ICES STATUS REPORT ON CLIMATE CHANGE IN THE NORTH ATLANTIC

EDITORS

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6 Chlorophyll and primary production in the North Atlantic

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6.1 Introduction

Marine plankton is a crucial component of life on Earth. The plants of the plankton (i.e. the phytoplankton, which include microalgae and photosynthetic bacteria) produce oxygen and change the composition of the air, as well as producing organic matter that sustains marine foodwebs. Annually, phytoplankton contributes approximately half of the net carbon fixation of the biosphere (Behrenfeld et al., 2006). Some of this organic matter is produced in excess of local consumption and becomes incorporated in bottom sediment as a carbon sink by means of the biological pump (i.e. the transfer of CO_2, fixed by photosynthesis in the surface, to the deep oceans in the form of dead organisms, faeces, and carbonated skeletons; Reid et al., 2009b). In a geological context, part of this sink has been transformed into fossil fuels, such as oil and gas. Through the rapid exploitation of fossil fuels, human beings are closing a cycle of millions of years in only a few centuries. Changing this pivotal process of Earth's ecology is likely to lead to imbalances that are difficult to foresee and may lead to pronounced effects on marine ecosystems (Denman et al., 2007).

The importance of marine phytoplankton for the biosphere includes the fixation of inorganic carbon, thereby reducing the concentration of CO_2 in the atmosphere. Phytoplankton also affects the chemical composition of other gases and aerosols (e.g. N_2O, O_2, dimethyl sulphide and sulphate) in the atmosphere, which, in turn, affect climate (Charlson et al., 1987). Increased atmospheric CO_2 has warmed the ocean through the greenhouse effect, but may also lead to shifts in ocean ecosystems because the acidification of marine waters may affect key processes of the biological pump, such as production, calcification, and sedimentation (Orr et al., 2005; Doney et al., 2009; Hofmann and Schellnhuber, 2009).

In addition to their large biogeochemical significance, marine phytoplankton also support foodwebs, including productive fisheries, worldwide. Spatial variation in fishery catch is significantly related to spatial variation in primary productivity (Ware and Thomson, 2005; Chassot et al., 2007). Fishing, as a top–down pressure, also influences catch and affects the movement of energy through ecosystems although, in relatively high productivity areas, increased productivity is associated with increased fishery yields (Frank et al., 2006; Chassot et al., 2010). Improved estimation of the energy transferred to higher trophic levels requires constraints on phytoplankton biomass losses. Apart from cell lysis, losses of phytoplankton are attributed to grazing by zooplankton and to aggregation (the formation and sinking of marine snow), which is responsible for the vertical flux of biomass out of the upper ocean's layers. Thus, understanding the variability of the bottom–up supply of energy from phytoplankton productivity is critical for successful ecosystem-based fishery management in the long term.

Phytoplankton requires adequate levels of light and nutrients for photosynthesis, and is therefore restricted to the upper layers of the ocean, where sunlight penetrates and a supply of nutrients is provided by convective mixing. Temperature of oceanic waters is not, in general, a limiting factor for phytoplankton production (Fasham, 2002). Temperature, however, is one of the main environmental factors affecting the degree of stratification (or, conversely, of mixing) of the surface layers of the ocean. Warming of the ocean surface triggers the development of an upper layer with a

reduced density that restricts both the dispersal of phytoplankton to the dark, deep ocean and the transfer of nutrients upwards from subsurface layers. The optimal environment for phytoplankton production requires some stratification near the surface and sufficient availability of nutrient-rich waters. For this reason, only a small fraction of the ocean displays high levels of primary production (Figure 6.1), but the large size of the less productive ocean explains its importance for global carbon uptake.
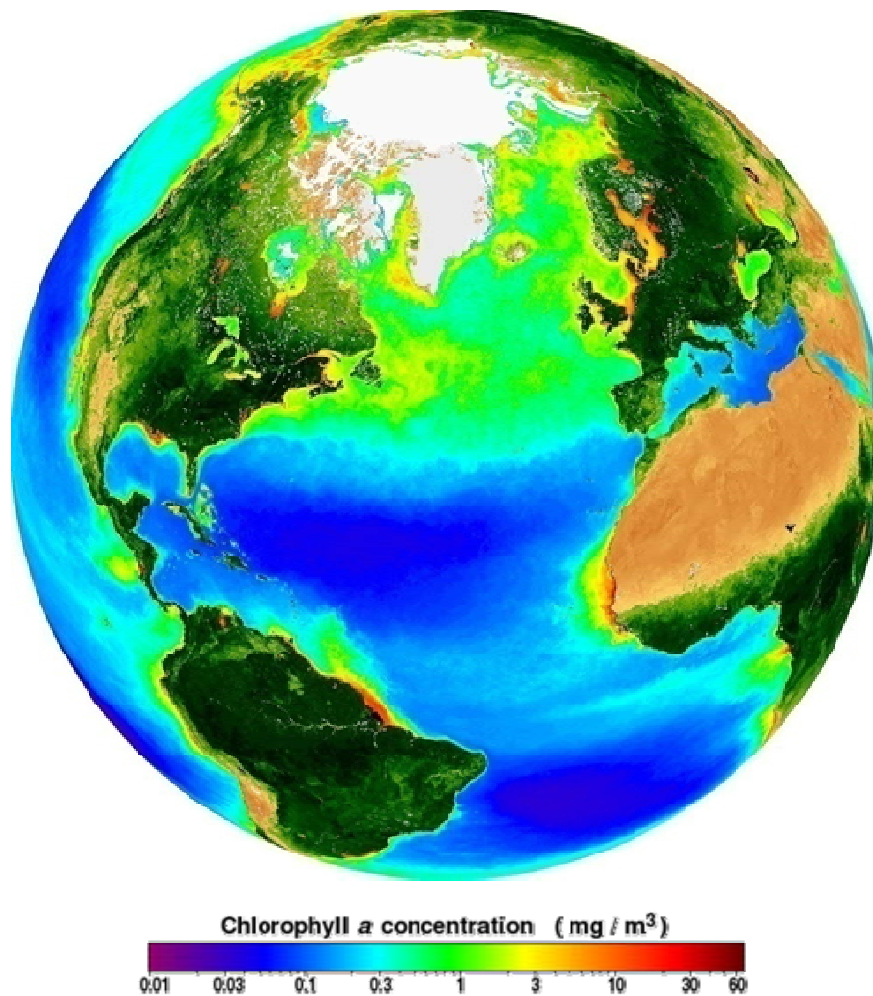
Figure 6.1. Composite image of annual mean surface chlorophyll in the North Atlantic as measured by the satellite-borne Sea-viewing Wide Field-of-view Sensor (SeaWiFS). Image obtained with the GES-DISC Interactive Online Visualization ANd aNalysis Infrastructure (GIOVANNI) of the Goddard Earth Sciences Data and Information Services Center (NASA).

Changes in climate are closely connected to variations in the productivity of the ocean. The warming trend of the atmosphere is already affecting the ocean surface (Revelle and Suess, 1957; Belkin, 2009) and deeper ocean layers, and contributing to modifications in currents and stratification (Bindoff *et al.*, 2007). In principle, higher temperature would favour an increase in primary production up to the optimal growth value and, therefore, greater removal of CO_2 from the atmosphere. Yet, at the same time, rising temperature forced from the surface will lead to the development of a more permanent stratification and a reduced supply of nutrients. The net result of these processes is predicted to be a reduction in global primary production (Behrenfeld *et al.*, 2006). However, the variability seen in data of satellite-derived

phytoplankton concentrations appears to be greater than that of sea surface temperature (SST). This is attributed to advection and mixing processes operating at a mesoscale level and contributing to the supply of nutrients to the upper productive layers (Klein and Lapyere, 2009). In addition, decadal and longer cycles in primary production related to warming and cooling of the ocean are still poorly known, thus limiting the present ability to predict future changes (Chavez *et al.*, 2011).

Human activities are increasing the discharge of nutrients from land (and the atmosphere) into coastal waters, which can lead to excessive levels of primary production and eutrophication (Druon *et al.*, 2004). In coastal and continental shelf regions especially, but also in the open ocean, other direct anthropogenic effects, such as pollution (Cabeçadas *et al.*, 1999) and overfishing (Cury *et al.*, 2000), are increasingly modifying marine ecosystems. Increased UV radiation (Forster *et al.*, 2007) reduces survival and production rates of phytoplankton and affects the turnover of oceanic organic matter, particularly at high latitudes (Moran and Zepp, 2000). However, it is not clear whether or not the increasing radiation would also increase the production of aerosols derived from phytoplankton, and in turn cloud coverage together with a negative feedback on radiation levels in the surface ocean (Charlson *et al.*, 1987), or if this effect would be of minor importance (Woodhouse *et al.*, 2010).

A number of hypotheses on the direction of change (i.e. increase, decrease, or no change) in the production of phytoplankton in the oceans have been proposed and have been tested recently in studies at local, regional, and global scales, with the aim of providing predictive clues for the state of the biosphere in the near future. In this review we will focus on two effects directly related to warming of the ocean.

1) **Thermal stratification** of the surface layers of the ocean induced by warming of the atmosphere is likely to lead to a severe reduction in the supply of nutrients from deeper water to the productive photic layer, thus reducing the production and biomass of phytoplankton, especially in oligotrophic low-latitude regions (Sarmiento *et al.*, 2004). This is the most important negative effect expected for most of the open ocean, where primary production is mainly limited by the input of nutrients from mixing. Where the North Atlantic is strongly influenced by outflow from the Arctic Ocean, stratification by low-salinity waters is intensified by increased meltwater from sea ice and large run-off from circumpolar rivers (Greene and Pershing, 2007). Similarly, evaporation in tropical waters may cause shallower mixed layers than thermal gradients suggest (Foltz and McPhaden, 2009). The ensuing haline stratification, like thermal stratification, can be expected to reduce or enhance primary production according to whether or not the phytoplankton is limited by the fluctuation of nutrients or light, respectively.

2) An increased **thermal gradient** between the land and the ocean (as the ocean responds more slowly to warming than the land) is expected to reinforce alongshore winds and, in turn, increase coastal **upwelling** of deep, nutrient-rich waters near the coast. Such upwelling may increase phytoplankton production in some coastal areas, as was predicted for the major upwelling regions off the east coasts of continents (Bakun, 1990). Modelling studies, however, contend that warming will decrease upwelling on a global scale (Hsieh and Boer, 1992). The outcome of these two major opposing scenarios is difficult to foresee because of regional differences and interactions with other factors, particularly near the land–

sea interface, where atmospheric, terrestrial, and oceanic forcings intersect (Cloern and Jassby, 2008; Beardall *et al.*, 2009).

