a new fine scale sampler. *Estuarine, Coastal and Shelf Science,* 65**,** (1-2), 94-108.

Maddock, L. and Swann, C. L. (1977). A statistical analysis of some trends in sea temperature and climate in the Plymouth area in the last 70 years. *Journal of the Marine Biological Association of the UK,* 57**,** 317-338.

Mantoura, R. F. and Llewellyn, C. A. (1983). The rapid determination of algal chlorophyll and carotenoid pigments and their breakdown products in natural waters by reversephase high-performance liquid chromatography. *Analytica Chimica Acta* 151**,** 297-314.

Margalef, R. (1978). Life-forms of phytoplankton as survival alternatives in an unstable environment. *Oceanologica Acta,* 1**,** 493-509.

Maritorena, S., Siegel, D. A. and Peterson, A. (2002). Optimization of a semianalytical ocean color model for global applications. *Applied Optics,* 41**,** 2705–2714.

Marquisa, E., Niquila, N., Delmasa, D., Hartmanna, H. J., Bonnetb, D., Carlottic, F., Herblandd, A., Labrye, C., Sautourf, B., Labordef, P., Vézinag, A. and Dupuya, C. (2007). Inverse analysis of the planktonic food web dynamics related to

phytoplankton bloom development on the continental shelf of the Bay of Biscay, French coast *Estuarine, Coastal and Shelf Science,* Volume 73 **(**1-2), 223-235

Mcquatters-Gollop, A., Raitsos, D. E., Edwards, M. and Attrill, M. J. (2007). Spatial patterns of diatom and dinoflagellate seasonal cycles in the NE Atlantic Ocean. *Marine Ecology Progress Series,* 339**,** 301-306.

Menden-Deuer, S. and Lessard, E. J. (2000). Carbon to volume relationships for dinoflagellates, diatoms, and other protist plankton. *Limnology and Oceanography,* 45**,** 569-579.

Miller, C. B. (2004). Biological Oceanography*,* Oxford, Blackwell, pp.402.

Moore, C. M., Suggett, D., Holligan, P. M., Sharples, J., Abraham, E. R., Lucas, M. I., Rippeth, T. P., Fisher, N. R., Simpson, J. H. and Hydes, D. J. (2003). Physical controls on phytoplankton physiology and production at a shelf sea front: an FRRF based field study. *Marine Ecology Progress Series,* 259**,** 29-45.

Moore, G. F., Aiken, J. and Lavender, S. (1999). The atmospheric correction of water colour and the quantitative retrieval of suspended matter in case II waters: Application to MERIS. *International Journal of Remote Sensing,* 20**,** 1713-1733.

Morales, C. E., Bedo, A., Harris, R. P. and Tranter, P. R. G. (1991). Grazing of copepod assemblages in the north-east Atlantic: the importance of the small size fraction *Journal of Plankton Research,* 13**,** 455-472.

Morel, A. and Bélanger, S. (2006). Improved detection of turbid waters from ocean color sensors information. *Remote Sensing of Environment,* 102**,** 237-249.

Moreth, C. M. and Yentsch, C. S. (1970). The role of chlorophyllase and light in the decomposition of chlorophyll from phytoplankton. *Journal of Experimental Marine Biology and Ecology,* 4**,** 238-249.

Morin, P., Corre, P. L., Marty, Y. and Helguen, S. L. (1991). Spring evolution of nutrients and phytoplankton on the Armorican shelf (north-west European shelf). *Oceanologica Acta* 14**,** 263-279.

Mousseau, L., Klein, B., Legendre, L., Dauchez, S., Tamigneaux, E., Tremblay, J. E. and Ingram, R. G. (2001). Assessing the trophic pathways that dominate planktonic food webs: an approach based on simple ecological ratios. *Journal of Plankton Research,* 23**, (**8), 765-777.

Nanninga, H. and Tyrrell, T. (1996). Importance of light for the formation of algal blooms by *Emiliania huxleyi*. *Marine Ecology Progress Series,* 136**,** 195-203.

Nedwell, D. B., Dong, L. F., Sage, A. and Underwood, G. J. C. (2002). Variations of the nutrients loads to the mainland U.K. estuaries: correlation with catchment areas, urbanization and coastal eutrophication *Estuarine, Coastal and Shelf Science,* 54**,** 951-970.

Nielsen, M. V. and Tonseth, C. P. (1991). Temperature and salinity effect on growth and chemical composition of *Gyrodinium aureolum* Hulburt in culture. *Journal of Plankton Research,* 13**,** (2), 389-398.

Ouchi, A., Aida, S., Uchida, T. and Honjo, T. (1994). Sexual reproduction of a red tide dinoflagellate *Gymnodinium mikimotoi*. *Fisheries Science,* 60**,** 125-126.

Peters, R. H. (1983). The ecological implications of body size*,* Cambridge, Cambridge University Press, pp.329.

Petersen, W., Colijn, F., Elliot, J., Howarth, M., Hydes, D. J., Kaitala, S., Kontoyiannis, H., Lavin, A., Lips, I., Pfeiffer, K. D., Proctor, R., Ridderinkhof, H. and Sørensen, K. (2005). European FerryBox project: from online oceanographic measurements to environmental information. *In* H. Dahlin, N. C. Flemming, P. Marchand and S. E. Petersson (Eds.) *European operational oceanography: present and future. Proceedings of the 4th EuroGOOS Conference.* Brest (France).

Petersen, W., Petschatnikov, M., Schroeder, F. and Colijn, F. (2004). Ferry-Box systems for monitoring coastal waters. *In* H. Dahlin, N. C. Flemming, K. Nittis and S. E. Peterson (Eds.) *Building the european capacity in operational oceanography, Proceedings from the 3rd EUROGOOS Conference.* Athens, Elsevier Oceanography Series.

