Chapter 2

Primary Production Processes

CHAPTER SUMMARY

Primary production is the starting point of all other life in marine systems. Primary producers in the oceans span many orders of magnitude in size from bacteria less than a micron (μm) in diameter through to 50 m long giant kelps that grow 0.5 m a day. Production is measured using bottled incubations or increasingly from space using satellite-borne ocean colour sensors that detect photosynthetic pigments in surface waters. The conversion of inorganic carbon into biomass, its subsequent sinking to the seabed and sequestration over thousands of years is fundamental for our understanding of the ocean as a potential sink for increasing levels of atmospheric carbon dioxide. This chapter introduces the major factors that control primary production, and how to measure it.

2.1 Introduction

The photosynthetic organisms of the ocean, as on land, are for the most part the fundamental food source on which marine ecosystems are based (Field et al. 1998; Falkowski et al. 2000). In coastal waters, the large stands of seaweeds exposed at low tide, submerged kelp beds or gently wafting meadows of seagrasses that fill coastal lagoons are the obvious plants. These primary producers grow in much the same way as their terrestrial counterparts: assimilating carbon through photosynthesis, and growing by taking up nitrogen, phosphorus, and a host of necessary other minerals and trace substances to generate new biomass.

When considering photosynthesis and the production of new biomass we need to consider both production and loss processes, and both are important for this chapter (Fig. 2.1). In the most simplistic terms, light energy is trapped and used to produce organic matter through photosynthesis, and this organic matter is broken down through respiration to release energy and heat.

● There is a large body of information on primary production processes in aquatic systems, and for this chapter, rather than an extensive list of citations and reference list (as used by other chapters), readers are rather encouraged to use the extended reading list at the end of the chapter. These have been selected for the overviews they give and the synthesis of the primary scientific literature. Citations are used for more specialized points, possibly not so widely covered in the more generalized texts.

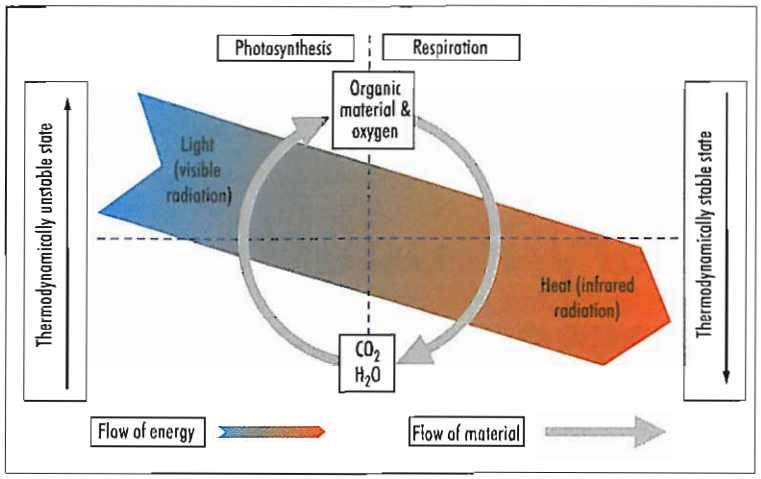


Fig. 2.1 The massive biological cycle. The energy of light, inorganic nutrients, CO_2, water, and salts are converted to a complex mix of organic compounds and oxygen by photosynthetic organisms. Respiration releases CO_2 and energy, at the expense of oxygen and recycles nutrients to the inorganic state. (Image: Peter J. le B. Williams).

The global scale of this cycle is massive and the annual cycle of production and consumption has been calculated to have the same energy production of about 1.5×10^{14} watts per year, equivalent to the annual output of around 150 000 nuclear power stations. It is also a relatively efficient process, with 40% of the solar radiation absorbed converted into organic material, which is slightly better than the best modern power station.

● Primary production is the formation of organic matter through the trapping of light energy and assimilation of inorganic elements.

2.1.1 Marine plants and algae

Looks can be deceptive. While the seagrasses are true flowering plants, the seaweeds are not. Seaweeds are algae, and although they are photosynthetic organisms, in contrast to the terrestrial plants, they are non-flowering and do not have roots, leafy shoots, or sophisticated tissues for transporting water, sugars, and nutrients. Their major evolutionary lineages remain controversial, although recent molecular advances clearly indicate that apart from a few of the green algal species the algae are only remotely linked to land plants.

● Seaweeds, seagrasses, and microscopic algae and bacteria are the primary producers in the oceans.

Seaweeds, or rather macroalgae as they are known, are a diverse group, ranging from mere encrustations on rock surfaces, to giant brown algae such as *Macrocystis prolifera* and *Nerocystis leutkaena*, which reach lengths over 50 m long (Fig. 2.2). The latter species is an annual, and grows taller than a mature oak tree in a single year.

Macroalgae are easily seen by the human observer, but we need the assistance of a microscope to observe the microalgae that generate most

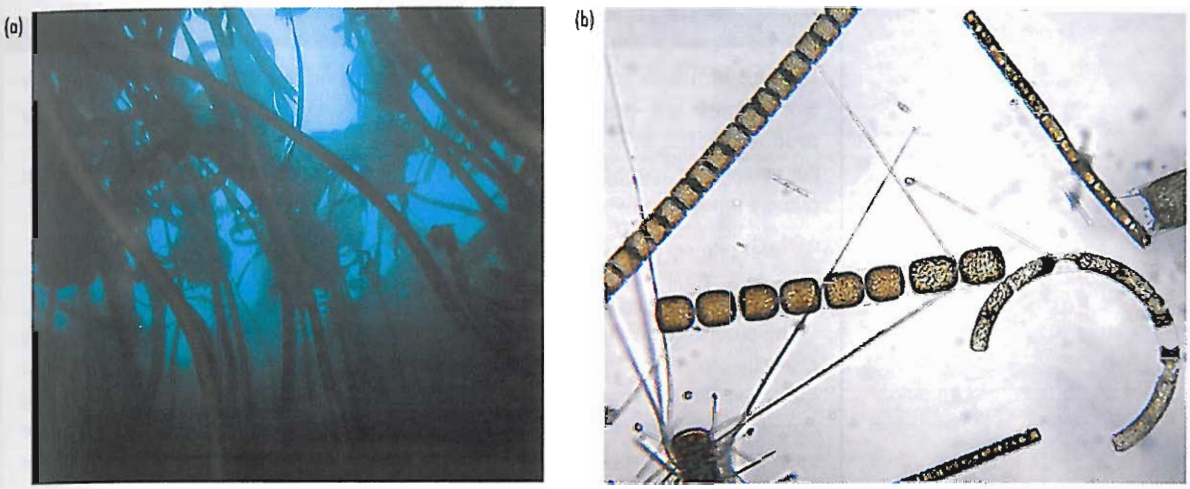


Fig. 2.2 The primary producers of marine systems range from large seaweeds (macroalgae) that grow attached to the sea floor (a), down to microscopic phytoplankton (b). Note the ×10 000 difference in scale between the two images. (Photographs: Ian Lucas/Gerhard Dieckmann).

of the primary production in the oceans (Fig. 2.2). We may not be able to see these individual **phytoplankton** cells, but we can certainly see their effects: clear waters can be turned brown almost overnight, when light, temperature, and nutrient conditions in the water are favourable, such that phytoplankton are induced to grow at such a rapid rate they form an **algal bloom**.

● Phytoplankton can bloom rapidly given enough light and a sufficient supply of inorganic nutrients.

2.1.2 Global ocean primary productivity

Global ocean net primary productivity estimates are numerous and varied (Geider et al. 2001). Most of the variability is largely to do with the methods used to measure ocean primary production, and the different metabolic processes that these methods quantify (Table 2.1). The most recent estimates based on satellite images of phytoplankton biomass in surface waters tend to range between 40 and 50 $Pg\,C\,y^{-1}$ (note: P = peta and 1 Pg is equivalent to 10^{15} g). Recent estimates of terrestrial primary production is estimated to be between 50 and 60 $Pg\,C\,y^{-1}$, which combined with the oceanic primary production gives a total primary production on Earth of *c.*10^{16} $g\,C\,y^{-1}$ (Table 2.1).

● Marine and terrestrial primary production are roughly the same at approximately 50 $Pg\,C\,y^{-1}$.

We can measure the distribution of phytoplankton from satellites in space (Fig. 2.3). Like all photosynthesizing organisms the algae contain chlorophyll. With modern-day satellites (see 2.13 below), it is possible to estimate the chlorophyll concentrations in the surface waters of the world's oceans and therefore monitor the growth of the phytoplankton.

Box 2.1 Comparison of terrestrial and aquatic primary production

The amount of bacterial, algal or plant biomass (**primary producers**) built up over time through the process of photosynthesis is generally referred to as **primary production**. This is normally expressed as the amount of carbon fixed by photosynthesis, per unit area of space or volume, per unit of time. Most estimates are expressed as net primary production, which takes into account the costs of respiration as well.

Net primary production
= Total photosynthetic carbon assimilation – respiration carbon losses

The production per square metre of seaweeds and seagrasses is equal to, or in many cases greater than, that of terrestrial plant based systems. For instance *Laminaria* spp. dominated communities have annual productivity rates of approximately 2 kg carbon $m^{-2}y^{-1}$, and the macroalgal sea palm *Postelsia* has been estimated to produce up to 14 kg carbon $m^{-2}y^{-1}$. These estimates contrast with those for mature rainforests and intensive alfalfa crop production (1 to 2 kg carbon $m^{-2}y^{-1}$), and temperate tree plantations or grasslands and prairies which are generally less than 1 kg carbon $m^{-2}y^{-1}$.

● Macroalgae can produce up to 14 kg carbon $m^{-2}y^{-1}$.

Macroalgae can be very productive, and *Laminaria* spp. dominated communities have annual productivity rates of approximately 2 kg carbon $m^{-2}y^{-1}$. (Photograph: David Roberts.)

● Although phytoplankton productivity is much less than that of macroalgae per unit area, on a global scale total phytoplankton productivity is far greater than that contributed by macroalgae.

Coastal phytoplankton annual production is also generally less than 1 kg carbon $m^{-2}y^{-1}$. One study estimated the annual productivity of all the seaweeds in a 1 m wide strip of shoreline, 360 m long, was *c.*600 kg carbon y^{-1}. An equivalent productivity by the phytoplankton in a 1 m wide strip of the adjacent seawater would require a stretch of water extending out 3.4 km from the shore. From figures like these it would be easy to think that the seaweed production is more important than that of phytoplankton production to the overall productivity of the oceans. However, compared to the vast area of the globe covered by the oceans (80%) in which phytoplankton grow, the seaweed covered strips of coastlines are rather small, and at best can be viewed as sites of intense localized production.

2.1.3 The phytoplankton

The microalgae vary considerably in size ranging from about 2 μm in diameter to over 200 μm. They are very varied in form, some of the most elaborate being the silicate (glass) encased diatoms that have beguiled

Table 2.1 Comparison of annual primary production between marine and terrestrial systems. It must be stressed that at best these values are good estimates, but they do allow a comparison of the magnitudes of primary production from various components of the biosphere.

Domain	Global Annual primary production ('Pg $C y^{-1}$)
Marine	
Temperate westerly winds	16.3
Tropical & subtropical trade winds	13.0
Coastal waters	10.7
Polar	6.4
Marshes/estuaries/macrophytes	1.2
Coral reefs	0.7
Terrestrial	
Tropical rainforests	17 8
Savannas	16.8
Cultivation	8.0
Mixed broadleaf & needleleaf	3.1
Needleleaf evergreen forest	3.1
Perennial grasslands	2.4
Broadleaf deciduous forests	1.5
Needleleaf deciduous forest	1.4
Broadleaf shrubs with bare soil	1.0
Tundra	0.8
Desert	0.5

'P = *peta*, and 1 Pg is equivalent to 10^{15} g.

naturalists since the first microscope lenses became available (Box 2.2). However, these **microphytoplankton** are not the only photosynthetic organisms to be found in the phytoplankton. Since the 1980s a host of much smaller **prokaryotic** photosynthetic organisms have been shown to be an important component of the phytoplankton. These include **cyanobacteria** such as those from the genus *Synechococcus*, cells about 1 µm in diameter, that are found in all waters except the polar oceans. Pelagic **prochlorophytes** in the genus *Prochlorococcus* (cells of 0.7 µm diameter) were discovered in the late 1980s. These very small **picoplankton** are thought to be found in most waters around the globe, and contribute a high percentage of the total primary production of open waters (Fig. 2.4). However, we are only just beginning to understand their role in global primary production, and in many oceanographic studies these tiny organisms remain overlooked (Binder et al. 1996; Karl 2002; Fuhrman & Capone 2001; Scanlan & West 2002).

● Femtoplankton – 0.02 to 0.2 µm;
Picoplankton – 0.2 to 2.0 µm;
Nanoplankton – 2.0 to 20 µm;
Microplankton – 20 to 200 µm;
Mesoplankton – 0.2 to 200 mm.

● Picoplankton, 0.2 to 2 µm in diameter, are important contributors to plankton primary production.

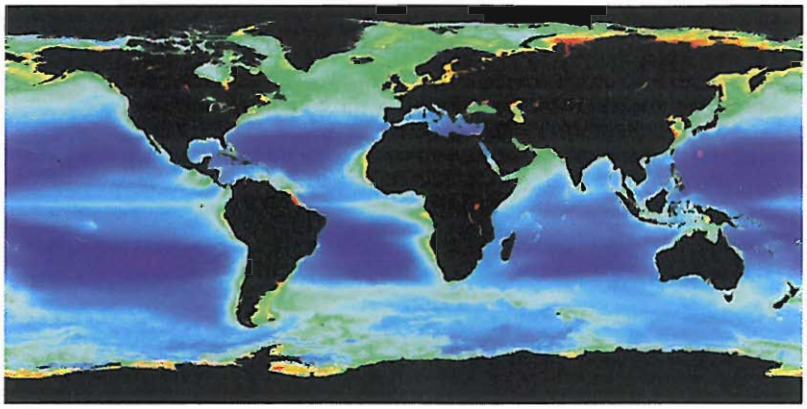


Fig. 2.3 The advent of satellite-borne ocean colour sensors enables scientists to look at the global distributions of phytoplankton in surface waters. This image shows the SeaWiFS average chlorophyll concentration collected from January 1997 to July 2005. (Image: SeaWiFS Project, NASA/Goddard Space Flight Center and ORBIMAGE).

This chapter describes production processes in marine systems with a focus on photosynthetic organisms and the constraints acting on this process, while in Chapter 3 we explore the role of non-photosynthetic organisms. The growth of all photosynthetic organisms is restricted primarily by the supply of light, carbon dioxide, oxygen, and the main macro-nutrients (phosphate, silicate, and nitrate). However, even when all these factors are adequate the lack of trace elements can be enough to restrict growth (see Box 2.7).

There are many other mechanisms for utilizing energy sources other than light, as well as different sources of carbon for the generation of new biomass. It is only proper that at least some mention is given to the diversity of metabolism, especially since this variety is fundamental for the microbial ecology (Chapter 3) and biogeochemical processes found within marine systems.

2.2 Photosynthesis

Algae (micro- and macroalgae) and cyanobacteria such as *Synechocccus* and *Prochlorococcus* are **photoautotrophs**, as they use light as their energy source and carbon dioxide (or one of its various forms in the water, see 2.2.1) to produce new organic matter.

● Photoautotrophs use light as an energy source and carbon dioxide to produce new organic matter.

The photosynthetic reaction can be divided into a **light** reaction and a **dark** reaction. The light reaction converts light into metabolic energy and reducing power. The dark reaction utilizes these to convert (**fix**) carbon dioxide and form organic material. The overall reactions are:

Light reaction: $2H_2O + light \Rightarrow 4[H^+] + metabolic\ energy + O_2$

Dark reaction: $4[H^+] + metabolic\ energy + CO_2 \Rightarrow [CH_2O] + H_2O$

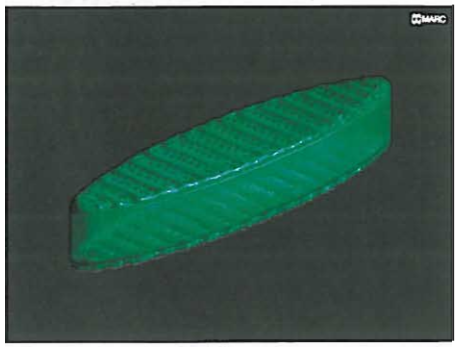
where $[CH_2O]$ is used as a general symbol for organic material.

Fig. 2.4 A concentrated water sample from the Arabian Sea, Indian Ocean, stained by the fluorescent DNA stain DAPI, and viewed by epifluorescence microscopy. Above: Under excitation by UV light, individual bacteria and flagellates are visible by their DAPI-induced blue fluorescence. Below: The same preparation under blue light excitation. Yellow (*Synechococcus* sp.) and even smaller red fluorescing picoplankton cells (*Prochlorococcus* sp.) are visible. Unlike in the upper picture, only the auto-fluorescence of the natural photosynthetic pigments can be seen. The large, very bright cell is a dinoflagellate (*Gymnodinium* sp., about 20μm in diameter). (Photographs: Marcus Reckermann).

Photosynthetic organisms contain specialized light sensitive pigments such as chlorophylls to absorb light energy, which is subsequently transferred to reduce CO_2 to organic compounds. CO_2 is fixed within the **Calvin cycle**, and the first step of the reduction of CO_2 in this cycle is catalysed by the enzyme **ribulose bisphosphate carboxylase/oxygenase** (**RUBISCO**). It is important that there is a high supply of CO_2 at the active site of RUBISCO. Many species of cyanobacteria and algae have

Box 2.2 The diatom frustule

(a)



Sophisticated models of diatom frustules, such as this computer-generated pennate diatom, are helping researchers understand how the structures of the silica cell walls are related to their ecology and evolution (Image: Christian Hamm, Alfred Wegener Institute).

Diatoms, a type of alga, are major contributors to the phytoplankton of marine and fresh water. There are also many diatom species that live within and on top of sediments, as well as species that grow as epiphytes on the surfaces of animals, plants, and macroalgae. The characteristic of all diatoms is that they produce cell walls made of silicate, which are not only very beautiful to look at, but also apparently very strong. Diatoms can form dense blooms in coastal waters, and are an important food source for protozoan and zooplankton grazers. However, once formed, the diatom cases, or frustules, dissolve only slowly, and in some regions of the world's oceans, the sediments are characterized by diatomataceous or siliceous oozes: massive accumulations of diatom frustules that have sunk from the surface waters over eons of time.

Many diatom species have highly ornate frustules, with spines, spikes, hooks, and other protrusions. Many of these adaptations are thought to resist sinking and aid colony/chain formation, but also deter grazers from attempting to eat them. Spined diatoms have even been known to clog fish gills and pierce delicate membranes in gill tissues.

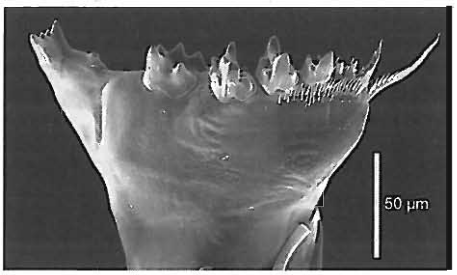
The strength of the diatom frustule seems to be a most remarkable feature of these algae. Although diatoms are grazed they are clearly not an easy food source to break into. The unique architectures and design of the frustules give them immense mechanical strength, and the diatom silica has material properties comparable to cortical bone with greater elasticity than glass. In fact, the grazers must exert tremendous force, and therefore expend extra energy, to break the frustules open and get to the cell contents. Recent studies using microscopic **crash tests** as well as computer-based simulations suggest that the diatom frustules have arisen from an **evolutionary arms race** in which the capability of grazing organisms to break open its prey has been pitched against the evolution of very strong elastic diatom frustules (Hamm et al. 2003). Both copepods and euphausiids, major consumers of diatoms, have silica-edged mandibles and gizzards lined with sharp crushing structures that function like teeth. It is likely that these structures have co-evolved with the development of the diatom frustule, just as the anti-grazing silica spicules in grasses have co-evolved with the evolution of teeth in animals that graze on land.

continues

● The Strength of diatom frustules is possibly linked to an anti-grazing strategy.

BOX 2.2 continued

(b)



Scanning electron micrographs of the mandibular gnathobases of the copepod *Calanoides acutus*. The gnathobases of this species have strong tooth-like structures that consist of a different material from the rest of the gnathobases. These structures are very suitable for cracking hard diatom frustules. (Photograph: Jan Michels, Alfred Wegener Institute).

active **carbon concentrating mechanisms** (CCMs) that maintain the required high levels of CO_2 within the cells (Box 2.3).

● Carbon concentrating mechanisms maintain high carbon dioxide levels at the RUBISCO enzyme.

