Chapter 7

The Impact of Climate Change and Feedback Processes on the Ocean Carbon Cycle

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7.1 Introduction

7.1.1 Climate and Change – Present Status

We have been aware of the concept of global climate change since the advent of modern science in the 17th Century and the emergence of disciplines such as geology. However, it is only in the last century that a putative link, termed the 'the Greenhouse Effect' (Wood 1909), has been suggested between the atmospheric concentrations of particular gases and climate. The composition of the atmosphere has been studied routinely since the late fifties/early sixties with the establishment of monitoring sites for atmospheric CO_2 (such as Mauna Loa) where the 40-year dataset clearly demonstrates the rise of atmospheric CO_2 (Keeling et al. 1995). Similar anthropogenically-mediated increases in the atmospheric concentrations of other gases such as nitrous oxide and methane have also been recorded in the last 40 years (Bigg 1996; IPCC 2001). Such increases in the concentrations of these gases in the atmosphere alter the radiative forcing globally by decreasing the long-wave radiative flux leaving the trophosphere (Houghton et al. 1990) which is thought to lead to climatic effects. Alongside the global monitoring of atmospheric concentrations and distributions of greenhouse gases, there have been concerted efforts to use mathematical models to better understand the nature of the relationship between the observed changes in gas concentrations, subsequent alteration of radiative forcing and climate.

While it is now well established that anthropogenic activities are responsible for observed increases in atmospheric gas concentrations such as CO_2 (IPCC 2001), the relationship between altered atmospheric composition and climate change is less well established. Nevertheless "there is new and stronger evidence that most of the warming observed over the last fifty years is attributable to human activities" (IPCC 2001), and that "emissions of greenhouse gases and aerosols due to human activites continue to alter the atmosphere in ways that are expected to affect climate" (IPCC 2001).

Recently, a synthesis of many observational studies indicates that the global average surface temperature has increased by ca. 0.6 °C in the 20th Century (IPCC 2001), and there is also strong evidence that the oceans are exhibiting a warming trend (Levitus et al. 2000). Indeed, the present rate of change in atmospheric CO_2 is without precedent, necessitating the development of a mechanistic understanding of the processes controlling climate change (IPCC 2001). In addition to contemporary changes in atmospheric CO_2, there is evidence of substantial climate change from the geological past with, for example, glacial core records showing large variations in temperature and greenhouse gas concentrations associated with glacial/interglacial oscillations over the last 400 000 years (the Vostok core record; Petit et al. 1999). Throughout this period, there are consistent trends of lower atmospheric CO_2 levels during the glacials, and higher levels during the interglacials (Woodwell et al. 1998). There has been much debate and many theories proposed as to what factors caused these shifts from interglacial to glacial periods (Archer and Johnson 2000; Schrag 2000; Sigman and Boyle 2000).

What is the role of the ocean in climate change? The ocean is inextricably linked with the atmosphere and the land, carries 50-fold more CO_2 (mostly in the form of Dissolve Inorganic Carbon, DIC) than the atmosphere, and thus dominates the global carbon cycle, playing a major role in climate change on a range of scales (Siegenthaler and Sarmiento 1993; Sigman and Boyle 2000). Current model and data-based estimates indicate that the ocean presently takes up approximately 2 Pg C yr^{-1} of anthropogenic carbon, or roughly a third of the atmospheric fossil fuel emissions (Battle et al. 2000; Doney et al., this volume). The potential influence of marine biota on atmospheric CO_2 levels suggest that a fully effective oceanic biological pump would result in an atmospheric CO_2 level of around 160 ppm (the unperturbed interglacial concentration of atmospheric CO_2 is 280 ppm) while an abiotic ocean would yield atmospheric CO_2 levels of ca. 450 ppm (Shaffer 1993). One of the goals of the Joint Global Ocean Flux Study (JGOFS) project is to "assess and understand the sensitivity to climate change of the ocean carbon cycle" and to "improve our ability to predict future climate-related changes" (JGOFS Science Plan 1991). JGOFS has produced comprehensive biogeochemical datasets from all major oceanographic regions. These datasets, which provide an unprecedented level of detail, enable us to define further biogeochemical provinces, and to understand better the functioning of the oceanic carbon cycle. Present coupled atmosphere-ocean climate or general circulation models (GCMs) are useful tools but have limited predictive abilities due to many uncertainties, in particular with regard to the response of the biota (Sarmiento et al. 1998; Doney 1999). A further aim of the JGOFS programme is to reduce these uncertainties by improving our understanding of the role of the biota in climate change.

The global climatic system is driven by a series of external and internal processes that influence global temperature and other climatic factors (Woodwell et al. 1998). External perturbations (such as variations in solar radiation, emissions of CO_2 from fossil fuel burning, human-induced alterations of surface albedo) elicit changes in the Earth's radiation balance and subsequently the climate (e.g., temperature, cloud cover, water vapour). These climate responses may in turn feedback on the initial perturbation. An example is the water vapour feedback where increased temperatures lead to higher atmospheric concentrations of water vapour, which is also a greenhouse gas leading to an amplification of the original temperature rise. Feedbacks may be classified as positive or negative i.e., in the case of climate change they may enhance or diminish the initial effects of anthropogenic perturbations on climate, respectively (Woodwell et al. 1998). Also, as feedbacks may be interactive (Lashof 1989) they can be viewed as the 'gears' of climate and as such may result in the non-linear effects that are increasingly receiving attention in climate research (Rahmstorf 1999).

This chapter provides examples of feedbacks, discusses the nature and dynamics of feedback mechanisms, identifies the main mechanisms reported to be relevant to climate change, and reviews aspects of feedbacks such as classification, forcing, magnitude and 'degree of belief' (after Pate-Cornell 1996). To be comprehensive both physically- and biogeochemically-mediated feedbacks have been included, but here only the latter are considered in detail. This is followed by an examination of case histories, from the JGOFS pro-

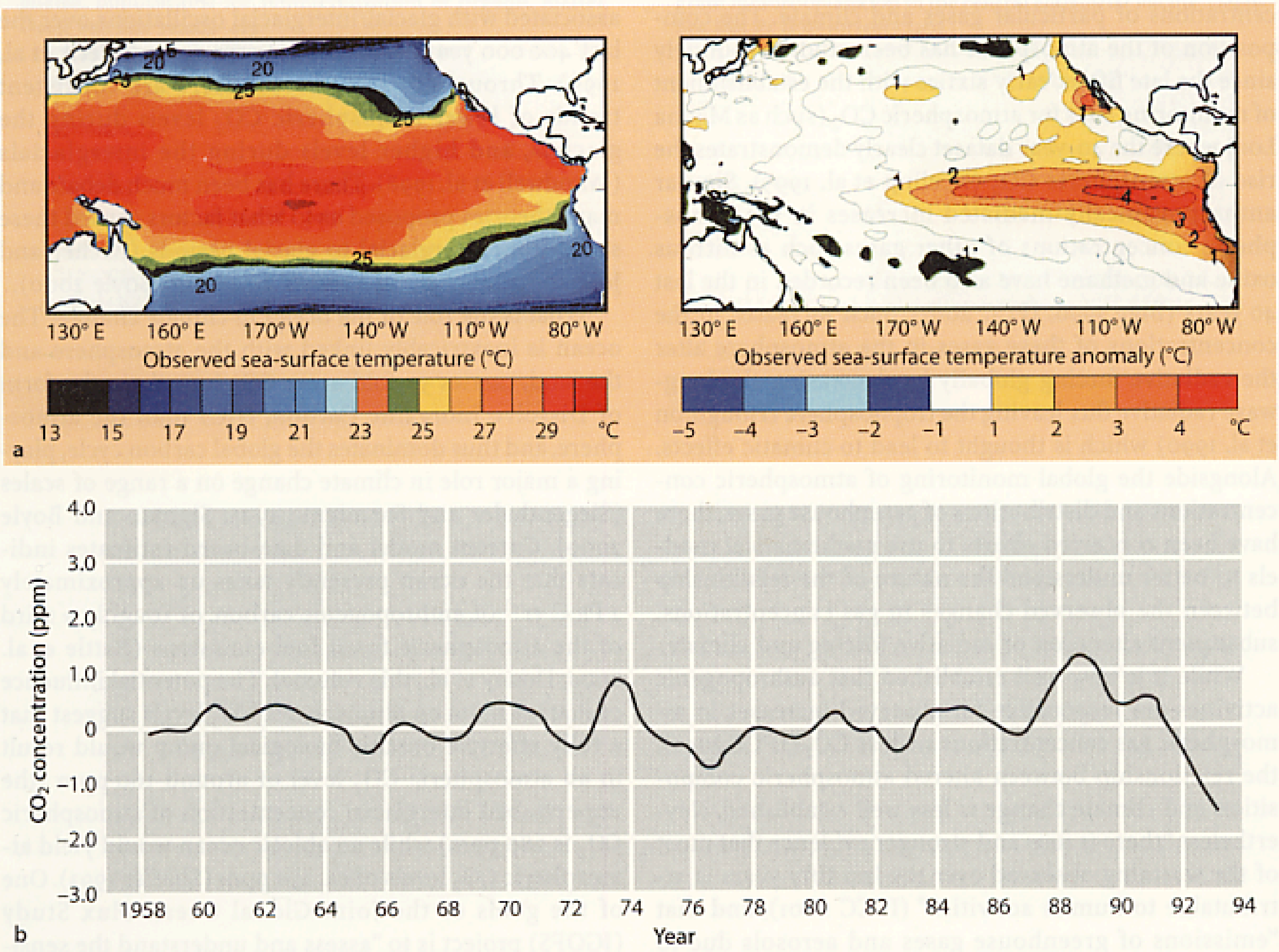


Fig. 7.1. Evidence of climate variability from **a** the 1997 El Niño event. The observed mean sea surface temperature (October 1997), and its deviation from the long-term (15 year) mean temperature for October are presented in the left and right panels respectively (reprinted by permission from Nature (Webster and Palmer 1997), © 1997 Macmillan Publishers Ltd.); and **b** the Mauna Loa CO_2 anomaly which displays the effects of El Niño events (1982–1983; 1986–1987) and the Pinatubo eruption (1991) (Sarmiento 1993). For details of the

gramme, that shed light on biotic feedbacks that were previously poorly constrained at the time of the second IPCC (International Panel on Climate Change) review (Denman et al. 1996). Finally, our present understanding of each feedback is appraised, the recent emergence of any new mechanisms is discussed, and the current scientific understanding is related to projection (modeling simulations) and detection (ocean observations) of feedbacks in the future.

7.1.2 Examples of Feedbacks in the Present and the Geological Past

Recent examples demonstrate that large amplitude climate variability can occur on short timescales, tens of years or less, both in the present (Fig. 7.1a), and in the geological past (the 'North Atlantic Trigger', Fig. 7.2). Each case illustrates the short timescales and large magnitude of the response by ocean-atmosphere feedbacks, and more importantly indicates how poor our understanding is of the complex interplay between feedbacks and the resulting shifts in the functioning of the global carbon cycle. Sarmiento (1993) demonstrated how the removal of the seasonal signal and long-term trends from the Mauna Loa atmospheric CO_2 record provides evidence of the effects of climate variability due to El Niño and other perturbations such as the Pinatubo eruption (Fig. 7.1b) on CO_2 levels. In the latter case, the eruption has been attributed to cause a –1.5 ppm change in CO_2. Sarmiento assesses the plausibility of potential candidate mechanisms to explain which feedbacks might have caused this marked shift in CO_2. These include both terrestrial (cooling/rainfall altering the balance of respiration and photosynthesis on land) and oceanic (iron-rich ejected rocks elevating ocean productivity; Watson 1997). Sarmiento concluded that the nature of the feedback mechanism(s) effecting atmospheric CO_2 were not clear, and that this analysis was restricted by our lack of understanding of the functioning of the global carbon cycle. However, the magnitude of such climatic variability – as in the case of Pinatubo – shows that the oceanic biota may potentially have a pronounced and rapid effect on atmospheric CO_2 concentrations. Severinghaus and Brook (1999) report on a 9 °C change in temperature over several decades around 15 000 years ago (i.e., the last glacial termination). This warming may have led to an abrupt increase in methane concentrations, and the authors put forward a causal mechanism comprising a suite of interactive feedbacks called the 'North Atlantic Trigger' (Fig. 7.2). Again in this example it is evident how interactions between feedbacks result in a marked amplification of the climatic signal over a relatively short time period.

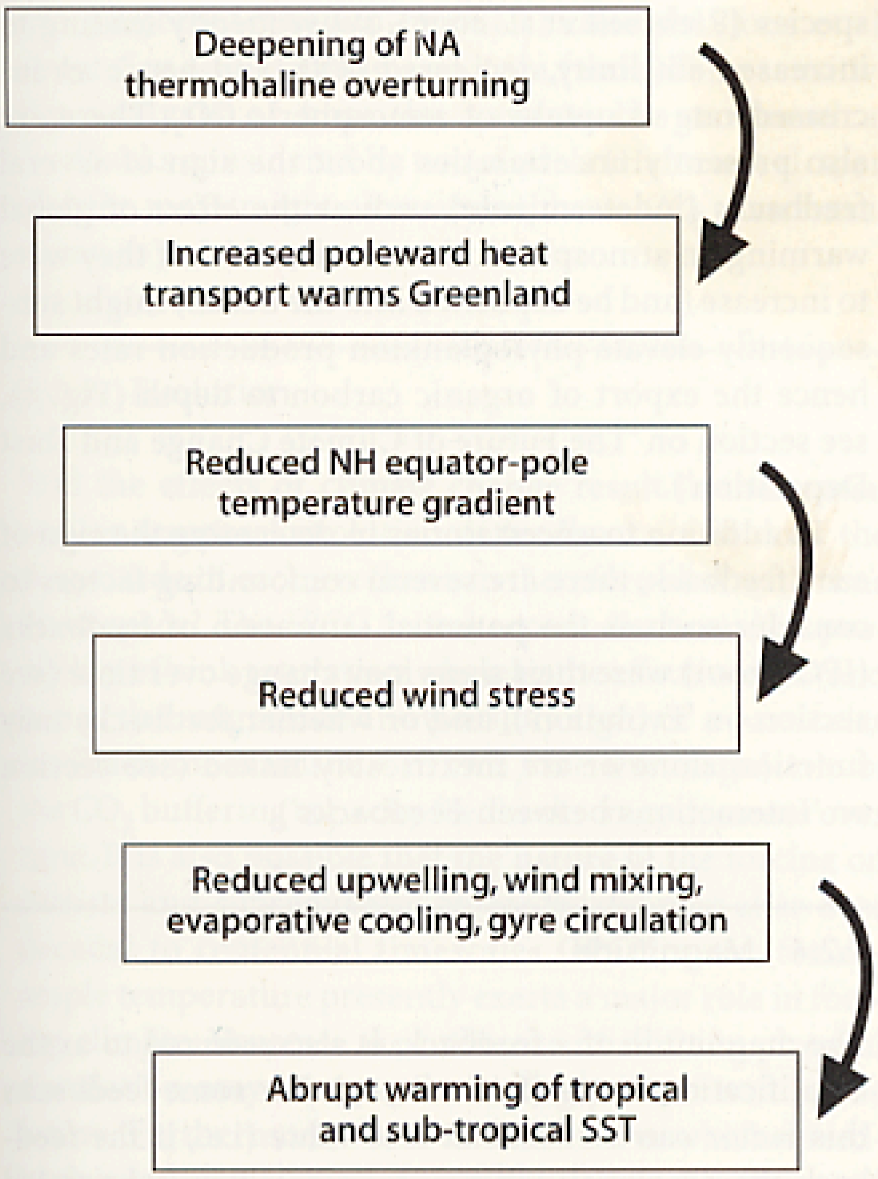


Fig. 7.2. A schematic of interactive feedbacks, chronologically arranged from the top of the panel downwards, hypothesised to drive the putative North Atlantic Trigger around 15 000 years ago (from

7.2 Feedbacks

7.2.1 Definition

In the field of climate change, the term feedback has often been used widely and loosely (Lashof 1989). Lashof refers to the term in a manner analogous to an electronic amplifier with the output (W) determined by the input signal (L) and a feedback signal proportional to W (such that the resultant (G), or gain is defined as $G = (W - L) / W$. Thus, if $G > 0$ the feedback is positive, and if $G < 0$ it is negative. In the case of the amplifier analogy, for clarity, care must be taken to use commensurate inputs and outputs. For example if the input is a 100 Pg increase in atmospheric CO_2, then the output will be the resulting change in atmospheric CO_2 due to terrestrial and oceanic carbon sources/sinks and climatic warming feedbacks.

7.2.2 Identification

Lashof (1989) divided feedbacks into those which are geophysically- and biogeochemically-mediated, exambility. It cannot be ruled out that there are other feedbacks that have yet to be identified. Geophysical feedbacks were defined by Lashof (1989) as those due to physical forcing (as opposed to chemical or biochemical processes) in the geosphere-biosphere that alter the radiative characteristics of the system in response to the initial radiative or temperature perturbation. Physical feedbacks, including the effect of water vapour, clouds, polar ice, and ocean heat storage, are usually included in GCMs (Woodwell et al. 1998). Biogeochemical feedbacks were defined by Lashof (1989) as those that involve the response of the biosphere and biogeochemical components of the geosphere, and at that time had seldom been considered in typical climate models (Lashof 1989). Examples of biogeochemical feedback mechanisms include short-term biological responses to warming and atmospheric CO_2 increases (e.g., changes in leaf area and terrestrial photosynthesis that in turn impact surface albedo and surface water vapour exchange), and longer-term effects due to the re-organisation of ecosystems (e.g., a shift in vegetation, forest to grassland; Lashof 1989). The biogeochemical feedbacks that have received most attention are those that impact biotic exchanges of greenhouse gases which are often sensitive to changes in temperature, radiation and moisture (Woodwell et al. 1998). Until recently, the latter have not been generally included in GCMs which have been generally driven by prescribed CO_2 concentrations rather than by prescribed emissions. Such biogeochemical feedbacks are complicated but potentially large and have the potential for either damping or accelerating global warming once begun (Woodwell et al. 1998). In the last few years there have been major efforts by climate modellers to include such biogeochemical feedbacks into coupled GCMs (e.g., Cox et al. 2000).

7.2.3 Classification

Feedbacks may be classified as positive (exacerbation), negative (diminution) (after Kellogg 1983), or in some cases indeterminate. Examples of those considered to be positive include the CO_2 buffering capacity feedback (where as the ocean takes up more CO_2 and becomes more acidic, the thermodynamic capacity of seawater to take up CO_2 (δDIC per unit CO_2) becomes smaller (Siegenthaler and Sarmiento 1993; IPCC 2001). Changes in ice and snow cover also constitute a positive feedback because warming the Earth reduces the planetary albedo and increases the surface shortwave heating by reducing the extent and persistence of sea-ice and snow cover (Lashof 1989). An example of a feedback viewed to be negative is the predicted decrease in pH, due to increased pCO_2, which in laboratory studies result in decreased calcification rate in several coccolithophorid species (Riebesell et al. 2000), subsequently leading to increased alkalinity, decreased pCO_2 and hence an increased rate of uptake of atmospheric CO_2. There are also presently uncertainties about the sign of several feedbacks (indeterminate) such as the effect of global warming on atmospheric dust levels, which if they were to increase (and be deposited into the ocean) might subsequently elevate phytoplankton production rates and hence the export of organic carbon to depth (Fig. 7.3, see section on 'The Future of Climate Change and Dust Deposition').

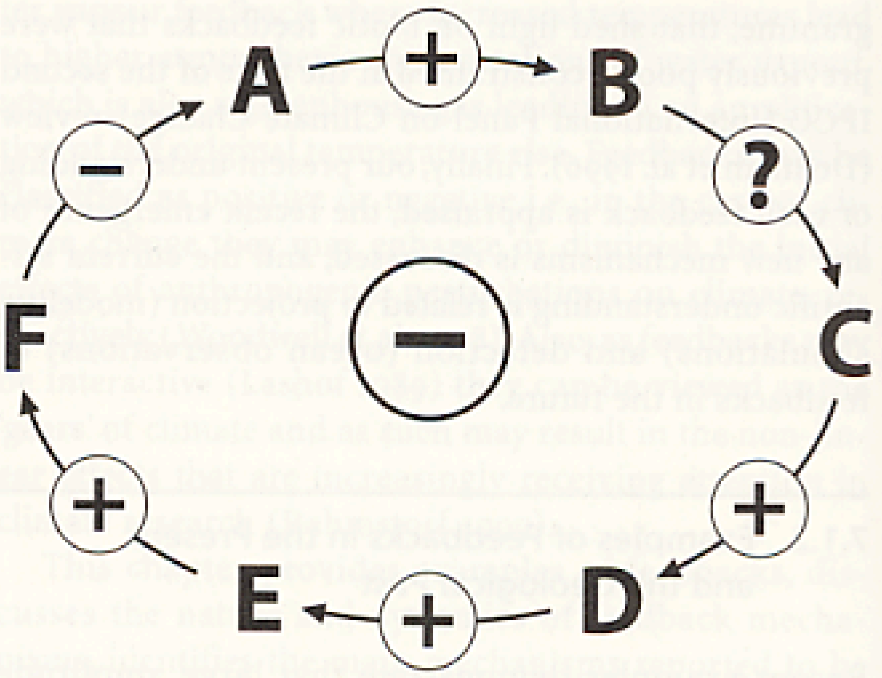


Fig. 7.3. A means by which to represent feedback loops (after Kellogg 1983). For example, the link between *A* increased atmospheric carbon dioxide concentrations, *B* warming, *C* enhanced aridification, *D* increased dust supply, *E* iron-elevated rates of primary production, and *F* higher downward particulate export fluxes. Positive (exacerbation) and negative (diminution) denote the signs of the feedbacks, note the relationship between B and C remains controversial/unproven (see Fig. 7.13). Although global warming is thought to increase aridity and hence the supply of iron-rich dust to iron-depleted phytoplankton (Falkowski et al. 1998), global atmospheric moisture content is predicted to increase as a result of global warming (Trenberth 1998), and thus it is not known if warming will result in an increase or decrease in iron-mediated phytoplankton production in the future

In addition to uncertainties in determing the sign of each feedback, there are several confounding factors to consider such as the potential saturation of feedbacks (IPCC 2001) were their signs may change over time (see section on 'Evolution'), and/or whether feedbacks may function alone or are inextricably linked (see section on 'Interactions between Feedbacks').