Petersen, W., Wehde, H., Krasemann, H., Colijn, F. and Schroeder, F. (2008). FerryBox and MERIS e assessment of coastal and shelf sea ecosystems by combining in situ and remotely sensed data. *Estuarine, Coastal and Shelf Science,* 77**,** 296-307.

Pingree, R. D. (1975). The advance and retreat of the thermocline on the continental shelf. *Journal of the Marine Biological Association of the UK,* 55**,** 965-974.

Pingree, R. D. (1978). Cyclonic eddies and cross-frontal mixing. *Journal of the Marine Biological Association of the UK,* 58**,** 955-963.

Pingree, R. D. (1980). Physical oceanography of the Celtic sea and English Channel. *In*: *The North-West European shelf seas: the sea bed and sea in motion. II. physical and chemical oceanography, and physical resources* (F. M. Banner and K. M.

Collins, Eds.). Amsterdam, Elsevier Scientific Publishing Company, pp.415-465.

Pingree, R. D. and Griffiths, D. K. (1978). Tidal fronts on the shelf seas around the British Isles. *Journal of geophysical research Journal of Geophysical Research,* 83**,** 4615-4622.

Pingree, R. D., Holligan, P. M. and Head, R. N. (1977b). Survival of dinoflagellate blooms in the western English Channel. *Nature,* 265**,** 266-268.

Pingree, R. D., Holligan, P. M. and Mardell, G. T. (1978). The effects of vertical stability on phytoplankton distributions in the summer on the northwest European shelf. *Deep Sea Research,* 25**,** 1011-1028.

Pingree, R. D., Holligan, P. M., Mardell, G. T. and Head, R. N. (1976). The influence of physical stability on spring, summer and autumn phytoplankton blooms in the Celtic sea. *Journal of the Marine Biological Association of the UK,* 56**,** 845-873.

Pingree, R. D. and Le-Cann, B. (1990). Structure, strength and seasonality of the slope currents in the Bay of Biscay region. *Journal of the Marine Biological Association of the UK,* 70**,** 857-885.

Pingree, R. D. and Le-Cann, B. (1992a). Three anticyclonic slope water oceanic eddies (swoddies) in the southern Bay of Biscay in 1990. *Deep Sea Research,* 39**,** 1147-1175.

Pingree, R. D. and Le-Cann, B. (1992b). Anticyclonic eddy X91 in the southern Bay of Biscay, May 1991 to February 1992. *Journal of Geophysical Research,* 97**,** (C9), 14353-14367.

Pingree, R. D., Maddock, L. and Butler, E. I. (1977a). The influence of biological activity and physical stability in determining the chemical distributions of inorganic phosphate, silicate and nitrate. *Journal of the Marine Biological Association of the UK,* 57**,** 1065-1073.

Pingree, R. D., Mardell, G. D. and New, A. L. (1986). Propagation of internal tides from the upper slopes of the Bay of Biscay. *Nature,* 321**,** 154-158.

Pingree, R. D., Mardell, G. T., Holligan, P. M., Griffiths, D. K. and Smithers, J. (1982). Celtic Sea and Armorican current stucture and the vertical distributions of temperature and chlorophyll. *Continental Shelf Research,* 1**,** (1), 99-116.

Pingree, R. D. and Pennycuick, L. (1975). Transfer of heat, fresh water and nutrients through the seasonal thermocline. *Journal of the Marine Biological Association of the UK,* 55**,** 261-275.

Pingree, R. D., Pugh, P. R., Holligan, P. M. and Forster, G. R. (1975). Summer phytoplankton blooms and red tides along tidal fronts in the approaches to the English Channel. *Nature,* 258**,** 672–677.

Poole, H. H. and Atkins, W. R. G. (1929). Photo-electric measurments of submarine illumination throughout the year. *Journal of the Marine Biological Association of the UK,* 16**,** 297-324.

Porra, R. J., Pfundel, E. E. and Engel, N. (1997). Metabolism and function of photosynthetic pigments. *In*: *Phytoplankton pigments in oceanography guidelines to modern methods* (S. W. Jeffrey, R. F. Mantoura and S. W. Wright, Eds.). Paris, UNESCO, pp.85-126.

Poulet, S. A. (1976). Feeding of *Pseudocalanus minutus* on living and non-living particles. *Marine Biology,* 34**,** (2), 117-125.

Puillat, I., Lazure, P., Jegou, A. M., Lampert, L. and Miller, P. I. (2004). Hydrographical variability on the French continental shelf in the Bay of Biscay, during the 1990's. *Continental Shelf Research,* 24**,** (10), 1143-1163

Puillat, I., Lazure, P., Jegou, A. M., Planque, B. and Lampert, L. (2003). Mesoscale, interannual and seasonal hydrological variability over the French continental shelf of the Bay of Biscay during the 1999s. *ICES Marine Science Symposia,* 219**,** 333-336.

Raine, R., Joyce, B., Richard, J., Pazos, Y., Moloney, M., Jones, K. J. and Patching, J. W. (1993). The development of a bloom of the dinoflagellate *Gyrodinium aureolum* (Hulbert) on the south-west Irish coast. *ICES Journal of Marine Science,* 50**,** 461-469.

Raine, R., O'boyle, S., O'higgins, T., White, M. and Patching, J. (2001). A satellite and field portrait of a *Karenia Mikimotoi* bloom off the south coast of Ireland, August 1998. *Hydrobiologia,* 465**,** 187-193.