2.2.1 Carbon dioxide and photosynthesis in the sea

Dissolved inorganic carbon occurs as several forms in seawater: carbon dioxide (CO_2) gas, carbonic acid (H_2CO_3), bicarbonate ions (HCO_3^-), and carbonate ions (CO_3^{2-}). The proportions of these forms in seawater are in an equilibrium that is primarily governed by the acidity (pH), salinity (Chapter 4), and temperature of the water.

$$HCO_3^- + H^+ \Longleftrightarrow H_2CO_3 \Longleftrightarrow H_2O + CO_2$$

● pH, temperature and salinity govern the form of inorganic carbon in marine systems.

In seawater of a salinity of 35 and a 'typical' pH of 8.1 to 8.3 (Box 2.4; Fig. 2.5) approximately 90% of the inorganic carbon occurs as HCO_3^-, with 2 mM of HCO_3^- and only about 10 µM in the form of CO_2. RUBISCO requires CO_2 as a substrate. CO_2 is taken up directly by marine algae but this is dependent on diffusion from low external concentrations compared with the high amount of carbon present in the HCO_3^- pool. Surprisingly, there is still debate as to which inorganic carbon form is the predominant form used by marine algae (Burkhardt et al. 2001). HCO_3^- is taken up by some algal species and this is converted within the cell to CO_2 by the enzyme carbonic anhydrase (Elzenga et al. 2000). In many algae carbonic anhydrase activity has also been measured on the outer cell surfaces converting HCO_3^- to CO_2, which is then taken up into the cells.

● Note that in chemistry we talk about a substrate, whereas later in this book we discuss seabed habitats: the substratum.

● The enzyme carbonic anhydrase converts HCO_3^- to CO_2 within and on the outside of some cells.

Generally photosynthesis (both light and dark reactions) is represented by the following equation:

$$6CO_2 + 6H_2O + 48\text{photons of light} \Rightarrow 6O_2 + C_6H_{12}O_6$$

This highly simplified equation masks the great complexity of the photosynthetic process. However, it does show that for these organisms

Box 2.3 RUBISCO

● RUBISCO is an enzyme – ribulose bisphosphate carboxylase/ oxygenase.

RUBISCO is an enzyme of very high molecular weight and in planktonic algae amounts to 50% of the protein of the cell. It is the most abundant protein on the planet (estimates of 40 million tonnes). Given this estimate and taking global productivity at 100×10^9 tonnes per year, 1 g of RUBISCO fixes about 2500 g C per year, *i.e.* about 10 g per day (this is equivalent to 70 CO_2 molecules per RUBISCO molecule per second (enzymes characteristically are much more reactive, catalysing 10 000 to 100 000 molecular reactions per second).

The carboxylase reaction catalysed by RUBISCO is as follows:

$$\text{Ribulose-1, 5-Bisphosphate} + CO_2 \Rightarrow 2(\text{3-Phosphoglycerate})$$

Then follows a complex sequence of reactions, from which the sugars glucose ($C_6H_{12}O_6$) and sucrose ($C_{12}H_{22}O_{11}$) are common initial products. RUBISCO is unusual as an enzyme in that it has a second and quite different function as an **oxygenase.** In this reaction rather than adding carbon dioxide onto ribulose-1,5-bisphosphate, oxygen is added:

$$\text{Ribulose-1, 5-Bisphosphate} + O_2 \Rightarrow \text{3-phosphoglycerate} + \text{phosphoglycolate}$$

This reaction, known as **photorespiration**, results eventually in the loss of carbon and the formation of CO_2. It is an important loss reaction in plants, especially tropical plants. The balance between the two alternative reactions is controlled by the ratio of O_2 and CO_2 concentrations at the enzyme:

Carboxylase (CO_2 fixing) reaction is **high at high** CO_2/O_2 ratios

Oxygenase (CO_2 releasing) reaction is **high at low** CO_2/O_2 ratios

Therefore:

At high CO_2/O_2 ratios $\Rightarrow$ carboxylase function $\Rightarrow$ CO_2 fixation & O_2 production

At low CO_2/O_2 ratios $\Rightarrow$ oxygenase function $\Rightarrow$ CO_2 production & O_2 utilization

By having carbon-concentrating mechanisms (CCMs – see above) the algae maintain high concentrations of CO_2 inside the cells where RUBISCO is situated, thereby ensuring that the carboxylase function dominates (Raven 1997).

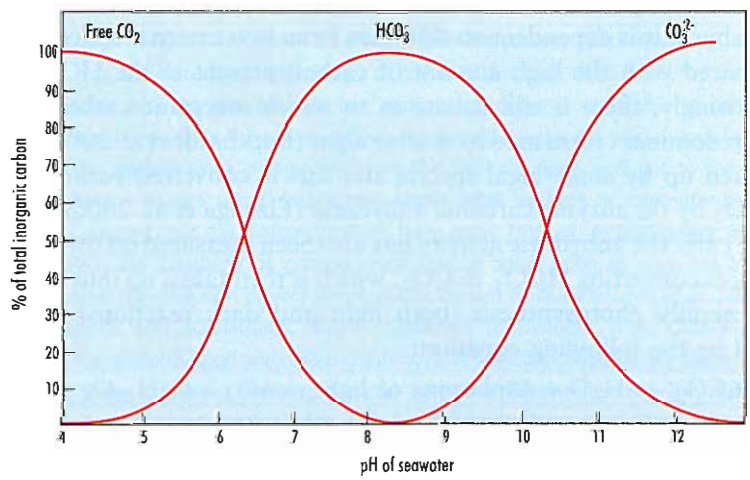
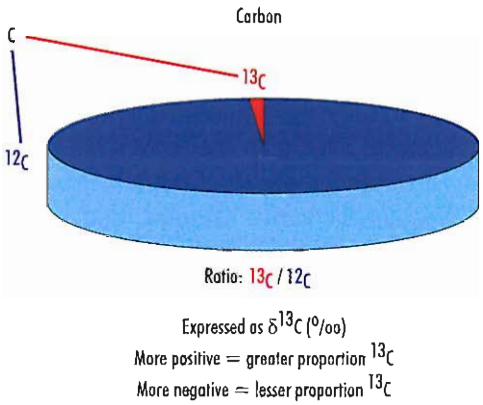


Fig 2.5 Relationship between pH and the relative proportions of dissolved inorganic carbon species in seawater.

Box 2.4 Photosynthesis and stable carbon isotopes

Carbon is present in nature in various isotopic forms: the radioactive isotope ^{14}C and the stable carbon isotopes, ^{12}C and ^{13}C. Photosynthetic carbon assimilation results in discrimination against ^{13}C, and as a result the produced biomass becomes enriched in ^{12}C whereas the remaining total dissolved inorganic carbon pool becomes relatively enriched in ^{13}C (Burkhardt et al. 1999a, 1999b; Riebesell et al. 2000).



Schematic illustrating the relative proportions (not to scale) of the stable carbon isotopes ^{13}C and ^{12}C.

This is reflected in their stable isotope ratio, which is commonly reported on a ‰ (parts per thousand) basis in the δ notation relative to the international standard Vienna Pee Dee Bellemnite (VPDB) as, $\delta^{13}C = 1000((R/R_{VPDB}) - 1)$, with $R = {}^{13}C/{}^{12}C$. Negative values indicate ^{12}C enrichment and more positive values indicating ^{13}C enrichment.

The isotope effect attributable to RUBISCO is about −27‰ in photosynthetic algae. In other words, the RUBISCO effect alone will result in a $\delta^{13}C$ of the photosynthetically assimilated organic carbon ($\delta^{13}C_{POC}$) that is more enriched in ^{12}C (i.e. isotopically lighter) than the CO_2 available for assimilation by an equivalent amount. This can be observed during growth in CO_2-replete conditions. However, the overall (net) biological isotope fractionation during photosynthesis and, hence, the final $\delta^{13}C$ values are a complex function of a number of factors, such as the dissolved CO_2 concentration, passive and/or active dissolved inorganic carbon transport into the cell, growth rate, cell size, and cell geometry. The departure from the chemical equilibrium value has been used by geochemists and palaeobiologists to identify the earliest evidence for life on the planet.

The $\delta^{13}C$ signatures have become a valuable tool for researchers interested in food webs (see later chapters). The signature tends to be conservative and maintained. Therefore an organism eating the primary producer will tend to assimilate carbon with the same isotopic signature (in line with the proverb 'You are what you eat'). By measuring the isotope signatures valuable information can therefore be gleaned for determining food web dynamics.

water is used as an electron donor to produce the reducing power in the overall metabolism, with oxygen produced as an end product. Because oxygen is produced these organisms are referred to as being **oxygenic photoautotrophs**.

2.2.2 Photosynthetic pigments

● Some types of photosynthetic bacteria only photosynthesize in anoxic conditions.

There are groups of photosynthetic bacteria that use other reductants, such as hydrogen, hydrogen sulphide, and ferrous iron, and do not produce oxygen. Oxygen can inhibit photosynthesis in these organisms, which include purple sulphur bacteria, purple non-sulphur bacteria, and green sulphur bacteria among others.

● A wide range of pigments, including chlorophylls are used by photosynthetic organisms to trap light.

There is a great variety of chlorophylls and other light absorbing pigments in photoautotrophs. Chlorophyll-*a* (Chl*a*), is the major chlorophyll of the algae, and is green because it absorbs blue (maximally at 430 nm) and red wavelengths (maximally at 680 nm) of light and reflects green wavelengths (Fig. 2.6). Because Chl*a* is such a ubiquitous pigment in a wide diversity of photosynthetic organisms it is used as a measure of algal biomass in water samples, and when photosynthetic

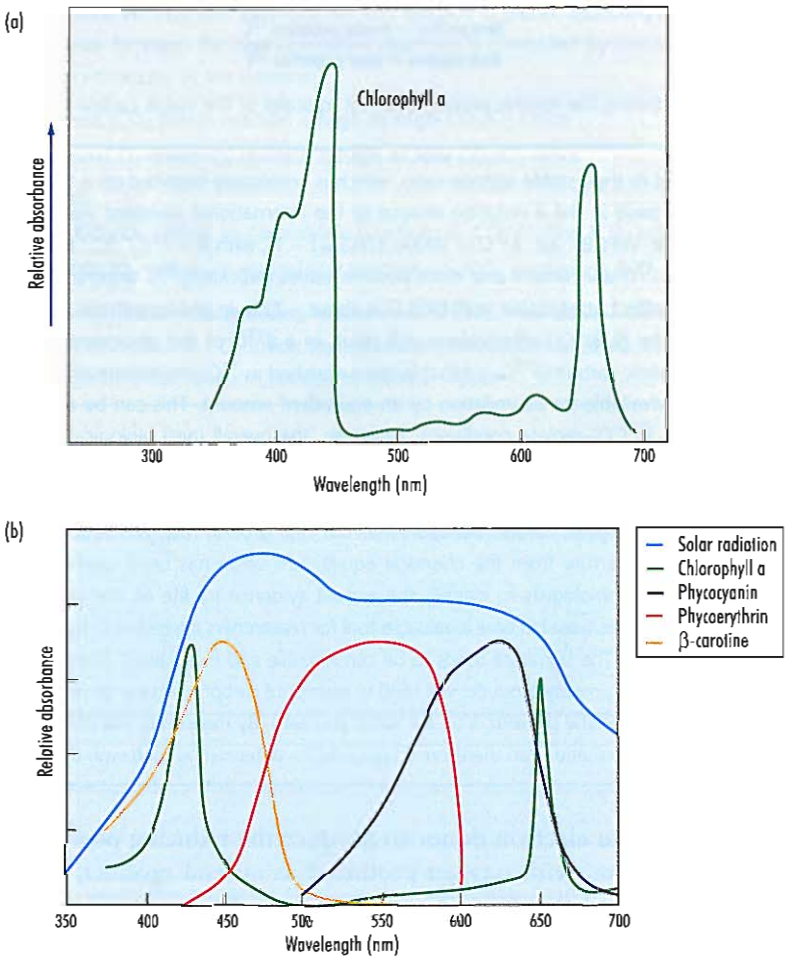


Fig. 2.6 (a) The absorption spectra of chlorophyll-*a*. (b) Absorption spectra of chlorophyll-*a* (green) and some accessory pigments: Phycocyanin (blue), Phycoerythrin (red) and *β*-carotene (yellow). The spectrum of photosynthetically active radiation (PAR) is overlain.

rates are calculated (see 2.13) they are often referred to the amount of chlorophyll present in the sample.

Carotenoids such as β-carotine and fucoxanthin, as well as chlorophyll-*b*, absorb in the green part of the light spectrum (400 to 520 nm), whereas phycoerythrin absorbs in a different range of the green region (490 to 570 nm) (Fig. 2.6b). Phycocyanins and allophycocyanins absorb light in the green-yellow (550 to 630 nm) and orange red (650 to 670 nm) parts of the spectrum respectively. These pigments are examples of **accessory pigments**. The wavelengths of light that range from 400 to 700 nm are called the **photosynthetically active radiation (PAR)**, and photosynthetic organisms adjust their light harvesting pigments to absorb various components of this spectrum of light which varies with water depth.

● Photosynthetically active radiation is the wavelengths 400 to 700 nm.

Among the prokaryotes the cyanobacteria have chlorophyll-*a*, as in eukaryotic photoautotrophs. However, other phototrophs such as the purple and green bacteria contain any of a large number of bacteriochlorophylls. These have different absorption characteristics than the algal chlorophylls. e.g bacteriochlorophyll-*a* absorbs maximally between 830 to 925 nm, whereas algal chlorophyll-*a* absorbs maximally at 430 and 680 nm.

2.3 Respiration

The other major metabolic pathway that needs to be introduced here is **aerobic respiration** (also see Chapter 3). When oxygen is present, compounds are oxidized using O_2 as an electron acceptor to produce CO_2 and adenosine triphosphate (ATP). *All* organisms carry out respiration, and unlike photosynthesis that can only take place in the light, respiration takes place continuously. Effectively the process of respiration can be exemplified by the reverse of the equation given for photosynthesis above:

$$6O_2 + C_6H_{12}O_6 \rightarrow 6CO_2 + 6H_2O + \text{energy}^*$$

(*When glucose is oxidized during respiration 2870 kJ mol^{-1} of energy is produced.)

The amount of energy produced is dependent on the nature of the starting material: one mole of fat (e.g. palmitic acid) results in the production of 9959 kJ of energy compared to the production of 2870 kJ when the same amount of glucose (a carbohydrate) is respired. For a given weight of material, fats yield at least twice as much energy as carbohydrates (hence their value as storage material and their occurrence in the eggs of most animals).

● The oxidation of fats yields far more energy than the oxidation of the same amount of simple sugars.

Where oxygen does not occur in sufficient concentrations for normal aerobic respiration, some organisms can use **anaerobic respiration**, and use nitrate, sulphate, carbonate, and organic compounds as electron acceptors.

Nitrate respiration is key to the **denitrification** process (Chapter 3), in which **denitrifying bacteria** reduce nitrate and nitrite to nitrous oxide or dinitrogen gas:

$$NO_3^- \rightarrow NO_2^- \rightarrow NO \rightarrow N_2O \rightarrow N_2$$

● Anaerobic respiration can result in the production of potentially toxic products such as hydrogen sulphide and methane.

Sulphur-reducing bacteria use sulphate, thiosulphate, and elemental sulphur as electron acceptors in respiration. The metabolism produces sulphide or hydrogen sulphide, the rotten egg smell, characteristic of many anoxic waters and sediments. **Methanogenic bacteria** use CO_2 as an electron acceptor producing methane (CH_4) as an end product.

Many of the products of anaerobic respiration are toxic (e.g. H_2S, which is even more toxic than hydrogen cyanide). This toxicity has very great ecological significance in water management, since plankton, zooplankton, and higher organisms (e.g. fish) are particularly susceptible to this toxicity and are at risk in environments that are prone to produce these compounds. Oxygen is always the preferred electron acceptor, and providing there is oxygen in the water, these toxic compounds will not be produced.

2.4 Heterotrophic Metabolism

● Heterotrophic organisms assimilate carbon derived from the oxidation of organic matter.

Organisms that use chemical compounds as an energy source, rather than light, are called **chemotrophs**. The **chemo-organotrophs** include those bacteria and fungi that live via the oxidation of organic compounds and in oxygenated habitats, they catabolize organic matter via aerobic respiration. Because these organisms do not get their carbon from CO_2, but rather from the oxidation of organic matter, they are called **heterotrophs** (c.f. Box 2.5). Those species that live in aerobic conditions use oxygen (**oxygenic heterotrophs**) as the external electron acceptor, whereas other species in anaerobic conditions (**anoxygenic heterotrophs**) can use other oxidized substrates such as nitrate and sulphate instead of oxygen as the terminal electron acceptor. The anaerobic heterotrophs are particularly important in anoxic sediments and the biogeochemical transformations that take place within these. These bacteria and fungi assimilate low molecular weight organic compounds such as sugars, amino acids, pyruvate, ethanol, and acetate, which are transported directly into the cells. These organisms release hydrolytic enzymes to break down larger organic compounds into low molecular weight substrates that can then be transported into the cell and then respired and built up into new biomass.

● Anoxic means without oxygen.

● Heterotrophic organisms obtain their carbon from the oxidation of organic matter, whereas autotrophic organisms obtain carbon from CO_2.

There are other groups of prokaryotes that use inorganic chemicals as their energy source (**chemolithotrophs**). Most of these organisms obtain their carbon from CO_2, and so are autotrophs. There are many sources

of inorganic electron donor used by these prokaryotes which include both bacteria and archaea. These include hydrogen sulphide, sulphur, ammonium, nitrite, and ferrous iron. Again some of these organisms can only survive in anaerobic conditions whereas others are tolerant of oxygen.

Examples of chemolithrophic bacteria include the **sulphur-oxidizing bacteria**, which grow in the tissues of hydrothermal vent organisms

Fig. 2.7 *Beggiatoa* form filaments that twine together to form the white mats shown here. *Beggiatoa* is found in habitats that have high levels of hydrogen sulphide, including deep hydrothermal vents, sulphur springs, sewage-contaminated water, and mud layers. (Photo: Paul Dando.)

● Mixotrophs use both phototrophic and heterotrophic means for assimilating energy.

Box 2.5 Switching metabolism

There are groups of organisms that can also switch metabolism. Good examples are the **anoxygenic phototrophic bacteria**. These bacteria are capable of utilizing organic carbon when it is available, but capable of photosynthetic light utilization and CO_2 metabolism when organic carbon sources are low. These organisms are abundant in the upper oceans and are estimated to make up to 11% of the microbial community.

There are also organisms, **mixotrophs**, which combine the use of phototrophic and heterotrophic nutrition (e.g. Stoecker 1999). Many phytoplankton species, **phagotrophs**, have been shown to be able to ingest particulate organic material to meet part of their nutritional requirements. These range from small nanoflagellates that ingest bacteria and cyanobacterial sized particles through to photosynthetic dinoflagellates that can consume phytoplankton and small ciliates more than 10 μm in diameter. Many phagotrophic algae increase their rates of particle ingestion in response to nutrient limited conditions in order to obtain growth limiting compounds and elements.

Some marine organisms, including some molluscs, foraminiferans, helizoa, ciliates, and dinoflagellates retain chloroplasts that they have ingested when grazing on photosynthetic organisms. The chloroplasts, although not fully integrated into the metabolism, can be a useful source of energy. In general the chloroplasts do not function for long periods of time in the new 'host', and their function gradually declines and they are lost. However, in some species, such as the ciliate *Mesodinium rubrum*, which is a major species in some 'red tides', are truly photosynthetic organisms (Dolan & Pérez 2000).

(a)

(b)

(a) Bloom of the autotrophic ciliate *Mesodinium rubrum* in surface waters of the North Sea. This an obligate phototrophic ciliate that contains endosymbiotic cryptophyte chloroplasts. (b) The relationship between corals and zooxanthellae are one of the best-known symbiotic relationships in marine systems. (Photographs: David Thomas).

continues

BOX 2.5 continued

One of the best-known symbiotic relationships in the marine world is that between photosynthetic dinoflagellates (zooxanthellae) and benthic corals. However, symbiotic relationships are also widespread in marine pelagic communities. A variety of algal species from several classes have been observed to form symbiotic associations with protozoans, medusae, turbellarians, and siphonophores. In most cases these relationships are highly species specific, most hosts only having one species as a symbiont. Certain species of heterotrophic dinoflagellates have cyanobacteria attached to their surfaces that sometimes reside within specialized pockets of the host's cell wall. Planktonic radiolarians and foraminifers can contain up to tens of thousands of symbiotic algae per individual.

● Symbiotic relationships are vital for coral species, but also for planktonic radiolarians, foraminifers, turbellarians, molluscs, and siphonophores.

It is clearly not an easy task to unravel the complexities of the metabolic pathways that are vital for the productivity in the oceans. With ever-increasing analytical tools the current trend for the discovery of new microbial components of the marine microbial world is likely to continue.

where sulphides are introduced into well-oxygenated seawater. Mats of *Beggiatoa* also grow on the reduced sulphur from the vents (Fig. 2.7). Purple sulphur bacteria are another example of organisms that oxidize H_2S and elemental sulphur:

$$H_2S + 2O_2 \Rightarrow SO_4^{2-} + 2H^+$$
$$S + H_2O + 3/2O_2 \Rightarrow SO_4^{2-} + 2H^+$$

● Nitrifying bacteria are important for nitrate regeneration in marine systems.