6.2 Regional approach and datasets

Given the large number and variety of regions within the oceans, phytoplankton is likely to show an equally diverse and complex response to changes in climate. In this section, we examine the evidence of change during recent decades in phytoplankton biomass and primary production, with special emphasis on the waters of the Atlantic Ocean north of 25°N. Studies reviewed include global scale analyses as per the United Nations Environment Programme (UNEP) Large Marine Ecosystem Report for the coastal ocean (Sherman and Hempel, 2009), and other analyses for deep ocean regions (e.g. McClain *et al.*, 2004; Antoine *et al.*, 2005; Gregg *et al.*, 2005; Behrenfeld *et al.*, 2006; Chavez *et al.*, 2011). Studies at regional or local scales, including long-term observations, were considered to display a variety of responses. The latter were illustrated by the contributions to the Theme Session on "Trends in Chlorophyll and Primary Production in a warmer North Atlantic" during ICES Annual Science Conference 2009 in Berlin. In addition, trends in phytoplankton biomass in North Atlantic waters were extracted from the time-series recorded in the ICES Zooplankton Status Report 2006/2007 (O'Brien *et al.*, 2008).

Phytoplankton biomass is represented in most studies by chlorophyll *a* concentrations, derived either from satellite measurements, as in global or regional studies (e.g. Behrenfeld *et al.*, 2006; Sherman and Hempel, 2009), or from direct determinations in field samples, the latter generally in local studies (e.g. Bode *et al.*, 2009b). Chlorophyll biomass is indicative of primary production over the past hours or days, reflecting the net result of production and losses through grazing, cell lysis, exudation of organic matter, and sedimentation. Primary production can be determined by several methods, but the most extended is ^{14}C-labelling in incubations of phytoplankton for a few hours. These measurements, however, are limited to a few depths and sites. As for chlorophyll, in global studies, primary production is computed from satellite data using models. These models are generally applied to weekly or monthly data, resulting in production estimates over large spatial scales that are less variable than *in situ* measurements. Temporal variability of chlorophyll and primary production is assessed using time-series. However, although ^{14}C measurements have been collected over the past 50 years, there are only a few *in situ* time-series that extend over ~2 decades. Such long-term data are needed to determine multivariate effects of the environment on primary production and biomass (see Chavez *et al.*, 2011). Global estimates of chlorophyll and production derived from satellites since 1997 are available (e.g. McClain *et al.*, 2004). Estimates of chlorophyll from satellite measurements are complicated by the presence of mineral particles, coloured dissolved organic matter, and other materials (Mobley *et al.*, 2004). These particles are more concentrated in coastal waters and can lead to errors in satellite estimates of chlorophyll compared with *in situ* measurements (Guðmundsson *et al.*, 2009). In this review, we use time-series of water-column integrated chlorophyll and primary production values derived from both satellites and *in situ* measurements, where available. In other cases, surface measurements are employed, because water column production is globally related to surface values (Chavez *et al.*, 2011).

Evidence of changes in phytoplankton biomass and primary production in ICES waters and in some additional areas to the west of Greenland are presented below. These geographic regions (Figure 6.2) have distinctive ecological characteristics. Linear trends in SST (1982−2007; Belkin, 2009) and phytoplankton biomass and

production derived from satellite data in this region (1998–2006; Table 6.1) were obtained from the study by Sherman and Hempel (2009), although the time-series is very short for interpretation of links to climate. The descriptions were completed with additional time-series data from field studies (e.g. Barton *et al.*, 2003; O'Brien *et al.*, 2008). Recent global phenological analyses (Cloern and Jassby, 2008; Zingone *et al.*, 2010) describe the timing and amplitude of recurrent features in the annual cycle of phytoplankton at many coastal sites within the North Atlantic regions under consideration.
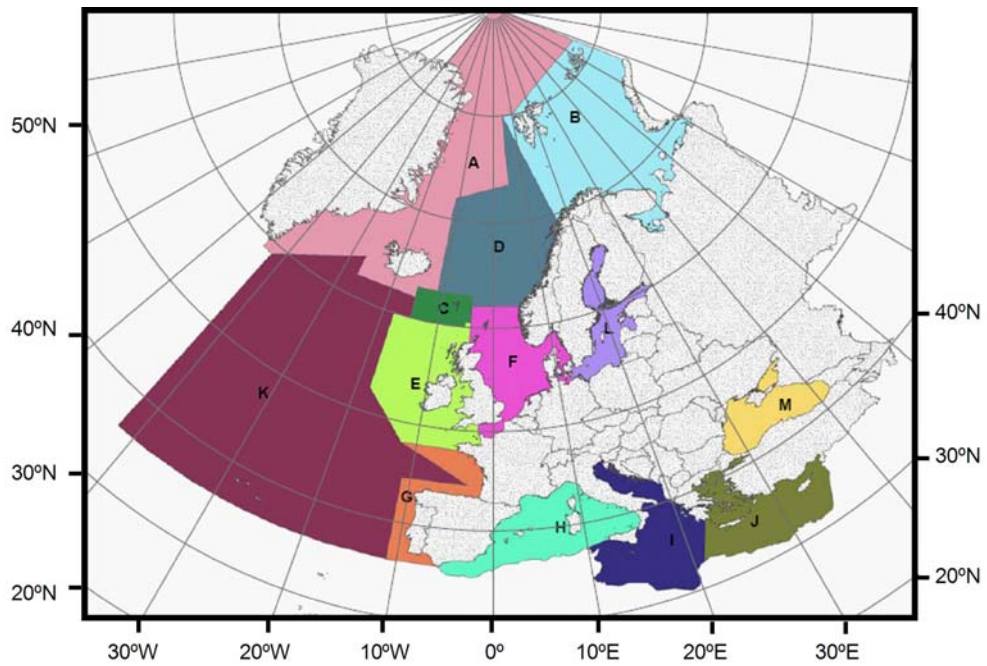

Figure 6.2. Ecoregions based on ICES Advice ACFM/ACE report (ICES, 2004a). A = Greenland and Iceland Seas, B = Barents Sea, C = Faroes, D = Norwegian Sea, E = Celtic Sea, F = North Sea, G = South European Atlantic Shelf, H = Western Mediterranean Sea, I = Adriatic-Ionian Seas, J = Aegean-Levantine Seas, K = Oceanic Northeast Atlantic, L = Baltic Sea, M = Black Sea. ICES Convention area (FAO area 27) includes regions A–G, L. Regions H–J, M are outside the ICES area.

Table 6.1. Linear trends in mean annual values of sea surface temperature (SST trend, °C (10year)$^{-1}$), chlorophyll *a* (B trend, mg Chl *a* m^{-3} year^{-1}), and primary production (PP trend, mg C m^{-2} year^{-1}) with time between 1982 and 2007 (SST) or 1998 and 2006 (B and PP). Mean values for chlorophyll (B, mg Chl a m^{-3}) and primary production (PP, mg C m^{-2} year^{-1}) for the whole period are also indicated. Significance of trends is shown by asterisks: * = $p<0.05$, ** = $p<0.01$. (Data and trend analysis from Sherman and Hempel, 2009.)

Large Marine Ecosystem	SST trend	B trend	PP trend	B	PP
Iceland seas	0.86	0.031	0.589	1.19	203
East Greenland	0.73	0.028*	1.674	0.80	130
West Greenland	0.73	0.021	0.277	1.00	149
Barents Sea	0.12	0.091**	4.812	2.45	240
Faroe Islands	0.75	0.031	3.403	0.81	174
Norwegian Sea	0.85	−0.003	−1.627	1.21	204
Celtic Sea	0.72	−0.002	1.051	1.26	225
North Sea	1.31	−0.007	−0.030	2.26	294
Southeastern European Atlantic Shelf	0.68	0.003	−0.359	0.53	156

Baltic Sea	1.35	0.094	10.499	6.87	601
Northwestern Atlantic (Newfoundland–Labrador shelf)	1.04	0.014	-0.689	1.07	181
Northwestern Atlantic (Scotian Shelf)	0.89	0.026	0.916	1.75	257
Northwestern Atlantic (US Northeastern shelf)	0.23	0.019	0.690	2.38	345

6.3   Changes at a global scale

The spatial scale of the distribution of phytoplankton that is relevant to climate response studies varies from metres to entire ocean basins (Fasham, 2002). There is, therefore, a need for global assessments of phytoplankton biomass and production that are based on long time-series of observations to ascertain the impact of climate change on these variables. Information on the spectral colour of the ocean surface has been gathered by satellites since the early 1980s and has been used to produce comprehensive global estimates of phytoplankton biomass and, later, using models, of primary production. The first long-term analyses (Antoine *et al.*, 2005) estimated an overall increase of ca. 22% in the global average of oceanic chlorophyll concentration between the period 1979–1986, when the first observations were made by the Coastal Zone Colour Scanner (CZCS), and the more recent period, 1998–2002, measured by the Sea-viewing Wide Field-of-view Sensor (SeaWiFS). The increment consisted of a large increase in the intertropical regions during spring and summer, a lower increase at higher latitudes, and a decrease in the oligotrophic gyres, and was not the result of the differences in methodology between the two periods. The Atlantic Ocean ranked second after the Indian Ocean in the level of increase (Antoine *et al.*, 2005). Later studies confirmed the global increase (estimated at 4.1% globally in the period 1998–2003) with the largest change (+10.4%) in coastal regions (Gregg *et al.*, 2005). Enhancement of coastal upwelling (Bakun, 1990) was considered a possible cause of the increase, although a direct effect of eutrophication by anthropogenic nutrient additions in most coastal regions could not be ignored.