Raitsos, D. E., Lavender, S. J., Maravelias, C. D., Haralabous, J., Richardson, A. J. and Reid, P. C. (2008). Identifying four phytoplankton functional types from space: an ecological approach. *Limnology and Oceanography,* 53**,** (2), 605-613.

Redfield, A. C. (1934). On the proportions of organic derivatives in sea water and their relation to the composition of plankton*,* Liverpool, pp.176-192.

Rees, A., Woodward, M. and Joint, I. (1999). Measurement of nitrate and ammonium uptake at ambient concentrations in oligotrophic waters of the north-east Atlantic ocean. *Marine Ecology Progress Series,* 187**,** 295-300.

Reid, P., Auger, C., Chaussepied, M. and Burn, M. (1993). North Sea subregion assessment report 1993, United Kingdom, France, Belgium, pp.153.

Richardson, A. J. and Schoeman, D. S. (2004). Climate impact on plankton ecosystem in the northeast Atlantic. *Science,* 305**,** 1609-1612.

Richardson, A. J., Walne, A. W., John, A. W. G., Jonas, T. D., Lindley, J. A., Sims, D. W., Stevens, D. and M.Witt (2006). Using continuous plankton recorder data *Progress in Oceanography,* 68**,** (1), 27-74.

Riebesell, U. and Wolf-Gladrow, D. (2002). Supply and uptake of inorganic Nutrients. *In*: *Phytoplnkton productivity carbon assimilation in marine and freshwater ecosystems* (P. J. Williams, D. N. Thomas and C. S. Reynolds, Eds.). Oxford, Blackwell publishing company, pp.109-140.

Rodriguez, F., Fernandez, E., Head, R. N., Harbour, D. S., Bratbak, G., Heldal, M. and Harris, R. P. (2000). Temporal variability of viruses,bacteria, phytoplankton and zooplankton in the western English Channel off Plymouth. *Journal of the Marine Biological Association of the UK,* 80**,** 575-586.

Roman, M. R. (1984). Utilization of Detritus by the Copepod, *Acartia tonsa*. *Limnology and Oceanography,* 29**,** (5), 949-959.

Sautour, B., Artigas, F., Herbland, A. and Laborde, P. (1996). Zooplankton grazing impact in the plume of dilution of the Gironde estuary prior to the spring bloom. *Journal of Plankton Research,* 18**,** (5), 835-853.

Sharples, J. and Holligan, P. (2006). Interdisciplinary studies in the Celtic sea (19,E). *In*: *The Sea, the global coastal ocean, interdisciplinary regional studies and syntheses* (A. Robinson and K. H. Brink, Eds.). Combridge, MA, Harvard University Press, pp.1003-1031.

Sharples, J., Moore, C. M., Rippeth, T. P., Holligan, P. M., Hydes, D. J., Fisher, N. R. and Simpson, J. H. (2001). Phytoplankton distribution and survival in the thermocline. *Limnology and Oceanography,* 46**,** 486-496.

Sharples, J., Ross, O. N., Scott, B. E., Greenstreet, S. P. R. and Fraser, H. (2006). Inter-annual variability in the timing of stratification and the spring bloom in the north-western North Sea. *Continental Shelf Research,* 26**,** 733-751.

Sharples, J., Tweddle, J. F., Green, J. A. M., Palmer, M. R., Kim, Y. K., Hickman, A. E., Holligan, P. M., Moore, C. M., Rippeth, T. P., Simpson, J. H. and Krivtsov, V. (2007). Spring-neap modulation of internal tide mixing and vertical nitrate

fluxes at a shelf edge in summer. *Limnology and Oceanography,* 52**,** (5), 1735-1747.

Short, S. M. and Suttle, C. A. (2003). Temporal dynamics of natural communities of marine algal viruses and eukaryotes. *Aquatic Microbial Ecology,* 32**,** 107-119.

Sieburth, M. J. (1979). Sea microbes*,* New York, Oxford University Press, pp.491.

Siegel, D. A., Doney, S. C. and Yoder, J. A. (2002). The North Atlantic spring phytoplankton bloom and Sverdrup's critical depth hypothesis. *Science,* 296**,** 730-733.

Silke, J., O'beirn, F. and Cronin, M. (2005). *Karenia*: an exceptional dinoflagellate bloom in western Irish waters, summer 2005*,* Galway, Ireland, Marine Institute, pp.48.

Simpson, J. H. (1998). The Celtic Seas. *In*: *The Sea* (A. R. Robinson and K. H. Brink, Eds.). John Wiley and Sons Ins., pp.659-698.

Smayda, T. J. (1980). Phytoplankton species succession. *In*: *The physiological ecology of phytoplankton* (I. Morris, Ed). Oxford, Blackwell Scientific, pp.493-570.

Smayda, T. J. (1997). Harmful algal bloom: their ecophysiology and general relavance to phytoplankton blooms in the sea. *Limnology and Oceanography,* 42**,** (5), 1137-1153.

Smayda, T. J. (1998). Some patterns of variability characterizing marine phytoplankton, with example from Narragansett Bay *ICES Journal of Marine Science,* 55**,** 668-679.

Smayda, T. J. and Reynolds, C. S. (2001). Community assembly in marine phytoplankton: Application of recent models to harmful dinoflagellate blooms. *Journal of Plankton Research,* 23**,** (5), 447-461.

Smetacek, V. and Passow, U. (1990). Spring bloom initiation and Sverdrup's critical-depth model. *Limnology and Oceanography,* 35**,** (1), 228-234.

Smith, W. O. and Lancelot, C. (2004). Bottom-up versus top-down control in phytoplankton of the Southern Ocean. *Antarctic Science,* 18**,** (4), 531-539.