7.2.4 Magnitude

The magnitude of a feedback, is also referred to as the amplification factor (Lashof 1989). For some feedbacks this factor can be taken at face value (i.e., if the feedback effect is global), whereas for others it must be scaled to take into account the regional nature of a particular mechanism (see Scales and Response Times). Although

Kellogg (1983) discussed several biogeochemical feedback scenarios, this was done in a qualitative manner. Lashof (1989) provided some of the first estimates of the magnitude of both geophysical and biogeochemical feedbacks. In general, based on modeling outputs, Lashof reported that geophysical feedbacks were all positive and had the largest magnitude (water vapour followed by ice/snow albedo and clouds). In contrast, although biogeochemical feedbacks were more numerous they had relatively small magnitudes, with some positive (ocean eddy diffusion) and negative (trophospheric chemistry). The cumulative effect of biogeochemical feedbacks was positive but only 25% of the magnitude (although of the same sign) of the geophysical feedbacks. Recently, Joos et al. (1999) performed a modeling experiment to assess the effects of various feedbacks on the global carbon cycle including sea surface temperature (SST), oceanic circulation, and some general biotic effects. They also included model runs employing different scenarios for the marine biota (such as more marine calcifiers). Joos et al. reported that the projected changes in the ocean carbon cycle produced modest changes in atmospheric CO_2 concentrations (a 4% and 20% increase by 2100 and 2500). The feedback with the greatest magnitude appeared to be a reduction in oceanic CO_2 uptake due to sea-surface warming. The projected changes in the biota due to climate change compensated in part for some of the projected physico-chemical changes (Joos et al. 1999). See also Denman and Pena (2000) for a sensitivity analysis of how the various biogeochemical feedbacks considered by two models (Heinze et al. 1991; Shaffer 1993) might alter atmospheric CO_2 concentrations.

7.2.5 Evolution

Will the effects of climate change result in the spatial and/or temporal evolution of feedbacks, and does the magnitude of each mechanism therefore alter with time or in space? The IPCC (2001) report discusses the possibility of 'sink saturation' whereby the effectiveness (and hence the magnitude and possibly sign) of a particular feedback mechanism – in this case the magnitude of the CO_2 buffering capacity feedback – may decrease over time. It is also possible that the nature of the forcing on climate and subsequently on feedbacks may alter over decadal to centennial timescales (IPCC 2001); for example temperature presently exerts a major role in forcing climate. However the influence of shifts in physical circulation may become increasingly important in the future. Furthermore, the areal extent over which a feedback is influential may presently be regional (uptake and storage of atmospheric CO_2 in the Southern Ocean, Calderia and Duffy 2000), rather than global (such as CO_2 buffering capacity, Siegenthaler and Sarmiento 1993), but may alter as climate changes. Parmesan (1996) examined the validity of the assumption that warming trends would result in a poleward expansion of the area occupied by certain terrestrial species and concluded that the existing small datasets had been overly upscaled. More recently, Lipschultz (1999) pointed to a poleward expansion of the oceanic biome for nitrogen fixers that might result from global warming. Future field/modeling experiments might include an assessment of whether there is a temporal sequence of feedbacks. It is unlikely that feedback mechanisms will remain as static features in the future, and such evolution needs to be taken into account when attempting to rank feedbacks.

7.2.6 Interactions between Feedbacks

Kellogg (1983) states that "in actuality, these various feedback (loops) cannot be considered by themselves – they all interact with each other – something that is well recognized by climate system modellers". The interactions between feedbacks is thought to be largely responsible for the non-linearity in response to climate (Rahmstorf 1999) observed both in the geological record (Broecker and Henderson 1998; Severinghaus and Brook 1999) and in the present day (El Niño, Webster and Palmer 1997; Chavez et al. 1999; Pinatubo, Sarmiento 1993). As such interactions usually result in enhanced system complexity, they will be difficult to assess, even qualitatively.

7.2.7 Scales and Response Times

At present, most climate model predictions with full three-dimensional GCMs only extend for 100 years or so into the future, and interest therefore has focussed on those feedbacks that will take place on decadal timescales (or less). To assess the contribution of each feedback mechanism, all of the relevant, and often wide-ranging time and space scales must be considered (such as algal physiology, Wolf-Gladrow et al. 1999; or ocean circulation, Calderia and Duffy 2000). Such temporal and spatial scales will also reflect the response time for each mechanism. Algal physiological responses are likely to be rapid and localised (hours/days Behrenfeld et al. 1996; Boyd et al. 2000) while those for foodweb shifts might take longer – from weeks (Boyd et al. 2000) to months (Chavez et al. 1999, see section on 'Regime Shifts'). Basin-scale might operate on a decadal/centennial time horizon (shutdown of North Atlantic Deep Water and subsequent alteration of thermohaline circulation, Broecker 1997). These time and space scales must be placed in context in the structuring of the coupled atmosphere/ocean models.

7.2.8 Degree of Confidence – Understanding Feedbacks

Prior to any ranking of feedbacks as is required to assign future research priorities, the degree of confidence in our understanding of their many aspects (magnitude, complexity – isolated vs. interactive) must be assessed. Such a synthesis must be made despite many uncertainties; it may be possible to adopt an approach analogous to that of Pate-Cornell (1996) who combined existing information on global climate change estimates with Bayesian probabilities that serve as a proxy for a 'degree of belief'. Climate scientists have recently begun to assign 'level of scientific understanding' or 'confidence' estimates for the expectations of forcing changes, responses and feedbacks (IPCC 2001). Similar exercises can be conducted for biogeochemistry. For example, the general consensus is that a decrease in pH is highly probable (99%) (Kleypas et al. 1999) while a decrease in calcification is perhaps only moderately likely (Riebesell et al. 2000). Here, the expected changes in the physicochemical environment of the future may be put forward as follows (in order of confidence): the most probable changes will be increased ocean DIC; decreased pH and [CO_3^--]concentration; probable changes include an increase in surface temperature; somewhat probable might be decreased solar irradiance because of increased cloudiness; coastal eutrophication; decrease in high latitude surface salinity (sea ice meltback and enhanced hydrological cycle); increased vertical stratification (temperature at low latitudes and salt at high latitudes); and increased storminess and hurricanes (Royer et al. 1998; Bates et al. 1998). The processes/changes that there is least confidence in our understanding of include changes in gyre shape/amplitude, dust deposition (see section on 'The Future – Climate Change and Dust Deposition'). On the basis of the unknowns raised so far in this chapter it is not possible to presently rank feedbacks in order of importance for climate change but a scheme by which to do so is presented in Fig. 7.4.

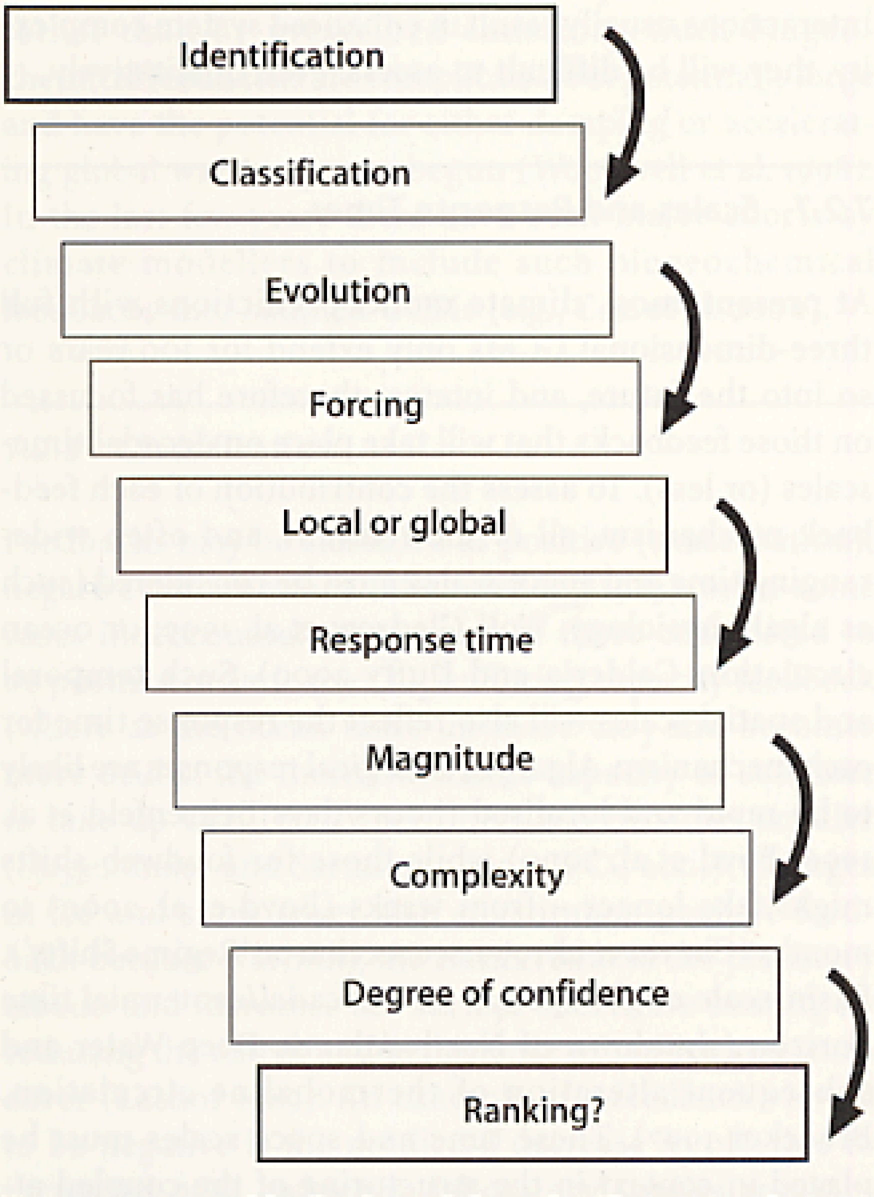


Fig. 7.4. Aspects of feedbacks and the order (from *top* to *bottom*) in which they should be considered to appraise our understanding/confidence in estimates of each feedback mechanism

7.3 What do Current Models Predict?

Current model estimates concur with data-based estimates indicating that the ocean takes up around a third of the atmospheric fossil fuel emissions (Schimel et al. 1995; Doney et al., this volume). Model projections suggest that the ocean will continue to play a major role in drawing down excess atmospheric CO_2 over the next several centuries (Fig. 7.5). As the magnitude of the anthropogenic impact on the climate system grows, significant changes in ocean physics and other external forcing factors will undoubtedly alter the uptake of an-

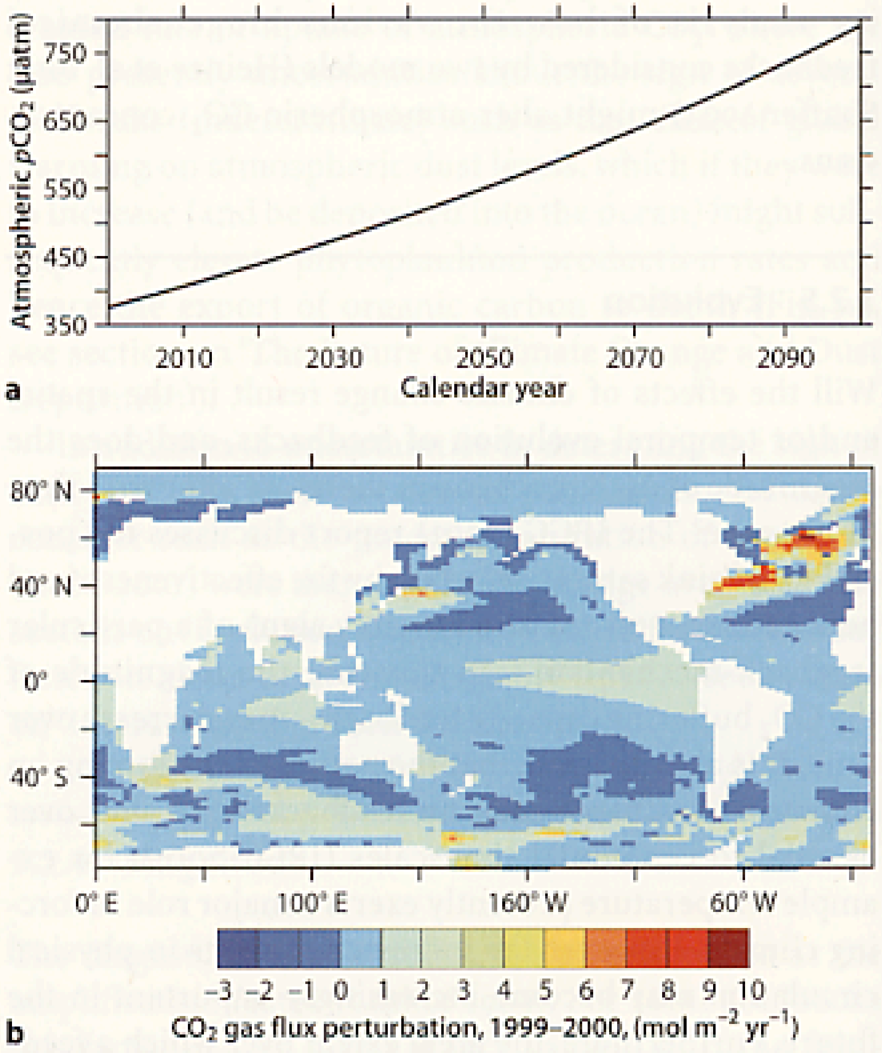


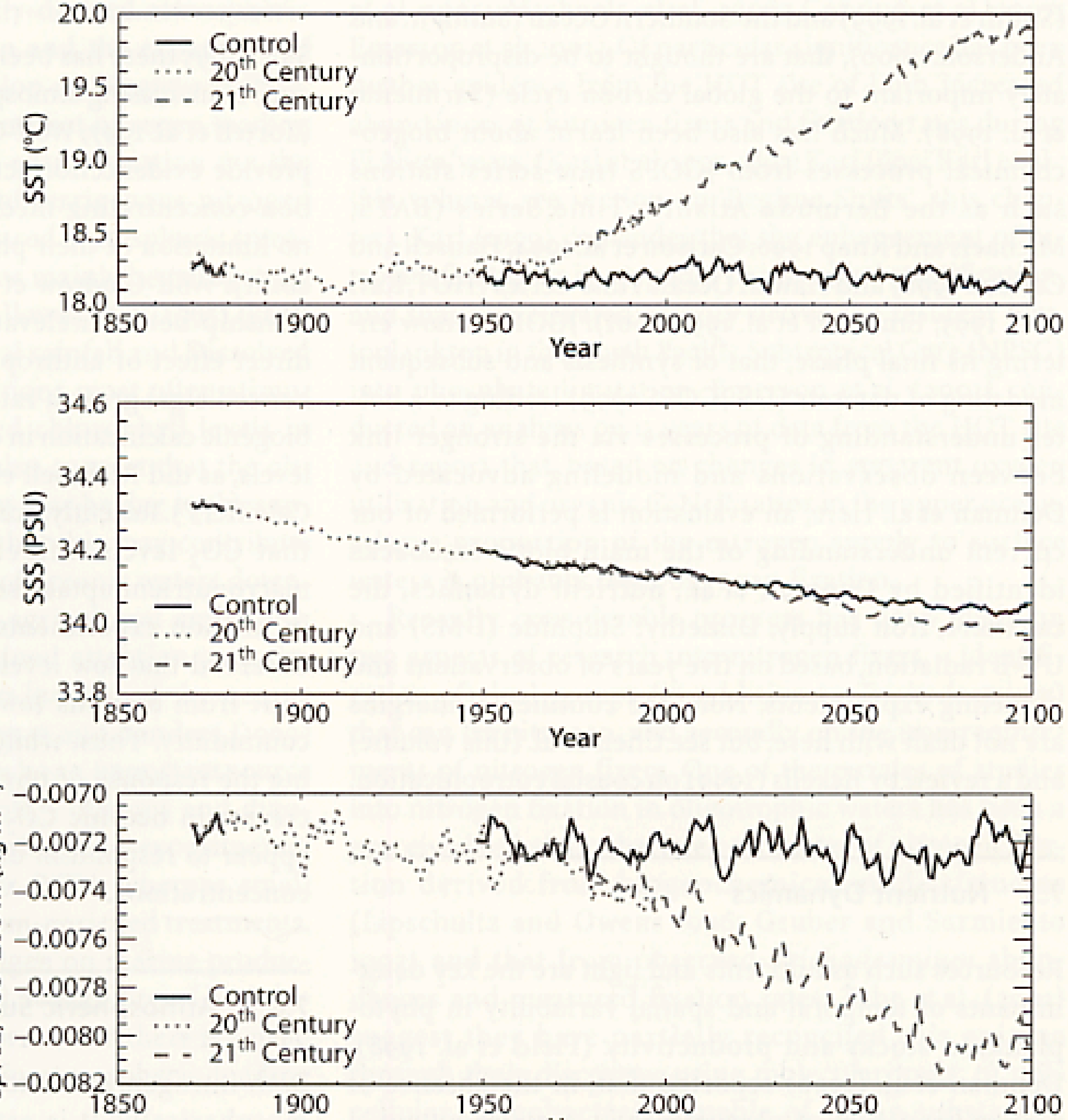
Fig. 7.5. Modelled projections for the next century of the rise in atmospheric CO_2 from the IPCC IS92A scenario (a) and the resulting magnitude of the global oceanic uptake of CO_2 (b) as a function of time from the NCAR (National Center for Atmospheric Research, Boulder, Colorado, USA) ocean model

thropogenic carbon and perturb the 'natural' biogeochemical carbon cycle, and these potential ocean feedbacks are a key topic of current research.

Recent advances in coupled ocean-atmosphere models (e.g., Manabe and Stouffer 1993; Boville and Gent 1998) have resulted in a series of reasonably credible physical scenarios for the next 100 years. Fossil fuel consumption and land-use change since the Industrial Revolution have led to substantial increases in the atmospheric levels of greenhouse trace gases such as CO_2, N_2O, CFCs and CH_4. The resulting net heating of the atmosphere is partially offset by cooling due to atmospheric sulphate aerosols over Northern Hemisphere industrial regions (Schimel et al. 1996). Calculating the full climatic impact of these perturbations, including feedbacks from clouds, sea-ice, and water vapour, requires the use of three-dimensional, coupled ocean-atmosphere models. The present generation of coupled simulations suggest continued surface warming of between 1.5–5.0 °C (above pre-industrial) and a strengthening of the hydrological cycle over the next century (e.g., Kattenberg et al. 1996).

From the perspective of ocean biogeochemistry, perhaps the most relevant features observed in almost all coupled model projections are a general warming of the upper ocean and thermocline and increased vertical stratification in both low latitude (warming) and high latitude (freshening) surface waters (Fig. 7.6). The regional patterns of climate change can differ considerably among coupled models (model intercomparisons provide useful tests to look at such regional variations, see Orr 1999) and should be viewed with some scepticism. However, many coupled model simulations show trends such as: reduction of polar sea-ice cover; shift toward more El Niño like conditions in the equatorial Pacific; and decreased deepwater production in the North Atlantic and Southern Ocean. Other potentially important physical climate forcings are changes in the pattern and magnitude of river runoff and thus nutrient input to the coastal ocean, a possible decrease in surface solar insolation under a more humid and cloudy atmosphere, and modified terrestrial dust iron deposition to the surface ocean (Mahowald et al. 1999). Terrestrial dust production and subsequent oceanic deposition depends on a complex mixture of physical climatic factors (e.g., soil moisture, see section on 'The Future Climate Change and Dust Deposition') and it is as yet unclear whether future dust depostion will increase or decrease. Finally, the basic ocean chemical state, and in particular the pH and carbonate system, will be dra-

Fig. 7.6.
Projections of the increases in global average sea surface temperature and salinity, and upper ocean (50 m) vertical density gradient (a measure of stratification) over the next century from the NCAR Climate System Model (CSM)



matically altered due to the uptake of anthropogenic CO_2. By the middle of the next century, the addition of CO_2 to the surface ocean will shift the acid-base chemistry by about −0.25 pH and reduce carbonate ion concentrations by about 30%, with the potential for significantly decreasing marine calcification (e.g., Kleypas et al. 1999). For future directions in ocean-atmosphere modeling see section on 'Modeling – Future Goals'.

7.4 Status of Our Understanding of Feedbacks

The most comprehensive review of marine biotic feedbacks was conducted by Denman et al. (1996) as part of the IPCC second scientific assessment of climate change. Their review identified and discussed several potential feedbacks, but concluded that their sign and magnitude were relatively poorly constrained. Moreover, Denman et al. stated that our most powerful tools to investigate feedbacks – climate models – could not adequately simulate complex ecosystem interactions, and that modeling and observational studies must be used in tandem to address these complex climate-feedback-responses.

Since 1995, the JGOFS programme has conducted further field studies in regions, such as the Arabian Sea (Smith et al. 1999) and the Southern Ocean (Smith Jr. and Anderson. 2000), that are thought to be disproportionately important to the global carbon cycle (Sarmiento et al. 1998). Much has also been learnt about biogeochemical processes from JGOFS time-series stations such as the Bermuda Atlantic Time Series (BATS, Michaels and Knap 1996; Carlson et al. 1994; Hansell and Carlson 1998) and Hawaii Ocean Time-series (HOT, Karl et al. 1995; Emerson et al. 1997, 2001). JGOFS is now entering its final phase, that of synthesis and subsequent modeling of datasets (US JGOFS 1999) leading to a better understanding of processes via the stronger link between observations and modeling advocated by Denman et al. Here, an evaluation is performed of our current understanding of the main biotic feedbacks identified by Denman et al., nutrient dynamics, the calcifiers, iron supply, Dimethyl Sulphide (DMS) and UV-B radiation, based on five years of observations and modeling experiments. Note, the continental margins are not dealt with here, but see Chen et al. (this volume) and a review by Jickells (1999) on coastal eutrophication.