Nitrifying bacteria are vital for nitrogen cycling and the regeneration of nitrogen forms that can be utilized for growth in other organisms (2.10, Chapter 3). Two groups of chemolithotrophic nitrifying bacteria exist, one group (including *Nitrosomonas*) oxidizing ammonium to nitrite and another group (including *Nitrobacter*) oxidizing nitrite to nitrate. The reactions in this vitally important process of nitrification are:

$$NH_4^+ + O_2 \Rightarrow NO_2^- + 4H^+ + 2e^-$$
$$NO_2^- + H_2O \Rightarrow NO_3^- + 2H^+ + 2e^-$$

2.5 Light in water

● Without light, photosynthesis cannot take place.

Although many factors interact to determine the net primary production of photoautotrophs in the oceans, naturally it is light that is the dominant factor that determines the rate and extent of photosynthetic activity (Kirk 1994). It is both the quality of the light, and the quantity of the light that reaches the chloroplasts within the cells that control these reactions. As anybody who has dived or snorkelled in open waters can testify, the penetration of light can vary greatly (Fig. 2.8a).

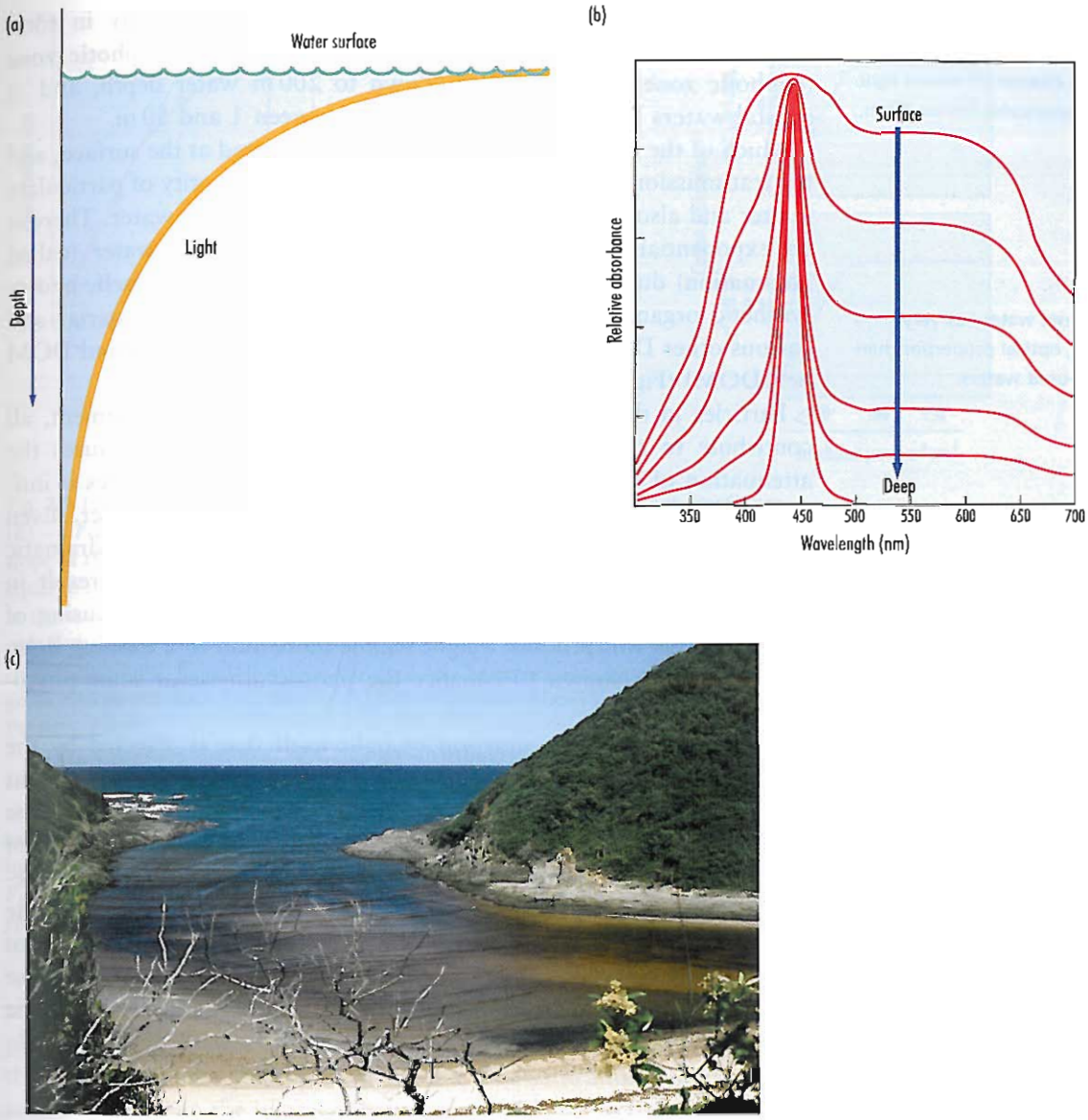


Fig 2.8 (a) Light decreases exponentially with water depth. (b) As light passes through a body of water, it is not just the amount of light, but also the spectral quality of light that changes. (c) River waters often contain high amounts of dissolved organic matter (DOM). In humic-rich rivers the DOM turns the waters brown. Where they mix with seawater the coloured waters can greatly influence the optical properties of coastal waters. (Photograph: David Thomas.)

In clear waters light can penetrate many hundreds of metres and in waters heavily laden with sediment or particulate matter it can be difficult to see a few metres. No matter how clear the water, below 1000 m water depth essentially no light penetrates and hence most of the world's

oceans with an average depth of 4000 m are permanently in total darkness (**the aphotic zone**) (Chapter 8). In general the **photic zone** (**euphotic zone**) seldom extends down to 200 m water depth, and in coastal waters light penetrates to depths between 1 and 50 m.

● In the clearest of waters light seldom penetrates below 200 m.

Much of the light incident on the water is reflected at the surface, and the transmission of light is then dependent on the quantity of particulate matter and also dissolved organic matter (DOM) in the water. There is an exponential loss of light as it passes through the water (called **attenuation**) due to absorbance of the light by the water itself, photosynthetic organisms, particles in the water, and humic material and various other DOM compounds that colour the water (**coloured DOM** or CDOM) (Fig. 2.8c).

● Coloured water has very different optical properties than non-coloured waters.

Particles in the water, such as bacteria, plankton, and sediment, all contribute to the scattering of light in the water, which causes the attenuation of light. Therefore the distribution of such particles is intimately linked to the transmission of light through the water. Even bubbles, ripples of water on the surface, and waves will have dramatic effects on the underwater light regime. These features may result in short-term fluctuations in irradiance, with focusing and defocusing of the light. This will produce a light regime more akin to a flashing light, which has been shown to enhance the photosynthesis of some phytoplankton species.

● Bubbles, particles, and surface ripples all greatly alter the light field underwater.

It is not just the transmission of light itself that is affected by the scattering and absorption of light, but also the spectral quality of the light (Fig. 2.8b). Water absorbs strongly in the red and infrared part of the spectrum, and so at deeper water depths the light is reduced in this part of the spectrum and effectively enriched in the blue and blue-green wavelengths. Water looks blue because of this differential absorption of the blue and red parts of the spectrum. Coastal waters have a large input of humic DOM or **yellow substances** (sometimes called *Gelbstoffe*). These reflect in the yellow-red part of the spectrum, and hence the characteristic yellow/brown colour of some river and coastal waters (Fig. 2.8c).

● Humic-rich dissolved organic matter often colours coastal waters.

2.6 Light and Photosynthesis

● *E* is the recognized symbol for irradiance.

The relationship between photosynthesis and irradiance is described by the characteristic ***P/E* curve** (Fig. 2.9) At low irradiance the photosynthetic rate is linearly proportional to increases in irradiance. At a particular irradiance the photosynthetic rate is equal to the respiration rate, the **compensation irradiance, E_c**. This irradiance is species specific, and within a single species can vary with season and even on shorter timescales. As irradiance increases the trend becomes gradually non-linear and a point is reached where further increases in irradiance do not

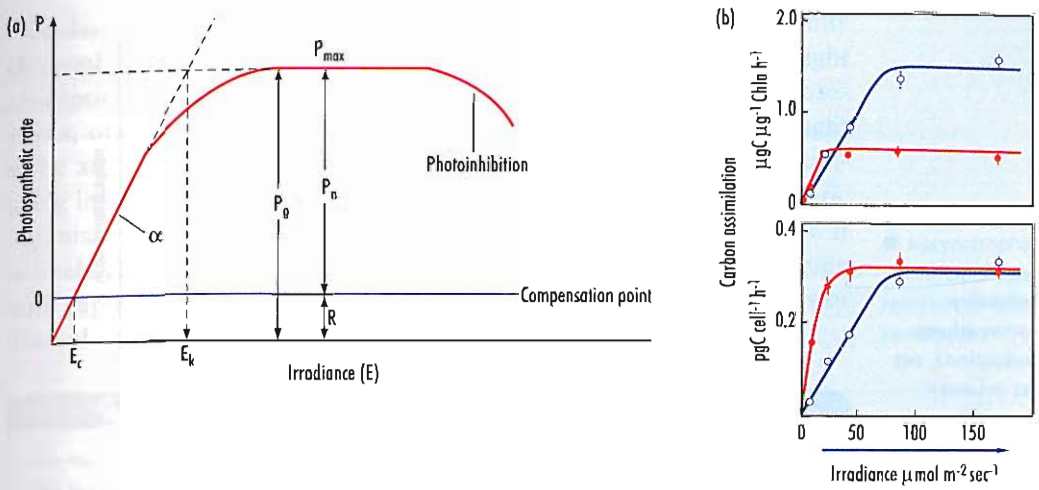


Fig. 2.9 (a) The response to photosynthesis (P) in response to changes in irradiance (E) – a P/E curve. With increasing light, photosynthesis increases linearly and the slope of the increase is α. At the compensation irradiance E_c the photosynthetic rate is equal to the respiration rate (R). With increasing irradiance the linear trend ceases, and at the saturation irradiance (E_k) the rate of photosynthesis is saturated (P_{max}). In some organisms, there can be a decrease in photosynthetic rates at high irradiances (photoinhibition). Respiration typically does not change with increasing irradiance, and gross photosynthesis is indicated by P_g and net photosynthesis by P_n (after Lalli & Parsons, 2004).

(b) P/E curves for phytoplankton cells grown in high (-○-) and low light (-●-). In the top set the rate of photosynthetic carbon assimilation is expressed as a function of chlorophyll concentration of the phytoplankton. In the bottom set, the same data is expressed on a per cell basis. The low-light algae have acclimated to the low light by increasing cellular concentrations of chlorophyll, and on a per cell basis reach the same P_{max} as the high-light acclimated algae, although their value of α is greater (i.e. more efficiently utilizing the lower irradiances).

result in increases in the photosynthetic rate. In other words, the rate of photosynthesis is light saturated (P_{max}). The slope of the linear part of the P/E curve is denoted by the symbol α. The **saturation irradiance, E_k**, is calculated from the intercept between α and P_{max}. In some organisms, there can be a decrease in photosynthetic rates at high irradiances. This decrease is a result of **photoinhibition**. This results from damage to components of the photosystems such as cellular membranes or electron-transport proteins.

● At high light levels maximum rates of photosynthesis can be inhibited, this is called photoinhibition.

Just as in the terminology used for primary production, **gross photosynthesis** is equivalent to the total photosynthesis, and **net photosynthesis** is equal to gross photosynthesis minus respiration (Fig. 2.10).

The characteristics P_{max}, E_c, E_k, and α are all species dependent, and also vary within a particular species depending on environmental conditions of light, nutrient status, and temperature. Generally P_{max}

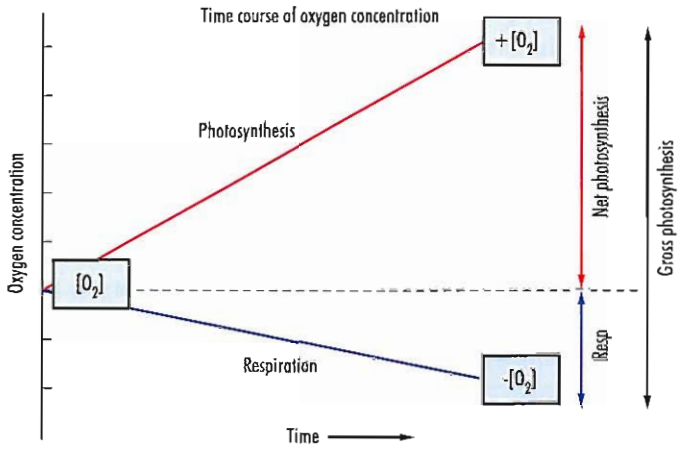


Fig. 2.10 The relationship between gross photosynthesis (gross primary production), net photosynthesis (net primary production), and respiration. (Image: Peter J. le B. Williams).

increases with increasing temperature (up to physiological limits), and is higher in organisms that grow at high rates in nutrient replete conditions compared with growth-limited cells in poor nutrient conditions.

2.6.1 Light acclimation

Within certain limits, most photosynthetic organisms are able to acclimate to a given light regime (MacIntyre et al. 2002; Raven & Geider 2003), mostly by altering the concentration of chlorophyll and/or accessory pigments per cell or per unit cell area. This process is called **photoacclimation**, and in low light conditions the Chlorophyll : Carbon (Chl*a* : C) ratio can be considerably greater than that for the same organism acclimated at higher light level (i.e. in the low light cells there is more chlorophyll per cell than in the cells at high light). Under nitrogen, phosphorus and trace metal (e.g. iron) limitation the Chl*a* : C ratio of a particular photosynthetic organism tends to decrease. Likewise in lower temperature acclimated cells, the Chl*a* : C ratio is lower than in cells acclimated at higher temperatures. The changing pigment concentrations of cells obviously have significant effects on the *P/E* characteristics of a particular algal species (Fig. 2.9b).

● By changing pigment content algae can photoacclimate to changing light regimes.

A Chl*a* : C ratio of 0.02 : 1 is often cited in the literature and used in models describing phytoplankton dynamics. However, because chlorophyll concentrations within phytoplankton cells can be altered due to external stimuli (temperature, irradiance, and the growth status of the algae) within time periods of hours, the utility of this ratio is rather dubious. Furthermore, ratios in the order of 0.01 : 1 to 0.005 : 1 are not uncommon in field populations (Lefevre et al. 2003).

Another feature, exhibited by some algal cells when exposed to changing light conditions, is an obvious movement of the chlorophyll-containing chloroplasts within the cells. The chloroplasts move along

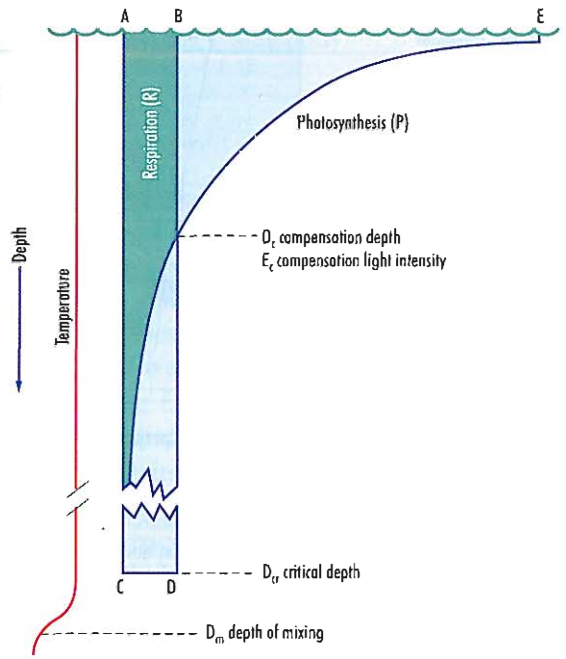
cytoplasmic strands in a process known as karyostrophy. Generally chloroplasts are distributed within the cell so that efficient light absorption can take place. However, in high light, clumping of chloroplasts, often around the nucleus, is frequently observed, and is thought to be associated with mechanisms to protect cell organelles from damaging light effects. Although not universal within aquatic photosynthetic organisms such mechanisms are known from terrestrial higher plants. It is likely that chloroplast movement processes are important for coping with rapidly changing light environments in turbulent surface waters or diurnal changes in light.

● Karyostrophy is a process by which chloroplasts move in reaction to changes light conditions.

Box 2.6 Compensation and critical depths

The euphotic zone is the upper part of the water column that supports photosynthesis. The bottom of this zone is generally defined as the depth at which 1% of the surface irradiance is measured. However, a better representation of the bottom of the euphotic zone is the **compensation depth**. This is the depth at which the gross photosynthetic carbon assimilation by phytoplankton equals the respiratory carbon losses, or when the net photosynthesis is 0.

● Compensation depth is the depth in a water column at which net photosynthesis is 0.



At the compensation depth (D_c) the phytoplankton photosynthesis is equal to the respiration, i.e. the compensation light intensity E_c. Phytoplankton is mixed in the water column, above and below the compensation depth, down to the depth of mixing (D_m). The critical depth is the water depth where the integrated water column photosynthesis is equal to the integrated water column respiration. In this diagram the area bounded by the points A, B, C, & D represents respiration, and the area A, C, & E represents the photosynthesis. At the critical depth these two areas are equal. When the depth of mixing is deeper than the critical depth, no net growth takes place. When, however, the

continues

BOX 2.6 continued

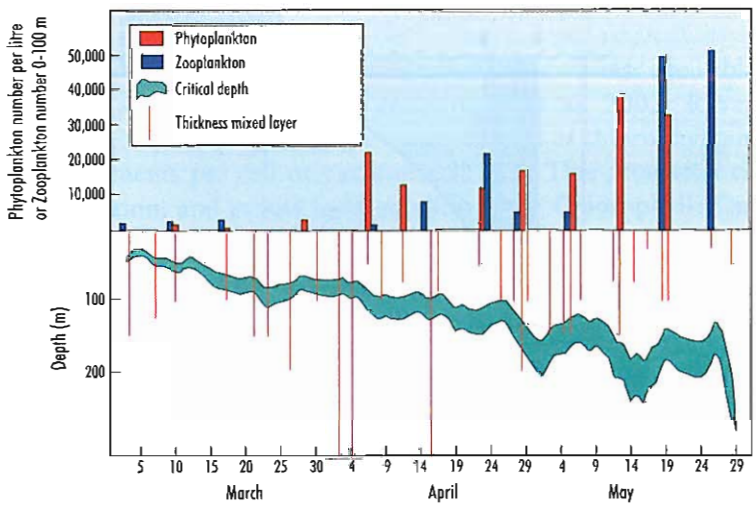
depth of mixing is shallower than the critical depth net phytoplankton growth occurs. (After Lalli and Parsons 2004).

It is worth noting that there is often a reduction in the photosynthesis rates measured at the surface of the water. This represents an often observed lowering of the photosynthetic rate due to photoinhibition in the very topmost meters of the water column.

Of course phytoplankton cells are not at a static depth as they and/or the water may move. In fact they are mixed either throughout the whole water column or, where water stratification takes place, within surface mixed water layers (Chapter 6). Because of this phytoplankton cells will be mixed above and below the compensation depth, to depths as deep as the **mixed layer depth**. When considering net phytoplankton growth it is therefore more pertinent to relate the daily integrated photosynthetic gains to the integrated respiration losses over the water column (day and night) to the mixed layer depth.

The **critical depth** is the water depth where the integrated daily photosynthetic carbon assimilation is balanced by the integrated daily respiratory carbon losses. As long as sufficient nutrients are present, net phytoplankton growth occurs when the mixed layer depth is shallower than the critical depth. When the mixed layer extends below the critical depth algal growth is limited by light, and there is no net phytoplankton growth (Sverdrup 1953; Smetacek & Passow 1990).

● The critical depth is the water depth where the integrated daily carbon assimilation is balanced by daily respiratory carbon loss.



Data from the Norwegian Sea in 1949 showing the relationship between mixed layer depth, critical depth, and phytoplankton and zooplankton abundance. Growth occurs only when the depth of mixing is consistently above the critical depth. (Illustration adapted from Sverdrup 1953).

The critical depth theory was first proposed by Sverdrup in 1953. In this theory the respiration losses are not just the algal respiration losses, but also losses due to grazing organisms and the respiration of bacteria and other heterotrophic organisms. Interestingly it led to a major advance in the design of freshwater reservoirs, where preventing algal blooms is an important part of their management.

The seasonal changes of mixed layer depth and incident light play a key role in the seasonal dynamics of phytoplankton (see below). These are discussed below in conjunction with the inorganic nutrient demands of growing phytoplankton populations.