Sournia, A. M. and Chretiennot-Dinet, M. (1991). Marine phytoplankton:how many species in the world ocean? *Journal of Plankton Research,* 13**,** 1093-1099.

Southward, A. J. (1960). On changes of sea temperature in the English Channel. *Journal of the Marine Biological Association of the UK,* 39**,** 449-458.

Southward, A. J. and Butler, E. I. (1972). A note on further changes of sea temperature in the Plymouth area. *Journal of the Marine Biological Association of the UK,* 52**,** 931-937.

Southward, A. J., Langmead, O., Hardman-Mountford, N. J., Aiken, J., Boalch, G. T., Dando, P. R., Genner, M. J., Joint, I., Kendall, M. A., Halliday, N. C., Harris, R. P., Leaper, R., Mieszkowska, N., Pingree, R. D., Richardson, A. J., Sims, D. K., Smith, T., Walne, A. W. and Hawkins, S. J. (2005). Long-term oceanographic and ecological research in the western English Channel. *Advances in Marine Biology,* 47**,** 1-105.

Steidinger, K. A. and Tangen, K. (1996). Dinoflagellates. *In*: *Identifying marine diatoms and dinoflagellates* (C. R. Tomas, Ed). New York, Academic Press, pp.387-598.

Stolte, W., Mccollin, T., Noordeloos, A. and Riegman, R. (1994). Effect of nitrogen source on the size distribution within marine phytoplankton populations. *Journal of Experimental Marine Biology and Ecology,* 184**,** 83-97.

Stolte, W. and Riegman, R. (1995). The effect of phytoplankton cell size on transient state nitrate and ammonium uptake kinetics. *Microbiology,* 141**,** 1221-1229.

Suttle, C. A. (2005). Viruses in the sea. *Nature,* 437**,** 356-361

Suttle, C. A. (2007). Marine viruses — major players in the global ecosystem. *Nature Reviews Microbiology,* 5**,** 801-812.

Sverdrup, H. U. (1953). On conditions for the vernal blooming of phytoplankton. *Journal du Conseil international pour l' exploration de la mer,* 18**,** 287-295.

Tappin, A. D., Hydes, D. J., Burton, J. D. and Statham, P. J. (1993). Concentrations, distributions and seasonal variability of dissolved Cd, Co, Cu, Mn, Ni, Pb and Zn in the English Channel. *Continental Shelf Research,* 13**,** 941-969.

Tett, P., Joint, I. R., Purdie, D., Baars, M., Oosterhuis, S., Daneri, G., Hannah, F., Mills, D. K., Plummer, D., Pomeroy, D., Walne, A. W. and Witte, H. J. (1993). Biological consequences of tidal stirring gradients in the North Sea. *Philosophical Transactions of the Royal Society: Physical and Engineering Sciences,* 343**,** 493-508.

Tilman, D. and Kilham, P. (1982). Phytoplankton community ecology: the role of limiting nutrients. *Annual Review of Ecology and Systematics,* 13**,** 349-372.

Tomas, C. R. (1997). Identifying marine phytoplankton, New York, Academic Press, pp.858.

Townsend, D. W., Cammen, L. M., Holligan, P. M., Compbell, D. E. and Pettigrew, N. R. (1994). Causes and consequences of variability in the timing of spring phytoplankton blooms *Deep Sea Research Part I,* 41**,** (5-6), 747-765

Trees, C. C., Clark, D. K., Bidigare, R. R., Ondrusk, M. E. and Mueller, J. L. (2000). Accessory pigment versus chlorophyll *a* concentration within euphotic zone. A ubipuitous relationship. *Limnology and Oceanography,* 45**,** 1130-1143.

Trees, C. C., Kennincutt, M. C. and Brooks, J. M. (1985). Errors assiciated with standard fluorometric determination of chlorophyll and phaeopigment. *Marine Chemistry,* 17**,** 1-12.

Treguer, P., Corre, P. L. and Grall, J. R. (1979). The seasonal variations of nutrients in the upper waters of the Bay of Biscay region and their relation to phytoplankton growth. *Deep Sea Resarch,* 26A**,** 1121-1152.

Trimmer, M., Gowen, R. J., Stewart, B. M. and Nedwell, D. B. (1999). The spring bloom and its impact on benthic mineralisation rates in western Irish Sea sediments. *Marine Ecology Progress Series,* 185**,** 46-47.

Tyrrell, T. (1999). The relative influences of nitrogen and phosphorus on oceanic primary production. *Nature,* 400**,** 525-531.

Tyrrell, T. and Merico, A. (2004). *Emiliania huxleyi*: bloom observations and the conditions that induce them. *In*: *Coccolithophores-rrom molecular processes to global impact.* (H. R. Thierstein and J. R. Youngs, Eds.). Springer, pp.75-97.

Uye, S. and Takamatsu, K. (1990). Feeding interactions between planktonic copepods and red-tide flagellates from Japanese coastal waters. *Marine Ecology Progress Series,* 59**,** 97-107.

Valdes, L., Beaugrand, G., Harris, R., Irigoen, X., Lopez-Urrutia, A., Moral, M. and Planque, B. (2001). Seasonal dynamics and year-to-year variability (1991-1999) of *Calanus helgolandicus and Acartia clausi* in the Bay of Biscay and Sea. *ICES Symposium on Hydrobiological Variability in the ICES area.* Edinburg (UK).

Valdes, L. and Lavin, A. (2002). Dynamics and human impact in the Bay of Biscay: an ecological perspective. *In*: *Large marine ecosystems of the North Atlantic: changing states and sustainability.* (K. Shermann and H. R. Skjoldal, Eds.). Elsevier Science B. V., Amsterdam, pp.293-320.