7.5 Nutrient Dynamics

Resources such as nutrients and light are the key determinants of temporal and spatial variability in phytoplankton stocks and productivity (Field et al. 1998). Denman et al. (1996) reported that, in the absence of

feedback resulting from climate change would be any alteration in the relationship between carbon and nutrients – via shifts in the supply of new nutrients to the open ocean, or to changes in the stoichiometry of nutrient uptake. Such shifts might result in an enhanced role of the biological pump in influencing climate, for example by fixing more carbon per unit of nutrient taken up. Much of their discussion of feedbacks was based on the decoupling of the carbon/macronutrient relationship. For new nutrients, Denman et al. focussed on atmospheric inputs (Michaels et al. 1993), nitrogen fixation (Carpenter 1973; Carpenter and Romans 1991) and coastal/riverine inputs (Schindler and Bayley 1993), while for altered nutrient uptake they discussed studies by Sambrotto et al. (1993), Banse (1994), and Karl et al. (1995). Denman et al. also reviewed the potential for uptake of presently unused nutrients (such as in High Nitrate Low Chlorophyll (HNLC) regions) due to changes in the supply rate of trace metals (such as iron), and the role of the continental margins in supplying new nutrients to the open ocean. Here, our present understanding of macronutrients is reported on, see section on 'Atmospheric Deposition of Iron' for details on changes in iron supply.

7.6 Phytoplankton and Carbon Limitation

Since 1995 there has been further research into the influence of increasing atmospheric CO_2 levels on algal growth (Tortell et al. 1997; Wolf-Gladrow et al. 1999). Tortell et al. provide evidence for active uptake of HCO_3^-, via a carbon-concentrating mechanism, in diatoms and hence no limitation of their photosynthetic rate by CO_2 availability. Wolf-Gladrow et al. reported evidence of a relationship between elevated CO_2 levels (mimicking the direct effect of anthropogenic CO_2 increases) and enhanced algal growth rates. They also observed reduced biogenic calcification in coccolithophorids at higher CO_2 levels, as did Riebesell et al. (2000) (see section on 'The Calcifiers'). Recently, Tortell et al. (2002) report evidence that CO_2 levels influence species composition and macronutrient uptake stoichiometry. During shipboard incubation experiments in the Equatorial Pacific they observed that low levels of CO_2 resulted in a floristic shift from diatoms towards a *Phaeocystis*-dominated community. Thus, while uncertainties remain regarding the response of phytoplankton to the projected increases in oceanic CO_2 levels, algal functional groups appear to respond in different ways to changes in CO_2 concentrations.

7.6.1 Atmospheric Supply of Nutrients

Both nitrogen and trace elements may be supplied at-

5–10-fold increase in sources of atmospheric pollution since the Industrial Revolution (Paerl and Whitall 1999). Model projections suggest that this source of nutrients might be 3- to 4-fold higher in 2020 (relative to 1980) in the coastal ocean (Galloway et al. 1994). However, increases in atmospheric inputs to offshore waters were predicted by these authors to be somewhat lower. Since 1995, research has focussed on several themes including the contribution of atmospheric nitrogen to ocean basin nitrogen budgets (Spokes et al. 2001), and the bioavailability of atmospheric nitrogen (Paerl et al. 1999; Peierls and Paerl 1997). Moreover, other atmospheric nitrogen sources such as dissolved organic nitrogen (DON) (Peierls and Paerl 1997) and urea (Cornell et al. 1998) have gained attention with respect to nitrogen loading of the oceans. Spokes et al. (2001) reported that up to 30% of new production in NE Atlantic waters could be supported by atmospheric inputs in spring. They identified that most nitrogen deposition occurred during short-lived, high concentration, SE transport events (i.e., when an airmass passes over Northern Europe first). In the SE Mediterranean Sea, estimates suggest that nitrogen inputs represent a 8–20% contribution to new production and point to possible phosphate limitation of algal growth in these waters (Herut et al. 1999).

Paerl and Whitall (1999) discuss the possibility of links between anthropogenically-derived atmospheric nitrogen, coastal eutrophication and the expansion of harmful algal blooms (see section on 'Regime Shifts'). Moreover, Paerl (1999) points out that nitrogen loading may uniquely mediate coastal eutrophication via the bypassing of estuarine filters of terrigenous nitrogen inputs. In the open ocean, enhanced atmospheric transport, via pollutants, of nitrate has mainly been reported in the oligotrophic Atlantic (Galloway et al. 1995). Paerl et al. (1999) point out that natural rainfall and Dissolved Inorganic Nitrogen (DIN) additions most often stimulated CO_2 fixation and elevated chlorophyll levels in western Atlantic waters. They also suggest that the observed high levels of stimulation may be due to the supply of both DIN and iron, and that this may contribute to the eutrophication potential of oceanic waters downwind of urban, industrial and agricultural emissions. Atmospheric DON has also gained attention as a significant new source of nitrogen loading of the oceans (Peierls and Paerl 1997). Seitzinger and Sanders (1999) report that DON in rainwater can be an important source of nitrogen to coastal ecosystems – diatoms and dinoflagellates dominated the assemblage in experimental treatments receiving rainwater DON, whereas small monads dominated in ammonium-enriched treatments. The effect of atmospheric nitrogen on marine productivity depends on the biological availability of both inorganic and organic nitrogen forms, and there is a need to include all nitrogen inputs in atmospheric loading estimates.

The effects of new nitrogen would appear to mainly impact the coastal ocean in the near future (see projections for 2020 in Galloway et al. 1994), but nonetheless provides interesting insights into ecological shifts 'not in the textbooks' that may be analogous to such shifts, in response to perturbations, in the open ocean (see section on 'Regime Shifts'). Also such nitrogen inputs appear to be regional rather than global, and include parts of the N Atlantic, Mediterranean Sea, Baltic Sea, North and Yellow Seas (Paerl 1999). Human alterations of the nitrogen cycle – rather than climate change per se – have approximately doubled the rate of nitrogen input into terrestrial systems globally (Vitousek et al. 1997). Thus, anthropogenic inputs rather than climate change will likely be the key determinants of the magnitude and impact of atmospheric nitrogen.

7.6.2 Nitrogen Fixation

The magnitude of the oceanic nitrate inventory is due to the balance between rates of nitrogen fixation and denitrification (Codispoti 1989, 1995). Nitrogen fixation by diazotrophs is observed over much of the subtropical and tropical oligotrophic oceans and is likely a major input to the marine and global nitrogen cycle (Karl et al. 1995; Michaels et al. 1996; Capone et al. 1997; Emerson et al. 2001). Of particular significance has been further evidence from the HOT site of both increased abundances of nitrogen fixers and fixation rates during El Niño 'years' (Karl et al. 1995, 1997; Karl 1999; Karl et al., this volume, see section on 'Regime Shifts', this chapter). Karl (1999) concludes that the enhancement of nitrogen fixation is in response to increased stratification, and that this elevated activity drives the resident phytoplankton in the North Pacific Subtropical Gyre (NPSG) into phosphate limitation. Emerson et al. (2001) conducted an analysis on 11 years of data from the HOT site and report that, based on changes in apparent oxygen utilisation and organic C:N:P ratios in the upper ocean, a large proportion of the nitrogen supply to surface waters is probably from nitrogen fixation.

Recently, considerable progress has been made on two aspects of research into nitrogen fixers – identification of algal groups (in addition to *Trichodesmium*) that can fix nitrogen, and secondly on the iron requirements of nitrogen fixers. One of the puzzles of studies into nitrogen fixation in oligotrophic waters has been a perceived imbalance between estimates of nitrogen fixation derived from biogeochemical models/studies (Lipschultz and Owens 1996; Gruber and Sarmiento 1997) and that from observed *Trichodesmium* abundances and measured fixation rates. Zehr et al. (2001) suggest they have partially reconciled this enigma through their discovery, using molecular tools, of unicellular cyanobacteria capable of fixing substantial amounts of nitrogen in oligotrophic regions such as the NPSG.

Theoretical studies of algal iron requirements (Raven 1990) suggested that nitrogen fixers such as *Trichodesmium* had relatively high iron requirements compared to diatoms. It was subsequently speculated that an upper limit on nitrogen fixation rates would be imposed by such high iron requirements (Falkowski 1997) and/or by phosphate limitation (Jickells and Spokes 2001). Thus, elevated iron supply to oligotrophic waters in the geological past might have increased the activity of nitrogen fixers and therefore the availability of new nutrients (Falkowski 1997), and has been invoked to explain the timing and magnitude of glacial/interglacial CO_2 changes (Broecker and Henderson 1998).

Recent experimental evidence suggests that phosphate rather than iron limitation of nitrogen fixers is evident in the subtropical Atlantic (Sanudo-Wilhelmy et al. 2001), which may be explained by the relatively high ambient dissolved iron concentrations (Martin et al. 1993; Powell et al. 1995). This mode of control may not be applicable to other oligotrophic waters as iron levels are lower in the NPSG (based on limited data, Karl 1999), and in the tropical Pacific there is evidence that the dominant cells (picophytoplankton) are iron-stressed (Behrenfeld and Kolber 1999). Furthermore, in the subtropical coastal waters off Australia, a laboratory study using *Trichodesmium* provides evidence that under iron-limiting conditions there is a marked decline in physiological rates such as nitrogen fixation (Berman-Frank et al. 2001). In the W Atlantic Shelf region, Lenes et al. (2001) add important observational data on this subject, via monitoring the response of *Trichodesmium* in these waters to a Sahara-derived dust deposition event. They report on a dust-mediated 100-fold increase in *Trichodesmium* stocks, the concomitant reduction in phosphate levels to below the limit of detection, and that the increased organic nitrogen levels associated with the bloom had the potential to support toxic algal blooms.

7.6.3 Changes in Nutrient Uptake Stoichiometry – the Redfield Ratio

The possibility that the uptake of nutrients might depart from fixed Redfieldian stoichiometry has been an overriding theme in discussions of the role and magnitude of biotic feedbacks (Sambrotto et al. 1993; Banse 1994; Anderson and Sarmiento 1994; Kortzinger et al. 2001), and provides a counter argument to the geochemical standpoint put forward by Broecker (1990). Denman et al. (1996) suggested that model simulations (Shaffer 1993) of ocean carbon cycle changes were particularly sensitive to changes in the Redfield ratio between carbon and the limiting nutrient. Denman and Pena (2000) provided evidence, via a sensitivity analysis of biogeochemical models (Heinze et al. 1991; Shaffer 1993), that a two-fold shift in the carbon:nutrient Redfield ratio might indeed result in the greatest change in atmospheric CO_2 levels (relative to two-fold shifts in other properties such as productivity, or ventilation rates).

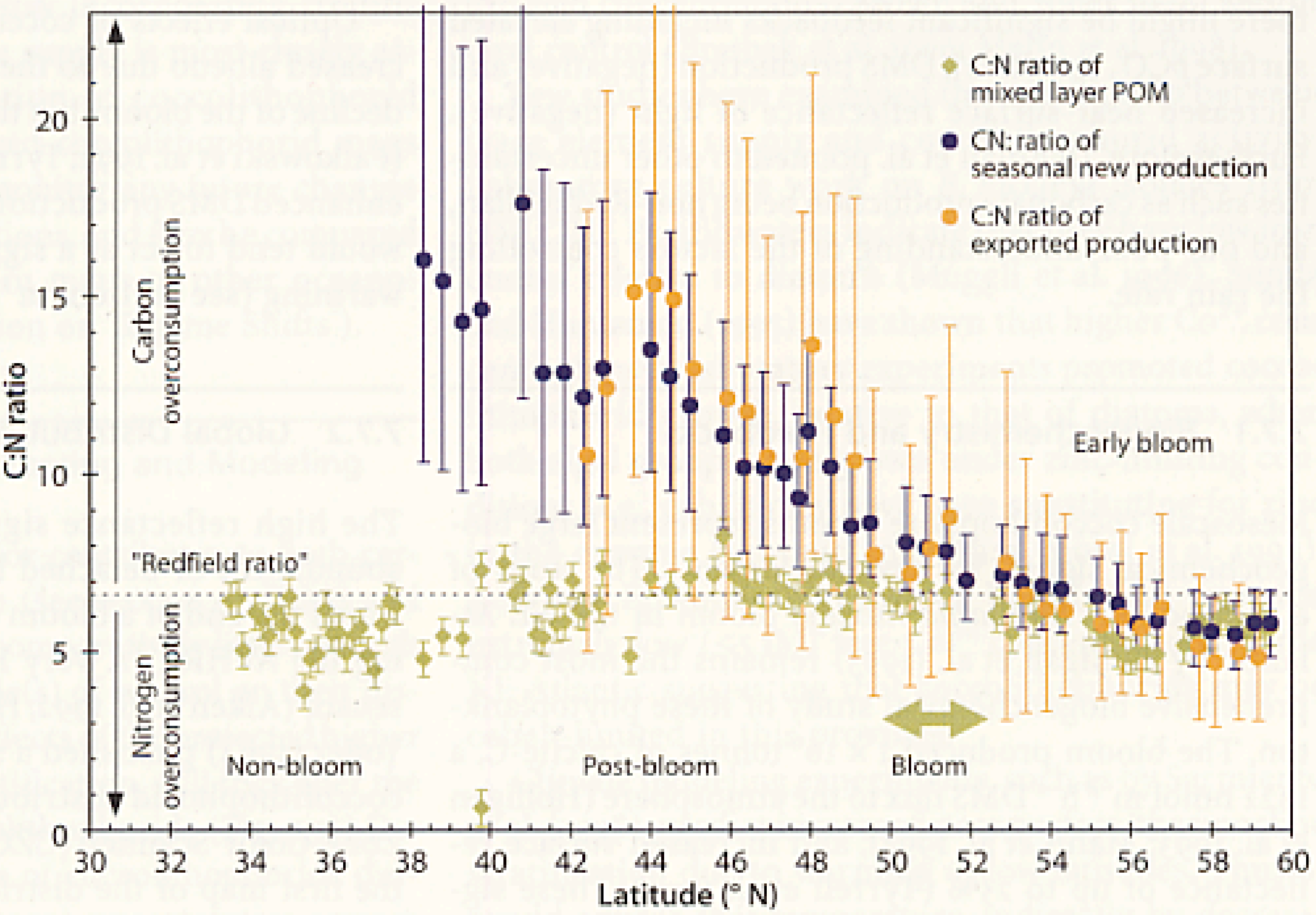
Sambrotto et al. (1993) presented evidence – based on estimates of nutrient utilisation ratios i.e., the net community drawdown of nitrate and DIC – of elevated carbon consumption relative to nitrate during the spring bloom in the NE Atlantic, Bering Shelf and Gerlache Strait, and asked whether this was evidence of widespread inconsistencies in the Redfield ratio. These variations in nutrient stoichiometry (with C:N ratios of up to 14 along the 20° W meridian in the NE Atlantic) were up to double that of estimates made by Takahashi et al. (1993) at a station (47° N) along this meridian in the same year. Mechanisms invoked for such elevated ratios include preferential recycling of nitrogen relative to carbon in the upper ocean (Sambrotto et al. 1993) or a high release of dissolved organic carbon (DOC) during an algal bloom (Toggweiler 1993). Furthermore, Lancelot and Billen (1985) had previously reported similarly elevated nutrient utilisation ratios during algal blooms and considered them due to a temporary imbalance between uptake of nitrogen and carbon consumption.

The study of Sambrotto et al. (1993) did not correct the observed macronutrient concentrations for abiotic factors such as evaporation minus precipitation, concurrent air-sea CO_2 flux, or to consider in their stoichiometric calculations the influence of winter reserve carbon and nutrient concentrations.

Since 1995 there has been only one published study to investigate further such aspects of the relationship between nutrient and carbon consumption (Kortzinger et al. 2001). They examined the C:N relationships in the mixed layer in the NE Atlantic in June/July 1996 using a transect (the 20° W meridian) as a proxy for the seasonal progression of biological events. Kortzinger et al. reported that in spring the system was dominated by nitrogen over-consumption, whereas during summer oligotrophy there was a marked carbon over-consumption (Fig. 7.7). Their study highlights the need to examine nutrient utilisation rates and stoichiometry over the entire algal growth season, and thus it is not presently known what the impact of such transient changes in C:N uptake stoichiometry have on the ocean carbon cycle over longer timescales.

Recently, there has been evidence of shifts in carbon/nutrient uptake stoichiometry due to changes in phytoplankton community structure (Arrigo et al. 1999), and in iron supply (Hutchins and Bruland 1998; Takeda 1998; Franck et al. 2000). Karl et al. (1995) have also observed shifts in the ratios of nitrogen to phosphorus at the HOT site between years due to pronounced changes in nitrogen fixation rates. In the Ross Sea, *Phaeocystis antarctica*

Fig. 7.7. Changes in the C:N ratio of mixed layer Particulate Organic Matter, new production and exported production along the 20° W meridian during late spring/summer in the NE Atlantic Ocean (reprinted from Deep-Sea Res I 48, Kortzinger et al. (2001) C:N ratios in the mixed layer during the productive season in the Northeast Atlantic Ocean. pp 661–688, © 2001, with permission Elsevier Science)



blooms under conditions of low light (Moisan and Mitchell 1999) due to deeper mixed layers (Arrigo et al. 1999), and are characterised by more carbon fixed per unit phosphate compared with diatom blooms. The latter are observed in summer (blooming under high light, shallow mixed layers, Arrigo et al. 1999). Evidence of the influence of iron supply on macronutrient uptake ratios comes from reports of decreased algal silicic acid:carbon and silicic acid:nitrate uptake ratios upon iron supply to phytoplankton from open (Takeda 1998) and coastal ocean HNLC waters (Hutchins and Bruland 1998). Such iron-mediated shifts in uptake stoichiometry, if sustainable over long timescales, have been shown to have important implications for increased drawdown of atmospheric CO_2 during glacial maxima (Watson et al. 2000).

7.6.4 Export Production and Remineralisation in the Deep Ocean

In a review of the ocean carbon cycle Siegenthaler and Sarmiento (1993) suggested that climate change might also influence the relationship between the relative magnitude of the export of carbon via either particulate or dissolved forms by causing a more rapid remineralisation of sinking organic particles. Moreover, Denman and Pena (2000) from a sensitivity analysis of biogeochemical models (Heinze et al. 1991; Shaffer 1993), suggested that shifts in remineralisation depth scales could have a pronounced effect on atmospheric CO_2 levels. Levitus et al. (2000) have reported that the surface waters of the World Ocean have warmed significantly during the last 40 years, with the largest warming occur-

This may have implications for bacterial ecto-enzyme activity (Smith et al. 1992; Christian and Karl 1995) which if it increased might reduce the depth scales for remineralisation for each major element (Christian et al. 1997).

Since 1995 considerable progress has been made in better understanding the role of DOC in carbon biogeochemistry, its relative contribution to export production (Carlson et al. 1994), and in its global and seasonal distributions and budgets (Hansell and Carlson 1998). However, in the latter study, the authors point to the need for more knowledge on the controls on the production and consumption of the semi-labile DOC pool. These are essential before the relative contribution of this pool to the downward export of biogenic carbon, and to the inter-hemispheric transport of DOC can be accurately assessed. Recent estimates that considered both DOC and POC fluxes at the HOT site suggest that the subtropical oceans may be responsible for a significantly higher contribution to the global biological pump than previously thought (Emerson et al. 1997).

7.7 The Calcifiers

The calcifiers include coralline algae, calcareous zooplankton (such as foraminifera) and coccolithophorids, but only the latter is considered here. Denman et al. (1996) focussed on this group as they are carbonate producers, influence the rain ratio (the ratio of organic carbon to carbonate in settling particles (see Denman and Pena 2000), help set the pCO_2 of surface waters via calcification, and have been linked to large changes in surface ocean DMS levels (Holligan et al. 1993; Westbroeck et al. 1993). Denman et al. suggested that if climate change there might be significant feedbacks including elevated surface pCO_2 (positive), DMS production (negative) and increased near-surface reflectance of light (negative). Furthermore, Denman et al. pointed to other uncertainties such as carbonate production being non-Redfieldian, and our poor understanding of the factors controlling the rain rate.

7.7.1 Biogeochemistry and Feedbacks

Mesoscale coccolithophore blooms represent large biogeochemical signals for several elements. The study of a 250 000 km^2 *Emiliania huxleyi* bloom in the NE Atlantic by Holligan et al. (1993) remains the most comprehensive biogeochemical study of these phytoplankton. The bloom produced 1×10^6 tonnes of calcite-C, a 1 122 nmol m^{-2} h^{-1} DMS flux to the atmosphere (Holligan et al. 1993; Malin et al. 1993), and increased surface reflectance of up to 25% (Tyrrell et al. 1999). These signals represent a relative increase of up to 50 µatm in surface pCO_2 in association with alkalinity and water temperature changes (Holligan et al. 1993), and were calculated to cause a 17% reduction in CO_2 uptake over the spring/summer growth period in the NE Atlantic (Robertson et al. 1994).

Model projections of the effect of global warming predict that pCO_2 in surface waters will increase, in line with increases in atmospheric CO_2 (IPCC 2001), leading to a corresponding decrease in the pH of these waters (Kleypas et al. 1999), and potentially a decrease in calcification rate. In laboratory culture studies, Wolf-Gladrow et al. (1999) and Riebesell et al. (2000) have examined the effects on coccolithophorids of increased CO_2 concentrations over a range predicted from IPCC GCM climate change scenarios (such as the 'business as usual' scenario IS 92a, which will cause carbonate ion concentrations and seawater pH to drop by ca. 50% and 0.35 units, respectively, relative to pre-industrial values). Both studies point to reduced biogenic calcification. Riebesell et al. report that, over a range of mean surface ocean conditions between pre-industrial times and that expected by the year 2100, the ratio of calcification to organic matter production of *E. huxleyi* and *Gephyrocapsa oceanica* is predicted to have decreased by 23% and 50%, respectively. Scanning electron microscopy revealed that malformed coccoliths and incomplete coccospheres increased in relative numbers with increasing CO_2, suggesting that predicted shifts in seawater carbonate chemistry on a decadal timescale may reduce the production of calcium carbonate in the surface ocean and its subsequent transport to depth. The predicted increases in algal growth rate, enhanced algal C:P ratios and reduced calcification reported by Wolf-Gladrow et al. (1999) are predicted to all increase the ocean's capacity to store

Optical effects of coccolithophore blooms cause increased albedo due to the detached liths that mark the decline of the bloom, but this effect is thought to be small (Falkowski et al. 1992; Tyrrell et al. 1999). In contrast, the enhanced DMS production associated with such blooms would tend to act as a significant negative feedback on warming (see section on 'DMS and the Biota').