2.7 Supply of Inorganic Nutrients

In addition to carbon, oxygen, and hydrogen, the plant must incorporate other elements into organic material. This arises as a consequence of the elemental composition of the various macromolecules, notably proteins and nucleic acids. The principal additional requirements are nitrogen and phosphorus and in aquatic ecology, these elements are commonly referred to as **nutrients** or **inorganic nutrients**

2.7.1 Nutrient status of water

Waters that have low concentrations of essential nutrients for algal growth are called **oligotrophic** and are regions of low primary productivity. In contrast **eutrophic** waters have high concentrations of nutrients, and generally support high levels of primary production. Waters between the two states are referred to as **mesotrophic** waters, and these sustain intermediate levels of primary production.

Most marine systems are classified on the basis of the annual primary production, which is another way of expressing the supply or production of organic matter in the water body:

Organic Carbon Supply	
Oligotrophic	$<100\,g\,C\,m^{-2}\,year^{-1}$
Mesotrophic	$100–300\,g\,C\,m^{-2}\,year^{-1}$
Eutrophic	$300–500\,g\,C\,m^{-2}\,year^{-1}$
Hypertrophic	$>500\,g\,C\,m^{-2}\,year^{-1}$

The process of **eutrophication** can be defined as **an increase in the rate of supply of organic matter to an ecosystem.** This occurs when there is a change in the concentration of a factor (can be more than one) that limits algal growth. This is often an increase in inorganic nutrients such as nitrogen or phosphorus, often associated with the run-off of artificial fertilizers from agricultural land (Chapter 14). The resulting increase in algal growth (both phytoplankton and/or macroalgae) if excessive (Fig. 2.11) can have deleterious effects for the whole ecosystem (Skei et al. 2000).

It is important to stress that eutrophication is a process or change and is not a trophic state. For example, an estuary may have been mesotrophic and is now classified as eutrophic, but it is not necessary undergoing further eutrophication. Although eutrophication is generally perceived as a detrimental process, it is also important to stress that it can be a reversible process. There are also instances when low levels of eutrophication can even be considered as being a positive state for increasing the productivity of a specific water body.

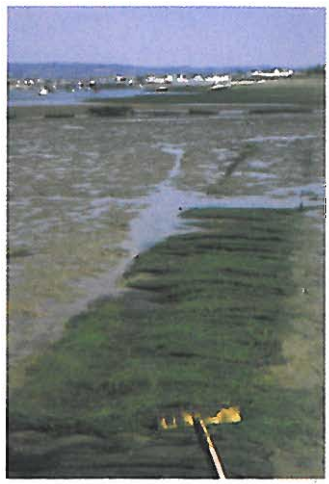


Fig. 2.11 Increased inorganic nutrient supply can result in excessive algal growth as shown by the mass of *Enteromorpha sp.* on clam cultivation plots in the River Exe, England. (Photograph: Brian Spencer.)

● Eutrophication can be defined as an increase in the rate of supply of organic matter to an ecosystem.

● Eutrophication is a reversible process and not always detrimental.

Strictly speaking eutrophication is a process by which the productivity of an aquatic system is increased, and can therefore be caused by factors other than nutrient input. These factors include reducing the suspended material in a water body and therefore increasing the light levels available for photosynthesis, or changing the residence time of water within a particular system. Therefore eutrophication is also a natural phenomenon, and is not always associated with anthropogenic activities. Coastal regions can receive high dosages of nutrients both directly via marine outfalls and by discharges from estuaries. This, coupled with their relatively long residence time, makes coastal ecosystems especially vulnerable to eutrophication (Chapters 7 and 14).

2.7.2 Supply of nutrients

Photoautotrophs require a diverse range of elements for balanced growth. These include nitrogen, phosphorus, silicon, sulphur, potassium, and sodium (all known as macronutrients). Many trace elements (micronutrients) are also required, including iron, zinc, copper, and manganese, as well as vitamins such as B_{12} (cyanocobalamin), biotin, and thiamine.

● A wide range of macro- and micronutrients are needed for algal growth.

Although each nutrient has the potential to limit the growth of photoautotrophs, in most marine environments it is either nitrogen or phosphorus that is generally the limiting element (c.f. Box 2.7 shown in section 2.9). It is actually the supply of the nutrient to the organism that is critical. A nutrient can be present in low concentrations, but if the uptake rate by the organism is low, only a low supply rate is required. Naturally growth can be limited by the supply of more than one nutrient at any one time: nutrients can be either biomass limiting or rate limiting. In the case of the former the nutrients are exhausted so that no more biomass can be produced. In contrast rate-limiting nutrients simply limit the rate of new biomass production by their rate of supply.

● Resupply of nutrients primarily takes place by molecular diffusion.

When a nutrient is taken up by an organism, there is immediately a reduction in that nutrient in the micro-environment surrounding the cell or organism. The resupply of nutrients takes place primarily by molecular diffusion from the bulk medium of water. Surrounding each cell or surface in water is a **diffusive boundary layer** (DBL) in which water movement and molecular diffusion is restricted. The thickness of the DBL surrounding the organism is therefore critical to determining the rate at which nutrients are transported to cell surfaces. The smaller the organism, the smaller the DBL due to the surface area : volume relationship (Chapter 3). This gives smaller organisms a physiological advantage at low nutrient concentrations and is presumed to be why small species of phytoplankton prevail in oligotrophic waters.

● Small phytoplankton species have a greater surface area : volume ratio than larger species.

It has been estimated that for cells less than 1 μm in diameter molecular diffusion is adequate for the resupply of nutrients, but for

Box 2.7 Iron and high-nutrient, low-chlorophyll regions

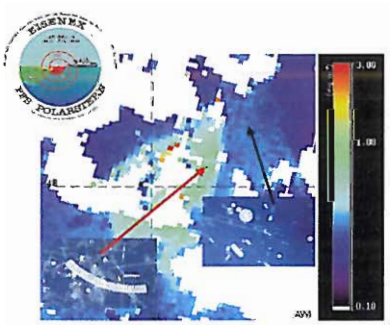
In some areas of the world's oceans the supply and assimilation of nitrogen, phosphorus, and carbon appear not to be linked. In these waters the phytoplankton standing stocks are never large enough to assimilate the N and P in the surface waters fast enough to deplete them at any time throughout the year. These are the 'high-nutrient, low-chlorophyll' (HNLC) waters of the subarctic Pacific, the Southern Ocean, and the equatorial Pacific.

● HNLC = 'high-nutrient, low-chlorophyll'.

Several hypotheses have been proposed to explain HNLC regions, including suggestions that in these regions light (either low or damaging high light intensity) limits production to a degree that inorganic nutrients are not utilized or that grazing pressure limits the standing stocks of phytoplankton. Whereas these factors clearly do play a role to varying degrees, the most compelling explanation is that the rate of supply of iron, an essential trace element for phytoplankton growth, is limited.

● Lack of iron may limit the growth of phytoplankton in 'high-nutrient, low-chlorophyll' regions.

Dissolved iron concentrations in offshore areas are extremely low, since the primary source of iron to the surface waters of the oceans is from the land, either via atmospheric dust deposition in offshore areas, or direct depositions from land masses. Atmospheric dust deposition in the two major HNLC areas – the Antarctic and equatorial Pacific Oceans – are the lowest in the world. Conversely, in the equatorial North Atlantic, which receives large amounts of dust from the Sahara, iron concentrations are sufficient for the complete assimilation of available nitrates and phosphates.



A satellite image of an iron fertilized patch during the Eisenex expedition to the Southern Ocean in 2000. The sparse phytoplankton outside of the patch is striking compared with the abundant growth of phytoplankton within the patch following fertilization. The satellite image shows the increase in chlorophyll (orange/red) compared to the waters surrounding the patch (blue). (Image: Philipp Assmy & Joachim Henjes, Alfred Wegener Institute).

In the late 1980s John Martin developed the idea that a lack of iron is the cause and laboratory experiments confirmed how vital iron is for phytoplankton growth. A series of experiments in the Equatorial Pacific Ocean, where large areas of the ocean (hundreds of square kilometres) were seeded with iron, led to substantial increases in phytoplankton growth. In particular diatoms grew and it appears that not all phytoplankton species are equally iron limited (Martin et al. 2002). Several oceanographic expeditions showed that during spring in the Southern Ocean phytoplankton bloom in iron-rich waters, but do not in waters with limited iron reserves (de Baar et a1.1995). It was pertinent to therefore extend the Pacific iron-fertilization experiments to the Southern Ocean. Several studies have now 'fertilized' Antarctic water bodies and in all of these diatoms did bloom in

continues

BOX 2.7 continued

response to the added iron. This growth was in turn responsible for the absorption of significant quantities of carbon dioxide from the water during the experiment (Boyd et al. 2000; Buesseler et al. 2004; Coale et al. 2004).

● Iron-fertilization experiments have resulted in increased phytoplankton growth within the fertilized patches.

It is this link between the phytoplankton growth and drawdown of atmospheric carbon dioxide that fuels a vigorous debate about these experiments. There is a concern that these results may be viewed as providing a simple answer for mopping up excess carbon dioxide, thereby curbing the effects of increasing greenhouse gases. It is thought by some that by spreading iron over huge swathes of the ocean, enhanced phytoplankton growth would effectively trap carbon dioxide. Such ideas about large-scale ecological engineering have little to do with the work of the scientists conducting the experiments. Iron fertilization is in fact a poor way to tackle greenhouse gas problems. Calculations show that iron fertilization of the Southern Ocean would not in fact be an effective mechanism for carbon dioxide removal. Levels of carbon dioxide are increasing at such a rate that even by maximizing biological uptake in these oceans by adding iron there would still be a net increase in atmospheric carbon dioxide (Chisholm et al. 2001; Buesseler et al. 2004).

● Fertilization of the oceans with iron will not be an easy fix for combating rising atmospheric carbon dioxide concentrations.

The real interest of this work comes from the implications for the understanding of the atmospheric carbon dioxide levels in past climate history. This new evidence supports the theory that low amounts of atmospheric carbon dioxide (measured in ice cores taken in the Arctic and Antarctic) during past ice ages may be linked to high amounts of iron in Antarctic waters that supported large standing crops of phytoplankton.

larger organisms it is a major limiting factor. Therefore mechanisms for reducing the DBL around the organism are key to the nutrient metabolism of aquatic organisms. Movement through the water, either by sinking or swimming, means that the nutrient depleted boundary layer is dragged with the organism causing fluid from the layer to be sheared away. This can then be replaced by nutrient-replete water. Clearly the velocity and magnitude of distance travelled will affect the degree of replacement. However, it is estimated that swimming significantly reduces diffusion limitation only in organisms greater than 100 μm diameter. In many of the organisms between 1 and 100 μm diameter, movement is a means of relocating into regions of higher nutrient concentration rather than addressing diffusion limitation by altering DBL properties. Any property of an organism that alters the organism's size and/or shape will alter the properties of the DBL. Therefore organisms that form colonies or chains, such as the diatoms, change their shape and therefore sinking rate, and also the characteristics of the DBL surrounding the colony or chain (Fig. 2.12).

● The diffusive boundary layer is key to determining nutrient supply to a cell, or surface of a macroalga.

In the case of macroalgae and seagrasses, relief or structures on the thallus or frond surface will cause eddy formation and turbulent motion of water passing over the surface (see also Chapter 7). This will have the effect of reducing DBLs and therefore enhancing nutrient exchange. As macroalgae and seagrasses cannot move in the water column by

● Ridges and structures on the surface of a macroalga can increase the rate of exchange of nutrients and dissolved gasses.

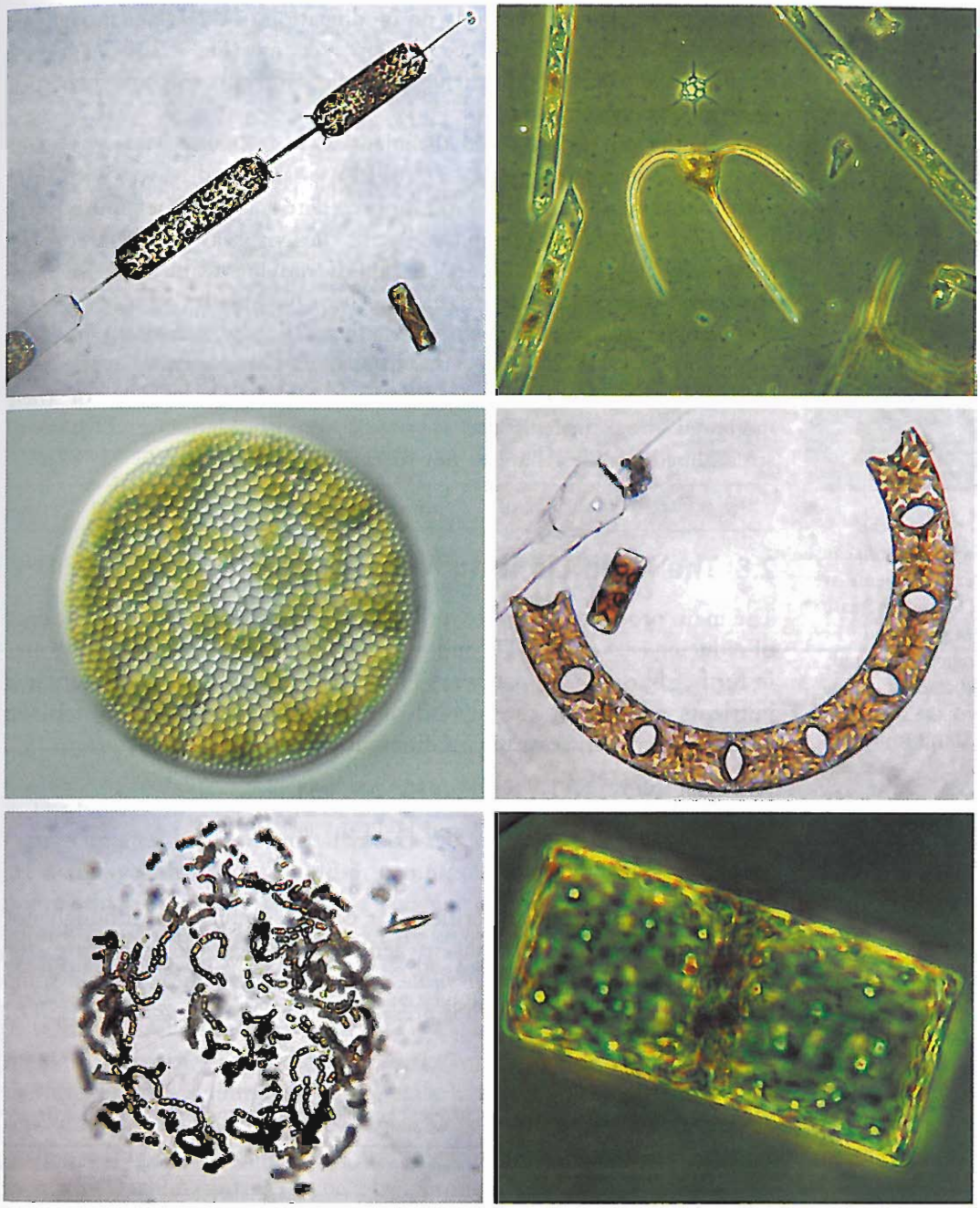


Fig. 2.12 Any property of an organism that alters the organism's size and/or shape will alter the properties of the diffuse boundary layer (DBL). Therefore the variety of shapes and forms of phytoplankton shown here will have very different sinking rates as well as different characteristics of the DBL surrounding the cells, colonies, or chains. Starting from top left and moving clockwise the images are: 1) *Ditylum brightwellii*, 2) *Ceratium tripos & Rhizosolenia* sp., 3) *Eucampia zodiacus*, 4) *Guinardia flaccida*, 5) *Chaetoceros socialis*, 6) *Coscinodiscus* sp. (Photographs: Ian Lucas).

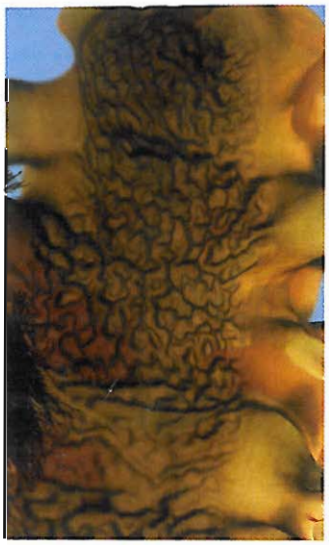


Fig. 2.13 Structures on the surfaces of macroalgae can cause turbulent water movements over the surfaces. This will increase the exchange of gases and inorganic nutrients compared with when undisturbed lamina flow passes over the surface. (Photograph: David Roberts).

swimming or sinking, they rely on modification of the water movement across their surfaces to enhance nutrient exchange (Fig. 2.13). Seagrasses are also able to take up nutrients from the sediments through their root and rhizome systems.

Naturally on exposed and turbulent wave influenced waters, water exchange is never going to be a problem. In sheltered waters with little water movement, diffusion limitation of nutrients becomes more of an issue. For example, the giant Pacific brown seaweed (*Nereocystis luetkeana*) has smooth blades in rapidly moving water, but in more sheltered waters its fronds are ruffled. The ruffled blades serve to increase the turbulence as water passes over them thereby increasing nutrient supply and gas exchange to the fronds. In faster moving waters the ruffled blades would increase the risk of tearing because of their increased drag; instead the seaweed's smooth blades tend to form streamlined bundles that are not so easily damaged.

2.8 The Main Limiting Nutrients for Growth

The main products of photosynthesis are sugars, reductant (the product of reducing enzymes), ATP, and oxygen, which are themselves substrates in further biosynthetic pathways (Table 2.2). The other major inorganic nutrients needed for the myriad of molecules that make up a living organism occur in seawater as different chemical species:

Nitrogen: NO_3^-, NO_2^-, NH_4^+, NH_3, N_2, and urea

Phosphorus: HPO_4^{2-}, PO_4^{3-}, and $H_2PO_4^-$

Sulphur: SO_4^{2-}, H_2S

● Nitrogen and phosphorus are the main growth-limiting nutrients in marine systems.

Particular nutrients are critical for certain organisms, although not limiting for photoautotrophs in general. An example is silicate, for diatoms and silica-scaled *prymnesiophytes* (and some cysts of some dinoflagellate species), which is present in several forms as well: H_4SiO_4, $H_3SiO_4^-$ and $H_2SiO_4^{2-}$.

Table 2.2 Typical percentage biochemical and elemental composition of algal cells.

Biochemical	% of an algal cell	% C	% H	% O	% N	% P	% S
Carbohydrate	40	44	6	49			
Protein	40	53	7	23	16		1
Lipids	15	69	10	18	1	2	
Nucleic acid & nucleotides	5	36	4	33	17	10	

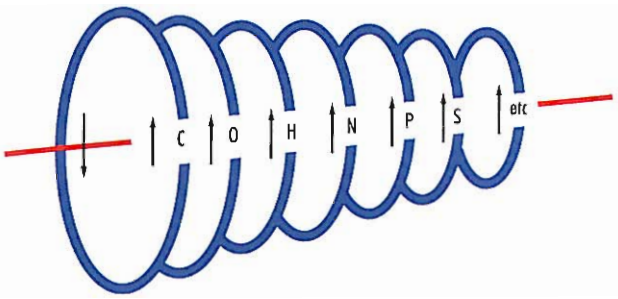


Fig. 2.14 There is a link between nutrient cycles and uptake of nutrients by primary producers. Ultimately these cycles and relative magnitudes are based on the biochemical composition of the organisms themselves. (Image: Peter J. le B. Williams.)

Table 2.3 Examples of nitrate, nitrite, ammonium, and phosphate concentrations in surface and deep waters of the Atlantic, Pacific, and Indian Oceans.

Ocean	Depth (m)	NO_3^- ($\mu mol\,l^{-1}$)	NO_2^- ($\mu mol\,l^{-1}$)	NH_4^+ ($\mu mol\,l^{-1}$)	$PO4^{3-}$ ($\mu mol\,l^{-1}$)
Atlantic	5	0–20	0–0.5	0–3	0.1–1
	4000	20	<0.5	<2	2
Indian	5	0–20	0–0.5	0–3	0.1–1
	4000	30	<0.5	<2	3
Pacific	5	0–20	0–0.5	0–3	0.1–1
	4000	35	<0.5	<2	3

The balance of these forms of any one element is highly dependent on many complex biogeochemical processes. Many of the trace nutrients are actually only mostly found in complexed forms with organic compounds in seawater (Table 2.3). The nutrient demands of individual species are naturally a reflection of its biochemical demands and composition. Clearly the proportion of the relative macromolecules, e.g. lipid (cf. nucleic acid), will determine the elemental composition of the cell and the relative demands for C, N, and P for growth. Although there is great variation in the composition of the cell, the functioning of the cell (i.e. the requirements for metabolism (enzymes – proteins) and reproduction (nucleic acid)) sets constraints on the relative proportions of the various macromolecules, and consequently the relative requirements for carbon, nitrogen, and phosphorus during photosynthesis.

2.8.1 Elemental composition of algae

There are obvious nutrient demands that are virtually universal, and these will be discussed here. However, it must be stressed that in many instances it is not the major inorganic nutrients (Table 2.4) that may

● A typical algal cell is 40% protein, 40% carbohydrate, 15% lipid, and 5% nucleic acids.