Valdes, L., Lo´Pez-Urrutia, A., Cabal, J., Alvarez-Ossorio, M., Bode, A., Miranda, A., Cabanas, M., Huskin, I., Anadon, R., Alvarez-Marques, F., Llope, M. and Rodrıguez, N. (2007). A decade of sampling in the Bay of Biscay: What are the zooplankton time series telling us? *Progress in Oceanography,* 74**,** 98-114.

Valdes, L. and Moral, M. (1998). Time series analysis of copepod diversity and species richness in the southern Bay of Biscay (Santander, Spain) and their relationships with environmental conditions. *ICES Journal of Marine Science,* 55**,** 783-792.

Van-Den-Hoek, C. D. and Mann, H. M. (1997). Algae an introduction to phycology, Cambridge, University press, pp.627.

Van-Haren, H., Mills, D. K. and Wetsteyn, L. P. (1998). Detailed observations of the phytoplankton spring bloom in the stratifying central North Sea. *Journal of Marine Research,* 56**,** (3), 655-680.

Varela, M. (1996). Phytoplankton ecology in the Bay of Biscay. *Scientia Marina,* 60**,** (2), 45-53.

Venrick, E. L. (1978). Estimating cell numbers- 7.1.2. How many cells to counts? *In*: *Phytoplankton manual* (E. Sournia, Ed). Paris, UNESCO, pp.167-179.

Venrick, E. L. (1982). Phytoplankton in an oligotrophic ocean: observations and questions. *Ecological Monographs,* 52**,** (2), 129-154.

Verity, P. and Smetacek, V. (1996). Organism life cycles, predation, and the structure of marine pelagic ecosystem. *Marine Ecology Progress Series,* 130**,** 277-293.

Vidussi, F., Claustre, H., Manca, B., Luchetta, A. and Marty, J. (2001). Phytoplankton pigment distribution in relation to upper thermocline circulation in the eastern Mediterranean Sea during winter. *Journal of Geophysical Research,* 106**,** (C9), 19939-19956.

Villate, F., Moral, M. and Valencia, V. (1997). Mesozooplankton community indicates climate changes in a shelf area of the inner Bay of Biscay throughout 1988 to 1990. *Journal of Plankton Research,* 19**,** (11), 1617-1636.

Wafar, M. V., Corre, P. L. and Birrien, J. L. (1983). Nutrients and primary production in permanently well-mixed temperate coastal waters. *Estuarine, Coastal and Shelf Science,* 17**,** (4), 431-446.

Waniek, J. J. (2003). The role of physical forcing in initiation of spring blooms in the northeast Atlantic. *Journal of Marine Systems* 39**,** 57-82.

Warner, A. J. and Hays., G. C. (1994). Sampling by the Continuous Plankton Recorder survey. *Progress in Oceanography,* 34**,** 237-256.

Wasmund, N., Topp, I. and Schories, D. (2006). Optimising the storage and extraction of chlorophyll samples. *Oceanologia,* 48**, (**1), 125-144.

Welschmeyer, N. A. (1994). Fluorometric analysis of chlorophyll a in the presence of chlorophyll b and pheopigments. *Limnology and Oceanography,* 39**, (**8), 1985-1992.

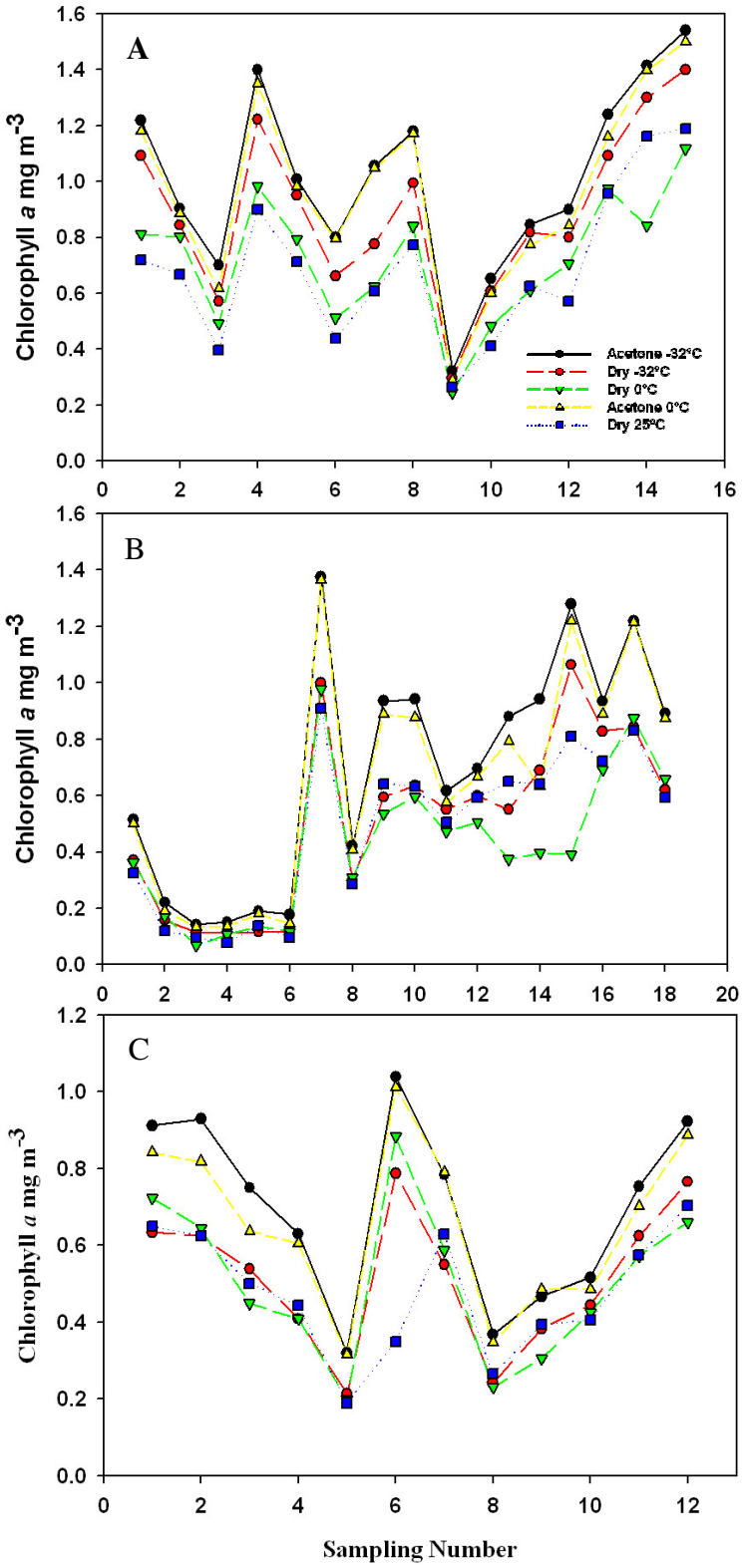
Williams, P. J. L. (1998). The balance of plankton respiration and photosynthesis in the open ocean. *Nature,* 394**,** 55-57.