More recent analyses, which considered water-column integrated production derived from satellite data, aligned the increases with cooling periods (including the *El Niño/La Niña* transition from 1997 to 1999), but demonstrated a general reduction in both phytoplankton biomass and production with warming at low latitudes and an increase at high latitudes (Behrenfeld *et al.*, 2006; Chavez *et al.*, 2011). This was attributed to increased stratification by surface warming that, in turn, would have reduced nutrient inputs by mixing and eventually primary production at low latitudes. In contrast, stratification would have increased the time for which phytoplankton cells were exposed to light at high latitudes, where primary production is limited by light (Figure 6.3). Oligotrophic gyres, characteristic of the subtropical areas of all oceans, were the most important regions for primary production and biomass, despite their low biomass of phytoplankton, because of their large size. The oligotrophic areas of the subtropical ocean have increased steadily in size since 1998 (McClain *et al.*, 2004; Behrenfeld *et al.*, 2006; Polovina *et al.*, 2008), probably as a consequence of a reduced input of nutrients caused by enhanced stratification. Even so, the input of nutrients caused by submesoscale processes is not well resolved in these areas (Klein and Lapyere, 2009). The changes in global primary production were correlated with variation in global climate, as indicated by the *El Niño*/Southern Oscillation index (Behrenfeld *et al.*, 2006; Chavez *et al.*, 2011), suggesting that global climate plays a major role in its variability. By extending the surface chlorophyll time-series back to 1899 using water transparency records, a general decreasing trend was found in most ocean basins (Boyce *et al.*, 2010),

although this result has been contested (Mackas, 2011; Rykaczewski and Dunne, 2011; McQuatters-Gollop *et al.*, 2011) The analysis by Boyce *et al.* also concluded that climatic oscillations (e.g. *El Niño*) accounted for most of the variability of surface chlorophyll. However, in these global studies, data from the productive continental shelves are generally outweighed by those from the larger oligotrophic areas of the ocean, where most of the production and chlorophyll is well below the surface layer, and does not include cyanobacteria and other small phytoplankton. Cyanobacteria (e.g. *Prochlorococcus*) and other small phytoplankton are found well below the surface layer in the larger oligotrophic areas. In any case, as corroborated by palaeoclimatic studies (see references in Chavez *et al.*, 2011), the computed linear trends in primary productivity are only indicative of the direction of change during a limited period when considering long-term oscillations in climate and primary productivity.
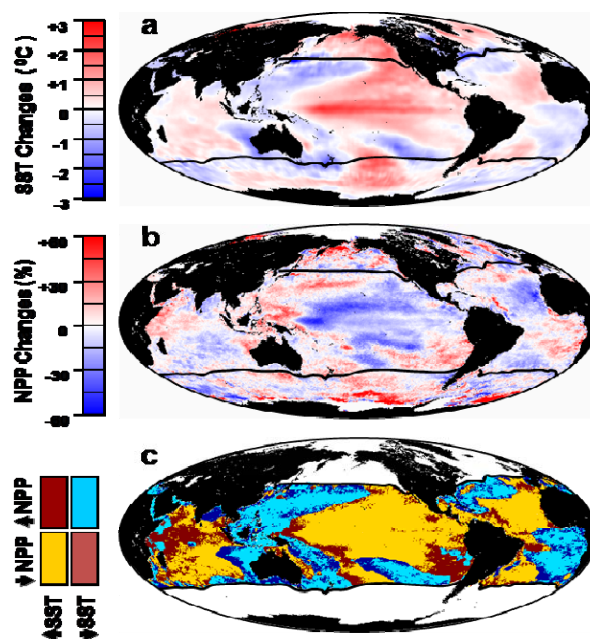

Figure 6.3. Climate controls on ocean productivity cause net primary production (NPP) to vary inversely with changes in sea surface temperature (SST). Global changes in: (a) annual average SST, and (b) NPP for the 1999–2004 warming period (c). For 74% of the permanently stratified oceans (i.e. regions between black contour lines), the NPP and SST changes were inversely related. Yellow = increase in SST, decrease in NPP; light blue = decrease in SST, increase in NPP; dark blue = decreases in SST and NPP; dark red = increases in SST and NPP. A similar inverse relationship is observed between SST and chlorophyll changes. (Source: Behrenfeld *et al.*, 2006, Figure 3. Courtesy of *Nature*.)

In contrast to the open ocean, an examination of variations in chlorophyll and primary production over the continental shelf did not reveal any consistent large-scale pattern of change between 1998 and 2006 (Sherman and Hempel, 2009). Out of 64 Large Marine Ecosystems (LMEs) analysed, only ten revealed statistically significant trends in mean annual chlorophyll and four in the case of primary production. Most of the trends, however, were positive, with significant decreases only in the eastern Siberian Sea (chlorophyll) and the Bay of Bengal (primary production). Such variability in coastal systems is to be expected, given the relative shortness of the time-series (9 years) and the multiple factors affecting primary production in the coastal ocean (e.g. stratification, nutrients, eutrophication, turbidity). Considering *in situ* time-series spanning the last 10–20 years, both chlorophyll and primary production increased at coastal sites, particularly at eastern

boundary continental margins, and were associated with major climate anomalies (Chavez *et al.*, 2011). These results suggest that, in general, productivity in coastal ecosystems benefits from warming and increased nutrient inputs from both open ocean and coastal sources. In turn, fishery biomass yields were enhanced with increasing primary productivity in all LMEs, particularly in areas with moderate warming (Figure 6.4).
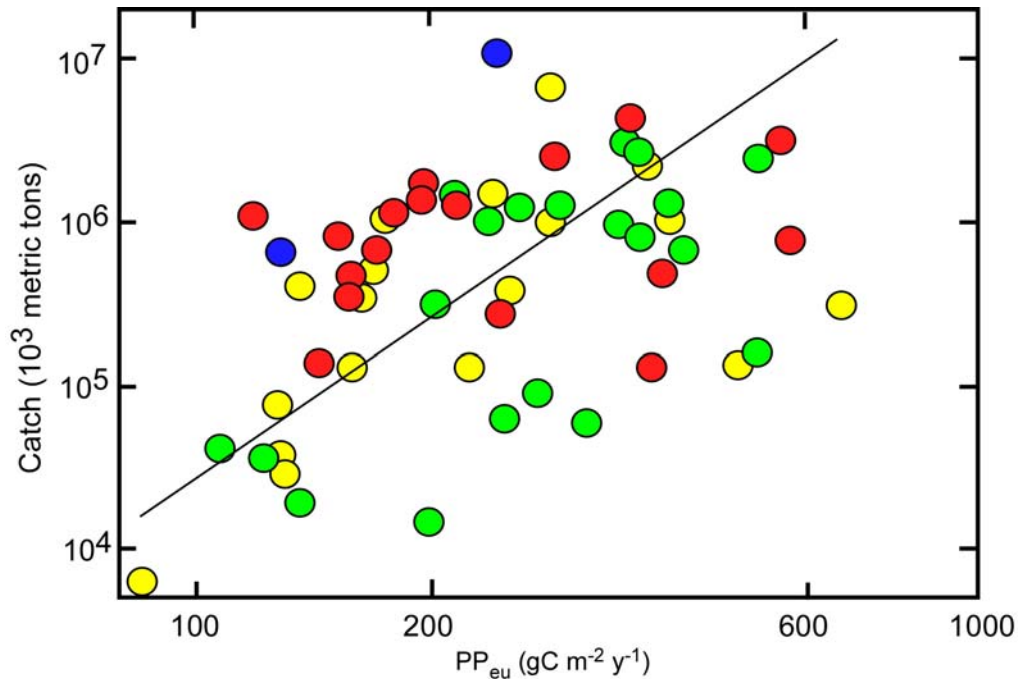

Figure 6.4. Positive correlation of 5-year mean annual fishery biomass yield with 9-year mean annual primary production in fast warming (red), moderately warming (yellow), slower warming (green), and cooling (blue) Large Marine Ecosystems (LMEs). Significance of regression line $p<0.001$. (Source: Sherman and Hempel, 2009, Figure 5a. Courtesy of UNESCO.)

From a biogeochemical perspective, however, the observed changes in phytoplankton biomass and production did not seem to have greatly influenced the capacity of the ocean to store carbon, which was estimated at $1.8 \pm 0.8 \, \text{Gt C year}^{-1}$ in the 1980s, $2.2 \pm 0.4 \, \text{Gt C year}^{-1}$ in the 1990s, and $2.2 \pm 0.5 \, \text{Gt C year}^{-1}$ between 2000 and 2005 Denman *et al.*, 2007). This suggests that major changes in physiology (e.g. increased respiration), foodwebs (e.g. increased predation), and biogeochemical processes (e.g. acidification and sedimentation rates) are occurring in parallel with the observed changes in phytoplankton production at the scale of the global ocean and affecting the carbon cycle on Earth (Figure 6.5).
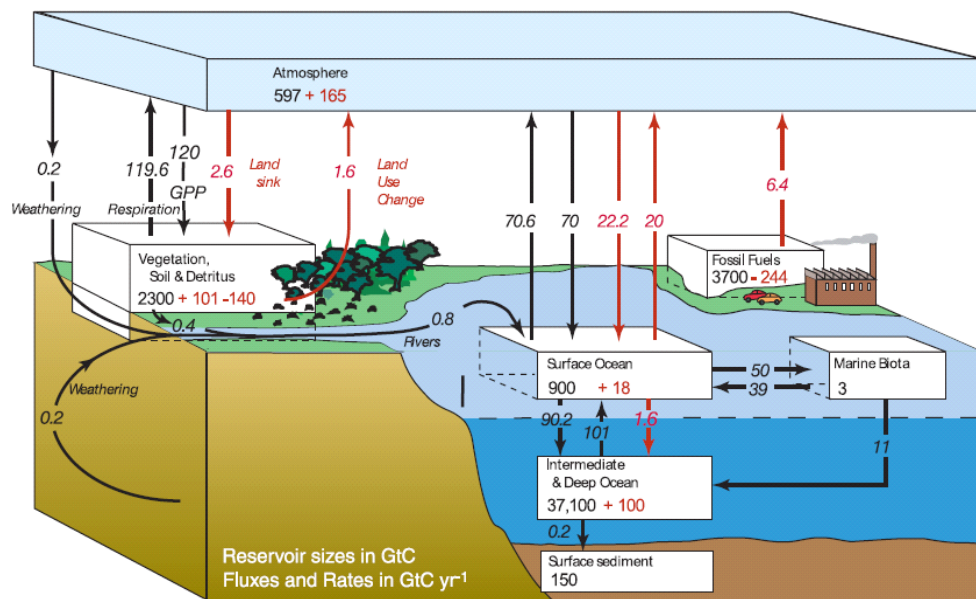
Figure 6.5. The global carbon cycle for the 1990s, showing the main annual fluxes in Gt C year^{-1}; black = pre-industrial "natural" fluxes; red = "anthropogenic" fluxes. Gross fluxes generally have uncertainties of more than ±20%, but fractional amounts have been retained to achieve overall balance when including estimates in fractions of Gt C year^{-1} for riverine transport, weathering, deep ocean burial, etc. GPP = annual gross (terrestrial) primary production. Atmospheric carbon content and all cumulative fluxes since 1750 are as of end 1994. (Source: Denman *et al.*, 2007, Figure 7.3.)