7.7.2 Global Distributions

The high reflectance signature associated with high abundances of detached liths of coccolithophorids towards the end of a bloom can be viewed from space using the AVHRR (A Very High Resolution Radiometer) sensor (Aiken et al. 1992; Holligan et al. 1993). Brown and Yoder (1994) published a series of global composites of coccolithophorid distributions using satellite Coastal Zone Color Scanner (CZCS) composites that provided the first map of the distributions of *E. huxleyi* blooms. Indeed, by comparing observed biogeographical patterns with global maps of other oceanographic properties Brown and Yoder suggested that low silicic acid concentrations might be related to the distribution of coccolithophorids (see section on 'Controlling Factors and Modeling'). The launch of the SeaWiFS sensor in late 1997 has provided a means to remotely-sense cocolithophore calcite concentrations from space (Gordon et al. 2001) and provided further detailed global coverage of coccolithophorid distributions (Fig. 7.8). Recently observed distributional trends, such as the appearance of high coccolithophorid abundances in the subarctic NE Atlantic, are similar to those from CZCS during the 1976–1984 (Brown and Yoder 1994). Such distributions suggest that coccolithophorids are dominant in distinct regions and that their response to climate change or variability might be on a regional, as opposed to a global scale.

Recently, Iglesiais-Rodreguez et al. (2002) have used SeaWiFS data on coccolithophorid distributions to construct a detailed monthly time-series, and by using probability analysis and modeling to assess what oceanographic properties best fit with these distributions. They

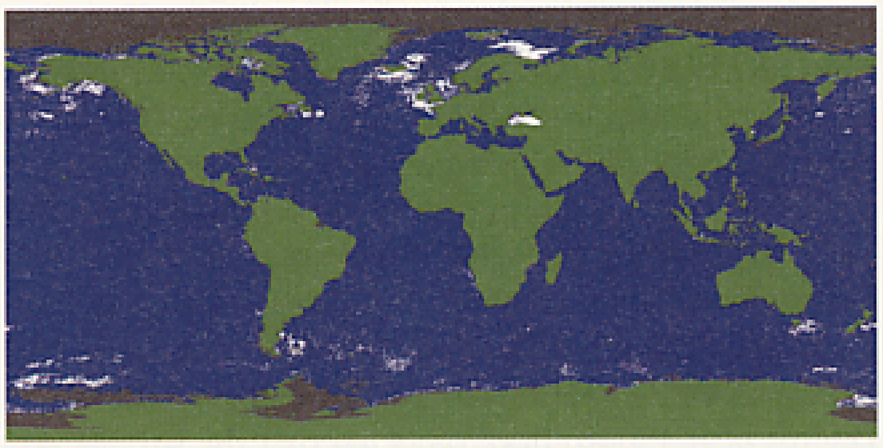


Fig. 7.8. An annual composite (1998/1999) of global coccolithophore distributions (denoted by *white areas*) derived from the SeaWiFS (Sea-viewing Wide-Field-of-View Sensor) in conjunction

suggest that a composite proxy incorporating stratification, insolation and nitrate supply is most closely associated with the distribution of coccolithophorid blooms. Thus, satellite-derived coccolithophorid maps provide a powerful tool to monitor any future changes in coccolithophorid distributions, and may be compared with any concurrent shifts in maps of other oceanographic properties (see section on 'Regime Shifts').

7.7.3 Controlling Factors, Forcing and Modeling

Coccolithophorids are a major contributor to both carbonate and DMS production (see section on 'DMS and the Biota'), yet until recently comparatively little research has been devoted to the mode(s) of control on their distributions. What will be the effects of the projected higher ocean temperatures and stratification, will they alter the global distributions of coccolithophorids (Fig. 7.9)? Despite biogeochemical studies of coccolithophorids during JGOFS (Holligan et al. 1993) uncertainties remain regarding what prompts the onset of such blooms, with inconclusive results from modeling studies (Tyrrell and Taylor 1995). Also little is known about the factors leading to the decline and collapse of such blooms (Boyd et al. 1998). Causative factors thought to control coccolithophorid blooms include conditions of high insolation/shallow mixed layer depths (<30 m) thought to favour the photophysiology of coccolithophorids (Nanninga and Tyrrell 1996), high irradiances and low phosphate levels, (cells using dissolved organic rather than dissolved inorganic phosphate) (Tyrrell and Taylor 1995), low silicic acid concentrations (Brown and Yoder 1994) and/or viral control (Bratbak et al. 1996; Malin et al. 1998).

Few studies have examined the relationship between trace element supply and coccolithophorid activity. Laboratory culture work on *E. huxleyi* isolates from HNLC NE Pacific waters indicate that they have low iron quotas relative to diatoms (Muggli et al. 1996). Sunda and Huntsman (1995) have shown that higher Co^{2+} concentrations in laboratory experiments promoted coccolithophorid growth, relative to that of diatoms, when both algal groups were grown under zinc-limiting conditions (i.e., cobalt may have been substituting for zinc in the enzyme carbonic anhydrase, Morel et al. 1994). Recently, Ellwood and Van den berg (2001) reported extremely low (<5 fM) free Co^{2+} concentrations in the NE Atlantic suggesting that coccolithophorids may be cobalt-limited in this province.

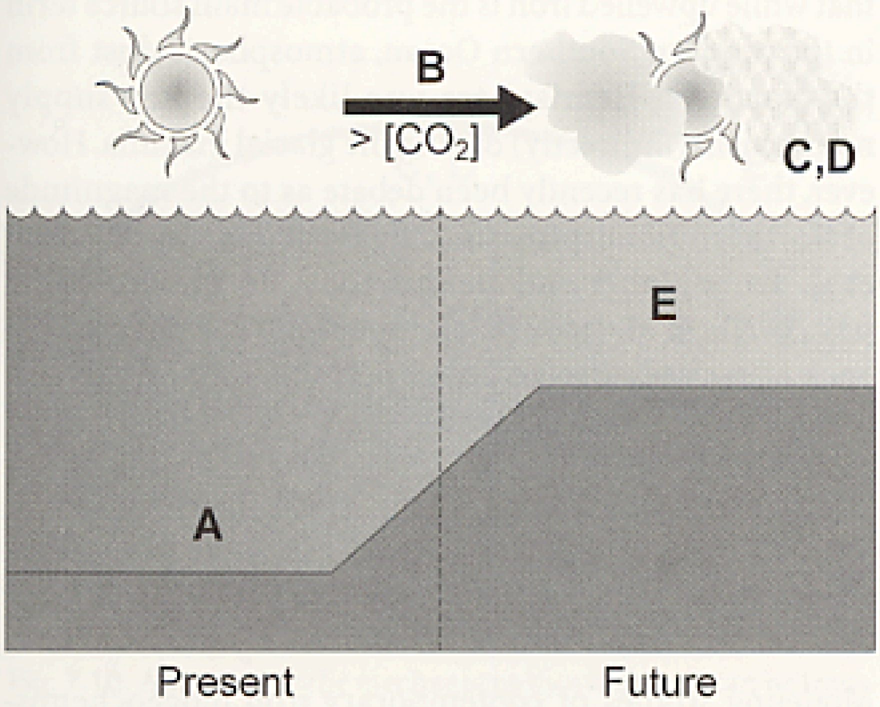


Fig. 7.9. A cartoon of the potential forcing functions that result in coccolithophorid blooms. *A* represents an increase in stratification/shoaling of the mixed layer depth (elevated mean light levels, Tyrrell et al. 1999), *B* an increase in atmospheric and hence upper ocean carbon dioxide levels (and its effect of calcification, Riebesell et al. 2000); *C* the degree of *cloudiness* (alteration of incident irradiances, Tyrrell and Taylor 1995); *D* changes in the aerosol dust supply (cobalt – Ellwood and van den berg 2001); and *E* increased *water temperatures* (Tyrrell et al. 1999)

Climate modeling experiments, such as by Sarmiento et al. (1998), predict increased near surface/thermocline stratification due to warming at low latitudes. Thus, it would appear that temperature, indirectly by decreasing mixed layer depths, might alter the biogeography of coccolithophorids. Furthermore, the effects of altering temperature and/or mixed layer depth are likely to reduce upper ocean nitrate, or phosphate levels. Therefore, if the general consensus, that high mean irradiances and/or low macronutrient levels (Nanninga and Tyrrell 1996; Tyrrell and Taylor 1995; Iglesiais-Rodreguez et al. 2002), promote coccolithophorid blooms then this conclusion in tandem with model predictions points to increased incidences of such blooms in the future. The impact of such forcing (i.e., increased stratification etc.) on the distributions of coccolithophorids must be reconciled with that of increased pCO_2 on their physiology (Riebesell et al. 2000). Although calcification rates may decrease significantly in response elevated atmospheric CO_2 levels, these changes may be offset if the incidence of coccolithophore blooms was to increase significantly due to impact of other oceanic forcing.

7.7.4 A Case Study – the Bering Sea

There is recent evidence in these waters of unprecedented incidences of coccolithophorid blooms over the period 1997–2000 (Napp and Hunt Jr. 2001; see section on 'Regime Shifts'). A bloom (>200 km length-scale) was initially observed in July–August 1997. A further bloom was recorded in 1998, and by summer 2000 a bloom was observed here for the fourth consecutive year suggesting a potential regime shift (Napp and Hunt Jr. 2001). The blooms were visible in SeaWiFS imagery and the duration of the 1998 bloom was 9 months – much greater than previously observed in the NE Atlantic (Holligan et al. 1993). Reports of the bloom in each year indicate that upper ocean temperatures were 2 °C above normal.

Napp and Hunt Jr. (2001) report that anomalous regional weather over the SE Bering Sea in spring and summer 1997 resulted in significant changes in the chemical and biological oceanography of this region. That these observations may be related to climatic shifts such as elevated temperatures and changes in sea-ice melt patterns, strongly suggests that we do not yet fully understand what controls the development of coccolithophorid blooms.

7.8 Iron Supply to the Oceans

The Iron hypothesis (Martin 1990) was based on the relationship between the magnitude of dust (a proxy for iron) and atmospheric CO_2 concentrations in the geological record, with dust peaks coinciding with CO_2 minima during each of the glacial maxima. Martin proposed that alleviation of iron stress in phytoplankton would enhance rates of both primary and export production, and increase carbon sequestration to depth during the glacial maxima. Such a mechanism may exist today, such that any climate-induced alteration of iron supply to the ocean might alter the magnitude of global primary production. Hence, this relationship has received particular attention over the last decade (reviewed by de Baar and Boyd 2000). Denman et al. (1996) summarised that there was mounting evidence of the role of iron in enhancing phytoplankton production when macronutrients were available in excess. Since then, advances in this field have included debate on what sets global oceanic iron concentrations (Johnson et al. 1997); the first detailed models of iron biogeochemistry (Fung et al. 2000; Archer and Johnson 2000) and the response of the biota to iron supply (Lancelot et al. 2000; Hannon et al. 2001); comprehensive upper ocean iron budgets (Price and Morel 1999; Bowie et al. 2001); in situ confirmation of iron limitation of algal growth in the Southern Ocean (Boyd et al. 2000); remotely-sensing global maps of aerosol dust distributions (Stegmann and Tindale 1999); revised estimates of dust-borne iron flux to the oceans (Jickells and Spokes 2001); and new interpretations, from modeling studies, on the magnitude of iron-enhanced carbon sequestration during the glacial terminations (LeFevre and Watson 1999; Watson et al. 2000; Maher and Dennis 2001).

7.8.1 How Much of the Ocean Is Iron-Poor?

The areal extent of iron-poor waters is now thought to be more widespread than previously acknowledged (Mullineaux 1999). In addition to open ocean HNLC regions (equatorial and north-east Pacific Ocean, Southern Ocean) which comprise around 30% of the World Ocean (de Baar et al. 1999), HNLC waters have been reported in coastal regions (Hutchins et al. 1998) where, due to the complex interplay of geomorphology, sediment distributions and riverine input, waters are iron-poor. Large expanses of Low Nitrate Low Chlorophyll (LNLC) waters such as the tropical South Pacific are reported to have iron-limited resident cells (mainly picophytoplankton, Behrenfeld and Kolber 1999).

7.8.2 The Supply of Iron to the Ocean

Denman et al. (1996) discussed the need to obtain estimates of current natural and anthropogenic iron inputs to the atmosphere and the ocean, which are critical to improved understanding of the control of iron supply on primary production rates in HNLC regions. At present, sources of iron to the open ocean include atmospheric (Duce and Tindale 1991; Piketh et al. 2000), upwelling (Martin et al. 1989), ice melt (Sedwick and DiTullio 1997, Sedwick et al. 2000), volcanic eruptions (Watson 1997; Boyd et al. 1998), and extra-terrestrial dust (Johnson 2001). The relative rate of supply by each mechanism varies regionally; Martin et al. (1989) concluded that aerosol iron was the greatest supply term in the NE subarctic Pacific, whereas de Baar et al. (1995) reported that upwelling was most important in the Southern Ocean. In coastal waters, iron from resuspended shelf sediments (and subsequent upwelling), rather than from riverine sources, is thought to be the main supply term (Johnson et al. 1999).

In the geological past, there is evidence that the main modes of iron supply may have altered; based on a modeling study, LeFevre and Watson (1999) concluded that while upwelled iron is the probable main source term in the modern Southern Ocean, atmospheric dust from the Northern Hemisphere was likely the key supply mechanism (indirectly) during the glacial maxima. However, there has recently been debate as to the magnitude of Northern Hemisphere dust fluxes at this time (Watson et al. 2000; Maher and Dennis 2001). In the geological past, Wells et al. (1999) also report on the likely influence of tectonic processes on periodic iron inputs into the eastern equatorial Pacific Ocean.

7.8.3 Atmospheric Deposition of Iron vs. Upwelling Supply

Modeling studies of contemporary iron biogeochemistry suggest that upwelling of iron is the dominant supply term (Archer and Johnson 2000), whereas Fung et al. (2000) in a model using longer timescales conclude that aeolian supply of iron is dominant. Both agree upon the large uncertainties in the present models. Climate change may result in shifts in the rate of upwelling to the surface ocean due to the projected changes in the degree of stratification (Sarmiento et al. 1998), and/or changes in aerosol deposition of iron (temperature/aridification, Falkowski et al. 1998; Berman-Frank et al. 2001), which will alter the magnitude of global productivity. Here the question of how climate change might influence the atmospheric deposition of iron is considered in detail.

7.8.4 Dust Supply – Global Maps and Fluxes

Duce and Tindale (1991) published the first global map of the supply of aerosol iron to the oceans, which evinced low inputs to HNLC waters, and that most of the global supply is to Northern Hemisphere waters. Their study, as they point out, was characterised by a paucity of data. This, along with the episodic nature of dust supply (Prospero 2000), introduces large uncertainties as to the accuracy of dust flux estimates. Recently, some of these uncertainties have been overcome by using by-products of satellite sensors for aerosols (CZCS, Stegmann and Tindale 1999; AVHRR, Husar et al. 1997; SeaWiFS, Husar et al. 2001; TOMS, Fig. 7.10). Thus, the detection of interannual variability in the global dust input to the ocean may be estimated indirectly from satellite observations. Such datasets also provide useful information on the seasonality of dust input (Stegmann and Tindale 1999) the intermittency of dust storms, and on the main dust routes (Husar et al. 1997, 2001; Fig. 7.10).

Dust supply can be converted into iron supply using the crustal abundance of iron and by assuming a dust solubility factor (Duce and Tindale 1991). Recently, Jickells and Spokes (2001) conducted laboratory experiments on the solubility of aerosol particles, and these presently provide the most reliable estimates (overall solubility of atmospherically-transported iron at seawater pH is 0.8–2.1% of the total Fe deposited) of how much aerosol iron is available to the biota, and in what regions the main depositional fluxes would occur. Jickells and Spokes (2001) also present revised estimates of total dust flux ($400–1\,000 \times 10^{12}$ g yr^{-1}), total iron input ($0.25–0.63 \times 10^{12}$ mol yr^{-1}), and total soluble iron input ($0.2–1.32 \times 10^{10}$ mol yr^{-1}) to the oceans.

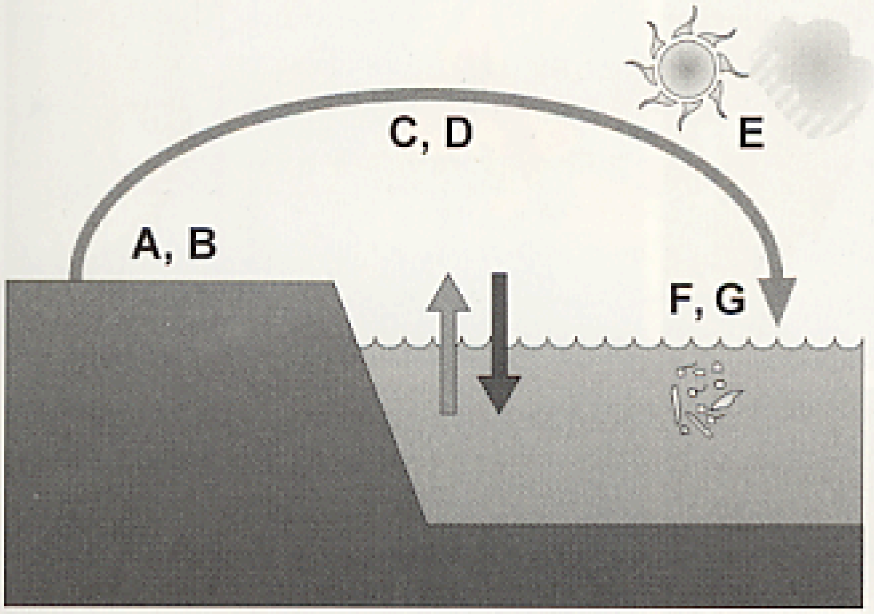


Fig. 7.10. A cartoon of the mechanisms by which iron can be transported from terrestrial sources to the open ocean. *A* Denotes changes in aridity, vegetation cover in arid environments (e.g., sensitivity to CO_2 fertilization and hydrology) and soil moisture (see also Fig. 7.11); *B* changes in land use (human activity) and/or in the dust size spectra; *C* alteration of atmospheric dust transport routes; *D* changes to the dust load/source-atmospheric carrying capacity, iron content and solubility; *E* nature (wet or dry) of deposition; *F* the iron status of the resident algal community (replete or deplete); *G* the iron requirements of the dominant species (diatoms vs. nitrogen fixers)

7.8.5 Dust Transport – from Soil to Phytoplankton

Many factors may influence the passage of dust from arid regions to the utilization by phytoplankton in the ocean (Fig. 7.10). In arid and semi-arid regions complex relationships between soil, micro-meteorology and dust production are apparent (detailed in Pye 1987; Nickovic and Dobricic 1996). Anthropogenic disturbances of soil (agriculture) and land use practices (Tegen and Fung 1995) will also influence significantly this transition from soil to dust. The uplifting and transport of dust depends on the size spectra of dust particles produced from the soil. Such transport is often episodic – via dust storms (Uematsu et al. 1983; Merrill 1989; Merrill et al. 1994), and both aridity and a rapid uplifting of the dust to altitudes above 1 km is needed to ensure long-range dust transport. Dust may then be deposited into the ocean by either dry or wet deposition which has implications for the solubility of aerosol particles (Jickells and Spokes 2001). The distance over which 50% of the dust load is lost from high altitude is thought to be around 500 km (Prospero et al. 1989). Finally, upon deposition into the ocean where a small proportion of the aerosol iron will be soluble, there are additional uncertainties, such as if and for how long the iron deposited will be 'bio-available' (Rue and Bruland 1997; Wu et al. 2001; Barbeau et al. 2001), and what are the iron requirements of the resident biota (nitrogen fixers have higher iron requirements than diatoms (Raven 1990; Berman-Frank et al. 2001).