Table 2.4 The major functions of some selected inorganic nutrients.

Nutrient	Examples of functions
Nitrogen	Major metabolic importance, structural amino acid, protein metabolism
Phosphorus	Structural in particular membranes and energy metabolism
Potassium	Osmotic regulation, protein stability
Calcium	Ion transport, enzyme activation, structural function
Magnesium	Ion transport, enzyme activation, pigments such as chlorophyll
Sulphur	Structural function, active in enzyme activity
Iron	Active in enzyme activity
Sodium	Ion transport, osmoregulation, enzyme activation
Manganese	Electron transport and membrane structure

limit growth, but rather the rate of supply of trace elements that restrict the growth rates (Box 2.7).

Typically marine phytoplankton are comprised of more than 40% protein, 5% nucleic acids and nucleotides, 40% carbohydrates, and 15% lipids. These proportions can vary greatly depending on the inorganic nutrient supply, age of the organism, temperature, and irradiance conditions. It is straightforward to categorize the average composition of the organic materials within the phytoplankton.

If we rewrite the simplified photosynthesis equation to take into account the need for nitrogen (mostly supplied as nitrate) and phosphorus (supplied as phosphate) we get:

$$106CO_2 + 16NO_3^- + HPO_4^{2-} + 122H_2O + 18H^+ \Rightarrow C_{106}H_{263}O_{110}N_{16}P + 138O_2$$

Typically from the equation above, the ratio of **carbon : nitrogen : phosphorus** in healthy, actively growing algal cells is **106 : 16 : 1**. This ratio is referred to as the **Redfield ratio**, after the oceanographer A.C. Redfield. Therefore the typical C : N ratio is 6.6 : 1. This is a commonly used parameter to measure the physiological status of algae, since when nitrogen is limited, or the algal cells are senescent or dying the ratio increases considerably (Burkhardt & Riebesell 1997; Lenton & Watson 2000; Geider & la Roche 2002).

● The Redfield ratio, carbon : nitrogen : phosphorus is 106 : 16 : 1.

The quotient of CO_2 to O_2 from the above equation is 1.3. This is known as the **photosynthetic quotient (PQ)** (Williams 1998). This quotient is highly dependent on the state of oxidation/reduction of the nitrogen source. When nitrate is taken up by an algal cell it has to be reduced within the cell to ammonium before it can be utilized in cellular metabolism (Fig. 2.17). Algae can also take up ammonium (NH_4^+) directly as a nitrogen source, avoiding the energy in the reduction stage when nitrate is assimilated (see below). Therefore growth on ammonium

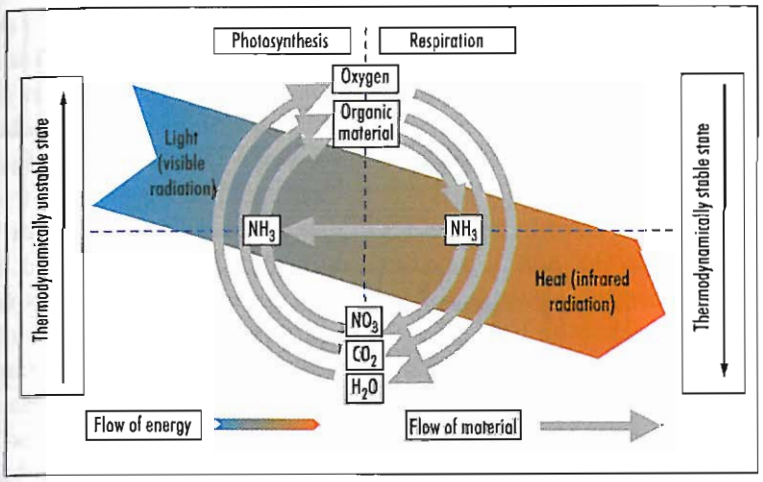


Fig. 2.15 The grand biological cycle is driving the biogeochemical pathways within marine systems. To simplify the diagram nitrate (NO_3^-) and ammonia are not shown in their charged forms. See further discussion in Chapter 3.

is about 19% more efficient on comparing the PQ values. The resulting PQ is lower at around 1.09.

● PQ = the moles of O_2 evolved per moles of CO_2 assimilated.

It must be stressed that this discussion of elemental ratios and typical cell composition is oversimplified. The cell composition (and therefore elemental ratios) will vary greatly at different life-history stages, and with changes in the prevailing temperature, light, and nutrient status. For example in older phytoplankton cells there is a marked switch from carbohydrate production to the accumulation of lipid reserves. When there is a lack of nitrogen in the surrounding water, protein synthesis is suppressed and the relative proportion of lipid and carbohydrates increase (Fig. 2.15).

2.8.2 Nitrogen

Nitrogen is present in seawater as dissolved molecular N_2, ammonium (NH_4^+), nitrite (NO_2^-), nitrate (NO_3^-), and as organic forms such as urea, amino acids, and a diverse range of complex dissolved organic nitrogen (DON) compounds (Fig. 2.16). In seawater ammonia (NH_3) exists as a mixture of the ammonium ion (NH_4^+) and NH_3. At seawater pHs (approx. 8) over 95% is in the form of NH_4^+. With increasing pH the relative contribution of NH_3 increases (e.g. at pH 9 NH_4^+ is about 75%).

● Only some species of cyanobacteria can fix nitrogen gas directly.

Nitrogen is the element that most frequently limits primary production in the oceans. Only some cyanobacteria, such as *Trichodesmium* species can reduce (fix) nitrogen gas, and these species thrive in waters where other forms of nitrogen are limited and thus restrict the growth of other phytoplankton (Berman-Frank et al. 2001). However, they still need sources of other nutrients such as phosphate.

● Nitrate is the primary form of nitrogen assimilated by marine primary producers.

Blooms of nitrogen fixing cyanobacteria are a feature of oligotrophic waters (particularly oceanic tropical coastlines), where nitrogen is

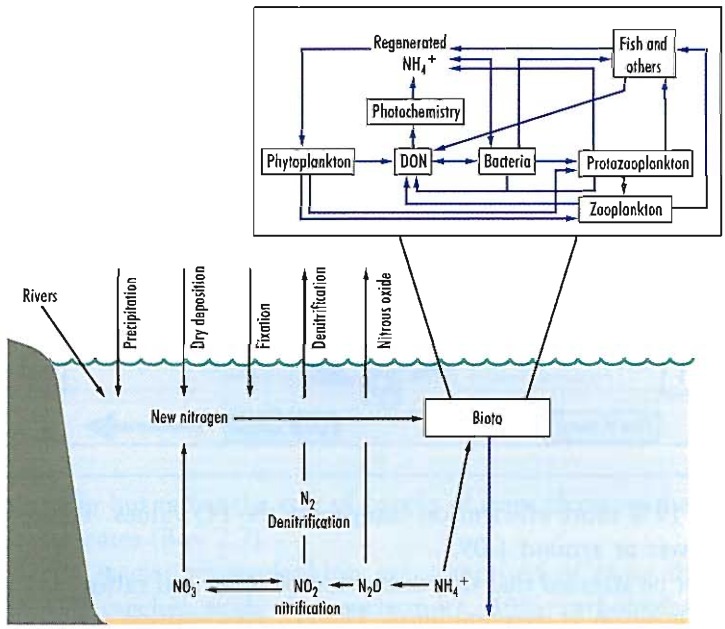


Fig. 2.16 Schematic of nitrogen in the ocean including input, transformation, and loss terms.

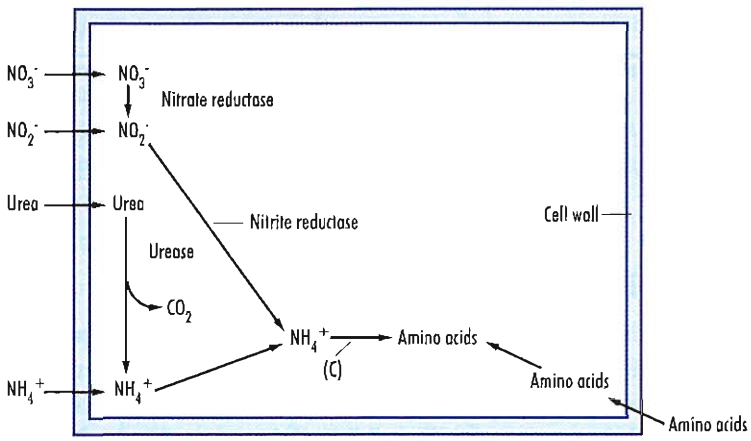


Fig. 2.17 Highly simplified schematic of major routes of nitrogen uptake and cellular transformation of inorganic nitrogen into amino acids by algae.

present in the water in very low concentrations, thereby restricting the algal growth. Other nitrogen fixers are also found growing on and in sediments in coastal regions, saltmarshes, and estuaries as well as in the roots of seagrasses and other saltmarsh grasses (e.g. *Spartina* spp.) where the nitrogen fixed by the cyanobacteria also supports the growth of the plants. In general, NO_3^- is the primary source of nitrogen utilized by algae, although NO_2^- and NH_4^+ can also be taken up (Fig. 2.17). Whatever the original source of nitrogen, NH_4^+ is the form utilized in cell metabolism and NO_3^- and NO_2^- have to be reduced by the enzymes **nitrate reductase** and **nitrite reductase** within the cell:

$$NO_3^- \rightarrow \text{nitrate reductase} \rightarrow NO_2^- \rightarrow \text{nitrite reductase} \rightarrow NH_4^+$$

As previously stated, changes in PQ indicate that production based on ammonium is 19% more efficient than production based on nitrate. In fact in some algal species nitrate uptake is inhibited when there are significant ammonium concentrations in the water. This inhibition is thought to be brought about by the inhibition of the nitrate reductase activity within the cells.

Primary production based on nitrate is referred to as **new production**. The breakdown, decomposition, and respiration of organic matter (Chapter 3) releases a range of other nitrogen species, ammonium, nitrite, and urea, and even amino acids that can be used as nitrogen sources for primary production. Primary production based on non-nitrate nitrogen sources is called **recycled production**.

The ratio of new production to total (new and recycled) production is called the **f-ratio**. The average global value is between 0.3 and 0.5. However, in oligotrophic deep ocean sites where there is little input of fresh nitrate into the upper mixed layer from below, the values can be well below 0.1 (Chapter 8). In contrast, in coastal regions or sites of coastal upwelling where input of nitrate can be high, the f-ratio can be up to 0.8 (Chapters 6 and 7). The inverse of the f-ratio gives the number of times the element recycles per year i.e., an f-ratio of 0.3 implies that an average nitrogen atom cycles round 3 times per year.

● The f-ratio is the ratio of new production to total (new and recycled) production.

2.8.3 Phosphorus

Following nitrogen, phosphorus is the second most common limiting nutrient in marine systems. Phosphate occurs in several forms in seawater, HPO_4^{2-}, PO_4^{3-}, and $H_2PO_4^-$, although at pH 8 and a temperature of 20 °C HPO_4^{2-} accounts for 97% of the free ions. Phosphorus is also present in a diverse range of organic compounds (organic phosphates). These can be broken down by enzymes (phosphatases) that are located in the membranes of many algal species. Phosphate limitation may also result in algae releasing alkaline phosphatases into the surrounding water to break down organically bound phosphorus. When external concentrations of inorganic phosphate are high, the production of alkaline phosphatases is repressed.

● Phosphorus can also limit primary production in some marine systems.

2.8.4 Sulphur

Sulphur is rarely a limiting nutrient as seawater is rich in sulphate, but it is a vital nutrient primarily for amino acid and protein synthesis. Curiously, in some macroalgae, such as the brown *Desmarestia*, the cells contain such high concentrations of sulphuric acid within their vacuoles that the low pH of the tissues deters grazers. Many species of macroalgae also contain large quantities of sulphated polysaccharides in their cell walls.

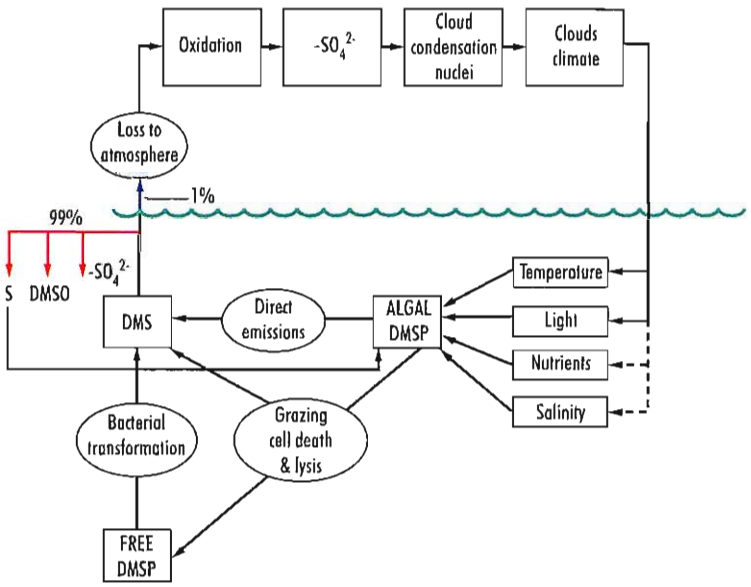


Fig. 2.18 Dimethyl Sulphide (DMS) released from phytoplankton and macroalgae (which contain DMSP) accounts for most of the non-marine salt sulphate in the atmosphere, and the oxidation of DMS to sulphur dioxide and the subsequent formation of aerosol particles and cloud condensation nuclei is part of a complex system of localized and global climate control. (NB Most of the DMS in the water is converted to DMSO (dimethyl sulphoxide), SO_4^{2-} and S, only 1% being exported to the atmosphere.) Image from Gunter Kirst.

Several phytoplankton species, as well as red and green macroalgae, produce a specialized compound, dimethylsulphoniopropionate (DMSP), which is used as an osmolyte in osmoregulation, a storage product, and possibly an antifreeze compound. In elevated external salinities intracellular concentrations of DMSP are raised in order to restore osmotic balance, and when external salinities are lowered DMSP is broken down proportionally into dimethyl sulphide (DMS) and acrylic acid (Fig. 2.18).

● DMSP is cleaved into DMS and acrylic acid.

DMSP is also broken down through the action of the enzyme DMSP-lyase and from grazing by proto- and metazoans, as well as viral infection. DMS released from phytoplankton and macroalgae accounts for most of the non-marine salt sulphate in the atmosphere, and the oxidation of DMS to sulphur dioxide and subsequent formation of aerosol particles and cloud condensation nuclei is part of a complex system of localized and global climate control (Malin & Kirst 1997). High concentrations of DMSP are also known to deter grazing of phytoplankton by protozoans (Wolfe 2000).

● DMS is important in the production of cloud condensation nuclei.

One of the most prolific producers of DMSP in coastal waters is the planktonic colonial alga, *Phaeocystis*. When these algae bloom, there is

a characteristic stench of DMS in the air, resulting from the breakdown of DMSP to DMS. Likewise intertidal green macroalgal species *Enteromorpha* and *Ulva* have high concentrations of DMSP, and following a rain shower during low tide, the DMS released from the *Enteromorpha* can be quite pungent.

2.8.5 Carbon

The supply of inorganic carbon for photosynthesis and algal growth is seldom (if ever) limiting in marine systems. However the role of oceans in the global carbon cycle has been the focus of intense study in the past decades, especially in relation to increasing carbon dioxide in the atmosphere as a result of anthropogenic activity (Siegenthaler & Sarmiento 1993; Takahashi et al. 1993; Feely et al. 2004; Sabine et al. 2004; Takahashi 2004).

The biggest pool of carbon in the oceans is that locked up in the sediments where globally about 10 million Gigatonnes (Giga is $\times 10^9$). In comparison there are about 39 000 Gigatonnes of dissolved inorganic carbon in the various forms discussed above. The next largest pool is that contained within the dissolved organic carbon (DOC) pool at about 700 Gigatonnes. It is striking to compare these numbers with the 30 Gigatonnes of carbon contained within the particulate organic carbon (POC) pool, which contains all of the organisms from bacteria to blue whales within the world's oceans (Fig. 2.19).

There are many algae that deposit calcium carbonate ($CaCO_3$) in their cell walls, sometimes together with smaller amounts of magnesium and strontium carbonates. In the phytoplankton, the most conspicuous

● 30 Gigatonnes of carbon is contained in all of the particulate phase biology compared to 700 Gigatonnes in the dissolved organic carbon pool and 39 000 Gigatonnes in the inorganic carbon pool.

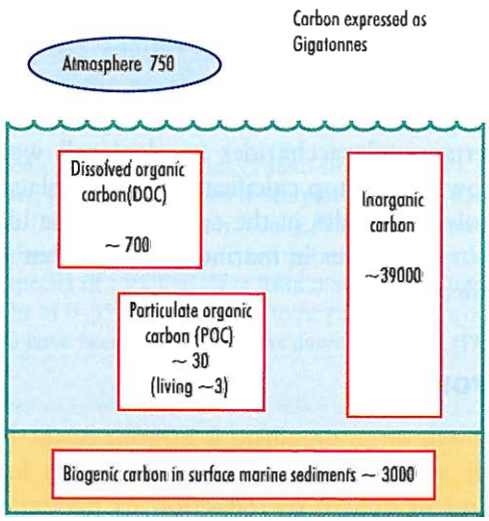


Fig. 2.19 Schematic to show the major pool of carbon within the oceans. Particulate organic carbon (POC) includes all organisms from bacteria-sized particles to whales. Dissolved organic carbon (DOC) is generally considered to be all carbon that can pass through a 0.2 μm filter. (Image: Rubén Lara.)

group of algae to exhibit calcification are the coccolithophorids that produce external 'shells' composed of calcium carbonate plates called coccoliths. These small phytoplankton species are common in all seas, although not as abundant in polar oceans. They can form extensive blooms where the ocean surface turns a milky white. One of the better-known species of coccolithophorid is *Emiliana huxleyi*, which can form blooms in the North Atlantic covering an area of the ocean equivalent to the size of Great Britain (Fig. 2.20). The coccoliths sink and are incorporated into sediments, where they can accumulate in huge amounts locking up $CaCO_3$ (Young & Ziveri 2000).

● Some microalgal and macroalgal species have calcified cell walls.

Normally when phytoplankton bloom there is a drawdown of CO_2 due to the assimilation through photosynthesis. However, the production of calcium carbonate structures by coccolithophorids can actually result in CO_2 being released to the atmosphere due to the formation of the calcium carbonate:

$$Ca^{2+} + 2HCO_3^- \Rightarrow CaCO_3 + CO_2 + H_2O$$

There are also many examples of calcareous brown, red, and green macroalgae, that is, species that have deposited calcium carbonate in the form of calcite or aragonite crystals within their tissue. This can be so extensive that these species can be important in the formation of tropical atolls and help to cement coral reefs together (Chapter 10). Calcite and aragonite never occur together in the same alga, and there is still some debate as to the metabolic processes that actually lead to the deposition. In some calcifying species the crystals are laid down outside the cells, such as in the green *Halimeda*, which causes aragonite crystals to precipitate in the spaces between the cells. In the fan-shaped brown *Padina*, aragonite is precipitated in concentric bands on the outer surface of the thallus. The corallines such as *Lithothamnion* and *Lithophyllum*, on the other hand, deposit calcite within their cell walls to the extent that the cells become encased, except for the cellular connections.

● In some coral reef systems over 70% of the reef can be made from calcified macroalgae.

Calcification is related to photosynthetic activity, and in particular the effects of pH on the dynamics of calcium and carbonate and bicarbonate in seawater. Certain polysaccharides in algal cell walls can actually block crystal growth and stop calcification taking place. The ability to produce these polysaccharides in the cell walls is the likely reason why calcification is not ubiquitous in marine algae and that relatively so few species are calcified.