6.4   Changes in North Atlantic regions

The large heterogeneity in the distribution of phytoplankton (as shown in Figures 6.1 and 6.3) is well represented in the North Atlantic waters studied by ICES (Figure 6.2). In this region, marine ecosystems range from the Arctic to temperate, mid-latitude waters, and from the deep ocean to coastal and shelf seas. It also includes enclosed or semi-enclosed seas, such as the Baltic Sea. The physical characteristics of the various subregions constrain phytoplankton production, mainly by determining the area and period where blooms can be produced. For instance, parts of the Arctic are covered by seasonal sea ice for an extended period of the year, thus restricting bloom development in open waters to a relatively short period after the ice melts, when light levels in the surface layer and nutrients allow phytoplankton growth. Melting of sea ice favours local increases of stratification because of the input of freshwater and also provides microalgae, fostering a bloom over large areas, which follows the melting front as it recedes (Sakshaug and Slagstad, 1992; Niebauer *et al.*, 1995).

In contrast, in open waters at lower latitudes in the ICES region, phytoplankton production is concentrated in spring and autumn. In this case, as the annual cycle of sunlight progresses, spring stratification developed by the gradual warming of the surface leads to a rapid uptake of nutrients by the phytoplankton. These nutrients are soon exhausted in the upper layer and remain at low levels throughout summer. In these circumstances, the only input of nutrients for phytoplankton growth comes from deeper waters through the pycnocline (i.e. where the water density gradient in the mixing layer is maximum) via eddy diffusion and from physical instabilities that induce mixing. The result is the development of a characteristic deep chlorophyll maximum, closely related to the nitracline (i.e. the maximum subsurface nitrate gradient). The deep chlorophyll maximum occurs at depths where phytoplankton growth critically depends on light and nutrients, and its maintenance and magnitude

is regulated by a close coupling of biological and physical processes (Varela *et al.*, 1992). Consumption by grazers is enhanced near this maximum, preventing further phytoplankton accumulation (Burkill *et al.*, 1993). The mixing of the surface and subsurface layers as the thermal gradient is disrupted during autumn results in new blooms in some areas, although the strong mixing and low light levels during winter restrict any further growth of phytoplankton. This seasonal pattern is modified over the continental shelf by the mixing effect of tides and by riverine and terrestrial inputs at intermediate (10–100 km) scales. In this way, coastal areas and semi-enclosed seas display a characteristically heterogeneous distribution of blooms for most of the year, although primary production is still maintained at low levels during winter (Smetacek, 1988).

Blooms are generally concentrated in the transitional periods between water-column mixing and stratification (i.e. winter–spring and summer–autumn) and the timing of changes in stratification, and bloom formation is crucial to many ecosystem processes, including the success of fish larvae (Cushing, 1990; Rodríguez, 2008). Increases in phytoplankton biomass during blooms and extension of the growing season were observed in the North Sea and in the Atlantic in the 1980s (Reid *et al.*, 1998; McQuaters-Gollop *et al.*, 2007). These changes also expanded to nearby regions and were related to changes in large-scale hydrometeorologic forcing (temperature and wind intensity and direction, and associated changes in the position of oceanic biogeographic boundaries) and reflect a pronounced change in climate (Beaugrand, 2004). A general trend in the North Atlantic, evident from global studies from 1979 to present, is an increase in phytoplankton biomass in shelf areas of both the Northeast and Northwest Atlantic, and to a decrease in phytoplankton biomass in the central North Atlantic Subtropical Gyre (Antoine *et al.*, 2005; Gregg *et al.*, 2005; Vantrepotte and Mélin, 2009).

Shelf systems also include ecosystems that are subject to seasonal coastal upwelling, induced by alongshore winds, which enhances primary production near the coast through the input of nutrients from deep waters. In this regard, the northwest Iberian coast represents the northern limit of the eastern boundary upwelling ecosystem of the North Atlantic (Alvarez *et al.*, 2008), which has a large impact on primary production and marine foodwebs in this region (Bode *et al.*, 1996; Alvarez-Salgado *et al.*, 2002; Valdés *et al.*, 2007; Bode *et al.*, 2009a, 2009b; Pérez, F. F., *et al.*, 2010). Local upwelling, caused by internal tides, also occurs along the shelf break, enhancing phytoplankton production (e.g. Pingree *et al.*, 1982).

6.4.1 Greenland and Icelandic seas

Warming of the sea surface has proceeded at a fast rate in this region since 1982 (Belkin, 2009), exceeding the global average of 0.2 °C decade^{-1} (Bindoff *et al.*, 2007). The warming was accompanied by increases in both phytoplankton biomass and production (Table 6.1), although only trends in annual average chlorophyll for the period between 1998 and 2006 in the Eastern Greenland Shelf were significant (P<0.05). On the West Greenland Shelf, increases in spring chlorophyll from 1994 to 2005 (Li *et al.*, 2006) have continued throughout 2009 (Labrador Sea Monitoring Group, 2010). It is often presumed that annual primary production in these waters is linearly related to the duration of the ice-free period through cumulative exposure to solar irradiance. However, the regions with the longest ice-free periods are also those where advective and convective supply of nutrients are extensive. It appears that annual primary production per unit area in seasonally ice-free waters is controlled

primarily by nitrogen supply and modulated by the light regime, which may affect phenology and species composition (Tremblay and Gagnon, 2009).

6.4.2 Barents Sea

In this region, there has been a minimal linear increase in SST, but average annual phytoplankton biomass (but not production) increased significantly (Table 6.1). These results are supported by a reduction in the oxygen saturation of bottom waters, as revealed by *in situ* measurements over the period 1957–2008 (Titov, 2009). The oxygen saturation of the near-bottom layers in the Barents Sea has decreased by ca. 1% in this period, and a prolonged period of low saturation was observed between 1998 and 2005 (Figure 6.6). The excess oxygen consumed can be considered a proxy for an increase in the degradation of organic matter produced by phytoplankton. As in the previous region, warming has favoured the melting of ice and enhanced the formation of hydrographic fronts with increased water column stability, allowing an expansion of areas that are suitable for the growth of phytoplankton populations.
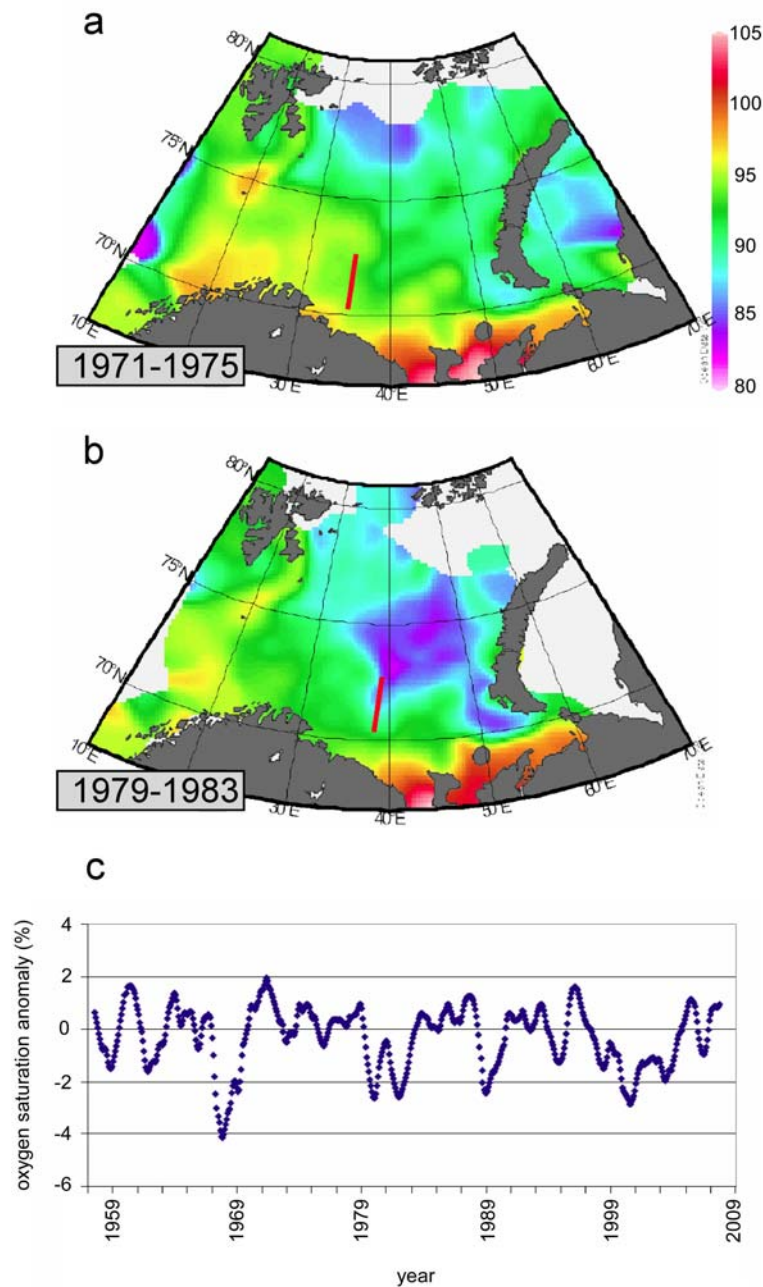
Figure 6.6. Oxygen saturation (%) of bottom layers in the Barents Sea averaged for periods of (a) high saturation (1971–1979) and (b) low saturation (1979–1983). The red line shows the position of the Kola section from where the mean anomalies smoothed by moving-average from the previous year are displayed (c). (Source: modified from Titov, 2009.)

6.4.3   Faroe Islands

As for other high-latitude regions, warming has proceeded at a fast rate in the sea around the Faroe Islands (Belkin, 2009), with SST values above the mean of the past century (O'Brien *et al.*, 2008). Satellite data since 1998 have revealed a small, but not significant, increase in both phytoplankton biomass and production (Table 6.1), although field data for the period 1990–2007 demonstrated no clear trend in chlorophyll values to the north or south of the Faroe Islands (O'Brien *et al.*, 2008).