7.8.6 Response by the Biota – Detection

What are the likely effects of dust inputs on the biota? DiTullio and Laws (1991) and Young et al. (1991) opportunistically sampled surface waters during a dust storm in the North Central Subtropical Pacific Gyre (NSPG), and observed transient increases in rates of primary production. Boyd et al. (1998) provided indirect evidence from the HNLC waters of the NE Pacific that episodic increases (of up to ten-fold) in phytoplankton stocks might have been driven by such episodic dust supply (Fig. 7.11). They also reported that the fate of such episodic algal blooms might be sedimentation to the deep ocean, resulting in up to 5-fold increases in POC export

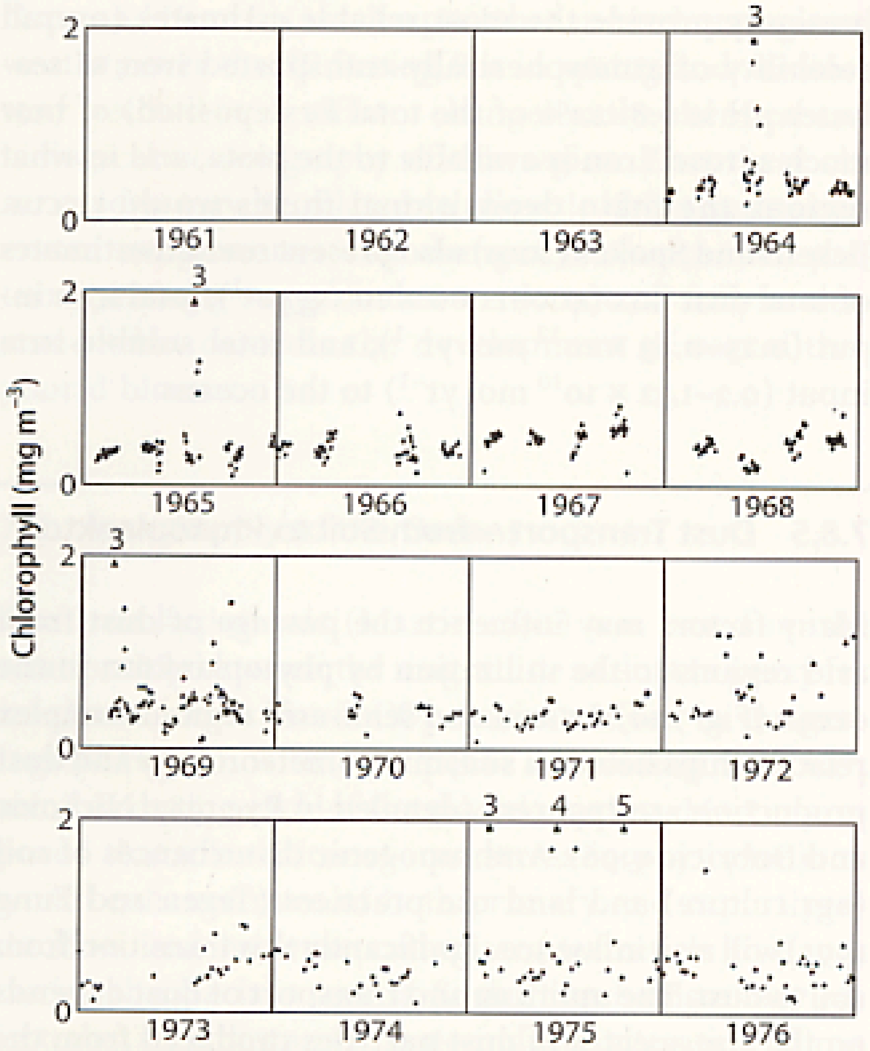


Fig. 7.11. A time-series of chlorophyll concentrations from the NE subarctic Pacific (Ocean Station Papa) in which episodic blooms in High Nitrate Low Chlorophyll (HNLC) waters were observed in 1964, 1965, 1969 and 1975 (numbers in each of these panels denote the highest chlorophyll levels (in mg m^{-3}) attained (data are from Parslow (1981))

(relative to ambient fluxes) over a month – equivalent to a 15% increase in POC export over the annual cycle. Clearly, the data of Boyd et al. (1998) indicate that the effects of dust supply in the present day may be episodic but are pronounced. Any increase in dust supply – due to climate change – might result in a relatively large response by the biota, but how can such a response be detected? Recent monitoring of HNLC waters has employed moored bio-optical sensors (Boyd et al. 1999) which record chlorophyll concentrations and other associated properties (temperature/irradiance) on an hourly basis. These platforms by providing the opportunity to monitor the expected biological responses to dust – such as increased levels of chlorophyll. Such mooring records, in conjunction with remotely-sensed evidence of dust storms (Fig. 7.12; Husar et al. 2001) may provide a means to both detect changes in dust supply to the ocean and the subsequent biological response.

7.8.7 The Future – Climate Change and Dust Deposition

In the future, if climate change results in elevated temperatures, it has been suggested that subsequent increases in aridification will result in enhanced dust input and increased primary productivity (i.e., a negative

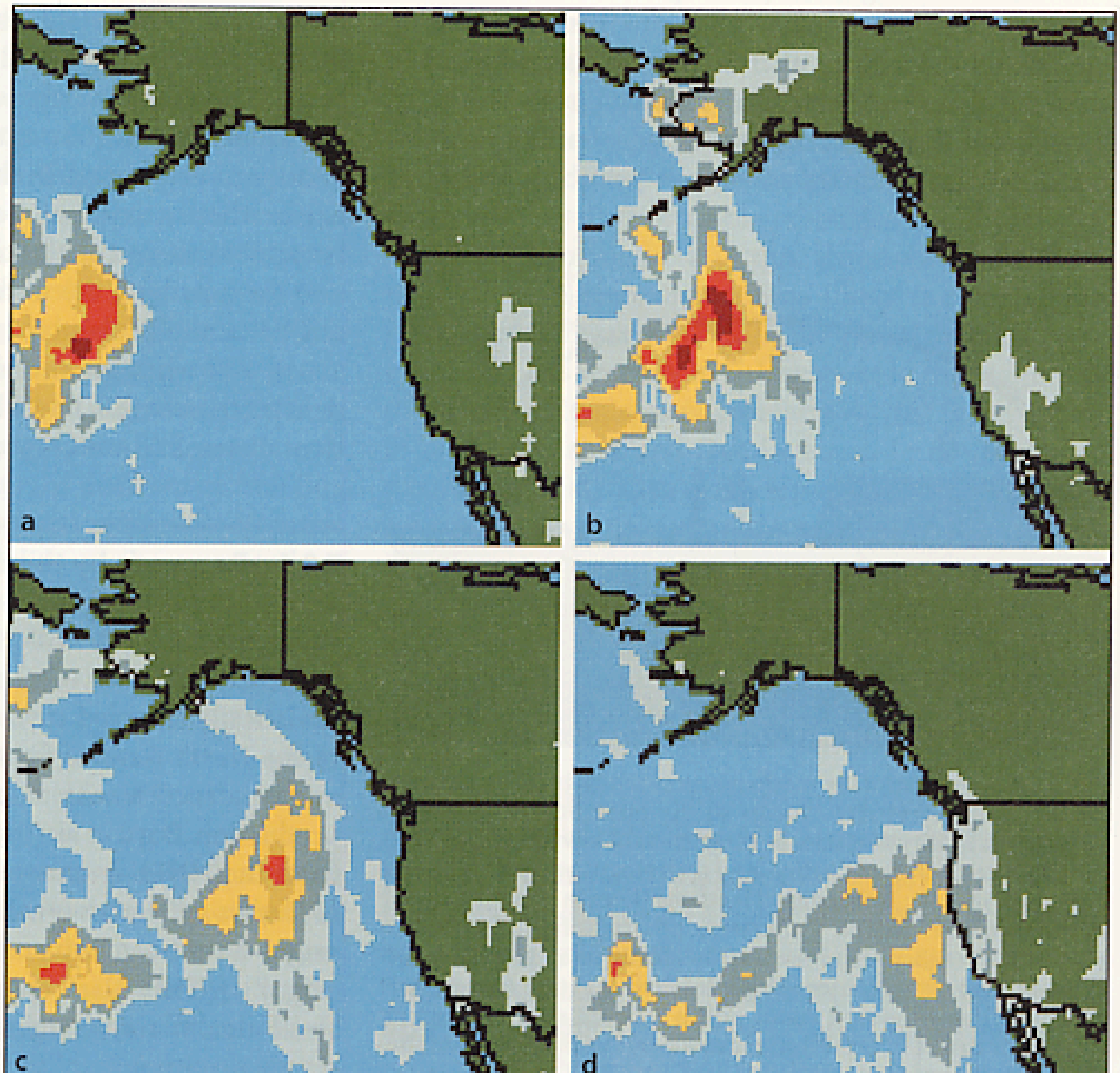


Fig. 7.12. Four consecutive daily plots of the aerosol index from the TOMS satellite in the North Pacific during the period 22–25 April 1998 (**a** April 22; **b** April 23; **c** April 24; **d** April 25;), showing the movement of a large dust storm from west to east. *Red* represents the highest dust concentrations, *blue* background levels. This was the largest dust storm to pass over the N Pacific in 10 years (Husar et al. 2001) but it did not appear to have any effect on the biota at Ocean Station Papa (P. Boyd, pers. comm.). This indicates that dust passing over the ocean may not always be deposited and thus such satellite images must be interpreted with due caution (images courtesy of TOMS/NASA)

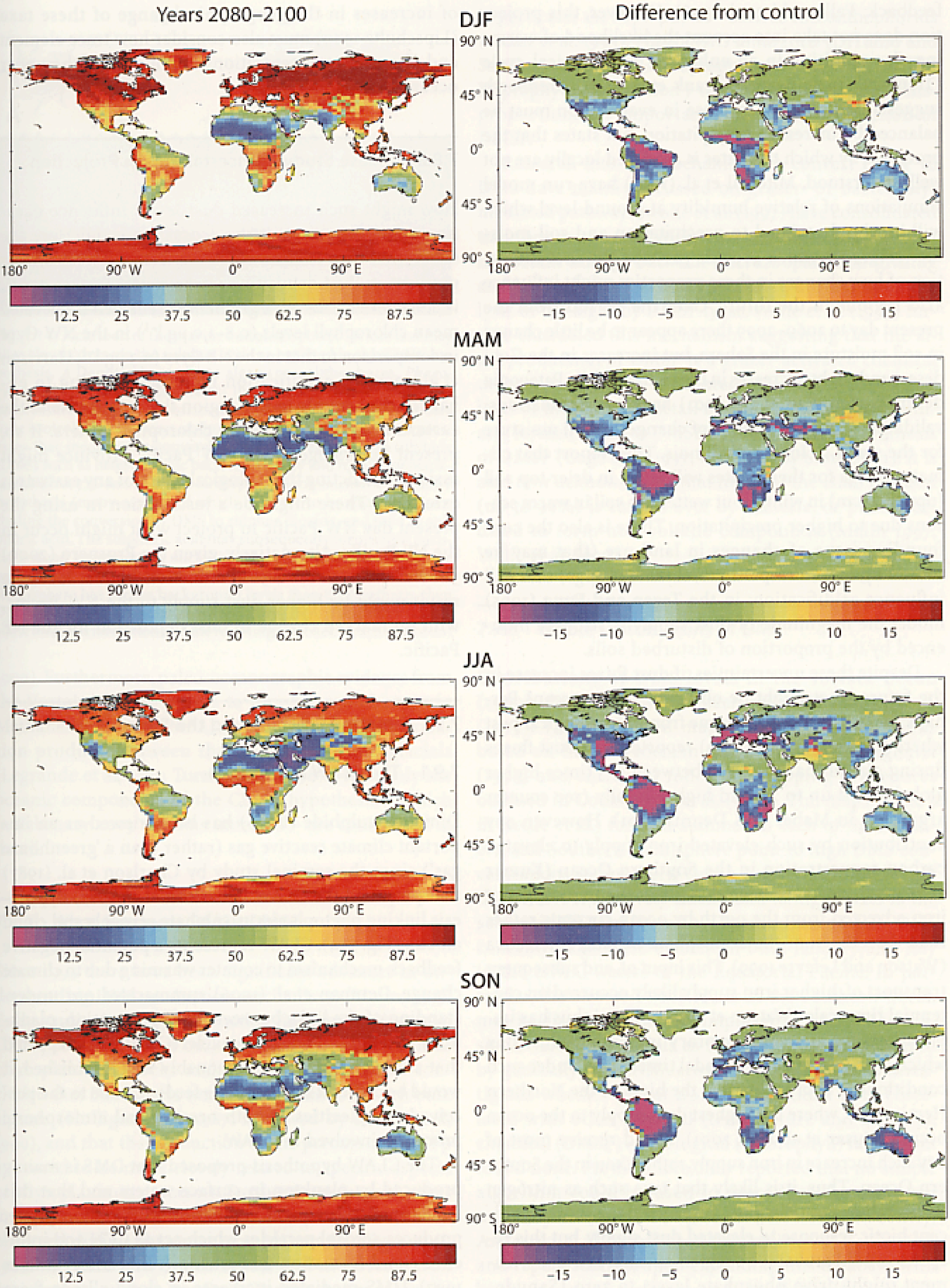


Fig. 7.13. Global projections of changes in relative humidity at 1.5 m (an important determinant of soil moisture) for each season (*DJF* is December, January, February) by the late 21th century based on simulations from the Hadley Centre model. The *left panel* shows the % relative humidity and the *right panel* the % difference from the control. Note the trends for the main arid regions such as the Sahara (slight decrease) and Gobi (little change to slight increase) deserts (redrawn with permission from Mitchell et al. 1998)

feedback; Falkowski et al. 1998). However, this projection does not take into account the likelihood of warming also resulting in an enhanced hydrological cycle (Trenberth 1998; Berman-Frank et al. 2001). Trenberth suggests that a global increase in evaporation must be balanced by increased precipitation, but states that the processes by which the latter is modified locally are not well understood. Mitchell et al. (1998) have run model simulations of relative humidity at ground level which will be closely related to precipitation and soil moisture (Fig. 7.13) which provide perhaps the first indication of how changes in these properties might influence arid regions in the future. Over the period from the present day to 2069–2099 there appear to be little change in soil moisture in the Sahara, but increases in the Gobi desert and slight decreases in the vicinity of the Patagonia desert region. Pan et al. (2001) have run simulations, validations, and projections of changes in soil moisture for the states of Iowa and Illinois. They report that climate change for these States will result in drier top soil (upper 10 cm) in winter, but wetter top soil in warm seasons due to higher precipitation. There is also the confounding issue of changes in land use (that may be caused by, or as a response to, climate change) that will influence aridification: in the Tegen and Fung (1995) model the magnitude of dust supply is strongly influenced by the proportion of disturbed soils.

Despite these uncertainties, if dust fluxes increase in the future what might be observed in the ocean? Perhaps the best indications come from the geological past where Mahowald et al. (1999) reported that dust fluxes during glacial maxima were between 2–3 times higher globally, and up to 20-fold higher locally (see counter argument in Maher and Dennis 2001). However, any contribution by such elevated iron supply to elevated carbon sequestration in the Southern Ocean (Kumar et al. 1995) may have been due primarily to a supply of iron advected from the north by ocean currents rather than directly from the atmosphere around Antarctica (Watson and Lefevre 1999). This input of, and subsequent transport of, higher iron supply likely occurred on centennial timescale (Watson et al. 2000), and thus has implications for any contemporary increase in dust flux which are likely to be on decadal timescales. Under such conditions, it is probable that the biota in the Northern Hemisphere, where the highest dust supply to the ocean occurs (Husar et al. 1997, 2001), would receive most of any such increase in iron supply, rather than in the Southern Ocean. Thus, it is likely that taxa such as nitrogen fixers, rather than diatoms, might yield the most significant biotic response to elevated dust supply, but this response would probably be region-specific as iron enrichment might drive phosphate levels to zero (Sanudo-Wilhelmy et al. 2001; Lenes et al. 2001; Berman-Frank et al. 2001). Thus, any temperature-mediated projections of increases in the geographical range of these taxa (Lipschultz 1999) must also consider how trace element and phosphate concentrations might alter in the upper ocean.

7.8.8 A Case Study – Uncertainties in Projection

How might such increased dust levels influence oceanographic provinces at the ecosystem level? Here the subarctic North Pacific, which has a strong west-to-east gradient in dust deposition (Jickells and Spokes 2001), is considered. This W-E gradient is reflected in elevated mean chlorophyll levels (0.8–1.0 µg l^{-1}) in the NW Gyre in comparison to that in the NE Gyre (0.3 µg l^{-1}; Harrison et al. 1999). If aridification increased, leading to enhanced dust supply in this region this might extend the eastern boundary of higher chlorophyll waters. If so, present knowledge of the NW Pacific Province might assist in predicting the ecological effect, of any eastwards extension. There might be a justification in using the present day NW Pacific to project what might occur in the NE Pacific. Alternatively, given the Prospero (2000) 500 km distance for a 50% reduction in dust load, the result might be higher dust supply to the NW Pacific, with no marked change in dust deposition for the NE Pacific.

7.9 Dimethyl Sulphide and the Biota

7.9.1 The CLAW Hypothesis

Dimethyl sulphide (DMS) has been viewed as an important climate reactive gas (rather than a 'greenhouse gas') since the seminal study by Charlson et al. (1987) that proposed the CLAW (Charlson et al. 1987) hypothesis linking phytoplankton, sulphate aerosols and cloud albedo (Fig. 7.14). CLAW represents a potential negative feedback mechanism to counter warming due to climate change. Denman et al. (1996) summarised our understanding of the links between DMS production, plankton and cloud condensation nuclei (CCN). They reported that although links were reasonably well established, it would be difficult to model this feedback due to the perceived complexities of both oceanic and atmospheric processes involved in CLAW.

The CLAW hypothesis proposed that DMS is mainly produced by plankton in surface waters and that this DMS, upon subsequent ventilation to the atmosphere, produces aerosol particles which act as CCN and influence cloud formation and albedo (reflectance) (Malin 1997). DMS-mediated increases in cloud albedo from elevated CNN abundances are estimated to potentially cool the planet globally by around 1 °K (Houghton et al.

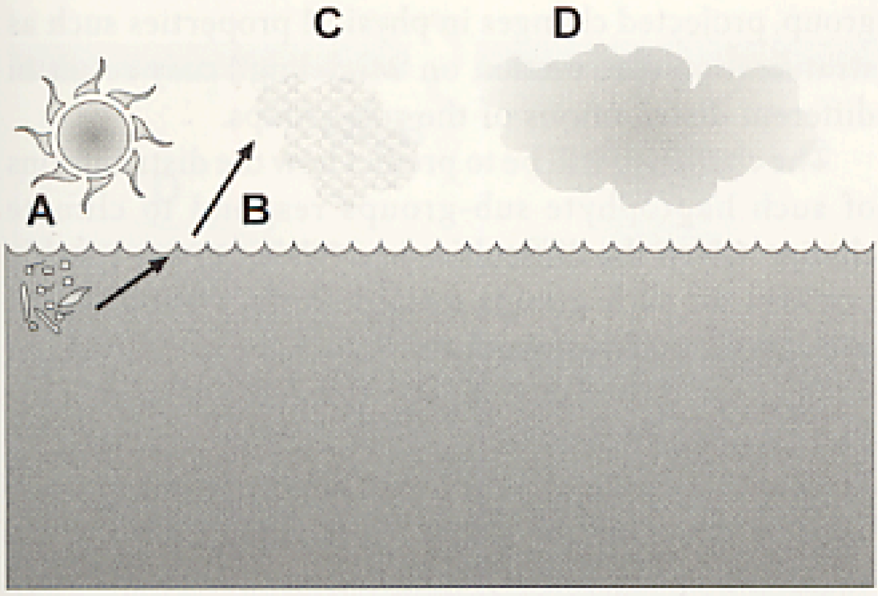


Fig. 7.14. A cartoon of the marine and atmospheric factors that may alter cloud cover via the sulphur cycle as outlined in the CLAW hypothesis. *A* Denotes haptophyte algae (coccolithophores, *Phaeocystis*, or 'HNLC' nanoflagellates) that produce dimethylsulfoniopropionate (DMSP); the distributions of these algal groups appears to be controlled by different environmental factors; *B* represents processes that mediate the conversion of DMSP to dimethyl sulphide (DMS) such as heterotrophic bacterial activity and micro-zooplankton herbivory; *C* and *D* denote atmospheric components of the CLAW hypothesis (many aspects of which have yet to be quantified), including the conversion of DMS to sulphur dioxide, and then to sulphuric acid. The sulphuric acid may subsequently form a new particle 'a cloud condensation nuclei' but this stage is dependent on the background abundances of condensation nuclei. As the Northern Hemisphere has higher background levels than the Southern, then DMS production in the latter will probably have a disproportionate effect on cloud formation and the resulting feedbacks (such as albedo)

1996). Furthermore, paleo-oceanographic evidence from the Vostok ice-core points to pronounced changes in Methanesulphonate (MSA, an atmospheric DMS oxidation product) between the glacials and interglacials (Legrande et al. 1991; Turner et al. 1996). Here, only the oceanic components of the CLAW hypothesis – which in February 2003 remains untested – are considered in detail.

7.9.2 What Produces DMSP/DMS?

Since 1995 there have been significant advances in understanding DMS production mechanisms (Malin 1997). Early studies investigated whether links existed between DMS production and bulk biological signals such as phytoplankton stocks and/or production. It was concluded that DMS levels were poorly related to such bulk signals (Holligan et al. 1987; reviewed by Kettle et al. 1999), and that the production of the precursor DMSPp appeared to be more closely related to specific aspects of phytoplankton processes. Furthermore, large changes in upper ocean DMSP and DMS concentrations have been observed during phytoplankton blooms (Holligan et al. 1993; DiTullio and Smith 1996), and mesoscale iron enrichments, such as IronEx II (Turner et al. 1996) in the equatorial Pacific, and SOIREE (Boyd et al. 2000) in the Southern Ocean. Therefore, algal community structure, in particular the haptophytes – such as coccolithophorids (Malin et al. 1993), *Phaeocystis antarctica* (DiTullio and Smith 1996), or 'HNLC' haptophytes (see section on 'The Haptophyte Connection') were reported to play a disproportionately important role in the production of DMSP.

Research into the mechanisms to convert DMSP to DMS have mainly focussed on grazer- or bacterially-mediated pathways. Wolfe et al. (1997) have consolidated their previous work (Wolfe et al. 1994) that proposed an important linkage between microzooplankton grazing and haptophytes (such as coccolithophorids) upon the lysis of the algae by DMSP lyase. Wolfe et al. (1997) further elucidated this mechanism suggesting that the algal production of DMSP is a grazer-activated chemical defence mechanism. Other studies have provided a new level of biochemical detail on the pathways/intermediates formed (such as DMSHB) involved in the synthesis of DMSP (Gage et al. 1997; reviewed by Simo 2001). It is also now acknowledged that much of the DMS released (up to 90%) is turned over by bacteria, or photo-oxidised to form non-volatile compounds (Malin 1997; Wolfe et al. 1999).