2.9 Algal Growth

The ultimate growth of an organism is a result of the balance between the energy input and the necessary energetic costs for cell processes to take place and of course reproduction to maintain the following

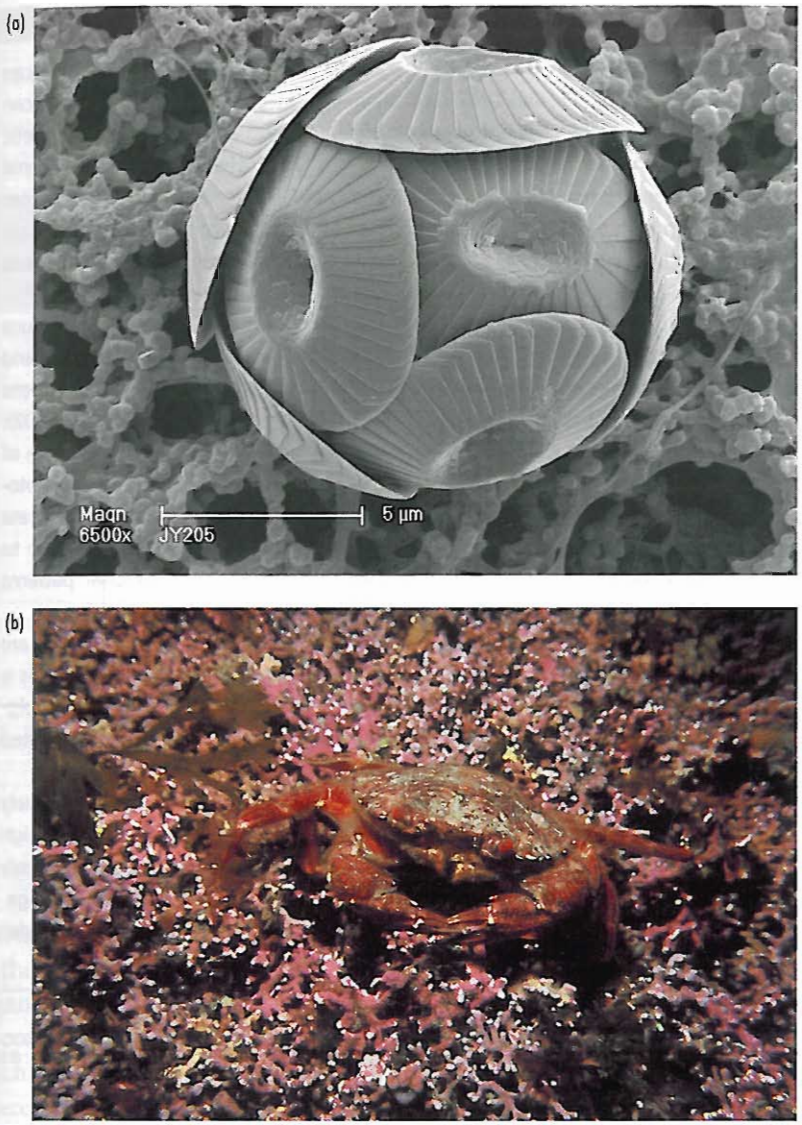


Fig. 2.20 (a) Planktonic coccolithophorids ('round-stone-bearers'), such as this *Coccolithus pelagicus*, synthesize exquisitely sculptured calcium carbonate cell walls known as coccoliths. (Photograph: Jeremy Young, Natural History Museum, London). (b) Several species of macroalgae have calcified cell walls, such as those comprising this maërl bed. Several species of coralline algae form maërl beds (Chapter 7), which are often found at depths of 0–35 m, although in some parts of the world free-living calcified macroalgae have been found at depths down to 200 m. (Photograph: Bill Sanderson).

Box 2.8 Ultraviolet radiation damage

Ultraviolet radiation (UV; UVA wavelength 320–400 nm and UVB 280–320 nm) can damage RNA transcription and DNA replication, and in particular UVB radiation can damage the photosystem II of photosynthetic organisms severely limiting photosynthetic carbon assimilation and therefore growth (Buma et al. 2001; Hebling et al. 2001). Some accessory pigments have a photoprotective role, and these are used to protect cells from damaging high light levels and also harmful UV radiation. Concentrations of these are usually low in light-limited algae, but form rapidly when the algae are transported into high light environments or high levels of UV radiation.

The effect of UV stress on many phytoplankton and macroalgal species is to produce UV screening agents such as β-carotene, mycosporine-like amino acids (MAAs), and photoprotective carotenoids (Hannach & Siglo 1998). These effectively act as sunscreens preventing damage to cell structures and DNA (Aguilera et al. 2002; Hoyer et al. 2002). The general response to increased UV radiation is a combination of a complex suite of cellular mechanisms including protection, repair, cell size, growth rates, and photoacclimation. Interspecific differences in response to this complex of factors will dictate any changes in phytoplankton composition. Therefore, the most likely scenario due to this environmental change is a shift in species composition or succesional patterns (Vincent & Roy, 1993).

One of the few generalizations that seem to be possible to make is that small cells are more vulnerable to UV radiation damage (Karentz et al. 1991; Buma et al. 2001). This is due to their surface area to volume ratios and the low effectiveness of screening pigments in small cells, although Helbing et al. (1992) found that UV radiation inhibited microplankton more than the nanoplankton.

It is not simply the amount of UV radiation that is damaging. This is because extremely low-light adapted algae are more susceptible to UV damage than algae grown in high light environments. Therefore algae growing in shade or low-light habitats suddenly exposed to high levels of UV radiations are highly susceptible to UV radiation damage. This may occur when subtidal stands of macroalgae are exposed on very low spring tides or phytoplankton cells are transported from deep waters to surface waters.

● A range of UV-absorbing compounds are produced by algae in high UV conditions to prevent cell damage.

generation (Box 2.8; Fig. 2.21). The energetic gains, investments, and losses of individual organisms include the following:

Material and energy gains: Photosynthesis or chemosynthesis

Material investments: Skeleton formation, production of energy storage compounds and formation of reproductive material

Energy and material losses: Movement, buoyancy, excretion, osmoregulation, nutrient uptake and respiration.

Growth is the expression of the integration of all of these losses and gains, within an organism. Thus, in general form:

Growth = Material and energy gains – Material and energy losses

This growth can be measured in material (mass) terms, e.g. dry weight, wet weight or in energy terms, kJ.

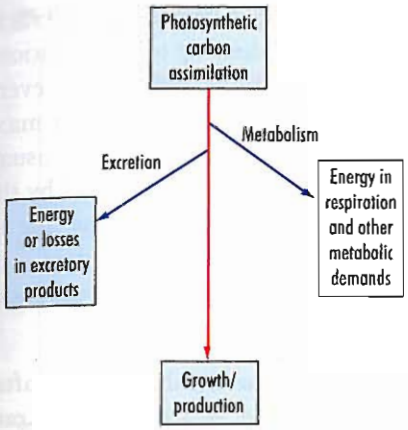


Fig. 2.21 The net carbon used for growth or production of a primary producer is a product of the photosynthetic assimilation minus several loss terms.

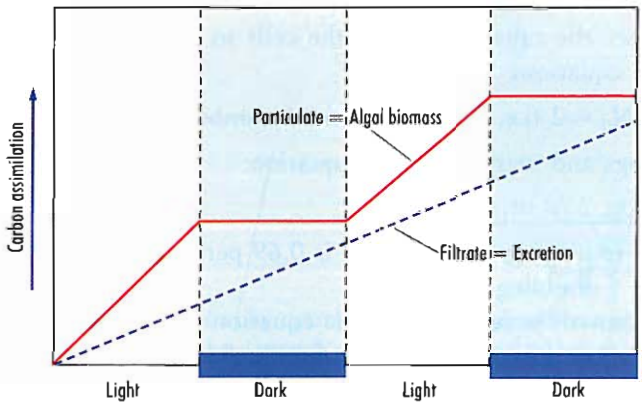


Fig. 2.22 Carbon assimilation by phytoplankton during light and dark periods. In the light, carbon is assimilated by the cells (particulate fraction), but not during the dark. In contrast carbon continues to be excreted by the cells (collected in the filtrate) in both the light and dark.

One of the striking features of algal growth is that significant amounts of the carbon assimilated during photosynthesis are released as excreted organic matter (see dissolved organic matter, Chapter 3). This varies greatly in composition from organic acids such as glycollate to vitamins, polysaccharides, fatty acids, amino acids, proteins, and simple carbohydrates. There are reports that up to 70% of carbon assimilated during photosynthesis can be excreted, but in general most values lie between 0 and 20%.

● Up to 20% of the carbon assimilated during photosynthesis can be excreted as dissolved organic carbon (DOC).

Some algal species increase the excretion of organic matter towards the end of a bloom, or when light and/or nutrients become limited. In contrast laboratory experiments have also shown that excretion of organic matter continues at a constant rate of about 10%. This excretion also continues during darkness and so is uncoupled from photosynthetic activity (Fig. 2.22).

2.9.1 Nutrients and growth

Algae can grow at high rates, given an adequate supply of light and no limitation in nutrient supply. Phytoplankton growth is usually expressed

as the rate of cell division or increase in biomass per unit of time. In ideal conditions, small picoplankton can divide to produce up to 3 generations per day (cf. bacteria growing in ideal conditions can divide every 20 minutes, or 72 generations per day). For most phytoplankton maximum growth rates of 0.3 to 1 generations per day are more usual. However, in natural conditions the growth rate is better reflected by the net rate of change in numbers or biomass including the gains due to reproduction and losses due to mortality or export from the system.

● Typically phytoplankton divide at 0.3 to 1 generations per day depending on the temperature and nutrients available.

The growth of phytoplankton can be expressed by the following equation:

$$N_t = N_o e^{\mu t}$$

where N_o is the starting number of cells, N_t is the number of cells after time t (the original N_o + the cells produced) and μ is the growth rate (which is species specific and depends on temperature, irradiance levels, and nutrient concentrations).

Therefore the time needed for the cells to double is given using the following equation:

$$N_t / N_o = 2 \text{ (i.e. double the initial number)} = e^{\mu t}$$

Taking logs and rearranging the equation:

$$t = \log_e 2 / \mu \text{ or, } t = 0.69 / \mu$$

Therefore if the growth rate (μ) is 0.69 per day the doubling time (t) would be 1 doubling per day.

When growth is described by the equation $N_t = N_o e^{\mu t}$, the growth of the population is exponential, and if natural logarithms of both sides of the equation are taken, the equation describes a straight line (Fig. 2.23a), the slope of which is μ:

$$\ln N_t = \mu t + \ln N_o$$

However, no population can continue growing exponentially for an indefinite period. Typically exponential growth ends following the utilization of one or another essential nutrient. When this happens a stationary phase is reached where there is no net increase or decrease in cell numbers (Fig. 2.23b). It is important to note that although there is no growth of the algal population, the cells continue to metabolize and produce and/or turnover cellular products. There may even be some cell division (growth), which is balanced by the numbers of cells dying during this phase. Ultimately as the stationary phase extends, the percentage of the cells dying increases and thereafter the population enters a death phase.

● Ideal algal growth includes a lag phase, exponential growth phase, stationary phase, and death phase.

If light and temperature conditions remain unchanged and losses due to grazing are not important, growth of algae is mostly limited by the availability of nutrients. The effects of nutrients on algal growth is described by the following equation:

$$\mu = \mu_{max} ([S/K_N] + S)$$

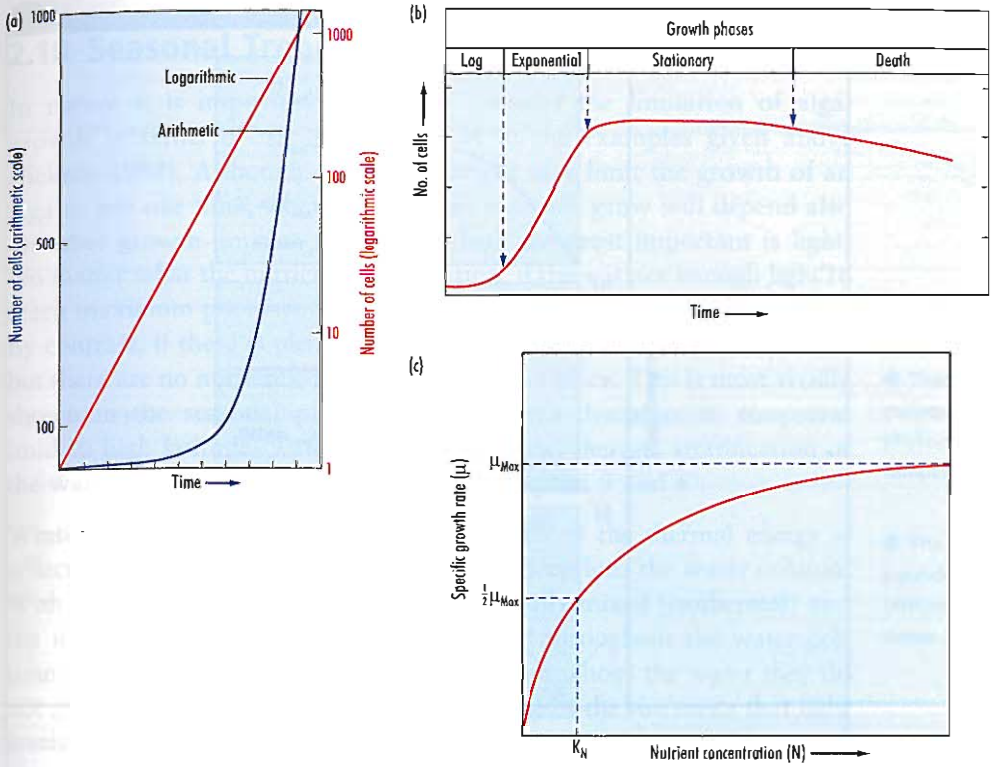


Fig. 2.23 (a) The growth rate of a phytoplankton culture expressed on both arithmetic and logarithmic scales. (b) Idealized growth curve for a phytoplankton population. (c) Relationship between nutrient concentration (N) and the growth rate of a primary producer. μ_{max} is the maximum growth rate, K_N the nutrient concentration at which growth rate is half the maximum ($0.5\,\mu_{max}$) – the half-saturation constant.

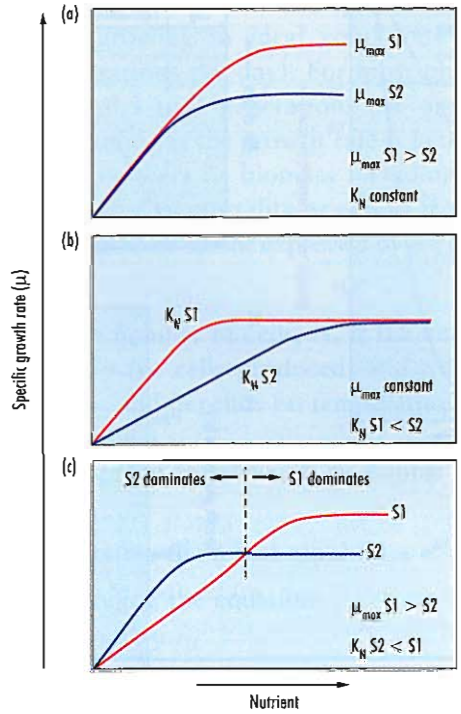
where S is the concentration of the nutrient and K_N is the half-saturation constant, or the concentration of the nutrient at which $\mu = \mu_{max}/2$.

This is a **Michaelis-Menten** relationship (as was the relationship between photosynthesis and irradiance, see above), and so when at low nutrient concentrations the rate of increase in growth rate increases rapidly with rising external nutrient concentration (Fig. 2.23c). At higher concentrations, increases in nutrient concentration add progressively less to the growth rate until the maximum growth rate is reached and further increases in nutrients do not affect the growth rate.

Each species of phytoplankton present in a body water (may be many tens to hundreds of species at any one time) has species-specific growth rate (μ and μ_{max}), and also a species-specific half-saturation constant (K_N) for all of the nutrients it needs to assimilate. This is one of the reasons why many different species of phytoplankton can coexist in a water body (Box 2.9).

Previously in the chapter it was described that small algae such as the picoplankton most efficiently take up nutrients because of diffusive

Box 2.9 Nutrient dynamics and phytoplankton growth



Examples of possible variations in nutrient growth curves of competing pairs of phytoplankton with different specific growth rates (μ), maximum growth rates (μ_{max}) and half saturation constants (K_N) for nutrient uptake (from Lalli & Parsons 2004).

In the first example (a) species 1 has a higher μ_{max} than species 2, but both have the same K_N. In this case both species grow at the same rate until a certain level of nutrients, after which species 1 continues to grow further until it reaches its maximum growth rate. In this case species 1 will dominate at nutrient concentrations greater than those at K_N.

In (b) both species 1 & 2 have the same value of μ_{max}, however, species 1 has a lower value of K_N than species 2. In this case species 1 reaches its maximum growth rate at lower nutrient concentrations than species 2. Therefore in low nutrient concentrations species 1 will dominate, although at higher nutrient conditions both species will grow equally.

In the third example (c) species 1 has a higher μ_{max} than species 2, but the latter has a lower K_N than species 1. At lower nutrient concentrations species 2 grows faster and dominates because it reaches its maximum growth rate at lower nutrient concentrations. However, at higher nutrient concentrations species 1 dominates because of its greater maximum growth rate.

boundary effects. Small photoautotrophs such as these also tend to grow at faster rates. Therefore why isn't there nothing else but the picoplankton? The answer is that in the discussions here, we have ignored a major controlling factor limiting algal standing stocks, namely, grazing by protozoans and zooplankton. In aquatic systems, grazing pressure exerts a major control on the dynamics and distribution of photosynthetic organisms.

2.10 Seasonal Trends in Primary Production

In nature it is impossible simply to consider the limitation of algal growth in terms of a single factor, as in the examples given above (Jickells 1998). Although only one nutrient may limit the growth of an alga at any one time, whether or not an alga will grow will depend also on other growth-limiting factors of which the most important is light. No matter what the nutrient concentration, if there is not enough light to reach maximum photosynthetic rates, growth rates will be compromised. By contrast, if there is plenty of light to saturate photosynthetic systems, but there are no nutrients, growth will not take place. This is most vividly shown in the seasonal phytoplankton growth dynamics in temperate (mid to high latitude) waters in which seasonal thermal stratification of the water column takes place (Fig. 2.24; Chapters 3 and 6).

● Thermal stratification of water masses is central to the seasonal phytoplankton dynamics in temperate waters.

Winter: The sun is low in the sky and much of the thermal energy is reflected. Winds tend to mix surface waters deep into the water column. With no thermocline, the water column is fully mixed (isothermal) and the inorganic nutrients are evenly distributed throughout the water column. Although phytoplankton are present throughout the water they do not grow because short days and the low angle of the sun mean that light levels are too low to support high rates of photosynthesis and growth.

● The thermocline is the boundary between dense cooler bottom water and warmer less dense surface water.

Spring: In spring the sun is higher in the sky and day length increases. This results in more solar energy absorption by the water and the development of a thermocline, which effectively traps phytoplankton in the surface waters. If the mixed layer depth is shallower than the critical

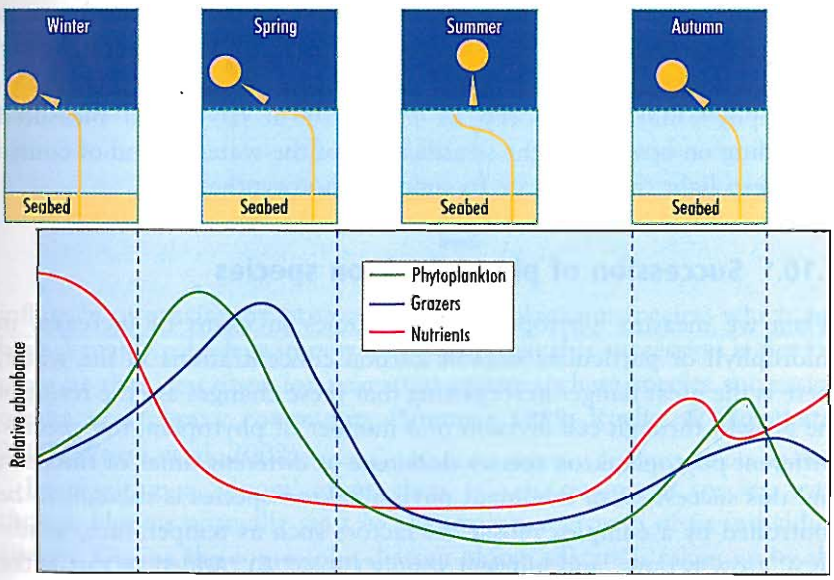


Fig. 2.24 Seasonal changes in phytoplankton, grazers, and inorganic nutrients (upper mixed layer) in temperate waters in relation to the seasonal thermal stratification of the water column.

depth (see above) phytoplankton will bloom, since there are abundant nutrients and adequate light to support maximal growth rates. This is termed **new production**.

Summer: The sun is high in the sky and day length is long. This results in the surface waters warming even more and the development of a strong thermocline that prevents any mixing between the surface and waters below the thermocline. Once the nutrients in the surface waters have been used up (typically nitrate and/or phosphate) phytoplankton growth ceases, despite the fact that light conditions are good enough for maximum photosynthetic rates to take place. Some growth will continue based on regenerated nutrients. This is termed **recycled production**.

Autumn: The sun is lower in the sky and day length shortens. The surface waters begin to cool and autumn winds tend to mix surface waters deeper leading to a breakdown in the thermocline. This results in nutrients from deeper waters mixing above the thermocline and this supports an autumn bloom of phytoplankton while light levels are still high enough to support photosynthesis. The autumn bloom is not as great as the spring bloom, because of lower light levels and also because concentrations of nutrients are not as great as at the beginning of spring. This is termed **new production**.