6.4.4 Norwegian Sea

No significant trends in satellite-estimated phytoplankton biomass and production were measured in the Norwegian Sea, which is characterized by high warming rates (Table 6.1). Chlorophyll measurements during spring cruises in the area since 1991 reveal a significant positive relationship between chlorophyll and stratification, with values in the Arctic generally exceeding those found in Atlantic waters (Figure 6.7). Temporal trends, however, were inconclusive in these series (Debes *et al.*, 2009).
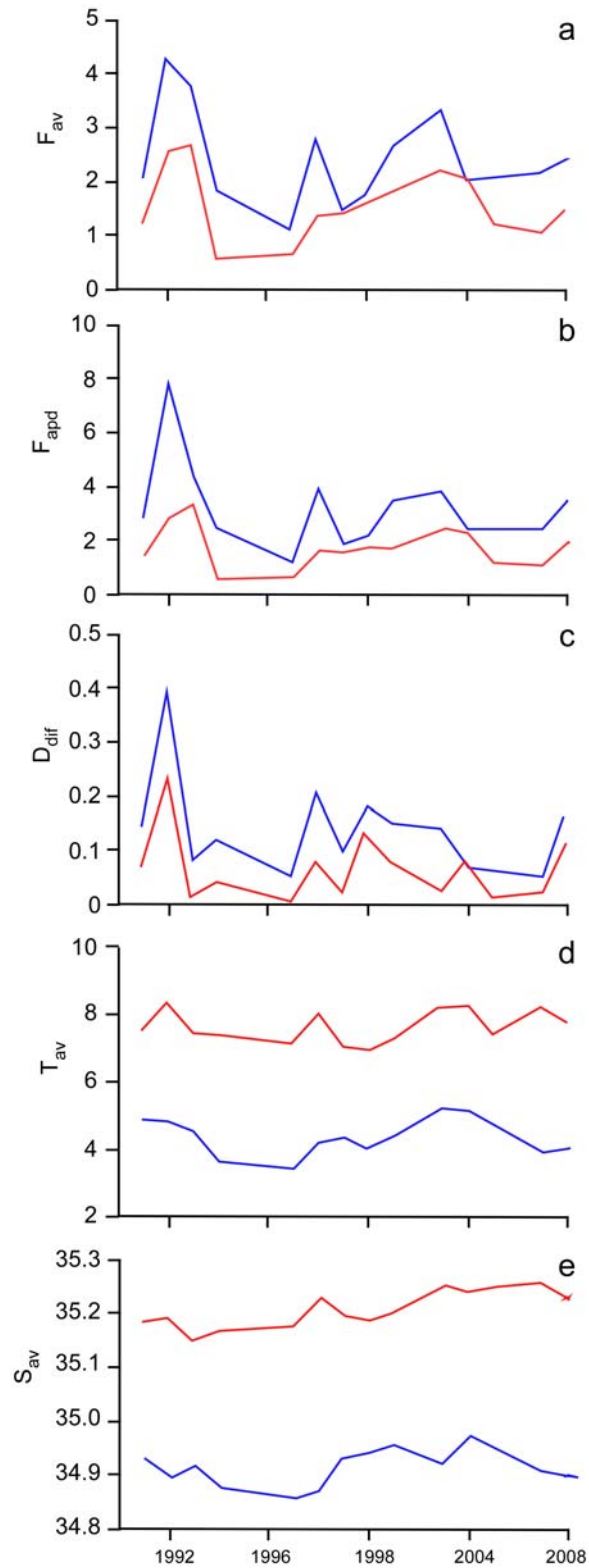
Figure 6.7. Time-series (from top to bottom) of: mean (±s.d.) chlorophyll *a* concentration (mg m⁻³) in the upper 50 m (F_{av}); chlorophyll *a* concentration (mg m⁻³) above the pycnocline (F_{apd}); density change (kg m⁻³) through the upper 50 m (D_{dif}); temperature (°C) in the upper 50 m (T_{av}); and salinity in the upper 50 m (S_{av}); measured in a transect of 14 stations running along 6°05′W, from 62°20′N to 64°30′N in the Norwegian Sea during May. Blue lines = Arctic Water; Red lines = Atlantic Water. (Source: Debes *et al.*, 2009).

6.4.5 Celtic Sea

Changes similar to those in the Norwegian Sea were also observed in the Celtic Sea (Table 6.1), where phytoplankton biomass and production did not change significantly over time, despite the rapid warming of surface waters. A more detailed analysis of satellite data emphasized the large variability observed within this region (i.e. no change or a reduction in the oligotrophic areas in the north and central part of the region and an increase in the south), although field studies also indicated no clear trend in the period 1992–2007 (O'Brien *et al.*, 2008). Similarly, a study of a time-series of annual primary production, based on nutrient inputs by mixing and estimated from additive models, revealed no clear pattern between 1960 and 2003, but demonstrated high production periods in the early 1960s and 1990s (Heath and Beare, 2008). The study revealed that primary production in stratified oceanic areas was correlated with the North Atlantic Oscillation (NAO) index and explained the high production periods as a response to an enhanced flux of nitrate-rich oceanic water in the early 1990s (Figure 6.8). In contrast, nutrient inputs from rivers and the atmosphere were of lesser importance for primary production than oceanic inputs into the Celtic Sea (Heath and Beare, 2008). Other studies noticed a marked increase in the Phytoplankton Colour Index (PCI, a proxy for phytoplankton biomass determined from the greenness of Continuous Plankton Recorder (CPR) samples) between 1958 and 2002 in a region of the Northeast Atlantic that includes the Celtic and North seas (Leterme *et al.*, 2005). Such an increase cannot be attributed to the effects of eutrophication by anthropogenic nutrients near the coast but is mainly the result of warm winters increasing stratification and the input of oceanic waters, along with an improvement in water clarity resulting from reduced turbidity (Leterme *et al.*, 2005; McQuatters-Gollop *et al.*, 2007, 2009).
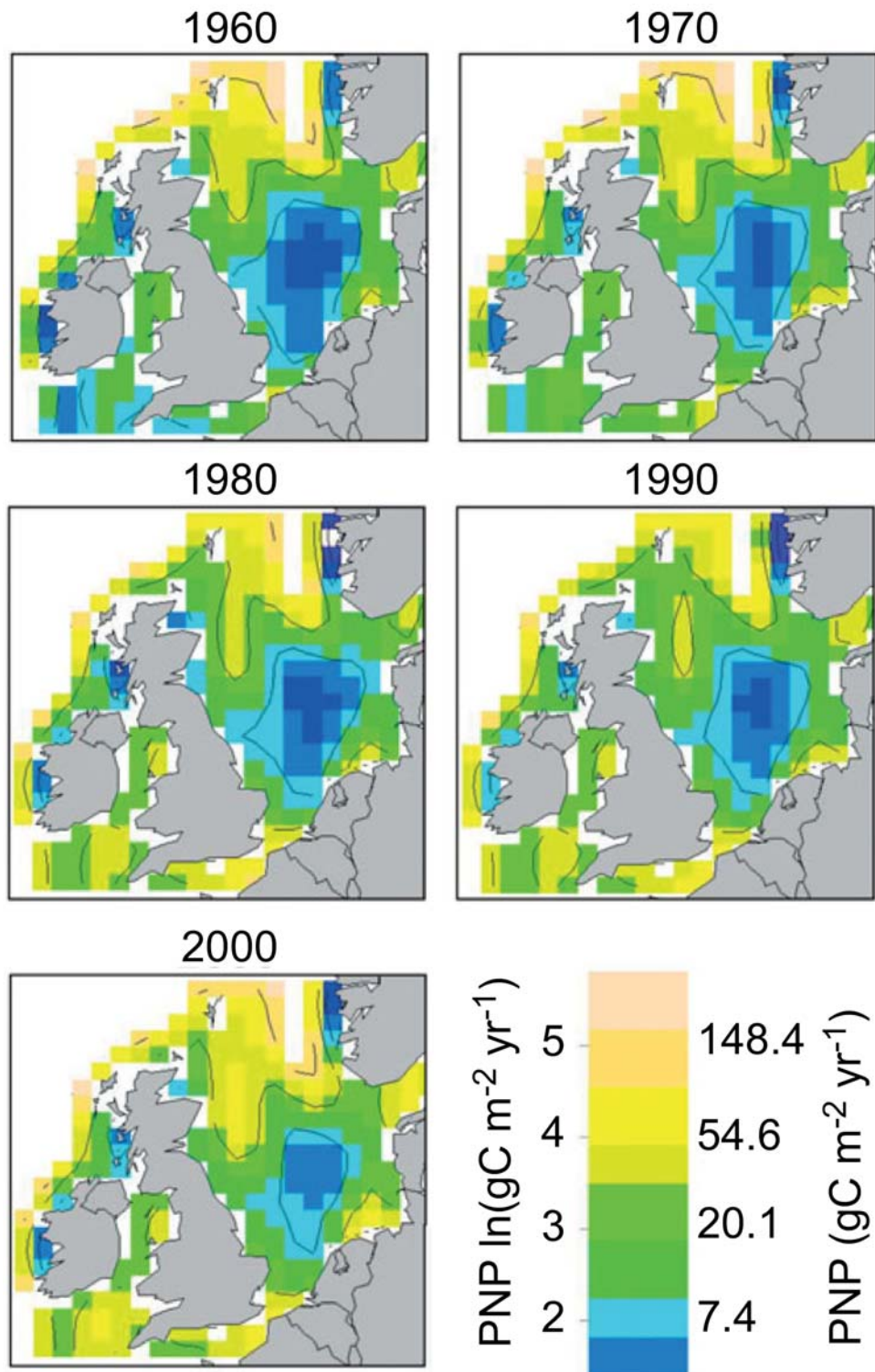
Figure 6.8. Spatial distributions of $\log_e$-transformed annual potential new primary production (PNP, ln g C m^{-2} year^{-1}) at 10-year intervals from 1960, estimated from the draw-down of nitrate in the water column. Contours shown at log-PNP values of 3, 4, and 5. (Source: Heath and Beare, 2008, Figure 5. Courtesy of Inter-Research.)