Winter, A. and Siesser, W. G. (1994). Atlas of living coccolithophores. *In*: *Coccolithophore* (A. Winter and W. G. Siesser, Eds.). Cambridge, Cambridge University Press, pp.107-160.

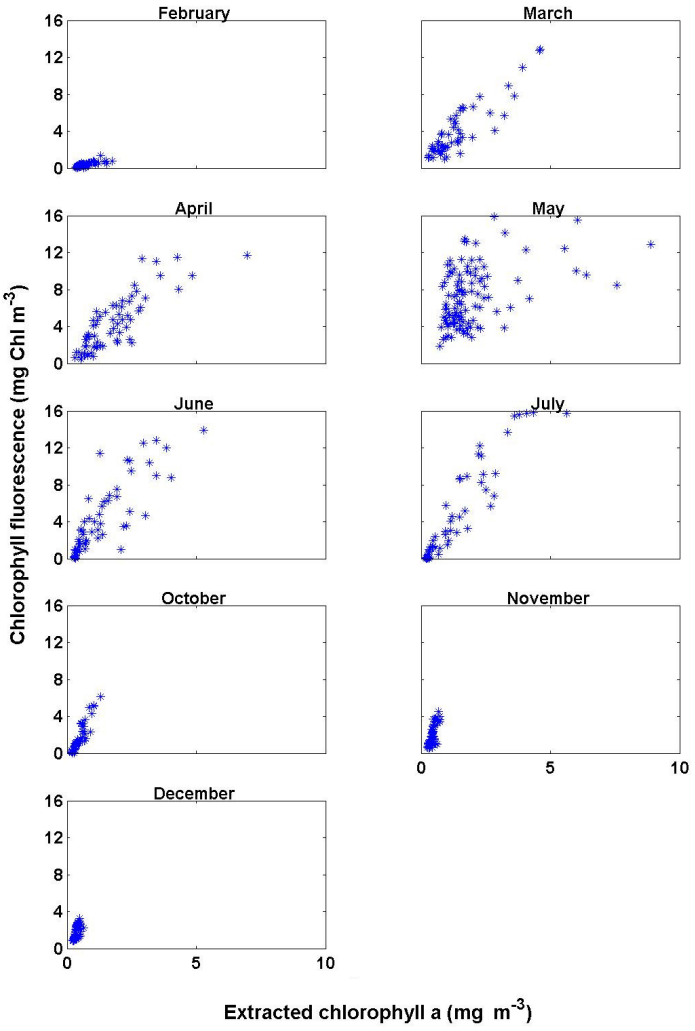
Zubkov, M. V., Sleigh, M. A., Tarran, G. A., Burkill, P. H. and Leakey, R. J. G. (1998). Picoplankton community structure on an Atlantic transect from 50° N to 50° S. *Deep Sea Research part I: Oceanographic Research Papers,* 45**,** 1339–1355.