7.9.3 Global Distributions of DMS

Distributions of DMS levels in the surface ocean (15 000 observations) have been collated by Kettle et al. (1999). They produced maps of DMS concentrations based on the biogeochemical provinces of Longhurst (1995) and corrected following mapping procedures outlined in Conkwright et al. (1994). The maps (plate 5 in Kettle et al.) for mid-summer in each of the Northern and Southern Hemisphere point to high DMS concentrations in Southern Ocean polar waters (although the dataset is relatively small), and to high levels in the subarctic NE Atlantic and NE Pacific. Intermediate DMS concentrations were evident in both January and July in the HNLC waters of the Equatorial Pacific. In particular, the elevated DMS levels in the Southern Ocean may be disproportionately important for sulphur emissions/CLAW hypothesis as this region is characterized by generally low CNN/aerosol levels. Kettle et al. investigated whether global DMS distributions were correlated with other physical (temperature and salinity), chemical (DMSP) or biological (chlorophyll) factors but found none. Furthermore, they reported that no simple algorithm could be used to reproduce the observed monthly fields of DMS concentrations. Recently, Anderson et al. (2001) used the database of Kettle et al. and report success, upon expanding this database with highly resolved nutrient and irradiance datasets, in predicting the global fields of DMS using a combination of chlorophyll, irradiance and nutrients.

7.9.4 The Haptophyte Connection

Anderson et al. (2001) have produced reliable simulations of the DMS global fields, based on a relatively simple relationship amenable to incorporation into a GCM. However, they caution that it is unlikely that DMS feedbacks (such as shifts in DMSP-producing species) on the climate system could be represented and thus realistically simulated using this approach. In addition, reports of inconclusive attempts to relate DMSP/DMS to bulk phytoplankton signals (Watanabe et al. 1995; Curran et al. 1998) are not surprising given the specificity of the mechanisms for DMSP/DMS (Wolfe et al. 1997, 1999). From field studies the main producers of DMSP are haptophytes, but different taxa may be particularly important in specific oceanic provinces. There are at least three groups in the open ocean (Fig. 7.14) that may responsible for the trends in global DMS maps (Kettle et al. 1999). In the NE Atlantic the impact of coccolithophorid (Holligan et al. 1993), and to a lesser extent *Phaeocystis pouchetti* blooms (Owens et al. 1989; Marra et al. 1995; Liss et al. 1994) on DMSP/DMS levels has been reported. Another haptophyte, *Phaeocystis antarctica*, dominates blooms in the Ross Sea and in the vicinity of the marginal ice zone (MIZ), regions which are subsequently characterised by elevated DMSP/DMS levels (DiTullio and Smith 1996). The third group – the so-called 'HNLC' haptophytes (<20 µm autotrophic flagellates) have been reported to be important during mesoscale in situ iron enrichments in HNLC waters. During both the IronEx II (Turner et al. 1996) and SOIREE (Boyd et al. 2000) studies a tripling of surface DMSP concentrations was recorded, which followed the evolution of the algal bloom, and although no specific candidates as to the biological source of DMSP were proposed for the former, the timing of increases in haptophyte abundances was similar to that for increases in DMSP during SOIREE (Boyd et al. 2000).

To predict how such DMSP producers might respond to climate change, more information on the enviromental control of each haptophyte group is required. Iron supply plays a role in the increases in DMSP, via increases in HNLC haptophyte stocks observed in the Southern Ocean (Boyd et al. 2000), and equatorial Pacific waters (Turner et al. 1996). In contrast, for coccolithophorids several factors such as stratification, insolation, nutrients and/or cobalt concentrations may determine the frequency and location of blooms (see section on 'The Calcifiers'). Another mode of control may best explain the dominance of the Ross Sea and MIZ waters waters by *Phaeocystis* – that of low light environments characterised by deep mixed layers with weak stratification (Arrigo et al. 1999). Moisan and Mitchell (1999) investigated the photophysiology of this taxa, and their laboratory culture results support the field observations of Arrigo et al. (1999). Thus, even within the haptophyte group, projected changes in physical properties such as stratification (see section on 'Modeling') may result in different distributions of the sub-groups.

The challenge will be to predict how the distributions of such haptophyte sub-groups respond to climate change. Given the difficulties in devising taxon-specific markers for such groups using remote-sensing (Ciotti et al. 1999), satellite-based studies will be of limited use in the near future, and field and laboratory perturbation experiments will be of particular importance (e.g., Riebesell et al. 2000; Boyd et al. 2000). Future projections might include a decrease in *Phaeocystis antarctica* abundances – with a shift to diatoms – due to increased stratification as predicted by GCMs and mediated by climate change (Sarmiento et al. 1998). For projected changes in coccolithophorid distributions see section on 'The Calcifiers', while for 'HNLC' haptophytes see the section on 'Atmospheric Deposition of Iron'.

The main pathway for the conversion of DMSP to DMS may be grazer-mediated (Wolfe et al. 1994, 1997, 1999). During SOIREE, the timing and magnitude of an increase in heterotrophic ciliate abundances was invoked as the most likley mechanism to explain the observed increase in DMS (and concurrent decrease in DMSP) (Boyd et al. 2000). However, it remains unclear whether such an iron-mediated increase in haptophyte stocks followed by an increase in herbivore stocks is a transient response on a time-scale of weeks, or part of a longer term and ongoing series of predator-prey oscillations. Thus, it is presently unknown whether persistently elevated DMS concentrations would result from a sustained and higher iron supply to the ocean (such as during the last glacial maxima, or due to increased iron levels from aridification).

7.10 UV-B and Ozone Depletion

The erosion of the protective ozone layer by depleting compounds (such as CFCs) has resulted in oceanic biota being exposed to elevated UV-B (280–320 nm) solar radiation. Denman et al. (1996) concluded that phytoplankton species-specific sensitivity to UV-B could result in shifts in community structure, particularly at high latitudes. They also acknowledged UV-B effects on heterotrophs and DOC. Here findings and observations on UV-B since 1995 are assessed (Fig. 7.15).

7.10.1 Present Status of Ozone Depletion

A report on ozone depletion by the World Meteorological Organisation (WMO Report No. 44, 1999) concluded that the total combined abundance of ozone-depleting compounds in the lower atmosphere peaked around 1994 and is slowly declining. The WMO estimated that, based on projections on the maximum allowances un-

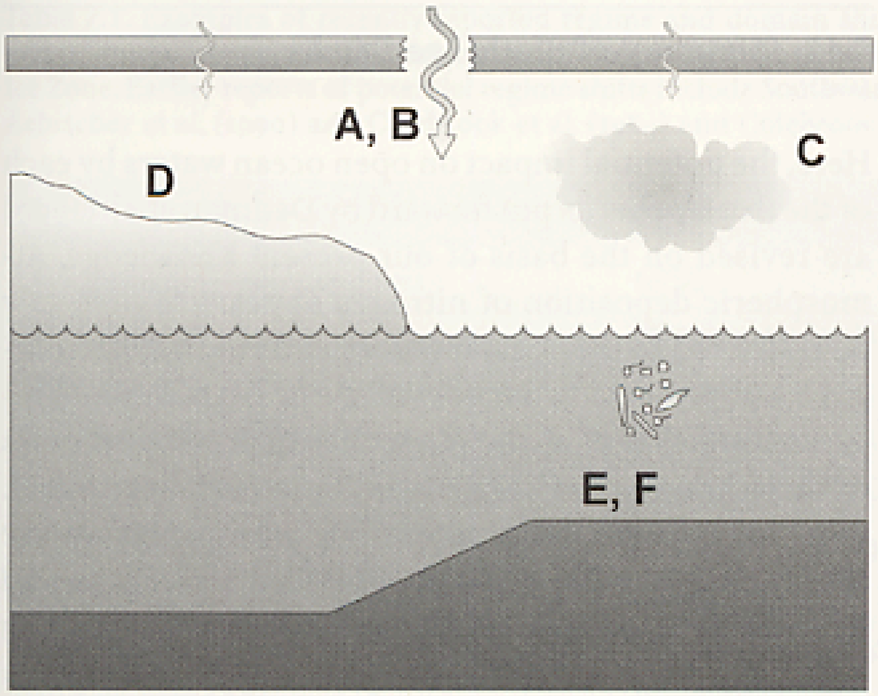


Fig. 7.15. A cartoon summarizing the factors controlling levels of UV-B reaching the upper ocean and its effect on the resident biota. *A* Denotes the influence of human activities resulting in the release of ozone-depleting compounds in the lower atmosphere (presently in decline under restrictions imposed by the Montreal Convention); *B* represents interactions between ozone depletion and the (cooling) effect of global warming on the stratosphere (Shindell et al. 1998); *C* the influence of cloud cover in the lower atmosphere (albedo) which can reduce UV-B penetration; *D* sea-ice cover which alters albedo (reflectance); *E* mixed layer depth, driven by wind stress and upper ocean stratification, which will also influence algal photoinhibition; *F* subsequent floristic and faunistic shifts than are driven by the degree of UV tolerance, in which organisms show differential sensitivity

der the Montreal Protocol, the period of peak ozone depletion is predicted to lie within at least the next 20 years. However, both identification of this maximum and evidence for the recovery of the ozone layer will require more than two decades. McKenzie et al. (1999) recently confirmed long-term decreases in ozone in the New Zealand region, and increases in the UV index. The authors point out that although stratospheric ozone loading is close to the minimum expected under the present control regime, there are concerns about the possible interactions between ozone depletion and the effects of global warming on the stratosphere. In this stratum, warming of the lower atmosphere results in radiative cooling which may delay the recovery of the ozone layer by decades (Shindell et al. 1998).

7.10.2 Phytoplankton and Primary Production

Previous studies established that elevated environmental UV-B reduces primary production rates in surface waters (Smith and Baker 1984; Fig. 7.15 this study), and led to the development of models on the spectral effects of UV on photosynthesis. Laboratory culture experiments, in which UV-B levels were manipulated, suggested that cells were able to counter the effects of UV-B inhibition within hours (Cullen and Lesser 1991). Since 1995, there has been progress in understanding the effects of UV-B on algal physiology with more emphasis on field studies and refining predictive models. Studies in the Weddell-Scotia Confluence (WSC) by Neale et al. (1998a) reported that the relationship between UV-B exposure and inhibition of photosynthesis was more complex that previously thought. In contrast to previous laboratory experiments (Cullen and Lesser 1991), resident cells demonstrated no ability to counter UV-induced inhibition of photosynthesis over <4 h periods, implying that UV inhibition was a non-linear function of cumulative exposure (Neale et al. 1998a). Furthermore, studies of algal assemblages in WSC waters with contrasting hydrographic conditions, indicated that both photo-acclimatory ability and species-selection against less UV-tolerant species were important determinants of the sensitivity of the phytoplankton assemblage to UV radiation. Thus, algal UV tolerance was highest in shallower mixed layers (with a proviso – the mixed layer must have been established for sufficient time to allow photoacclimation) whereas low light adapted cells in deeper mixed layers had the lowest UV-tolerances.

Models to predict the relative biological effects of UV-B dosage must incorporate a Biological Weighing Function (BWF), i.e., a UV wavelength-dependent function (Cullen et al. 1992). Their model successfully described the majority of the spectrally-dependent experimental variations in photosynthetic rate in the WSC region. However, as the model yielded 6 specific BWFs for the resident cells, Neale et al. concluded that no single BWF was applicable to the WSC, and that the development of a suite of BWFs was required for Southern Ocean waters. A further modeling study (Neale et al. 1998b) of the interactive effects of ozone depletion and vertical mixing indicate that inhibition of photosynthesis can be enhanced or decreased by vertical mixing, and was dependent on both mixed layer depth and mixing rate. They conducted a sensitivity analysis of various factors to a worst case scenario in which ozone levels were suddenly reduced by half, and reported that column-integrated production could decrease by up to 10%. However, their analysis points to more pronounced inhibitory effects on primary production rates due to alteration of other factors that may be influenced by climate change such as vertical mixing rates, or the degree of cloudiness.

7.10.3 Dissolved Organic Matter and Heterotrophic Bacteria

UV-B radiation may also alter rates of marine bacterial and viral activity, and rates of photodegradation of DOM (Dissolved Organic Matter) from different sources (Moran and Hodson 1994). Recent studies indicate the relationship between UV radiation, DOM source, DOM reactivity, and subsequent utilisation by bacteria are complex (Pausz and Herndl 1999). They report that algal exudates of DOM become more resistant to bacterial utilisation upon UV exposure in the water column. This contrasts with the findings of Amon and Benner (1996) who observed that refractory DOC after UV exposure was more labile for bacterial utilisation. Other recent studies (Visser et al. 1999) have provided evidence of UV damage to heterotrophic bacterial DNA, and inhibition of protein and DNA synthesis in microbial communities in the Caribbean Sea.

7.10.4 Pelagic Community Response

In addition to specific UV damage or inhibitory effects on plankton at the molecular or physiological level (reviewed by Vincent and Neale 2000), the resulting interactive effects of UV damage at the ecosystem level must also be considered. Bothwell et al. (1994) observed that differential sensitivities to UV-B for freshwater algae and herbivores led to a counter-intuitive increase in algal biomass in habitats exposed to UV-B. Bothwell et al. cautioned that predictions of ecosystem response to elevated UV-B should not therefore be made using assessments of a single trophic level. A further plea for careful interpretation of experimental results was also made by Cabrera et al. (1997) who provided evidence of species-specific differences in UV sensitivity of herbivores in high altitude Andean lakes. Cabrera et al. advocated the careful definition of timescales for such manipulative experiments since different trophic groups may have different response times. A mesoscosm experiment by Mostajir et al. (1999) in the lower St Lawrence estuary indicates that UV-B exposure may alter the structure and dynamics of the pelagic foodweb, from large to small organisms, and thus favour a microbial rather than a herbivorous foodweb (sensu Legendre and Rassoulzadegan 1995). Thus, the carbon pool of the foodweb may primarily be within small organisms with implications for the proportion of carbon (or other elements) that are recycled or exported from the system.

7.10.5 The Future

Uncertainties remain as to how such inhibitory effects of elevated UV-B on the biota will interact with other projected shifts due to climate change. For example, the implications of predicted increases in upper ocean stratification, particularly in the Southern Ocean, due to increased freshening (Sarmiento et al. 1998) must be carefully related to the complex relationship between vertical mixing and UV-B dosage (Neale et al. 1998b). Superimposed on these changes, are the often counter-intuitive effects of UV-B radiation at the ecosystem level, and the potential changes in other factors controlling UV-B levels, such as cloud cover, aerosol extinctions, stratospheric temperatures, or albedo (McKenzie et al. 1999).

7.11 Summary of Biotic Feedbacks

Here, the potential impact on open ocean waters by each of the five feedbacks put forward by Denman et al. (1996) are revised on the basis of our present knowledge. Atmospheric deposition of nitrogen appears to presently be restricted to the coastal waters and continental margins, and projected changes will be greatest in these regions (Galloway et al. 1994). Further to previous reports of variations in the C:N Redfield ratio (Sambrotto et al. 1993) other examples of alterations of nutrient uptake stoichiometry have been put forward (Hutchins and Bruland 1998; Arrigo et al. 1999). However, caution is urged as to how robust and significant such trends in carbon: nitrogen uptake stoichiometry might be over longer timescales (Kortzinger et al. 2001). In contrast, iron-mediated decreases in the silicic-acid:carbon uptake ratio, if sustained over centennial timescales, may play a significant role in modulating atmospheric CO_2 levels during the glacial maxima (Watson et al. 2000).

Laboratory studies on coccolithophorids have demonstrated that elevated atmospheric CO_2 concentrations result in decreased calcification (Riebesell et al. 2000), yet little is known about what controls the onset or decline of these blooms of calcifiers. This points to the dangers of making projections based on only one set of perturbed conditions, and to the need for a holistic approach whereby the effects of climate-mediated shifts at all levels (physiological to biogeographical) are taken into account when making such projections. There is now evidence that the main DMSP producers reside within three distinct sub-groups of the haptophytes. However, blooms by each group may be triggered by different environmental factors; much may be learnt from the approaches developed to determine what factors control phytoplankton processes in HNLC regions (reviewed by de Baar and Boyd 2000). Iron limitation of phytoplankton growth is now more widespread that previously thought and has been observed in both coastal HNLC and oceanic LNLC regions. Defining the controls on iron supply in the present, geological past, and future will be central to understanding the biogeochemical functioning of much of the surface waters of the World Ocean. Although the Montreal Convention appears to be slowly redressing the 'balance' with respect to ozone depletion which is forecast to decrease on a timescale of decades, uncertainties remain on the interactive effects of UV-B and global warming.

Denman et al. (1996) in their IPCC review considered these main potential marine feedback mechanisms discretely. However, a point may have been reached whereby it is simplistic to think in terms of discrete feedbacks, since there are strong links between them, such as the role of iron supply on the algal uptake ratio of silicic acid to carbon, or that of elevated UV-B levels on the photo-

Table 7.1. Examples of recently reported regime and domain shifts in phytoplankton community structure, at higher trophic levels, and potential impacts on the magnitude of the biological pump. NSPG denotes North Subtropical Pacific Gyre; *MIZ* denotes Marginal Ice Zone. Earlier reports of potential regime shifts include Southward (1963, English Channel); Venrick (1971), Venrick et al. (1987) (NPSG); Aebischer et al. (1990) and Colebrook et al. (1984) and Colebrook (1986) (NE Atlantic)

Biota	Region	Reference
Phytoplankton – nitrogen fixers	NPSG	Karl et al. (1995, 1999); Karl (1999)
Phytoplankton	NE subarctic Pacific	Whitney et al. (1998)
Phytoplankton – pico to large diatoms	Equatorial Pacific	Chavez et al. (1999)
Small to large phytoplankton[a]	NE subarctic Pacific	Parslow (1981)
Coccolithophores	Bering Sea	Napp and Hunt Jr. (2001)
Phytoplankton	NE Atlantic and North Sea	Reid et al. (1998)
Euphausids	Bering Sea	Napp and Hunt Jr. (2001)
Zooplankton and salmon	NE subarctic Pacific	Beamish et al. (1999)
Calanoid copepods	North Sea	Heath et al (1999)
Krill and Salps	Polar Southern Ocean	Loeb et al. (1997)
Krill and Salps	Southern Ocean – East Antarctica	Nicol et al. (2000)
Penguin stocks	MIZ – Antarctic Peninsula	Smith et al. (1999)
Cod stocks	North Sea	O'Brien et al. (2000)
Elevated export to depth	NE subarctic Pacific	Boyd et al. (1998)
Fulmar populations	N Atlantic	Thompson and Ollason (2001)

[a] By inference – see Boyd et al. (1998).

chemistry of iron or DOM. Denman et al. acknowledged the significance of observations by Karl et al. (1995) of higher abundances of nitrogen fixers at the HOT site as evidence of a marked change in the composition of a pelagic community (often termed a regime or domain shifts, Karl et al. 1997). However, Denman et al., while also citing previous evidence of interdecadal variations in planktonic stocks in the N Pacific (e.g., Venrick 1971, 1982; Venrick et al. 1987), cautioned that potentially confounding effects of methodological changes over time might account for much of this apparent variability.

One striking trend since 1995 has been the number of studies reporting evidence of regime or domain shifts (summarised in Table 7.1), and how they may provide the best clues as to the likely response of the biota to climate change (see below).

7.12 Climate – Variability vs. Change

7.12.1 Climate Change

There is evidence of pronounced shifts in the magnitude of many properties over the geological record – for example in the Vostok ice core there are gradients of 6–7 °C in temperature, and accompanying shifts of 100 ppm in atmospheric CO_2, tenfold changes in dust (iron) levels, and five-fold shifts in both MSA concentrations and methane levels. This contrasts with a 20 ppm change in atmospheric CO_2 between 1958 and 1990 (Keeling et al. 1996; Archer and Johnson 2000). Research has focussed on the relative timing of these events to assist in the identification of forcing functions for shifts in temperature and CO_2, and the phasing of these changes such that the mechanisms for abrupt climate change may be elucidated. Plausible biotic mechanisms considered so far include elevated iron supply and nitrogen fixation (Broecker and Henderson 1998). In a recent modeling study, Watson et al. (2000) conclude that increased iron supply during the last glacial periods may account for up to 30% of the observed 100 ppm change in atmospheric CO_2, and that multiple feedbacks are probably responsible for pronounced biogeochemical gradients at the glacial terminations. These paleo-oceanographic studies provide estimates of the magnitude of change due in part to feedbacks, and offer compelling evidence for relatively abrupt changes in properties brought upon by non-linear responses (Hasselmann 1999; Rahmstorf 1999). Yet such changes are mainly on centennial or millennial timescales, and thus tell us little about the response time in the present day of feedbacks to climate change predicted to occur on annual to decadal timescales (Sarmiento et al. 1998).

In only a few cases from the geological past are there records of changes occurring on decadal timescales as are predicted from present models. One example is derived from changes in nitrogen and argon isotopes in trapped air from the Greenland ice record which indicates that the Greenland summit warmed 9 ±3 °C over a period of several decades around 15 000 years ago. Furthermore, atmospheric methane concentrations (possibly from wetlands) rose abruptly over a 50 yr period not long after the onset of this abrupt temperature change (Severinghaus and Brook 1999; see Introduction to this chapter). The mechanisms behind other climatic anomalies such as the Medieval Warming Period or the Little Ice Age may also assist in explaining the magnitude of such events (Reid 1997). However, to obtain a mechanistic understanding of the role of such feedbacks, more comprehensive datasets than can currently be provided by the paleo-oceanographic record are required.

7.12.2 Climate Variability

A close examination of trends in atmospheric CO_2 concentrations over the last three decades suggest that large shifts, due to interannual climate variability such as the effects of El Niño events, are superimposed onto the pronounced rate of increase in CO_2 concentrations (Sarmiento 1993). Furthermore, there is strong evidence of links between such transient events and modes of atmospheric variability – indices of climate such as El Niño Southern Oscillation (ENSO), or NAO (North Atlantic Oscillation). For example in the North Atlantic, Sutton and Allen (1997) analysed patterns of sea surface temperature during the winter and reported that the trends appeared to be 'remarkably organised' over a decadal time-scale. McCartney (1997) proposed that the long-term variability in westerly winds (as evidenced from the NAO) may be driven by temperature variations in the ocean (see counter-argument in Seagar et al. 2000). While such climatic variability potentially confounds the detection and interpretation of any such climate change, it does provide information on the response times of oceanic processes to climatic variability (and vice-versa). Furthermore, with the improved resolution of ocean time-series observations (such as BATS) there are increasing opportunities to compare observed trends in biogeochemical properties with such climatic indices.