6.4.6 North Sea

The North Sea is one of the most studied regions of the North Atlantic, displaying one of the fastest rates of warming in recent years (Belkin, 2009). When considering the whole region, average annual phytoplankton biomass and production

demonstrated little change in the period 1998–2006 (Table 6.1). Studies of field data, however, indicate a large variability in observed responses. Phytoplankton chlorophyll decreased in the northeast of the region (Skagerrak), although no clear trend was found in the northwest (Stonehaven) in the period 1994–2007 (O'Brien *et al.*, 2008). Over a longer period (1946–2002), a stepwise increase in phytoplankton biomass, as deduced from PCI values, occurred after the major late phase-shift of the 1980s (regime shift) in oceanography that affected many physical and ecosystem variables in the North Sea (Reid *et al.*, 2001a; Beaugrand, 2004; Leterme *et al.*, 2005; Weijerman *et al.*, 2005). This increase in phytoplankton biomass has been largely attributed to the climatic effect of warm winters that increased water column stratification, reduced turbidity (McQuatters Gollop *et al.*, 2007), enhanced the nutrient input from oceanic waters (Reid *et al.*, 2003a), and favoured phytoplankton production.

Like the Celtic Sea, the estimated production during the period 1960–2003 revealed no clear pattern (Figure 6.8), with a high production period in the early 1990s (Heath and Beare, 2008). Although the influence of nutrients provided by riverine and atmospheric sources was, on average, larger than that calculated for the Celtic Sea, the concentration of nitrate in the water appeared to be determined more by the concentration in ocean source waters than in river inputs (Hydes *et al.*, 2004). The production maximum in the early 1990s was attributed mainly to oceanic inputs driven by climate (Reid *et al.*, 2003a; Heath and Beare, 2008). At local scales, field data also revealed frequent periods of increase and decrease. For instance, Lindahl (1995) reported an increase in phytoplankton biomass and annual primary production at a coastal site in the Skagerrak in the period 1985–1994, caused in part by large blooms in 1987–1988. The changes were attributed to an increase in nutrient inputs but their source (oceanic or terrestrial) was not identified. However, an extension of the dataset to 1996 and new analyses revealed that the increasing trend in primary production was not significant and that climate-driven oceanographic changes may have triggered a lagged response of the phytoplankton (Lindahl *et al.*, 1998).

Similarly, Cadée and Hegeman (2002) found an increase of phytoplankton biomass in the coastal Wadden Sea from 1973 to 1985, then a small decrease until 2000. Primary production also increased, in this case from 1964 to 1974, and then decreased as reported for biomass. Coastal eutrophication has been invoked to explain earlier increases, with subsequent reductions in both biomass and production attributed to improvements in the removal of excess (anthropogenic) nutrients in river waters (e.g. Hickel *et al.*, 1993), but recent interpretations assign a major role to changes in the nutrient inputs from oceanic waters (Carstensen *et al.*, 2005; McQuatters-Gollop *et al.*, 2007, 2009; Schlüter *et al.*, 2009). However, coastal (<10 km offshore), estuarine, and isolated areas, which are not being monitored by the CPR programme, are likely to be affected by nutrient discharges from the continent.

6.4.7 Southeastern European Atlantic Shelf

This region is characterized by a transition between open ocean and shallow coastal waters on the one hand, and south–north and east–west reducing gradients in the intensity of upwelling (Lavín *et al.*, 2004) on the other. As a consequence, multiple fronts and alternating extremes influence the photic zone where phytoplankton production occurs (Bode *et al.*, 1996; Alvarez-Salgado *et al.*, 2002). This may explain why overall trends in phytoplankton biomass and production were small and insignificant (Table 6.1), even when sea-surface warming proceeded at a relatively high rate. Annual mean values of phytoplankton biomass appeared to increase in the

period 1958–2002, considering the whole region and the changes observed in PCI (Leterme *et al.*, 2005), but such changes were not significant when considering only the upwelling-influenced southwest of the region and extending the data period to 2006 (Bode *et al.*, 2009a). For coastal and offshore waters located farther south, in the vicinity of the Galician Rías Baixas, a significant decrease in net primary production, estimated from new nutrient inputs and accompanied by shifts in phytoplankton dominant groups, was associated with weakened upwelling over a 40-year period (Pérez, F.F., *et al.*, 2010).

Analysis of local time-series of *in situ* measurements in the southern Bay of Biscay also revealed years of high and low phytoplankton biomass over the period 1989–2007 (O'Brien *et al.*, 2008). An extended analysis of two coastal time-series with updated datasets (Figure 6.9) revealed a lack of clear patterns in annual mean phytoplankton biomass at the site that was influenced by upwelling, although maximum values occurred at both ends of the series at the site that was only marginally affected by upwelling (Bode *et al.*, 2009b, In press). These changes can be related to parallel variations in the input of nutrients, particularly phosphate, owing to changes in the origin of the intermediate water masses, related in turn to atmospheric forcing in winter at the formation area and the advection of western waters (van Aken, 2001). High nutrient inputs, such as those found in 2005, could be the result of deep mixing of the water column during extremely cold winters which reduced the stratification of the upper layers for several years (Somavilla *et al.*, 2009). An apparent linear reduction in primary production measured *in situ* in the southern Bay of Biscay between 1993 and 2003 was attributed to a decrease in surface nutrients (Llope *et al.*, 2007) and enhanced thermal stratification induced by the warming of the sea surface (Valdés *et al.*, 2007).

These patterns are part of the variability of response by coastal sites to the influence of upwelling and annual variations in the input of nutrients from the ocean (Bode *et al.*, 2009b, In press). In this way, mean annual primary production increased fourfold at the coastal upwelling site between 1989 and 2006, whereas in the southern Bay of Biscay it first decreased until the early 2000s but increased thereafter (Figure 6.9). Analysis of *in situ* chlorophyll data from the southeast of the Bay of Biscay also revealed no evidence of change in the period 1986–2008 (Revilla *et al.*, 2009), although winds that are favourable to upwelling have reduced in this region since the 1960s (Alvarez *et al.*, 2008). The inconclusive changes, or even the increases observed in total primary production, could be the consequence of an increase in the input of regenerated nutrients (Pérez, F. F., *et al.*, 2010).
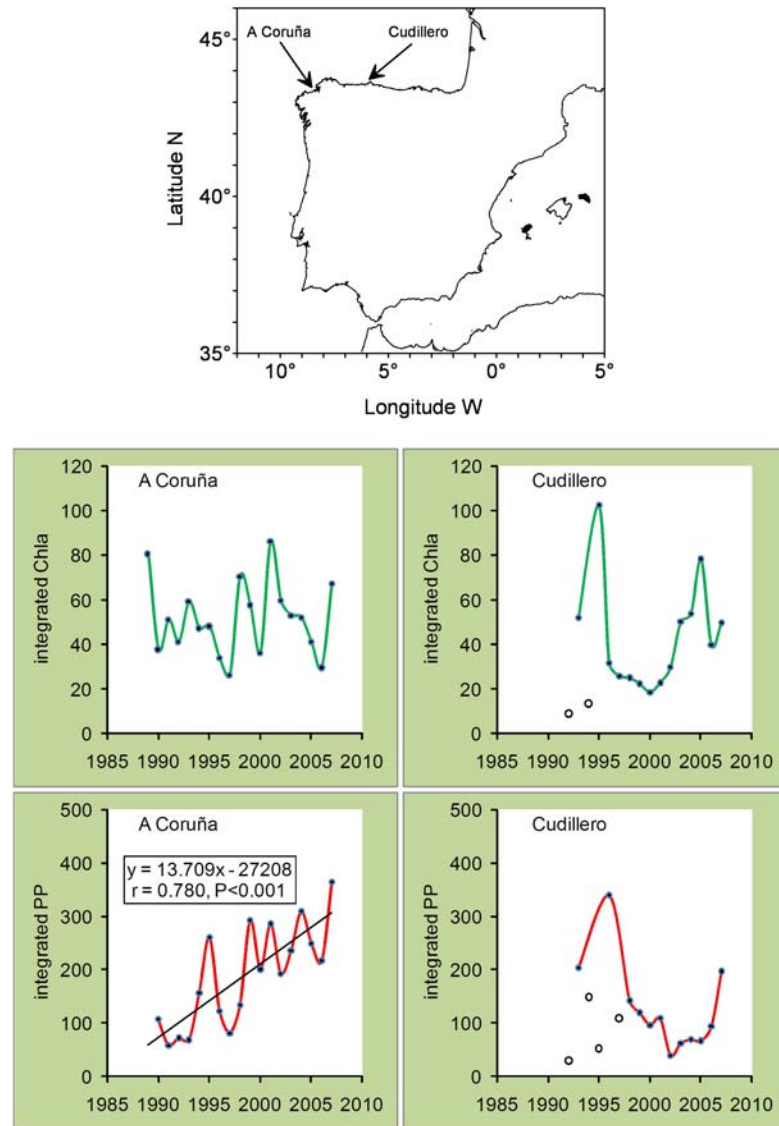
Figure 6.9. Annual mean water-column integrated chlorophyll *a* concentrations (mg m⁻²) and primary production (PP, ¹⁴C uptake, mg C m⁻² h⁻¹) measured at two coastal stations in the southern Bay of Biscay. Open circles represent mean values computed from <8 monthly observations and not used in the estimation of trends by linear regression. (Source: modified from Bode *et al.*, 2009b).