The depletion of nutrients in surface mixed water layers results in the establishment of a **nutricline** between the surface waters and deeper water: a gradient of low to high nutrients with increasing depth. There is therefore a potential flux of nutrients from below to above, and the maximum flux will be in the region of the nutricline. If the nutricline occurs above the critical depth in stable stratified waters, sub-surface chlorophyll layers form. These can occur in seasonally stratified waters (e.g. in summer), but are more characteristic of more permanently stratified waters found in tropical and subtropical oceans (Fig. 2.25). Chlorophyll maxima as deep as 20 to 100 m have been measured depending on how stable the stratification of the water is, and of course how deep light can penetrate to support photosynthesis.

2.10.1 Succession of phytoplankton species

When we measure phytoplankton dynamics in terms of increases in chlorophyll or particulate organic carbon concentrations in the water, there is the great danger in forgetting that these changes are the result of the growth through cell division of a number of phytoplankton species. Different phytoplankton species dominate at different times of the year, and this succession of dominant phytoplankton species is thought to be controlled by a complex mosaic of factors such as temperature, irradiance, growth rates, and nutrient supply (Box 2.6). Added to this is the

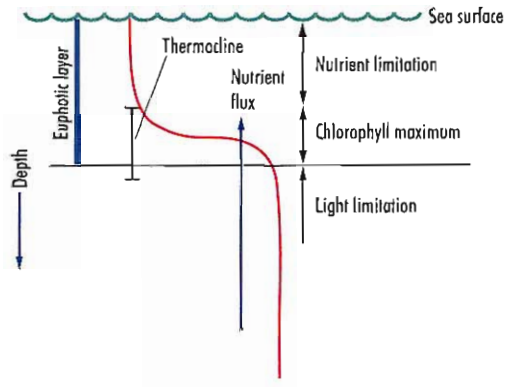


Fig. 2.25 In stratified waters nutrients may become limiting in the surface waters. However, nutrients may diffuse from deeper waters upwards across a thermocline. If this layer is in the euphotic zone (above the critical depth) phytoplankton growth can occur leading to the formation of sub-surface chlorophyll layers.

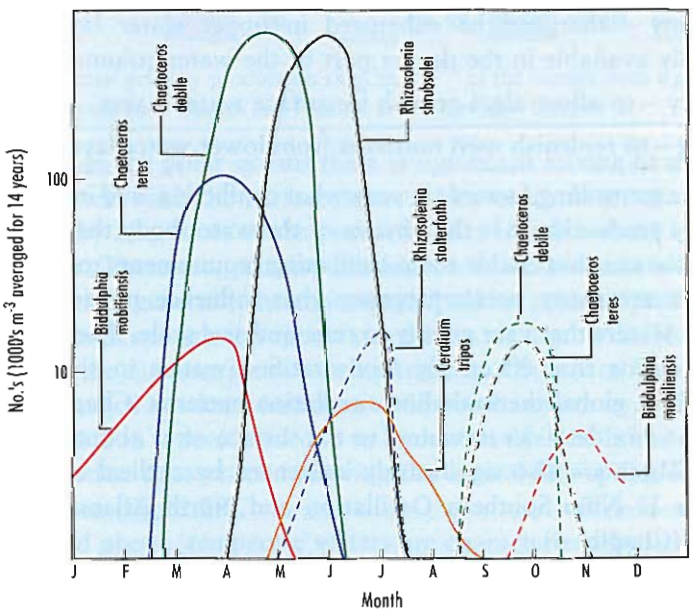


Fig. 2.26 Seasonal succession of dominant phytoplankton species in the Irish Sea averaged over 14 years (from Barnes & Hughes 1999).

influence of grazing by protozoan and zooplankton species, which can have a major role. It is important to note that this succession is *not* the same as that described for terrestrial systems where species succession results in a climax community (Sommer 1989; Roelke & Buyukates 2002; Worm et al. 2002).

Even within a 'bloom' event, there is a succession of species, even though blooms normally start by the explosive growth of an individual species. During the course of a diatom bloom silicate is taken up by the

● Many species make up the phytoplankton, and there is a succession of species throughout a bloom or from one season to the next.

diatoms to build silicate frustules. As the concentrations of silicate fall in the water due to this uptake there can be a progression from large diatom species to small diatom species that have less demanding silicate requirements for growth.

2.11 Global Trend in Primary Production

When considering primary production on a global scale, the advent of satellite colour images of chlorophyll distribution around the globe have been very successful in showing us that primary production is far from uniform at a large scale (Chapter 1, Fig. 1.6). Indeed, large-scale patterns in primary production are partly used to define distinct regions or biomes of the world's seas (see Chapter 7, Table 7.2). Ultimately there are four major factors that govern primary production in marine systems (Falkowski et al. 1998):

Light – only available in the upper part of the water column (max 200 m).

Nutrients – that can be exhausted in upper water layers, but are generally available in the deeper part of the water column.

Stability – to allow algal growth in surface water layers.

Mixing – to replenish used nutrients from lower water layers to surface.

● Ultimately it is the physics of a water body that controls the primary production.

These controlling factors are somewhat conflicting, and in areas of high primary production it is the physics of the water body that gives rise to circumstances that enable these conflicting requirements to be met.

There are many ocean processes that influence nutrient supply to surface waters that vary greatly in time and size scale. These range from storm events that effectively mix stratified waters in shallow waters through to global thermohaline circulation patterns (Chapters 6, 7 and 11) that mix deep ocean waters to the surface after about 500 years or more. These are also significantly influenced by cyclical oceanic events such as El Niño Southern Oscillation and North Atlantic Oscillation events (Chapter 6).

In tropical and sub-tropical waters, there is normally permanent thermal stratification due to the high degree of solar heating of the surface waters. Irradiances in these waters are high, and the clear waters result in light passing deep into the water column (>200 m). These conditions are of course conducive to high primary production, but because of the lack of mixing of inorganic nutrients from the deeper waters, tropical waters generally only support low primary production, although at a rather constant level throughout the year. When storm events do mix surface and deeper waters, phytoplankton blooms can result from the input of nutrients. Likewise tropical waters are sensitive to eutrophication processes, since when nutrients are introduced the high light levels support a rapid build up of primary producers (Fig. 2.28).

● Tropical waters have generally low primary production due to low surface water nutrient concentrations.

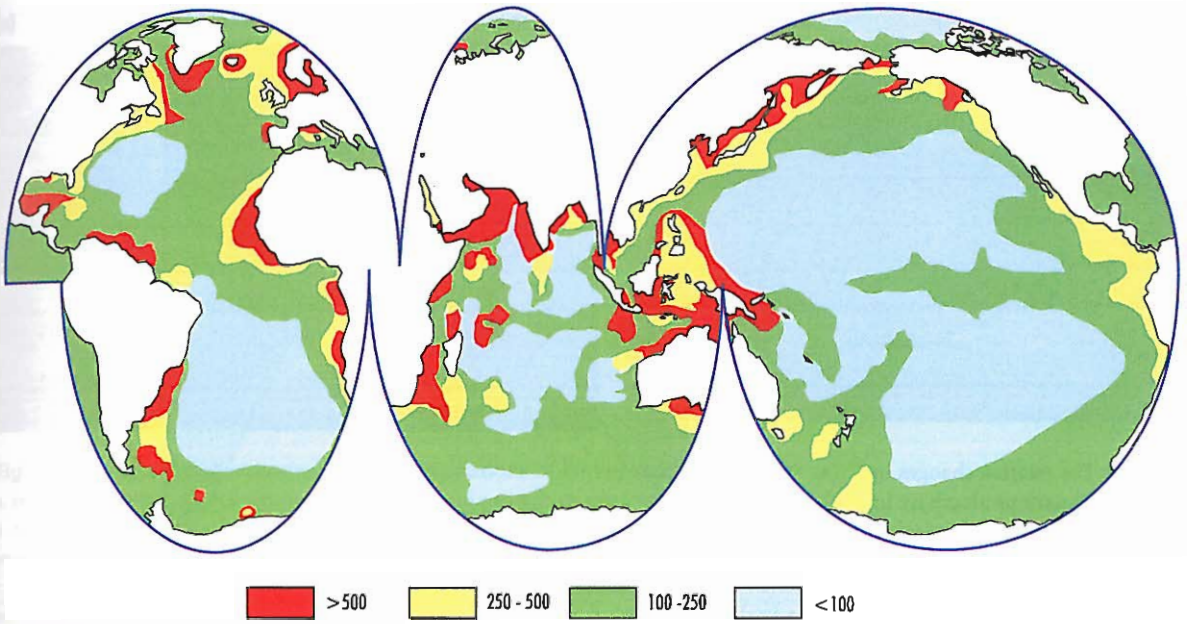


Fig. 2.27 The annual primary production as $gCm^{-2}\ y^{-1}$ of the oceans from a global perspective. Adapted from Barnes and Hughes 1999. (See also Chapter 1)

In contrast, in the **polar oceans** there is significant mixing of nutrient rich lower waters with the surface waters. However, these regions are characterized by long times of the year when day length is short and sun angles shallow. Therefore, primary production in these waters is limited by irradiance, and generally there is a single peak of primary production when light is high enough to support net gain in algal growth. There are differences in the nutrient status of the Arctic and Southern Oceans. In the latter the major nutrients (nitrogen and phosphate) are in excess, but primary production is restricted due to limitation of iron. In the Arctic, nutrient limitation does occur following the annual late-spring/summer plankton bloom (Fig. 2.28).

● Primary production in polar waters is restricted to short seasonal windows when light is available.

As described above, **temperate waters** are characterized by a suite of complex of seasonal dynamics of light and thermal stratification. These seasonal variations impart a distinctive seasonality in primary productivity: spring and autumn blooms of phytoplankton, with low standing stocks of phytoplankton in summer and winter (Fig. 2.25).

Large **oceanic gyres** are a conspicuous feature of the Atlantic, Pacific, Indian, and Southern Oceans. In the northern hemisphere these gyres move in a clockwise direction and anticlockwise in the southern hemisphere. These **anticyclonic gyres** tend to deepen the thermocline, moving water towards the centre of the gyre. Therefore nutrient replenishment into surface waters does not take place, and these anticyclonic gyres tend to be regions of low primary productivity (Chapter 6).

● Anticyclonic gyres are regions of low primary production whereas cyclonic gyres sustain higher rates of primary production.

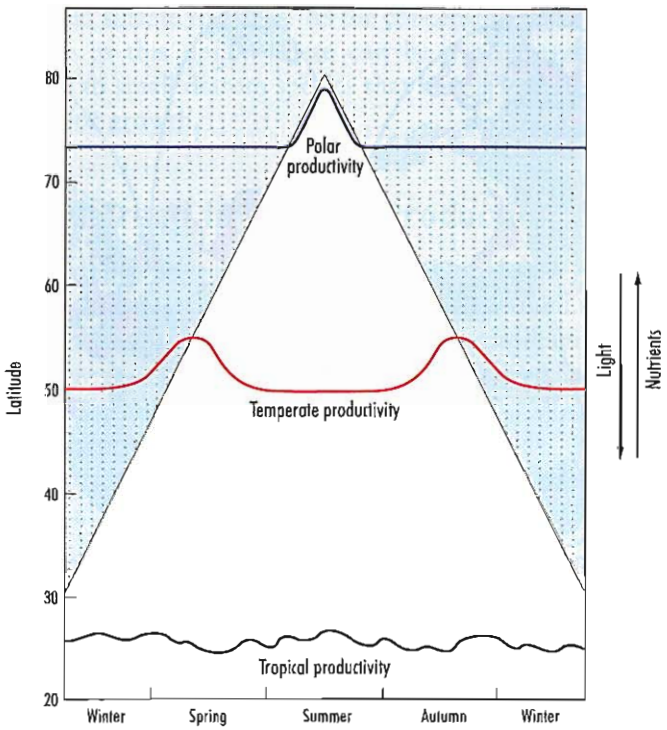


Fig. 2.28 The relative changes in seasonal primary productivity in polar, temperate, and tropical latitudes as a result of light- and nutrient-limited growth. The relative differences in light (unshaded) and nutrients (shaded) at the different latitudes are represented. (After Lalli & Parsons 2004).

However, **cyclonic gyres** (anticlockwise in northern hemisphere and clockwise in southern hemisphere) actually result in water being mixed from below the thermocline into surface waters, due to water being transported outwards from the centre of the gyre. Therefore in such gyres higher rates of primary production are supported, due to the mixing of nutrient rich water into surface waters.

Upwelling of nutrients in nutrient rich waters is characteristic of several coastal regions. Offshore winds give rise to offshore transport of nutrient-depleted surface water that is replaced by upwelling nutrient-rich water, supporting high rates of primary production. Upwelling also occurs at major ocean frontal systems in the open oceans, such as the equatorial regions where north-east and south-east trade winds generate two westerly flowing surface currents, the North and South Equatorial Currents. The **Coriolis effect** causes the currents to be deflected northwards in the northern hemisphere and southwards in the southern hemisphere. The divergent flow of these surface waters from the equator promotes nutrient-rich water upwelling, supporting higher rates of primary production (Chapter 6).

● Regions of upwelling are important sites of high primary production.

Coastal waters and waters overlying continental shelves (<200 m) support the greatest primary productivity. This is because many coastal waters are shallower than the critical depth (see Box 2.6), and also

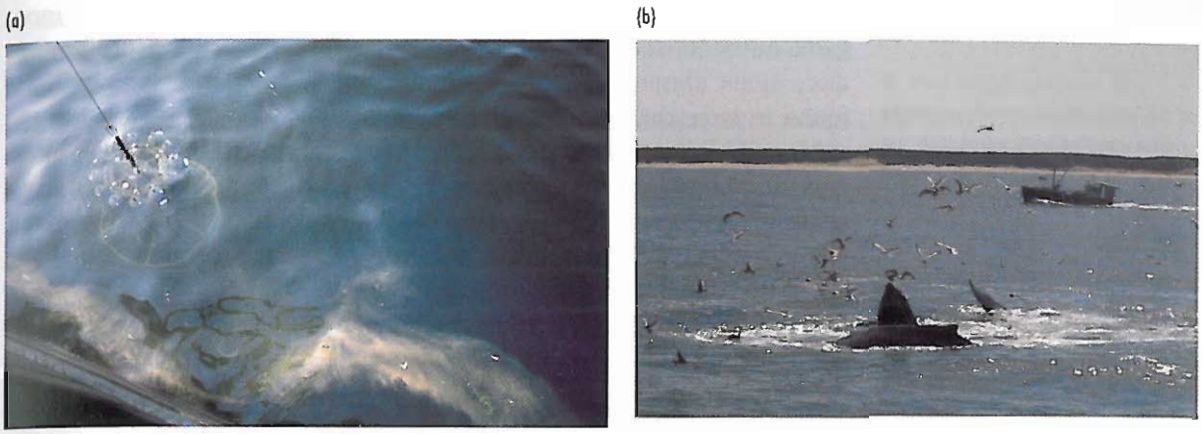


Fig. 2.29 (a) Fronts can be zones where concentrations of biology are found, either as a result of physical concentration or by increased growth of organisms. Here there is a huge concentration of photosynthetic ciliate *Mesodinium rubrum* in the surface waters of a front in the North Sea, as well as bird feathers, and green macroalgae concentrated on the water's surface. (Photograph: David Thomas) (b) Frontal systems are enhanced zones of biological activity, as seen here by the whales and birds feeding on plankivorous fish at a front. (Photograph: Michel Kaiser).

because coastal waters receive large amounts of growth limiting nutrients from river inputs into the coastal zone (Jickells 1998). There are many different types of frontal systems in shelf seas, and these tend to be associated with increased primary production, e.g. fronts associated with river plumes and shelf-sea fronts (tidal fronts) where the water column changes from being tidally mixed to being stratified. Typically the dense accumulations of plankton that occur at fronts attract feeding aggregations of fish, birds, cetaceans, and fishers (Fig. 2.29; Chapters 6 and 7).

● Frontal systems tend to be regions of enhanced biological activity, either from increased primary production or a concentration of organisms through physical processes.

The high standing stocks of plankton at tidal fronts may simply result from physical concentration by the water dynamics in the frontal zone. However, the conjunction of two separate water bodies can result in an exchange of nutrients (or other components) from one body of water to the other.

2.12 Primary Production in Seaweeds and Seagrasses

Much of this chapter has concentrated on primary production in planktonic photoautotrophs, since these contribute the greatest proportion to the primary production in the oceans. However, in coastal waters, the intertidal seagrasses and macroalgae are a very dominant

feature. These have a huge influence on the dynamics of coastal inorganic nutrients and cycling of organic matter (Chapter 9). More general discussions about the ecology of macroalgae and seagrasses will be found in later chapters (Chapters 5, 7, and 9).

Nevertheless seaweeds on a shore can grow at impressive rates, amassing large biomass (Fig. 2.30a). The productivity of seaweeds and seagrasses is equal to, or in many cases greater than, that of terrestrial plant systems. For instance *Laminaria* dominated communities have annual productivity rates of approximately 2 kg carbon $m^{-2}y^{-1}$. Seagrass meadows are extremely productive with annual production rates up to 6 kg carbon $m^{-2}y^{-1}$ measured at some tropical sites, far exceeding estimates for even tropical rain forests and monocultures of crops (Chapter 9).

● The annual primary production of seaweed and seagrass meadows can be in excess of rainforest or crop species.

In water, seaweeds obtain the carbon needed for photosynthesis from CO_2 or from HCO_3^-. When they are exposed to air, there is no bicarbonate and photosynthesis can only take place by the uptake of carbon dioxide from the air. As long as the seaweeds do not dry out, many species photosynthesize in air at rates similar to those measured when they are fully submerged. However, when they begin to dry out there are considerable differences in capacities for photosynthesis. Photosynthesis

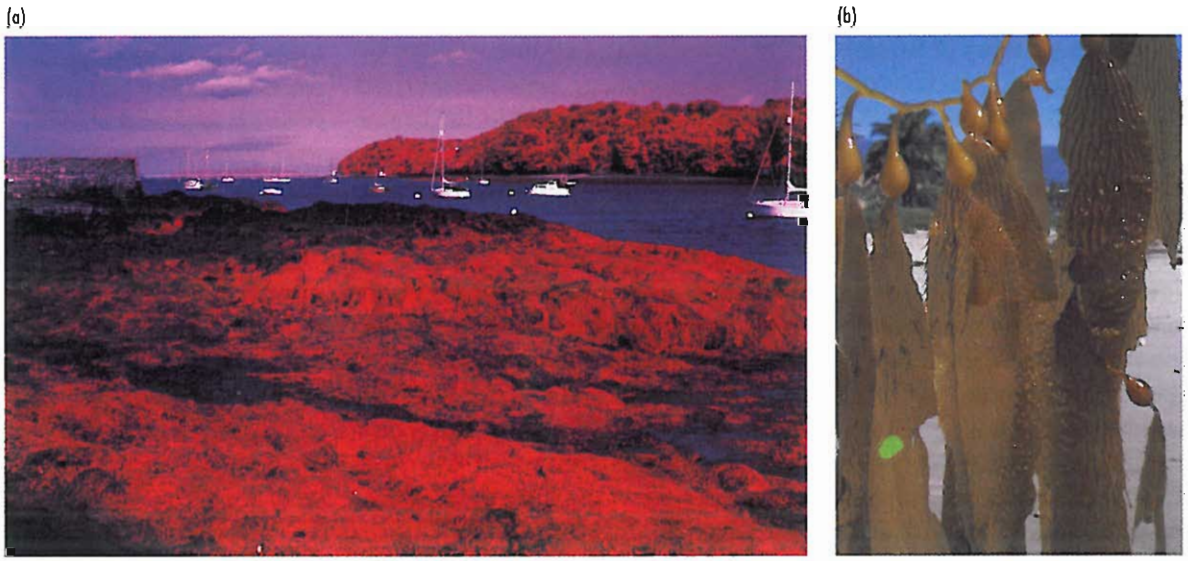


Fig. 2.30 (a) Infrared image enabling a comparison to be made of terrestrial and intertidal primary producers. The trees in the background show up red (due to the fluorescence of chlorophyll) in the image, as do the large standing stock of macroalgae on the shore in foreground. (Photograph: David Roberts.) (b) Air bladders at the end of each *Macrocystis pyrifera* blade help to support the giant algae in the water, and maximize exposure to the incident light. (Photograph: David Thomas.)

in the low shore kelps such as *Laminaria*, even when mildly desiccated, is greatly reduced, whereas the green alga *Ulva*, often found in intertidal zones, continues photosynthesis down to 35% water loss. *Fucus vesiculosus*, *F. serratus*, and *F. spiralis* can all photosynthesize even when desiccated down to a point where the remaining tissue water content is less than 30% (Dring & Brown 1982).

● Macroalgae continue to photosynthesize when exposed to air, and some species even when harshly desiccated.

When submerged, considerable energy is expended in maximizing the amount of light getting to the chloroplasts. This is especially important in turbid coastal waters full of plankton and suspended particles that reduce light penetration to a few metres or less. There are several morphological features common to many species of seaweed that help to address this problem. The first is the **stipe** that supports the bulk of the photosynthetic tissue at the surface of the water where incident light is at a maximum. *Nereocystis luetkena* is a superb example of this, with a stipe of over 30 m long supporting up to 100 blades each several metres long. In this case the stipe acts very much like the trunks of canopy species of trees in a rain forest, getting the maximum surface area of photosynthetic cells as close to the incident light as possible (Fig. 2.30b).