APPENDIX

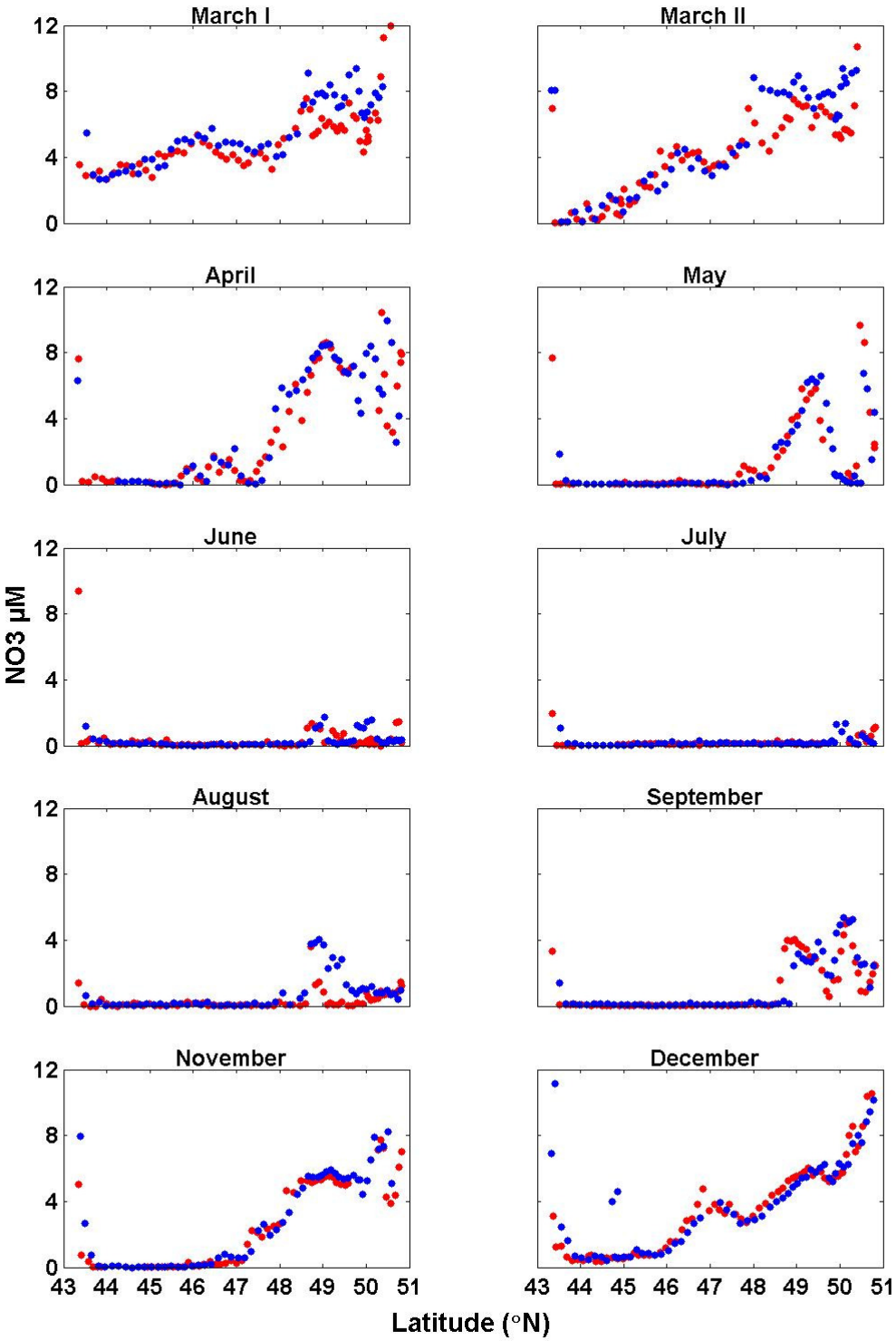
Appendix 1: Comparison of chlorophyll *a* using different sample storage methods (acetone -32^{o} C, dry -32^{o} C, dry 0^{o} C, acetone 0^{o} C and dry 25^{o} C) in A: August, B: September and C: October 2003.



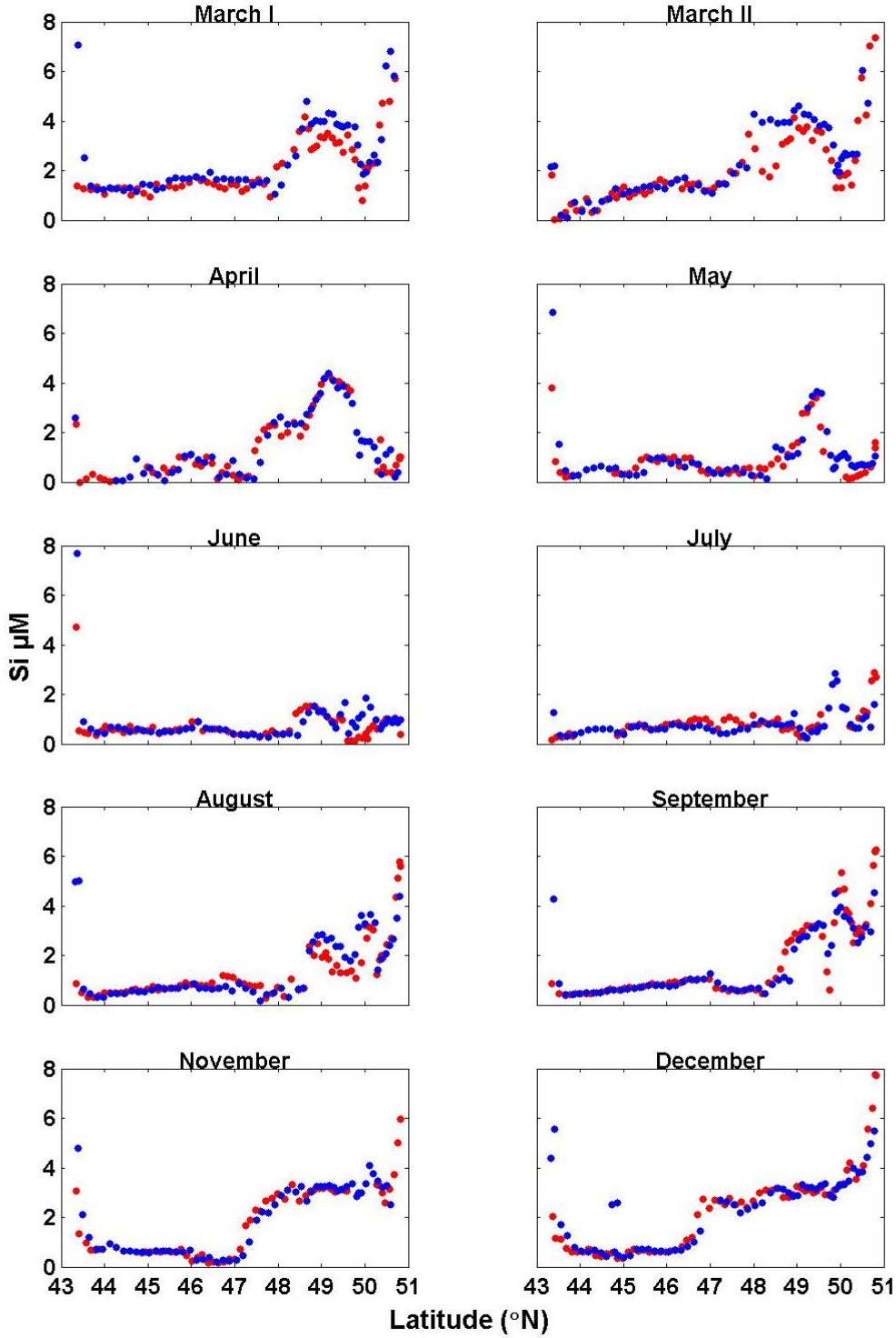
Appendix 2: Plots of in-vivo fluorescence against chlorophyll *a* measured by fluorescence for each calibration crossing in 2004.