6.4.8 The oceanic Northeast Atlantic

Evidence of changes in phytoplankton in the oceanic North Atlantic areas comes mostly from satellite data. Behrenfeld *et al.* (2006) and O'Brien *et al.* (2008) demonstrated contrasting trends of change in primary production in this region, ranging from net increases in southern areas to net reductions in the north during the 1999–2004 warming period. Data based on the PCI also indicate a decrease in biomass to the south of Iceland to ca. 1997 (Figure 6.10); since then, there has been a large increase (Leterme *et al.*, 2005; Reid, 2005) that has been linked to the westward retreat of the Subpolar Gyre (Hátún *et al.*, 2009a). The convergence and mixing of subtropical and subpolar waters west of Ireland causes a transition zone where the mixing layer depth attains optimal conditions of light and nutrient for phytoplankton production. This transition zone shifts west and north as the Subpolar Gyre weakens, as observed in the period post-1995 (Hátún *et al.*, 2009a).
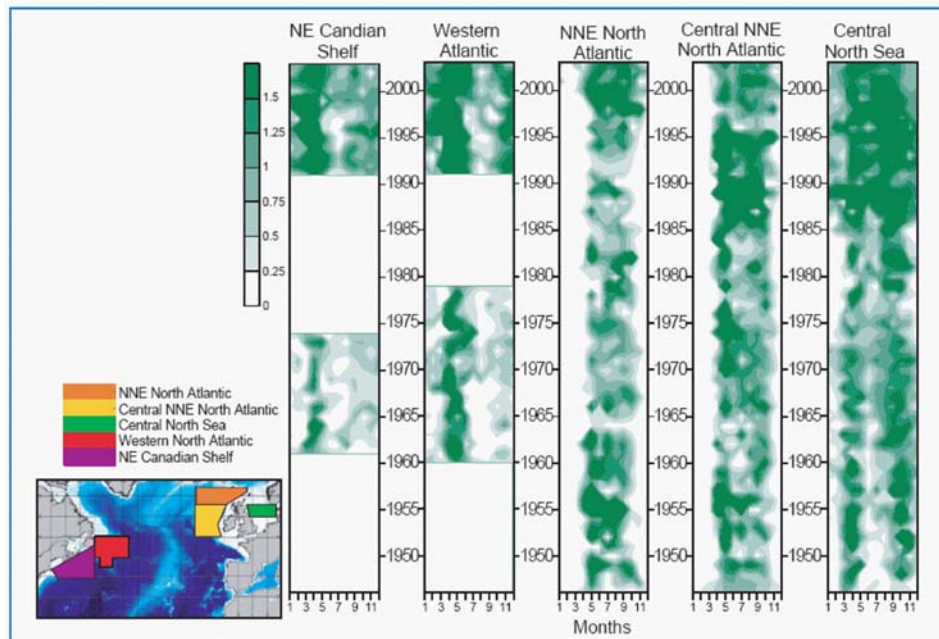
Figure 6.10. Contour plots of the mean monthly Phytoplankton Colour Index (PCI) from the Continuous Plankton Recorder for the northeastern Canadian Shelf, Western Atlantic, NNE North Atlantic, Central NNE North Atlantic, and Central North Sea. (Source: Reid, 2005, Figure 1. Courtesy of GLOBEC).

6.4.9 Baltic Sea

The Baltic Sea displayed one of the highest linear trend values in recent sea surface warming of all world regions, equivalent to the trend found in the North Sea (Belkin, 2009). No clear patterns, however, were found in mean annual phytoplankton biomass and production (Table 6.1). Increased freshwater inputs, along with warming, may have caused the large values in primary production estimated for recent years (Sherman and Hempel, 2009). Analysis of *in situ* chlorophyll measurements from local time-series (O'Brien *et al.*, 2008) revealed an increase in mean values for the Gulf of Finland (1993–2007) and in the Southern Baltic (1979–2007), although no clear trend was found in other areas, such as the Gulf of Riga (1993–2007) and the northern Skagerrak (1994–2007). The changes in the areas with increases in the concentration of chlorophyll were attributed to higher levels of nutrient caused by enhanced mixing of bottom waters in spring during years of warm winters, producing earlier and longer spring blooms than those years with cold winters (O'Brien *et al.*, 2008). A recent analysis using open and coastal water data, including all seasons and stations from the Baltic Proper demonstrated a very slowly decreasing trend for median chlorophyll *a* from 1974 until 2005 (Håkansson and Lindgren, 2008). The time-series of primary production data reveal a change in the annual maxima in recent years, with one in March and another between July and September, that were not recorded in the 1950s and 1960s (Rydberg *et al.*, 2006). The results also indicate that annual primary production has clearly increased between the 1950s and 1980. Intensive anthropogenic influence in this enclosed sea, however, makes it difficult to separate the effects of eutrophication from those of climate-driven changes.

6.4.10 Northwest Atlantic

The rate of increase in SST was highest in the Newfoundland–Labrador region, moderately high in the Scotian Shelf, and equivalent to the global ocean average in the

northeastern shelf of the US (Belkin, 2009). Phytoplankton biomass and production estimated from satellite data revealed small but positive increases in all three areas except for the Newfoundland–Labrador region, which displayed an apparent reduction (Table 6.1). Further examination of these data, extending the time-series from 1987 to 2007 and considering more subareas, indicated positive increases in biomass in all areas, except for Georges Bank (Figure 6.11), where tidal currents are considered a more important contributor to phytoplankton biomass than climate forcing (Hyde *et al.*, 2009). The tidal contribution, however, should even out and not affect interannual changes. In the Mid-Atlantic Bight phytoplankton blooms (particularly those of autumn and winter) have declined from the 1970s and 1980s to the last decade (Schofield *et al.*, 2008). The decrease in autumn blooms was attributed to a late erosion of surface stratification, whereas that of winter blooms may be associated with an increase in winter winds that enhance winter mixing, thus increasing light limitation of the phytoplankton. Field studies covering large areas are generally consistent with recent increases in biomass. For instance, Leterme *et al.* (2005), analysing PCI data in mostly off-shelf areas, found a marked increase in biomass between 1958 and 2002 that was attributed to the production of earlier and larger blooms in years with a positive NAO index; this situation would have enhanced water column mixing and the input of nutrients from below the photic layer. Time-series of chlorophyll and primary production rates measured in the Sargasso Sea between 1988 and 1998 did not reveal any clear pattern of change (Steinberg *et al.*, 2001). The lack of variation is considered to be a consequence of the dominance of mesoscale over climatic factors in determining primary production in this oceanic area. High primary production rates, however, were related to positive anomalies of the NAO index.
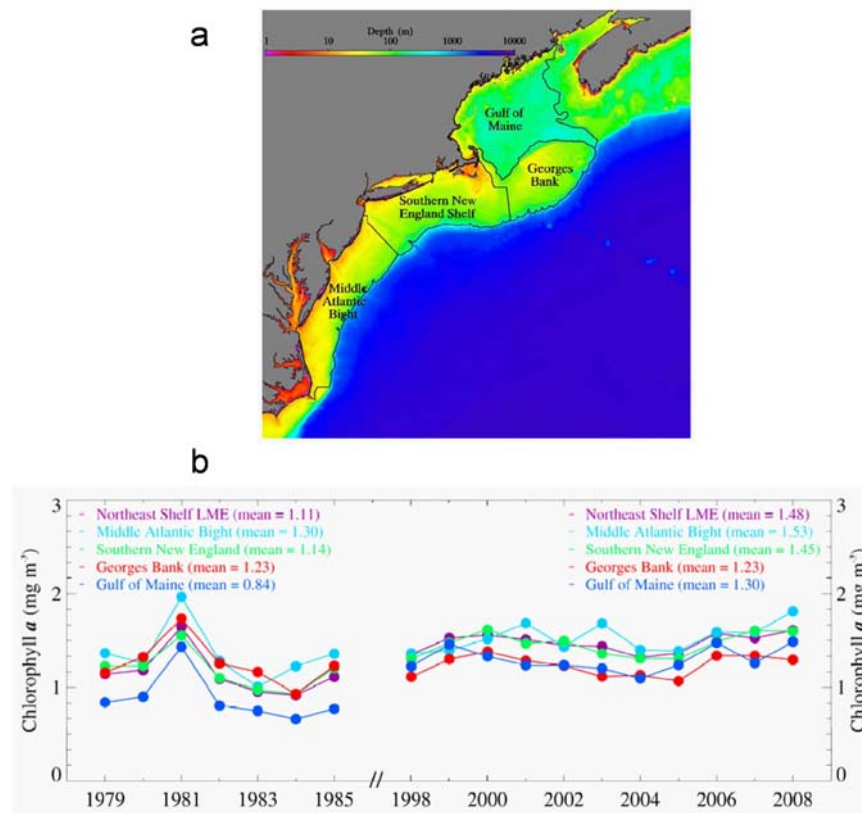

Figure 6.11. Subregions of the US Northeastern Atlantic Shelf (a) and annual chlorophyll *a* means (b) from 1979–1985 (estimated from the Coastal Zone Color Scanner) and from 1998–2008 (estimated from SeaWiFS; Source: modified from Hyde *et al.*, 2009).

Over the Scotian Shelf, an increase in mean chlorophyll in spring and a decrease in autumn was detected for the period 1997–2009 (Li *et al.*, 2006; Li, 2009). Both trends were balanced out at an annual level, with no net change in biomass but a potential impact on foodweb dynamics (Ji *et al.*, 2010). Nevertheless, at a local scale in Bedford Basin adjoining the Scotian Shelf, and using a frequently sampled long time-series, it is possible to discern multidecadal change in chlorophyll associated with nutrient enrichment (Li *et al.*, 2008), as well as interannual phytoplankton variability associated with climate-driven stratification (Li and Harrison, 2008).

In the Labrador Sea, the situation is complicated by the variability of the modes of phytoplankton regulation (light or nutrient limitation) at different times of the year and in different regions of the sea (Harrison and Li, 2008). Earlier analysis of a 12-year time-series indicated chlorophyll decreases in the Labrador Basin and on the Labrador Shelf (Li *et al.*, 2006), but the interannual trends have flattened with additional observation in more recent years (Labrador Sea Monitoring Group, 2009, 2010). In Labrador waters, a net reduction in primary production was found (Li, 2009) and attributed to changes in the availability of nutrients caused by an increase in thermal stratification. In contrast, average chlorophyll concentrations were reduced in most time-series obtained at coastal sites, except for the St Lawrence Estuary (O'Brien *et al.*, 2008). A detailed analysis of satellite data revealed large spatial heterogeneity in local responses, despite the trends observed in their core or averages within a given region (Devred *et al.*, 2009).