Although the dataset is small, several studies suggest indirectly that oceanic biota may have a pronounced and rapid response to climate variability, with a concomitant effect on atmospheric CO_2 concentrations (Fig. 7.1). The biota may respond to climate variability or change, by alteration of rates of bulk properties, such as primary production, and/or via shifts in ecosystem structure (Falkowski et al. 1998). Recently, Behrenfeld et al. (2001) provided the most comprehensive estimate of how rates of primary production might alter in response to marked climate variability. They report an increase of around 10% in global primary production (derived from SeaWiFS via a productivity algorithm) over the 3 yr duration of an El Niño event, i.e., a negative feedback.

In contrast, because ecological processes are highly dynamic (Field et al. 1998) little is known about the timing or magnitude of climate-mediated floristic and/or faunistic shifts, and how they might in turn impact climate via feedbacks. However, detailed oceanographic datasets, from SeaWiFS, time-series sites, mooring arrays and shipboard surveys/experiments have provided clues as to how ecosystem structure might respond to climate variability (Table 7.1). These studies suggest that ecological shifts (often termed regime or domain shifts) may subsequently influence the biogeochemical cycles of several elements via feedback mechanisms. As such, these detailed observations on climate-mediated regime shifts may be viewed as fortuitous experiments under which conditions for an entire ecosystem were altered for a sustained period of time (months), such as shoaling the mixed layer depth (Karl et al. 1995), or in-

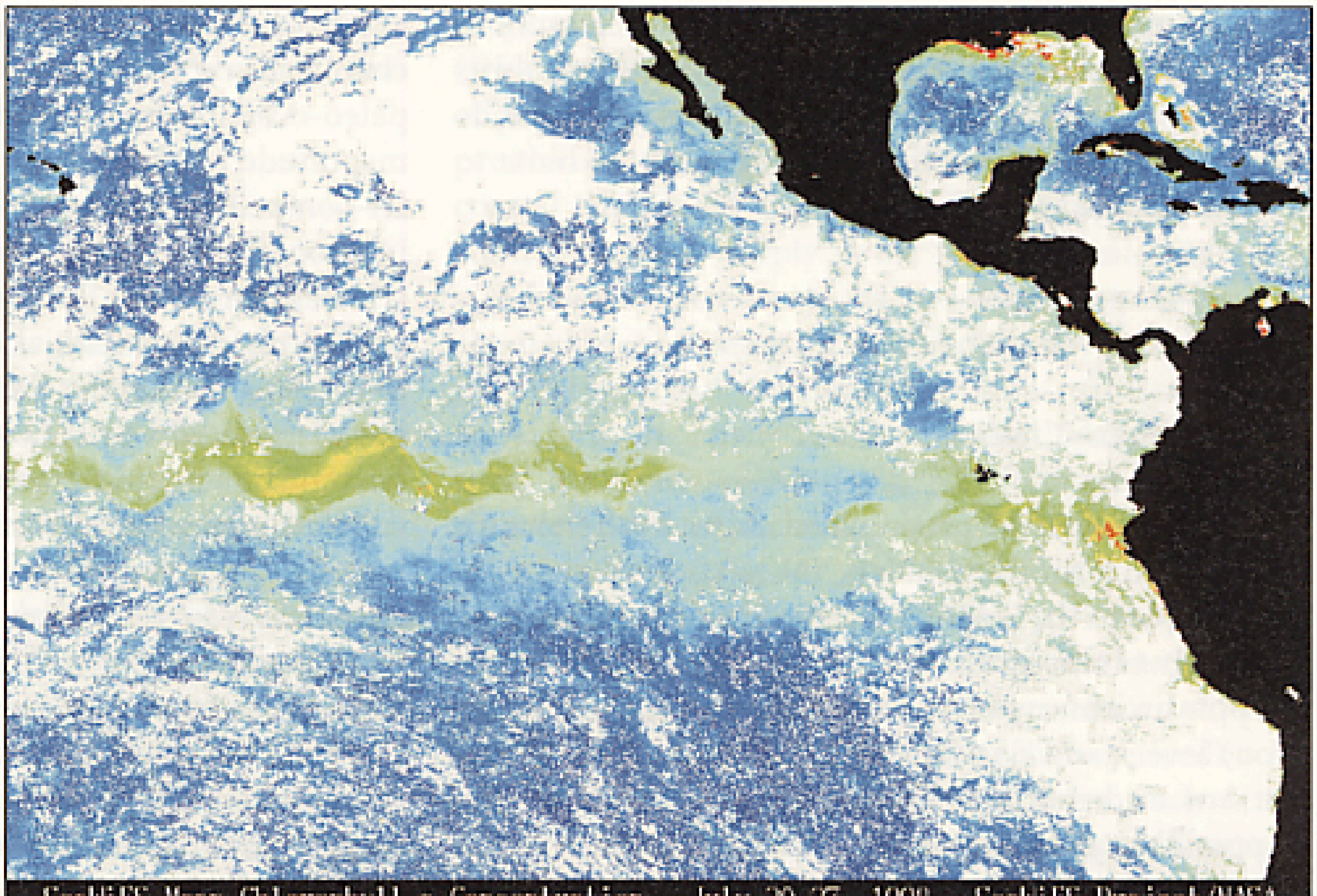


Fig. 7.16.
An example of a rapid (six months) shift in algal stocks and community structure in the waters of the E Equatorial Pacific as evidenced by a ribbon like filament of high chlorophyll waters (*green*) surrounded by HNLC waters (*blue*). Shipboard sampling of these waters indicated that they were diatom-dominated (rather than the usual picophytoplankton dominated HNLC community), with signi-ficantly high rates of primary and export production being driven by elevated upwelling of iron-rich waters during the La Nina condition (SeaWIFS data reprinted with permission from Chavez et al. (1999) Biological and chemical response of the equatorial Pacific Ocean to the 1997–1998 El Niño. Science 286: 2126–2131, © 1999, American Association for the Advancement of Science)

creasing the rate of upwelling of nutrients (Chavez et al. 1999; Fig. 7.16) in a way that could not be mimicked in the laboratory or in mesocscale field experiments (Coale et al. 1996). This approach offers the best means to investigate the response time of the biota to climatic variability and hence will likely provide our best indicators of how biotic feedbacks might respond to climate change.

Such evidence of regime shifts may represent a departure in how climate-mediated alteration of pelagic marine systems are perceived. Previously, researchers examined datasets with a view to detecting changes in the phytoplankton signals. Several studies have suggested little evidence in the archives of change in algal stocks etc (Falkowski and Wilson 1992), whereas most of the reported regime shifts are characterised by floristic changes which may have marked implications for the strength of feedback mechanisms (nitrogen fixers, *Phaeocystis*, and also large vs. small cells and their influence on particulate export flux, Fig. 7.17). Thus, it has led to perhaps the largest single shift in the emphasis of research since Denman et al. (1996), the investigation of how feedbacks are controlled or forced at the taxon-level rather than solely via alteration of bulk signals.

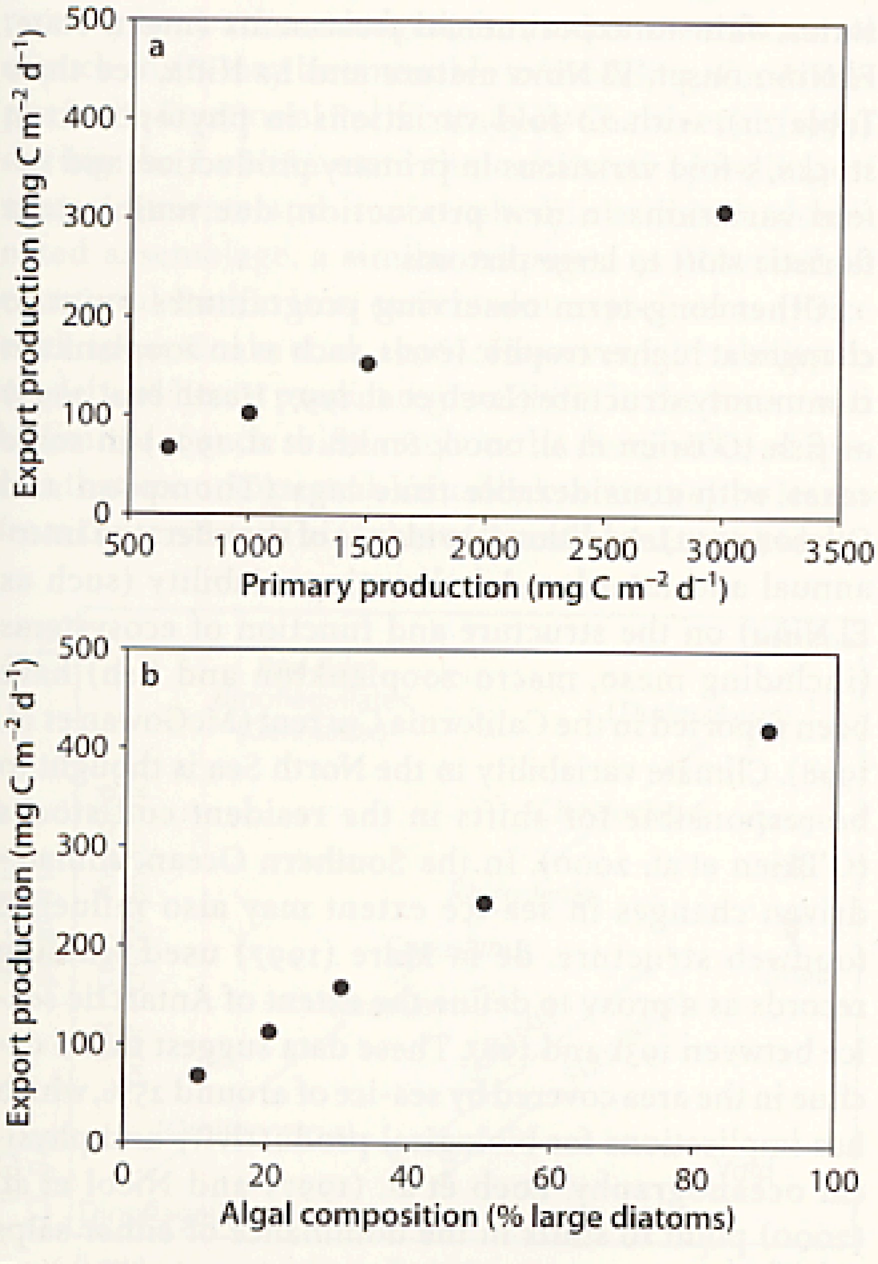


Fig. 7.17. A comparison of the effect of increasing rates of primary production without changing community structure (in a population dominated by picophytoplankton, with few large cells), and altering community structure from small to large cells without increasing rates of primary production (mean rate is 660 mg C $m^{-2} d^{-1}$) on the potential export production from the base of the mixed layer to depth. Projections are based on the approach of Boyd and Newton (1999) and using data from the HNLC

7.12.3 Regime Shifts

There is increasing evidence for strong links between climate variability and changes in biological populations (Smith et al. 1999; Wuethrich 2000). Such variations in climate may result in a shift in algal taxa (e.g., Karl et al. 1995, 1997) and may also have implications at higher trophic levels (Heath et al. 1999, Table 7.1). In terrestrial systems climate variability may result in complex biological responses resulting from the triggering of several chains of ecological events that cascade through an ecosystem (Wuethrich 2000; Smith et al. 2000). Such shifts are referred to in the literature as regime or domain shifts but care is required in the usage of this term, and a distinction should be made between isolated events or curios, and shifts that are repeatedly observed over several years (summary in Table 7.1).

In the ocean, there is compelling evidence of regime shifts in response to climatic variability (such as based on SOI and El Niño events) in both the NPSG (Karl et al. 1995, 1997, this volume; Karl 1999) and in the NE subarctic Pacific (Whitney et al. 1998). Both regions are characterised by long time-series records, suggesting that regime shifts of a similar magnitude may also be occurring in other oceanic regions but have so far not been detected due to a paucity of data. Several other studies provide evidence of a shift in phytoplankton community structure in response to climatic changes (Reid et al. 1998; Chavez et al. 1999; Napp and Hunt Jr. 2001). Here three examples of such shifts are considered in detail.

In the NPSG (HOT site) Karl et al. (1995) reported ecosystem changes in response to the 1991–1992 El Niño. They present evidence of a shift from a nitrogen- to a phosphorus-limited system caused by a floristic shift towards greater abundances and activity of nitrogen-fixers. Karl et al. summarise this domain shift as resulting in changes in the proportion of nitrogen fixers during El Niño and non El Niño years, with enhanced nitrogen fixation in response to increased stratification in El Niño year (which has major implications for nutrient cycling in this region and for future shifts due to climate change), and a suggestion that such a shift in the degree of nitrogen fixation is driven by nitrogen limitation. The increased rates of nitrogen fixation results in a phosphate-limited ecosystem (for details see Karl et al., this volume). In the Western Tropical Pacific, Hansell and Feely (2000) hypothesise that water column stratification, forced by high net precipitation, favours enhanced rates of nitrogen fixation in these waters. Such changes may be driven by a more active hydrological peratures. Projected increases in upper ocean stratification due to future climate change (Sarmiento et al. 1998) might result in a shift towards increased nitrogen fixation and hence a negative feedback. Furthermore, Lipschultz (1999) has suggested that with the projected warming of the ocean there might be a potential polewards increase in the geographical range of nitrogen fixers. The ability to remotely-sense blooms of nitrogen fixers is required to answer these contentions (Subramaniam et al. 1999a,b; Dupouny et al. 2000).

Whitney et al. (1998) provide evidence of interannual variability in nitrate supply to surface waters of the NE subarctic Pacific (Fig. 7.18), and report shifts between the El Niño/La Nina cycles in salinity, temperature and nitrate. During the El Niño period the reduced nitrate supply was estimated to have reduced new production over the growth season by 40% (2 million t C) over a 290 000 km^2 area. This resulted in a shift to an oligotrophic system (characterised by a subsurface chlorophyll maximum) as opposed to the previously observed mesotrophic system akin to the NE Atlantic. There is anecdotal evidence of subsequent changes in the magnitude of production and the composition of the higher trophic levels due to this climatic variability (Beamish et al. 1999; Mantua et al. 1997).

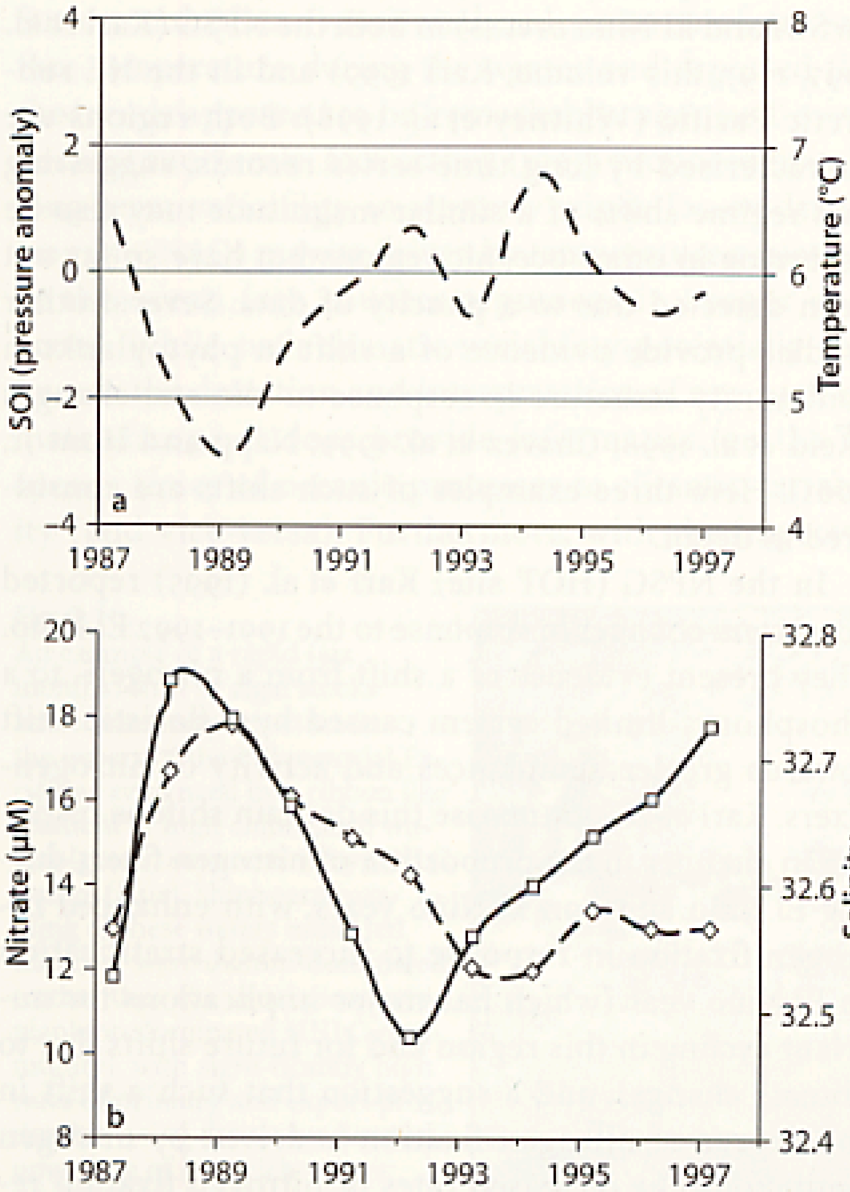


Fig. 7.18. **a** Changes in the Southern Oscillation Index (SOI, derived from the monthly mean pressure anomalies between Tahiti and Darwin, Australia) for the N Pacific in relation to **b** the observed shifts in winter reserve nitrate and salinity for these waters between 1993 and 1997. The nitrate changes resulted in massive fluctuations in the productivity of this region between these years (redrawn with permission from Whitney et al. (1998) Interannual variability in nitrate supply to surface waters of the Northeast Pacific Ocean. Marine Ecology Progress Series

Other regime shifts in the NE subarctic Pacific include transient events in which phytoplankton processes were altered in the HNLC waters (Ocean Station Papa, OSP). In three of ten years there was evidence of a temporary shift from HNLC conditions to those characterised by transient bloom events (Parslow 1981; Fig. 7.17 this study). Such events, may be due to diatoms as evidenced by occasional exceptionally large drawdown of surface silicic acid levels at OSP (Wong and Matear 1999; see section on 'Atmospheric Deposition of Iron').

In another province, the equatorial Pacific, Chavez et al. (1999) recently reported marked biological and chemical changes driven by the 1997–1998 El Niño event. There were shifts in the upwelling rate of macronutrients, CO_2 and iron, resulting in subsequent changes in community structure, increases in phytoplankton stocks, and in the proportion of new production during La Niña compared to the mean, El Niño (onset and mature) conditions. Thus, variations in conditions resulted in four states, akin to experimental treatments (mean state, El Niño onset, El Niño mature and La Niña, see their Table 7.1), with 20-fold variations in phytoplankton stocks, 5-fold variations in primary production and 20-fold variations in new production, due mainly to a floristic shift to large diatoms.

Other long-term observing programmes point to changes at higher trophic levels, such as in zooplankton community structure (Loeb et al. 1997; Heath et al. 1999) or fish (O'Brien et al. 2000; Smith et al. 1999) in some cases with considerable time lags (Thompson and Ollason 2001). Additional evidence of the effects of interannual and interdecadal climatic variability (such as El Niño) on the structure and function of ecosystems (including meso, macro-zooplankton and fish) have been reported in the California Current (McGowan et al. 1998). Climate variability in the North Sea is thought to be responsible for shifts in the resident cod stocks (O'Brien et al. 2000). In the Southern Ocean, climate-driven changes in sea-ice extent may also influence foodweb structure. de la Mare (1997) used whaling records as a proxy to define the extent of Antarctic sea-ice between 1931 and 1987. These data suggest that a decline in the area covered by sea-ice of around 25%, which has implications for biological productivity and physical oceanography. Loeb et al. (1997) and Nicol et al. (2000) point to shifts in the dominance of either salps or krill in response to shifts near the ice-edge.

The reportage of a wide range of regime shifts points to a change in the dominant flora or fauna which may have marked effects on biogeochemical cycles due to both alterations in community structure and rates of production (Karl et al. 1997). Several studies evince a rapid response time for such shifts in some cases within

6 months (Chavez et al. 1999). Due to the wide range of these shifts, they may be less amenable to model or predict than that, for example, of a direct (temperature-driven) increase in the rate of growth or primary production with no concurrent floristic shift. Moreover, these domain shifts appear to regional in scale (Karl et al. 1995; Whitney et al. 1998), and indicate the need to assess such changes or feedbacks on a regional basis (sensu Longhurst 1995, 1998) before attempting to determine the cumulative or global effects of biotic feedbacks due to climate change (see section on 'The Future'). Thus, to comprehensively estimate the influence of such regime shifts, scales of biotic response from physiological (Beardall et al. 1998) to shifts in the areal extent of biogeographical provinces must be taken into account.

7.12.4 Unexpected Biological Responses to Climate Change

Although the significance of regime shifts, and their use as proxies of biotic responses to climate change, has only recently been acknowledged, the environmental control of such shifts may be amenable to modeling. For example, in the Equatorial Pacific study by Chavez et al. (1999) during the La Niña state the enhanced upwelling of macronutrients and iron resulted in a diatom-dominated assemblage, a similar response as observed in equatorial Pacific iron enrichment experiments (Price et al. 1994; Coale et al. 1996). However, our ability to model and hence predict regime shifts in the future will be limited if such shifts result in the dominance of species that are unexpected. Valuable lessons may be learnt from the terrestrial biosphere (Pounds et al. 1999) where "widespread amphibian extinctions in seemingly undisturbed highland forests may attest to how profound and unpredictable the outcome can be when climate change alters ecological systems". In the ocean the proliferation of toxic algal blooms in the nearshore eutrophic environment (Paerl 1999) or the recent sustained presence and overwintering of a cocolithophore bloom in the Bering Sea (Napp and Hunt Jr. 2001) may be examples of such unpredictable changes. Several terrestrial studies have investigated the ecological impact of species invasions (either natural or anthropogenic) and conclude that there is considerable difficulty in predicting the outcome, due to the transient nature of such systems (Petchley et al. 1999; Sait et al. 2000). In the ocean, Margalef (1997) has come closest to exploring such ecological concepts. His phytoplankton mandala (nutrient concentrations vs. turbulence, Fig. 7.19) is an example of the type of predictive conceptual frameworks that will be required to tackle these issues.