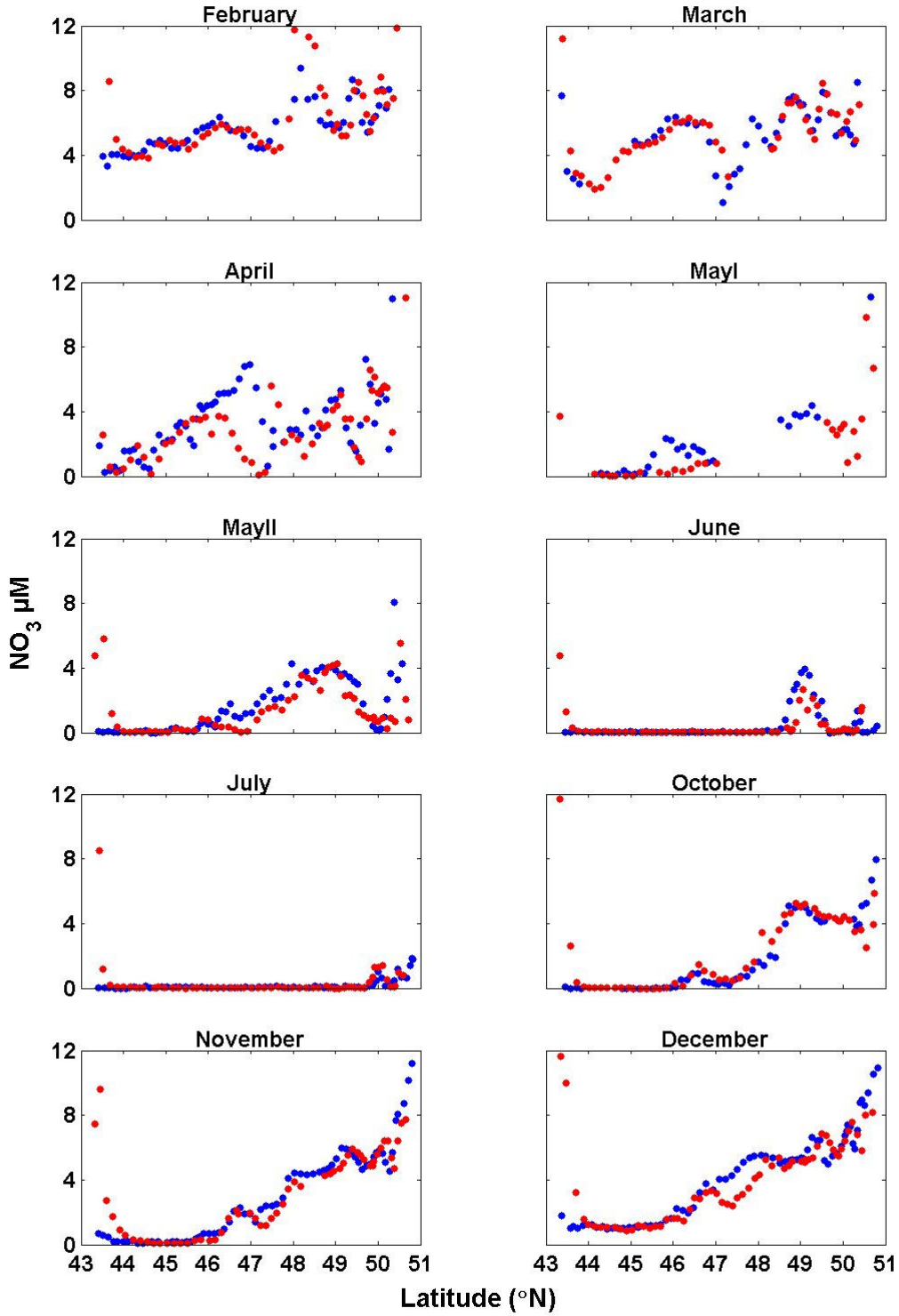
Appendix 3: Plots of nitrate values for each calibration crossings in 2003. The blue and red dots represent the tracks from Portsmouth (P) and from Bilbao (B) respectively.



Appendix 4: Plots of silicate values for each calibration crossings in 2003. The blue and red dots represent the tracks from Portsmouth (P) and from Bilbao (B) respectively.



Appendix 5: Plots of nitrate values for each calibration crossings in 2004. The blue and red dots represent the tracks from Portsmouth (P) and from Bilbao (B) respectively.



Appendix 6: Plots of silicate values for each calibration crossings in 2004. The blue and red dots represent the tracks from Portsmouth (P) and from Bilbao (B) respectively.