6.5 Phytoplankton productivity, foodwebs, and biogeochemistry in the North Atlantic

6.5.1 Biomass and production

Despite the marked differences between the mean values of chlorophyll *a* and primary production between the different areas, there is no clear relationship between the variability of SST, as an index of changes in stratification, and trends in chlorophyll or primary production when considering the whole region. In some cases (e.g. Subarctic waters) the increase in water column stratification induced by moderate warming seems to stimulate phytoplankton production and the accumulation of biomass. However, the stratification leads to reductions in primary production and biomass in other areas (e.g. subtropical waters). An independent study using time-series of chlorophyll from both eastern and western regions of the North Atlantic (Morán *et al.*, 2010) also established a significant negative relationship between average water column chlorophyll and temperature (Figure 6.12a). Century-scale trends also point to a global reduction in surface chlorophyll (Boyce *et al.*, 2010), although this remains contentious. Model simulations and the available high-resolution palaeorecord suggest that plankton biomass is highly sensitive to changes in the meridional overturning circulation of the North Atlantic (Schmittner, 2005). A severe disruption of the overturning circulation would lead to a collapse of plankton biomass owing to increased shoaling of the winter mixed layer, which becomes isolated from the reservoir of nutrients in deep waters. In turn, the amount of biogenically fixed carbon would decline as integrated export production declines.
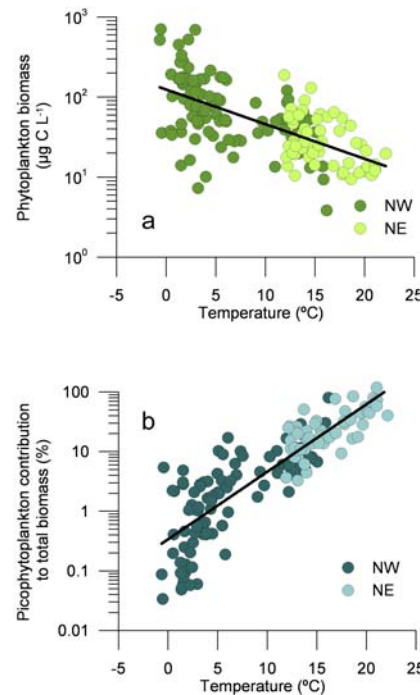
Figure 6.12. Relationship between temperature and: (a) phytoplankton biomass (estimated from chlorophyll), and (b) percentage contribution of picophytoplankton to total phytoplankton biomass in two regions of the North Atlantic. Fitted lines are least-squares linear regressions for the pooled datasets (p<0.001). (Source: Morán *et al.*, 2010, Figures 1 and 4. Courtesy of Wiley-Blackwell.)

Primary production includes a particulate and a dissolved fraction. The latter is frequently not measured, contributing less to total rates (10–30%), but it is especially important for heterotrophic bacteria. Knowledge of the effect of ocean warming on primary production partitioning is still scarce, but results from perturbation experiments suggest higher fluxes of dissolved organic carbon (DOC) with increasing temperatures (Morán *et al.*, 2006; Wohlers *et al.*, 2009). It is unclear how these extra inputs of dissolved compounds will affect bacterial metabolism in the long term, but some studies point to an increase in microbial loop processes in parallel with a weakening of the strength of the biological pump (Hoppe *et al.*, 2008; Wohlers *et al.*, 2009; Kirchman *et al.*, 2009). Different temperature sensitivities of phytoplankton and heterotrophs also underlie predictions of a shift in planktonic metabolism towards net heterotrophy in a warmer ocean (López-Urrutia *et al.*, 2006; O'Connor *et al.*, 2009).

6.5.2   Shift to smaller species

The study by Morán *et al.* (2010) revealed that a reduction in total phytoplankton biomass was accompanied by an increase of picoplankton (<2 µm of equivalent spherical diameter) cells with temperature (Figure 6.12b). According to their analysis, picoplankton constituted >50% of the phytoplankton biomass as water temperatures approach 20°C. This dominance of picoplankton at higher temperatures may be explained by a combination of the temperature–size rule, predicting lower cell sizes at high temperatures, and the inverse relationship found between total cell abundance and individual cell size. In warmer conditions, the average size of organisms in a community would reduce and, because smaller organisms have lower absolute energy requirements than their larger equivalents, the number of phytoplankton cells that can be hosted will be higher. A shift to smaller cells is also favoured under strong stratification because small cells are more effective in

acquiring nutrients and less susceptible to gravitational settling than large cells. An increasing abundance of picoplankton in freshening Arctic waters (Li *et al.*, 2009) may be propagated to parts of the North Atlantic that are influenced by Arctic outflow. Although nutrients undoubtedly play a role in determining organism size (e.g. Finkel *et al.*, 2010), consistent observations within various phytoplanktonic groups of a decrease in mean cell size with increasing temperature (Atkinson *et al.*, 2003; Daufresne *et al.*, 2009; Finkel *et al.*, 2010) support the prediction that, on average, phytoplankton cells will be smaller in the next few decades.

6.5.3 Foodwebs

Notwithstanding changes in species composition (e.g. Richardson and Schoeman, 2004; Schlüter *et al.*, 2009), a general reduction in the rates of primary production and in the size of phytoplankton cells as a consequence of severe warming imply profound transformations in the foodweb. Export rates of biologically fixed carbon to the sediments, for instance, are likely to be greatly reduced, as small cells are rapidly degraded in the water column (Bopp *et al.*, 2001), further reducing the capacity of the ocean to remove CO_2 from the atmosphere (Denman *et al.*, 2007). In addition, regional studies demonstrated changes in bacterioplankton abundance that were coherent in direction and magnitude with those of phytoplankton biomass (Li *et al.*, 2006; Li, 2009) in agreement with the idea of changes at the ecosystem level directed by climate variations. Foodwebs based on progressively smaller primary producers and having lower absolute rates of primary production will not be able to sustain current fish populations, implying that pronounced changes will take place in the size and composition of fish catches as temperatures rise as a result of climate change (Sherman and Hempel, 2009). As fish catches have been increasingly limited by primary production for the past 60 years (Chassot *et al.*, 2010), this effect will exacerbate problems arising from increasing pressure from the fishery, with unpredictable consequences for ecosystems.

6.5.4 CO_2 uptake

The increase in ocean CO_2 concentration may not have large direct effects on photo-synthetic rates, but some phytoplankton species (e.g. coccolithophorids) are likely to show significant stimulation of growth (Orr *et al.*, 2005; Iglesias-Rodríguez *et al.*, 2008; Beardall *et al.*, 2009). Interactions between temperature rise, CO_2 levels and sensitivity of phytoplankton to UV radiation may modify primary productivity and the assemblage composition of phytoplankton. The results of simulation models indicate that the fraction of anthropogenic CO_2 taken up by the ocean (from $42 \pm 7\%$ during 1750 to 1994 to $37 \pm 7\%$ during 1980 to 2005) will decline if atmospheric CO_2 continues to increase (Denman *et al.*, 2007). At the same time, ocean CO_2 uptake has lowered the average ocean pH by approximately 0.1 units. The consequences for marine ecosystems may include reduced calcification by shell-forming organisms (Orr *et al.*, 2005), and in the longer term, the dissolution of carbonate sediments (Doney *et al.*, 2009). Other effects of rising CO_2 levels include an increase in DOC exudation by phytoplankton, enhancing the formation of transparent exopolymer particles (Engel, 2002), and possibly affecting carbon export (Arrigo, 2007; Riebesell *et al.*, 2007). Laboratory experiments suggest that increasing CO_2 concentrations will affect phytoplankton carbon fixation rates, but its importance in modifying oceanic primary production remains uncertain (Riebesell, 2004; Riebesell *et al.*, 2007; Beardall *et al.*, 2009). Nevertheless, nitrogen-fixing cyanobacteria may enhance productivity in oligotrophic areas because of their sensitive response to high CO_2–low dissolved-nutrient conditions (Barcelos e Ramos *et al.*, 2007).

6.6   Conclusions

Available observations show an overall increase in global oceanic phytoplankton biomass since the 1970s. Regional changes, however, vary from increases in Subpolar and large upwelling regions to net decreases in the Subtropical Gyres. Alleviation of light limitation for phytoplankton growth by enhanced stratification provided by surface warming is likely the cause for the increases in chlorophyll found in areas typically characterized by well mixed waters. On the contrary, a reduction in mixing exacerbates nutrient limitation in areas with near permanent stratification. In the northern North Atlantic, the available evidence also supports a general increase in the average biomass and primary production of phytoplankton that is associated with rising SST. The observed changes, however, are not uniform either spatially or temporally. The increase in biomass and production in subpolar (and probably also in temperate shelf waters) can be related to warming and wind patterns but also to shifts in the position of the Subpolar and Subtropical Gyres, causing marked shifts in nutrient inputs and ecosystem composition and production. An example of the interactions between different factors is the large regime shift displayed by the North Sea in the late 1980s, which was attributed to the joint effect of warming, change in wind intensity and direction, and an increase in the inflow of oceanic waters. In these ocean and shelf areas, the effect of anthropogenic nutrient enrichment on primary production is in general of minor importance compared with climatic and large-scale oceanographic factors. However, along most of the temperate and tropical margins of the Atlantic, although primary production is largely regulated by the flux of nutrient from below the nutricline, additional factors such as high frequency perturbations from tides to storms, run-off, and agricultural eutrophication can make it difficult to discern the effects of climate in these regions.

Increases in total primary production in the upwelling region off the northwestern Iberian peninsula can be related to variations in the input of nutrients caused by mixing during the formation of intermediate waters. Near the southern Galician coast, a 40-year reduction in upwelling intensity and frequency has led to a reduction in the input of new nutrients so that total primary production depended increasingly on nutrient regeneration. In contrast, reductions in phytoplankton biomass in the southeastern Bay of Biscay were attributed to increasing stratification by warming and a reduced influence of upwelling, but the trend may be reversed in years of high mixing of the water column during winter. Changes in the Baltic and other enclosed coastal areas, however, are difficult to ascertain owing to the interaction of climate and eutrophication, as the observations generally indicate larger values of primary production and biomass in recent years compared with historical records. Variability of trends on both sides of the Atlantic is similar, with a general increase in phytoplankton biomass and production in most shelf waters but with large local variability. Blooms have reduced in intensity and changed timing in some regions of the western Atlantic (e.g. Mid-Atlantic Bight and Labrador waters) although no clear pattern of change was found for the eastern Atlantic. Climate-driven changes in the position of oceanic gyres and in the mixing depth of waters during winter interact with stratification caused by surface warming thus affecting the availability of nutrients and light for phytoplankton production in the whole area, but particularly in the transition region between subpolar and subtropical waters. Because of interactions between direct (e.g. CO_2 and temperature increases) and indirect effects (e.g. nutrient inputs) of climate change, the exact nature and direction of future changes in phytoplankton production is difficult to establish without having long-term (i.e. >30 year) time-series of observations as reliable baselines against which to

interpret the effects of abrupt or gradual changes. These series must be methodologically consistent and representative of the main ecosystem types.

Acknowledgements