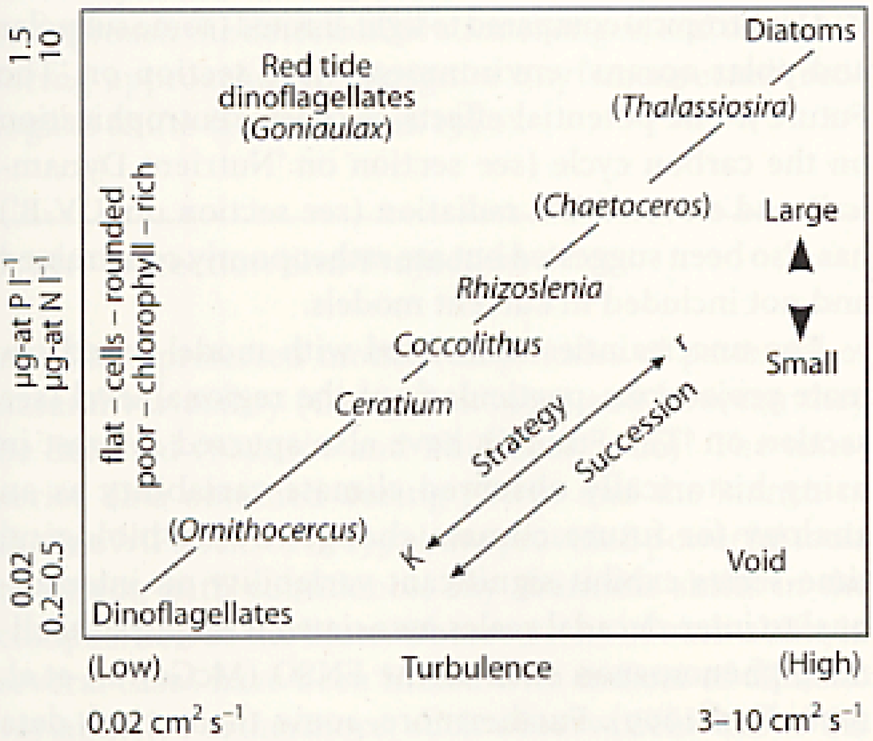


Fig. 7.19. The phytoplankton mandala of Margalef that summarises conceptually the role of forcing (gradients in nutrient supply and turbulence) in determining phytoplankton species and size composition (reprinted with permission from Margalef R (1997) Our biosphere. In: Kinne O (ed) Excellence in Ecology. Ecol-

The evidence presented for regime shifts suggests that future climate change is unlikely to result solely in the alteration of one trophic level, that such shifts may be abrupt, and have subsequent ramifications for higher trophic levels, the export of carbon to depth, and for pathways of nutrient recycling (Karl et al. 1995). Thus, a multi-stranded approach comprising laboratory culture (Riebesell et al. 2000) and mesoscale (Coale et al. 1996) experiments, remote-sensing of algal distributions (Fig. 7.8), and time-series observations (Fig. 7.11) are needed to predict the nature and geographic extent of regime shifts in the ocean in response to climate change.

7.13 Modeling – Future Goals

Numerical models play an important dual role in climate change research with respect to ocean biogeochemistry. Firstly, physical climate models are required to estimate the manner and degree to which the environment may change, and secondly ocean biogeochemical models are needed to predict the subsequent response to and possible feedbacks of biota and biogeochemistry to these forcings. The two are of course linked because one of the main driving factors of climate change, atmospheric CO_2 levels, is modulated by the ocean carbon cycle (Siegenthaler and Sarmiento 1993). Indeed, the future levels of atmospheric greenhouse gases such as CO_2 have become one of the major uncertainties associated with climate predictions through the next few centuries (Hansen et al. 1995). Robust ocean biogeochemical models are required for hind-casting past historical climate change and projecting future effects and feedbacks. Particular focus should be on the nature, times-scale and magnitude of changes that might be observed over the next few decades, providing observationalists attempting to detect climate change with some suggestions for future fieldwork

A summary of state of biogeochemical ocean modeling at the time of the last IPCC report (Denman et al. 1996) commented on the limitations of the available coupled atmosphere-ocean GCMs. They reported that the coupled GCMs included only the physical climate system with no explicit inclusion of the chemical or biological processes related to climate-reactive gases and atmospheric aerosols. The only consideration of the relationships between climate change and biological processes was via box models (Shaffer and Sarmiento 1995). At that time Denman et al. pointed to the lack of data to formulate, calibrate and evaluate marine climate effect models as being the greatest limitation to modeling efforts. Recently, there have been substantial improvements with coupled GCMs now including physical and biogeochemical feedbacks in a simplified form.

The results from current coupled ocean-atmosphere models on the extent of secular climate change predicted for the next century under greenhouse warming scenarios are at present based on a series of four coupled ocean-atmosphere experiments looking at the effects of climate change on ocean sequestration (Sarmiento et al. 1998; Joos et al. 1999; Matear and Hirst 1999; Cox et al. 2000). These simple ocean carbon cycle models have been run with either intermediate complexity (e.g., Joos et al. 1999) or fully coupled 3-D atmosphere-ocean GCM simulations (Sarmiento et al. 1998; Matear and Hirst 1999; Cox et al. 2000). The physical effects of warming of the surface ocean and reduction in meridional overturning, convective mixing, and isopycnal mixing combined lead to a 30–40 μatm decrease in CO_2 over the next century. The biogeochemical response is governed by two opposing factors, a reduction in the upward nutrient supply due to the increased stratification, which leads to decreased export production and CO_2 uptake, and a decrease in the upward vertical flux of dissolved inorganic carbon. The latter factor generally dominates in the present (biologically-unsophisticated) simulations, so that the effect of altered biogeochemistry is a net positive CO_2 uptake partially compensating the physical effects.

Numerical models are being improved dramatically as better, data-based mechanistic parameterizations are developed and evaluated based in part on the JGOFS process study, time-series and global survey data (Doney 1999; Doney et al., this volume). With respect to climate change, processes that need further observational and modeling attention include (Doney and Sarmiento 1999): direct physiological effects due to alterations in ocean temperature, pH etc.; sensitivity of HNLC regions, particularly in the Southern Ocean and subtropical waters (with resident nitrogen fixers) to changing dust deposition; and response of algal community structure, export flux and subsequently air-sea carbon exchange to projected increased water column vertical stability. As shown in Fig. 7.20, a number of potential feedbacks are

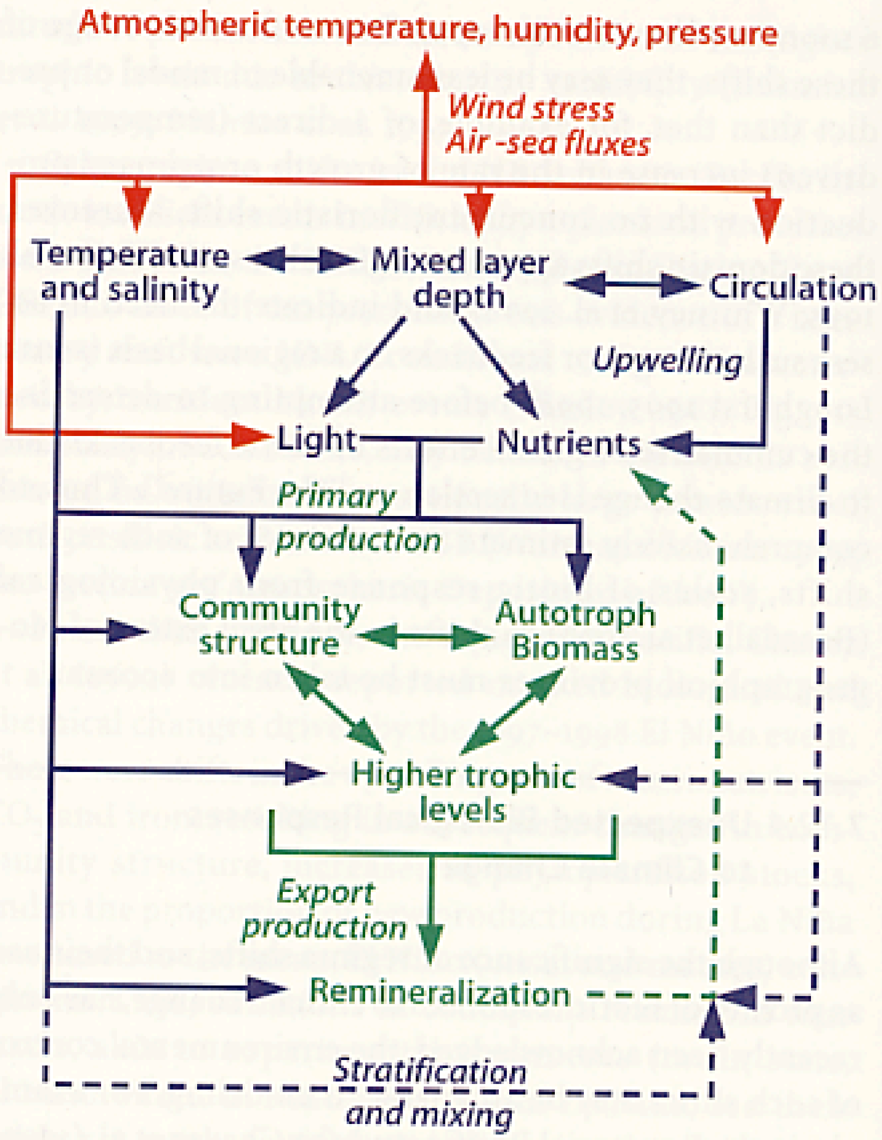


Fig. 7.20. Schematic of ecosystem level responses to physical factors of climate change including both rapid local effects (e.g., sea surface temperature, mixed layer depth) and longer term, non-local effects (e.g., sub-surface nutrient distributions)

ing altering mixed layer depth) and non-local associated with changes in large-scale circulation patterns and the depth of the nutricline etc. Observational (Polovina et al. 1995) and preliminary modeling studies (Bopp et al. 2001) suggest that enhanced stratification can have different impacts on rates of primary production in nutrient-limited (subtropics) compared to light-limited (some subpolar and polar oceans) environments (see section on 'The Future'). The potential effects of coastal eutrophication on the carbon cycle (see section on 'Nutrient Dynamics') and elevated UV radiation (see section on 'UV-B') has also been suggested but are rather poorly constrained and not included in current models.

The uncertainties associated with model-based climate projections, particularly at the regional level (see section on 'The Future'), have also spurred interest in using historically observed climate variability as an analogy for future climate change. Ocean biological time-series exhibit significant variability on inter-annual to inter-decadal scales associated with physical climate phenomenon such as the ENSO (McGowan et al. 1998; Karl 1999). Furthermore, some theoretical, data analysis, and modeling studies argue that climate change may project significantly onto these existing modes of natural variability (Corti et al. 1999). Thus, one could infer the biogeochemical climate change response by extrema. However, the projected physical climate change for the next century greatly exceeds observed natural variability, and the ecosystem response to physical forcing may be time-scale dependent and quite non-linear (Fig. 7.20). Most climate variability studies focus on bottom-up control of autotrophic production (e.g., nutrient supply, irradiance), but top-down control from higher trophic levels are also possible. The feedbacks associated with gyre scale circulation, large-scale nutrient distribution, planktonic community structure, and top-down controls have inherently longer time-scales and may not be well resolved by interannual climate variability. The paleoclimate record offers another valuable resource (see section on 'Climate Change') yielding information about the state of ocean biogeochemistry under climate perturbations of similar magnitude (though not rate of change) to projected anthropogenic effects and to a variety of climatic conditions both colder and warmer than today.

7.14 The Future

A central goal of JGOFS was to assess and understand the sensitivity to climate change of the ocean carbon cycle, and to "improve our ability to predict future climate-related changes". The decade long JGOFS programme has enabled us to reduce uncertainties in our understanding of the carbon cycle but, as reported here, to make smaller advances in our predictive abilities with respect to climate change. The legacy of JGOFS will be to provide datasets, directions and design criteria for future programmes – the progeny of JGOFS – to supply a suite of projections for the biogeochemical shifts induced by climate change, and recommendations on how to approach the detection of such changes, and on monitoring approaches to recognise any 'unexpected' ecological shifts (Pounds et al. 1999).

7.14.1 Detection and Projection

Are there preferred modes (amplitudes of patterns) of natural variability (Corti et al. 1999) and how can they be detected (Fedorov and Philander 2000)? The time-series data obtained during JGOFS and the launch of the SeaWiFS sensor in 1997 have provided powerful tools to detect, with confidence, any dramatic shifts in the composition of the biota. Observations of such shifts in several cases have been linked with indices of climatic variability. Furthermore, such observations are at the ecosystem or domain level and provide an invaluable 'domain wide' set of trends resulting from climatic variability. In the future the present suite of ocean observatories must be supplemented in selected locations that repre- will provide the detection of shifts and/or feedbacks to climate change. In tandem with detection will be projection, derived from increasingly sophisticated coupled ocean atmosphere models embedded with sub-models with higher resolution biological detail. These two strands together offer 'Earth system' analysis – a macroscope to look at global change (Schellnhuber 1999).

7.14.2 Does the 'Initial' Condition Still Exist?

Climate-mediated shifts in ocean properties may already be underway (Sarmiento et al. 1998; Broecker and Henderson 1998; Calderia and Duffy 2000) such as shutting down of midwater convective processes in the Southern Ocean. This in conjunction with the relatively large oscillations around the mean state due to climatic variability (IPCC 2001) may make specifying the 'baseline' condition, i.e., prior to any marked change in climate, difficult. Thus, a further requirement of field programmes, in addition to ocean observatories (McGowan 1990; Macilwain 2000), will be additional surveys and process voyages to obtain the 'baseline' condition in oceanographic provinces. Leading examples of such comprehensive studies include the JGOFS time-series sites, the CALCOFI study (McGowan 1999), the Gulf of Mexico observatory (Blaha et al. 2000), and in the Ross Sea by the ROVVERS group (which also includes a modeling component; Arrigo et al. 1999, 2000).

7.14.3 The Need for a Regional Approach

The siting of additional observatories should reflect one of the main conclusions of this chapter – the regional nature of biotic feedbacks – in contrast to physico-chemical feedbacks, which tend mainly to be global in their impact. Although the modeling study of Joos et al. (1999) suggests that the feedbacks with the greatest magnitude are physico-chemical, the impact of increased stratification on ocean ecosystems is likely to be pronounced (Falkowski et al. 2000). At present little is known globally about the effects of stratification on floristic or faunistic shifts (Margalef 1997). Shifts in the degree of stratification and depth of the mixed layer will probably have different effects on the dominant biota in each oceanic province (Fig. 7.21). For example, in the NPSG it may result in a shift towards nitrogen fixers (Karl et al. 1995, 1997), or a shift from a *Phaeocystis* to a diatom-dominated community in the Ross Sea (Arrigo et al. 2000; Moisan and Mitchell 1999), whereas in the NE Atlantic altered stratification may lead to the predominance of coccolithophores (Tyrrell and Taylor 1995), or diatoms in the Equatorial Pacific (Chavez et al. 1999). Each floristic shift will have associated feedbacks

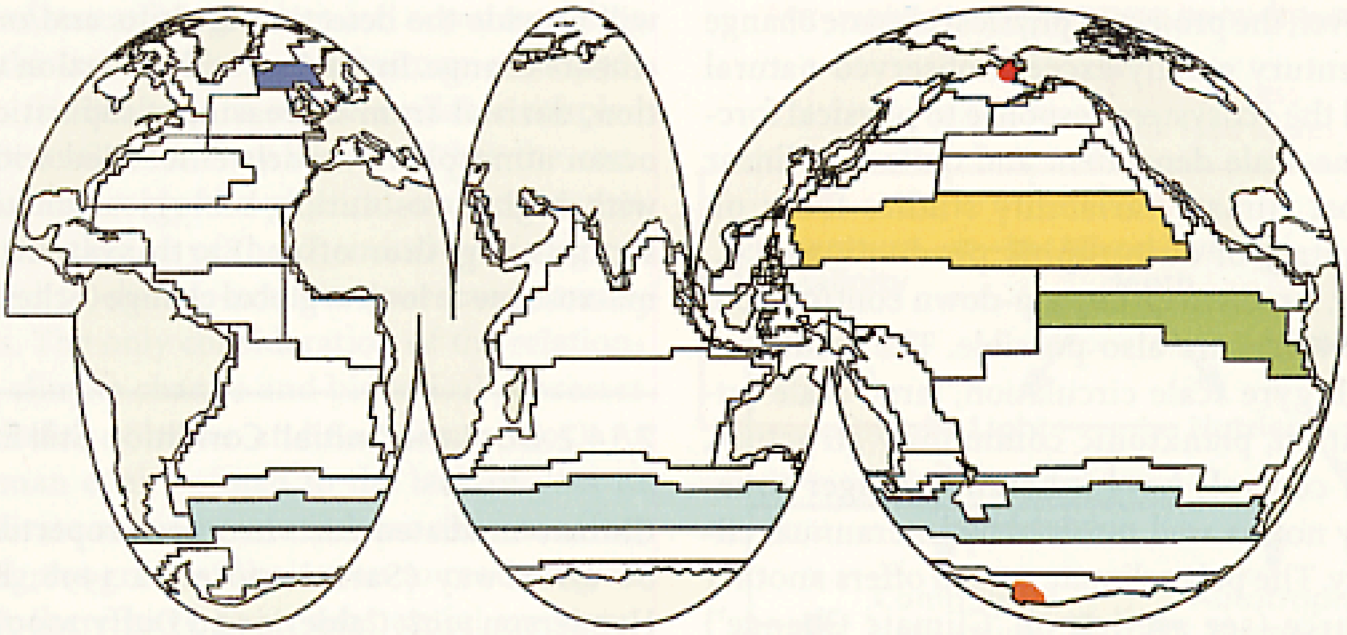


Fig. 7.21. A summary of the likely effects of increased stratification and decreased mixed layer depths on flora in various ocean provinces, based on the scheme of Longhurst (1995, 1998). Note the forcing will result in different outcomes in each region. *Yellow* denotes increased abundances of nitrogen fixers (Karl et al. 2001; a negative feedback); *brown* represents fewer *Phaeocystis* but more diatoms (Arrigo et al. 1999; positive feedback). *Green* denotes a shift to more diatoms (see Fig. 7.17, Chavez et al. 1999; a positive and negative feedback – as waters with higher carbon dioxide concentrations will also be upwelled along with iron). *Red* denotes the persistence of coccolithophorid blooms in the Bering Sea that may have been initiated by the warming of surface waters and increased stratification (Napp and Hunt Jr 2001); *blue* represents subantarctic waters where a decrease in mixed layer depth – in the presence of iron enrichment – results in elevated diatom stocks (Boyd et al. 1999; Blain et al. 2001); *purple* denotes changes in phytoplankton stocks and the length of the growth season in response to climate variability (Reid et al. 1998)

7.14.4 A New Definition of Biogeochemical Provinces?

JGOFS has produced comprehensive biogeochemical datasets from all major oceanic regions. These datasets, which provide an unprecedented level of detail, enable us to refine further the definition of biogeochemical provinces. They also, for the first time, permit us to focus in detail on the complex physicochemical and biological feedback mechanisms that may result from climate change. The observed regional nature of regime shifts and hence biotic feedbacks requires that we adopt a regional-based approach akin to the 'ecological geography' provinces put forward by Longhurst (1995, 1998). Existing criteria for dividing the ocean into provinces has been criticised and referred to as arbitrary (McGowan 1999). Perhaps it is now time to better define ecological boundaries with new goals in mind, to relate them to our improved understanding of ocean physics from the WOCE (World Ocean Circulation Study), to reformulate them so that they are not static and rigid but can be dynamic and alter in time in step with projected changes in ocean circulation. This will be a considerable task beyond the scope and efforts of one individual (Banse 1998). However, this approach will yield a more reliable assessment of the magnitude, evolution, ranking and degree of confidence that presently available for each biotic feedback. It would also be helpful to relate such site-specific observations regionally using remote sensing (Hansen et al. 1995; Chavez et al. 1999). By linking this regional approach with remote-sensing may reduce the dangers of upscaling – 'the process of extrapolating from the site-specific scale at which observations are usually made to the smallest scale that is resolved in global scale models' (Parmesan 1996; Harvey 2000).

7.15 Summary

The most dramatic shift in our perception of marine biotic feedbacks over the last five years has been the widespread occurrence of regime shifts in response to climate variability. Their detection has been possible by using ocean time-series datasets, the first step towards an ocean-observing system. Observations indicate that such regime shifts are relatively rapid, may be forced by a number of different environmental factors, and influence many aspects of biogeochemistry, such as nutrient inventories and the fate of fixed carbon. Furthermore, these regime shifts and their associated feedbacks encompass and overlap the original five feedbacks identified by Denman et al. (1996), suggesting that such biological responses to climate change are likely to be interlinked and complex. In contrast to many of the physicochemical feedbacks, such as stratification or gas solubility, which are amenable to global modeling (Kleypas et al. 1999), biotic feedbacks as manifested by regime shifts appear to be regional in nature. Thus, any modeling attempt must take place initially at this regional level. Datasets from both WOCE and JGOFS will be useful in understanding better how each feedback and/or shift is mediated and forced. Perturbation experiments can provide data needed on the physiological and ecological responses, and this information together with data from satellites on global distributions and geographical extent may be used to define the environmental mode(s) of control on taxa. In addition, a series of ocean-observing systems will be required in the main biogeochemical provinces to permit further assessment of these shifts over time. Such observatories, in tandem with remote-sensing and mathematical models will be needed to obtain 'baseline' conditions for each biogeochemical province. The final goal will be to assess the cumulative impact of such biotic feedbacks, in response to climate change, on the global ocean.

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