The long stipe of *Nereocystis* is rather flexible, and the blades only sit on the surface because the apex of the stipe terminates in an approximately 15 cm diameter float, or **pneumatocyst**. This large gas-filled bladder ensures that the blades are floating as high in the water as possible. In contrast, the giant kelp (*Macrocystis pyrifera*) has a different arrangement with a small gas bladder at the base of each of its thousands of blades, which connects them to the highly branched stipe.

● Gas-filled bladders are important in many macroalgal species for maintaining photosynthetic tissues as close to the incident light as possible.

Although not as impressively large, many other species use gas-filled bladders in a similar fashion, e.g. *Ascophyllum*, *Sargassum*, *Fucus*, and the bead-like *Hormosira*. The gases within the bladders contain oxygen and nitrogen in roughly the same proportion as in air, and varying amounts of carbon dioxide. Curiously the huge pneumatocysts of *Nereocystis* contain up to 10% carbon monoxide, although why this should be remains unclear.

As in trees that form terrestrial forests, the stipes of the seaweeds also act as surfaces for epiphytes to grow on. These can vary from other macroalgal fronds through to biofilms made from bacterial and/or microalgal assemblages. Colonial animals such as Bryozoa can also form dense cover on the outside of large macroalgal species both on the stipe and blades. Epiphytic growth can reach such densities that they restrict the exchange of gases and inorganic nutrients and cut down on light that reaches the photosynthetic cells of the host. They can also increase drag to such an extent that they make their hosts more prone to being washed away in strong water currents (Fig. 2.31). To avoid such problems, 'skin shedding' is widespread among large seaweed species

● Epiphytes growing on the surfaces of seaweeds restrict gas exchange and the supply of inorganic nutrients, as well as increasing drag.

Fig. 2.31 Macroalgae, like many other structures, can quickly become host to other algae and sessile animals that grow on their surface. Here a frond of *Fucus serratus* is nearly overgrown by the epiphytic brown *Ectocarpus sp.* (Photograph: David Roberts.)

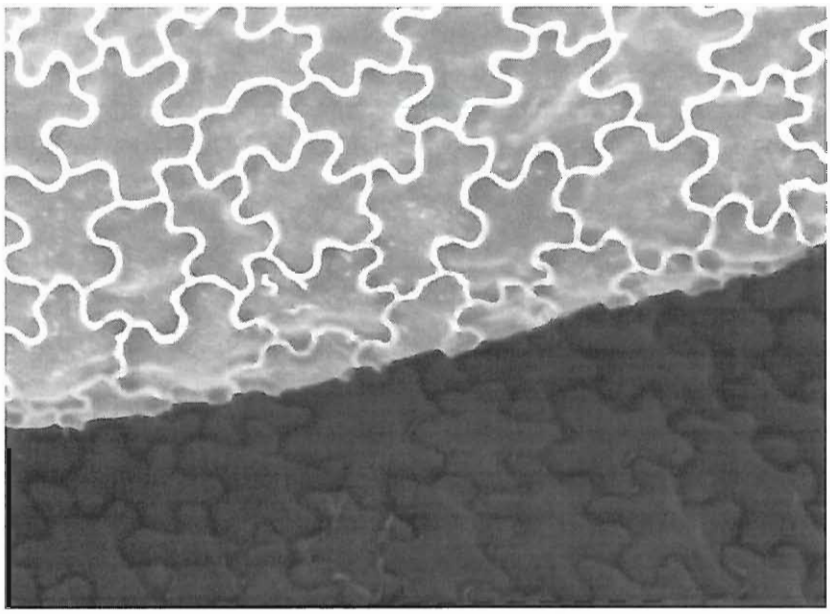


Fig. 2.32 One of the mechanisms by which several seaweed species overcome problems derived from epiphyte growth on their surfaces, is the periodic shedding of outer layers of cell walls. In this scanning electron microscope image, the outer layer of cell walls of the brown alga *Himanthalia elongata* can be seen lifting off, with the pattern of the underlying cells imprinted. (Photograph: George Russell.)

(Russell & Veltkamp, 1984). Layers of cell walls are shed from the outer surfaces of the seaweed carrying any attached epiphytes along with them (Fig. 2.32).

Seagrass blades are also renowned for supporting dense epiphytic growth. The biomass of epiphytes can range from 25 to 80% and production from 50 to 100% that of the seagrasses. Skin shedding is not carried out by seagrass species, but rather they produce large numbers of shoots, and blades heavily laden with epiphytes break off and are lost.

2.13 Measurement of Primary Production

The act of observation alters the object being observed (rough interpretation of Schrödinger's Cat thought experiment).

One of the key issues facing biological oceanographers trying to get good measurements of primary production rates is how to translate the measurements they can make to the conditions from where their field samples are taken. For the past 50 years the key techniques to measure primary production have been to measure directly the carbon assimilation during photosynthesis and/or the oxygen production and oxygen uptake during photosynthesis and respiration respectively.

● Primary production is mainly estimated by measures of the fluxes of carbon dioxide and/or oxygen.

The amount of carbon or oxygen flux per unit of time is then related to the biomass of the photosynthetic organisms creating the fluxes. Commonly used biomass terms are amount of chlorophyll, or the weight/concentration of the organic carbon contained within the photosynthetic organisms. Therefore the production is expressed as: **change in concentration of O_2 or CO_2 per unit of time per unit of mass or concentration of algae.**

The combinations of units are diverse, depending on the types of measurements being made and/or whether it is phytoplankton or macroalgae/seagrasses that are under investigation. For phytoplankton, rates of gas flux are often expressed per unit of chlorophyll or particulate organic carbon (POC). Measurements with macroalgae and seagrasses are normally expressed on the basis of fresh or dry weight, since these are easy to determine.

● Rates of primary production are usually based per unit of chlorophyll, particulate organic carbon or in seaweeds on a dry or wet weight basis.

To be most realistic, the incubations during which the fluxes of gas are measured should be made under the exact light regime that would be experienced in nature (Fig. 2.34). In a few instances it is possible to take a sample of phytoplankton, or macroalgae, from a particular water depth, put it in a container and then perform the incubations back at the same depth and then subsequently measure the gases produced or consumed over the incubation. However, the simple act of using a closed vessel introduces changes to the system that some researchers claim result in unrealistic measurements.

● How realistic 'bottle incubations' are is open to debate.

It is logistically difficult to deploy *in situ* incubations, especially if incubations are made throughout the euphotic zone, which may extend down to 200 metres in the open ocean. It is also preferable to make incubations last for whole diurnal periods so that the carbon and/or

● Although ideal, *in situ* incubations are often difficult to employ.

oxygen changes can be integrated over daily periods, thereby including periods of darkness where photosynthesis is absent, but respiration continues. These measurements are onerous; hence compromise is necessary, as discussed below.

2.13.1 Radiocarbon labelling – the '^{14}C method'

Primary production is basically the measure of the amount of inorganic carbon that is assimilated through photosynthesis to create new organic matter over a period of time and over a specified area. Intuitively therefore direct measurements of the decrease in the external inorganic carbon pool or the increase in the organic carbon pool would seem the most obvious way to measure primary production.

In the1950s the Danish scientist Einer Steemann Nielsen introduced the use of radiolabelled isotope ^{14}C for measuring carbon assimilation in phytoplankton. Since then, the '^{14}C method' as it is often referred to has become probably the most standard technique for measuring primary production in both phytoplankton and macroalgal studies.

● Uptake of radioactive ^{14}C is a widely used way to estimate primary production, although it is not clear whether net or gross production is being measured.

^{14}C in the form of $NaH^{14}CO_3$ is added to the incubation water surrounding a macroalgal sample or into a sample of phytoplankton. The photoautotrophs assimilate the ^{14}C during photosynthesis and at the end of an incubation period the quantity of radioisotope within the photoautotrophs is measured. This is directly converted into the amount of carbon that has been photosynthetically assimilated during the incubation.

Technically the method is rather straightforward, however, there is still much controversy about what it actually measures in terms of net or gross production. The other major disadvantage of the method is that it is not possible to measure dark respiration rates and, therefore, estimate gross primary production.

2.13.2 Oxygen determinations

It is possible to measure both photosynthetic oxygen production and respiratory oxygen consumption during incubations. The most widely used accurate oxygen determination method is based on Winkler titrations for determining the oxygen concentration of water. When performed with care, this chemical titration determination method is able to measure precisely very small changes in oxygen concentration, vital where respiration and photosynthetic rates are low.

● By measuring oxygen fluxes both photosynthesis and respiration can be measured, enabling both gross and net photosynthesis to be estimated.

The method involves measuring the increase in oxygen concentration in glass bottles (ranging in size from 10 to 200 ml) in which photosynthesis has taken place and the decrease in oxygen concentration in darkened bottles in which only respiration has taken place. One major

difference between this and the '^{14}C method' is that the oxygen fluxes due to bacterial, protozoan, and zooplankton respiration present in the sample will be included, because in reality it is impossible to screen these out of field samples without completely disrupting the photoautoptrophs. Therefore the oxygen methods tend to measure community metabolism, whereas in general the ^{14}C method is measuring activity of only the photoautotrophs.

The advantage of the oxygen system for the estimation of primary production is that both rates of respiration and photosynthesis can be directly measured, and so there is no ambiguity about whether or not net or gross production is being measured. The major difficulty comes in the conversion of the oxygen measurements into carbon terms. The **photosynthetic quotient** (PQ) is the term that describes the moles of oxygen evolved per moles of CO_2 assimilated, and is often quoted as 1.25. However, as described above, the PQ varies with different nitrogen and/or phosphorus supply. If lipids are being predominantly produced the PQ is significantly different than if carbohydrates are being produced. **Respiratory quotients** (RQ) are the inverse of the PQ and describe the respiratory relationships between oxygen consumption and CO_2 production, and are typically taken to be 1.0. Although less variable than PQ values, there will be variations around this value, making standardized conversions less certain.

● Photosynthetic and respiratory quotients are important to convert oxygen fluxes into units of carbon in primary production studies.

2.13.3 Electrodes

There is an increasing array of electrodes that can measure pH, O_2, CO_2, as well as sulphur and nitrogen species (de Beer 2000). These are not typically used to measure the fluxes of O_2 or CO_2 in incubations as described above, but rather are used in field deployments to measure temporal trends and estimate fluxes. Since the 1980s there have been great advances in technology that have enabled reliable electrodes with tip diameters of less than 50 μm to be constructed. These have been revolutionary in measuring small-scale fluxes in photosynthesis and respiration at surfaces such as biofilms and sediments. Estimates of primary production using these techniques have been greatly enhanced by the engineering of miniature light sensors with tip diameters of approximately 100 μm. Therefore the prevailing light regime can be measured at the same time as the chemical fluxes (Fig. 2.33).

● Increasingly electrodes are used to measure pH and gas fluxes, especially for fine-scale work on the surfaces of sediments.

The latest generation of equipment capable of measuring small-scale fluxes are the micro-optodes. In these, light of a specific wavelength is conducted via fine glass fibres to the measuring tip, which can be less than 20 μm. The tip contains a fluorescent dye that fluoresces at a different wavelength to the exciting light. The intensity of fluorescence depends on the concentration of the substance being measured.

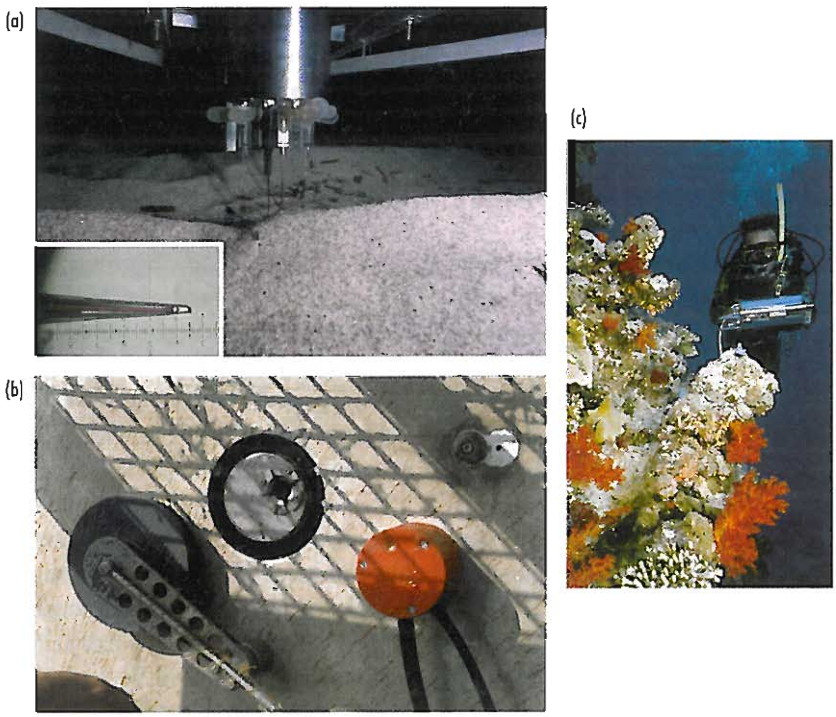


Fig. 2.33 (a) Microelectrodes are now available for several parameters including oxygen and carbon dioxide. These have incredibly small diameter tips (insert) enabling scientists to profile mini-scale (μM) differences in primary production and respiration, in particular in benthic systems. The images shows a 'lander' equipped with several electrodes, which it automatically pushes into the sediments. It logs the chemical data measured by the electrodes for downloading when the lander is retrieved. (Photographs: Dirk de Beer, Microsensor Group, Max Planck Institute for Marine Microbiology, Bremen and Christian Lott, Hydra institute.) (b) *In situ* fluorometer (window in centre) that can be deployed for long periods of time (months) to measure concentrations of chlorophyll in the water. Note that instruments left in the sea become fouled by growth of sessile organisms, requiring the antifouling washing arm shown to clean the fluorometer window periodically. (Photograph: David Thomas.) (c) Measuring photosynthetic activity on algae, corals, and sponges (symbiotic algae) in the Red Sea with the *in situ* chlorophyll fluorometer DIVING-PAM. (Photograph: Camillo Weis, Heinz Walz GmbH, Germany, **www.walz.com**.)

2.13.4 Fluorescence measurements

The measurement of changes in biomass is one route to estimate primary production. One of the most commonly employed methods for measuring chlorophyll is by measuring its fluorescence either within the cells directly or after extraction from the organism by a solvent. The chlorophyll is excited by carefully defined wavelengths of light and the resulting fluorescence measured directly (Krause & Weis 1991). Since the 1970s reliable instruments have been available for measuring the chlorophyll

fluorescence in open waters. These send out pulses of light and the fluorescence generated is measured. Many systems that profile for salinity (conductivity), temperature, and pressure (depth) (CTD sensors) can also be easily adapted to have *in vivo* chlorophyll fluorescence sensors attached and this information relayed back to the ship together with the temperature and salinity data. Such instruments have become invaluable for determining the distribution profiles of phytoplankton through the water column. For instance, such profiles often help scientists determine from which depths they should take water bottle samples for their oxygen or ^{14}C incubations for primary production determinations.

● Fluorescence sensors are used for the determination of *in situ* concentrations of chlorophyll, and therefore phytoplankton biomass.

Such sensors can also be deployed for the long-term measurement of fluorescence on moorings, automated underwater vehicles (AUVs), or on seabed platforms (see below). These can be left for periods of over a year and the data logged to allow the seasonal dynamics of phytoplankton biomass to be elucidated in fine detail for that particular site (Chapter 6).

It is possible to derive more information from the fluorescent characteristics of a photoautotroph than from the simple measures of *in vivo* chlorophyll concentrations. Pulse Amplitude Modulated (PAM) fluorometry is becoming a widespread tool for measuring *in situ* photosynthesis (Fig. 2.33). PAM fluorometers use a range of flashing (pulsed) lights to measure the photosynthesis from the fluorescense induced by the flashes of light (e.g. Glud et al. 2002). Generally the fluorescence is excited at high repetition rates by microsecond pulses of different wavelengths of light from light emitting diodes (LED).

● Fluorometric methods are used for direct measurements of primary production.

The accurate measurement of the variable fluorescence characteristics of phytoplankton is the basis of profiling devices that can measure 'real time' primary production as they are lowered through the water. These are known as Fast Repetition Rate Fluorometers (FRRF). The fluorescence excitation system generates excitation flashes at rates exceeding 200 kHz. The stimulated fluorescence and excitation flashes as well as the photosynthetically active radiation are all measured simultaneously. These measurements are then used to calculate various biophysical parameters that allow rates of photosynthesis and therefore primary production to be calculated (Suggett et al. 2003).

2.13.5 Remote sensing

Probably one of the most significant changes in biological oceanography over the past twenty years has been the development and deployment of satellite- and aircraft-borne colour sensors that can record the colour of water masses and, using sophisticated algorithms, can allocate the colour to concentrations of dissolved constituents such as coloured dissolved organic matter (CDOM), suspended solids, and (most importantly for primary production) chlorophyll and other algal pigment concentrations.

● Increasingly sensors on satellites provide information on primary production on a global scale.

Such satellite ocean colour sensors provide the only means we have for looking at the large-scale distributions of phytoplankton so that monthly and annual distribution patterns can be created (Fig. 2.3).

These large-scale distribution studies are fundamental to our understanding of the large scale processes in the oceans and how these affect primary production, e.g. the interannual variability due to massive cyclical phenomena such as the North Atlantic Oscillation (NAO) or the El Niño Southern Ocean Oscillation (ENSO). Naturally as more satellites are deployed carrying such sensors, and more years of information are collected, these methodologies will greatly enhance our understanding of large-scale ocean processes.

● Surveys of water bodies using aircraft give rapid information about phytoplankton distribution in surface waters.

Ocean colour sensors can also be deployed on aircraft and have been used successfully to record the dynamics of phytoplankton blooms, especially in coastal waters within the operational ranges of the aircraft. Light Detection and Ranging (LIDAR) flights use a variety of pulsed lasers to stimulate phytoplankton chlorophyll and other pigments to fluoresce, and the fluorescent signals are then detected by sensors on the aircraft.

One advantage of such data is that it can be collated rapidly by scientists on board the aircraft and relayed to colleagues on the ground or on research vessels. In this way the research vessels can be directed to particular areas of research interest such as developing phytoplankton blooms, or phytoplankton dynamics associated with water frontal systems. Increasingly research expeditions will rely on information such as this, as well as 'on-line' satellite information to plan and modify cruise tracks to conserve expensive ship time.

● Many remote sensing methods only give information in surface waters, they cannot give information about sub-surface phytoplankton distribution.

The major disadvantage of ocean colour sensors, either aircraft- or satellite-borne, is that it is only the colour of the very top few metres of the oceans that is measured. As has been discussed above (section 2.10), this is unlikely to be a reflection of much of the phytoplankton biomass in any one body of water. In particular features such as sub-surface chlorophyll maxima and accumulations of chlorophyll associated with sub-surface processes are not accounted for using these sensors.

2.13.6 Automatic measuring devices

● The typical daily cost of an ocean going research vessel is between $US20 000 and $US50 000 depending on size and sophistication.

Naturally such ground truth exercises are limited to the rather restricted activities of research vessels. Although many millions of dollars are spent each year on maintaining research ships at sea, the coverage of global oceans at any one moment of time is minimal. Many research vessels now have the technology to measure the chlorophyll content of surface waters continually during the whole of their cruise track by pumping surface waters past a sensor that measures the fluorescence, which can then be converted to phytoplankton biomass. This technology is robust enough to deploy on other ships, such as commercial freighters,

container ships, and ferries. These vessels tend to keep to well-defined routes, and so information can be collected that will document seasonal changes with high precision.

As well as chlorophyll concentrations, automated measuring systems are being developed for measuring temperature, salinity, and inorganic nutrients such as nitrate, phosphate, and silicate, as well as dissolved gases. Increasingly such devices will be deployed on a variety of ships (including ferries and commercial shipping), together with fluorescent sensors for phytoplankton determination (e.g. Cooper et al. 1998). This will enable the determination of seasonal biological and chemical dynamics along specific routes to be well defined. Naturally these measurements still suffer from the limitation that they are only measuring surface waters, since the water is normally pumped from seawater inlets in the keel of the ships, only a few metres below the water surface.

● Coupled biological and chemical sensors are deployed on ships that have regular routes, enabling large-scale collection of data over long periods of time.

The opportunity to profile the concentrations of phytoplankton and the parameters that determine primary productivity over greater water depths is clearly the next step. Very important information may be gained using towed platforms that undulate during towing from the surface to depths of 500 m (Fig. 2.34). These **undulators** can be towed at speeds up to 12 knots (*c.*6 ms^{-1}) and their 'flight-paths' can be set by the operators. These platforms can support a multitude of sensors such as fluorescent

● Towed instrument platforms that undulate between the surface and depths of 500 m can provide valuable information about the biological and chemical characteristics of a water body.

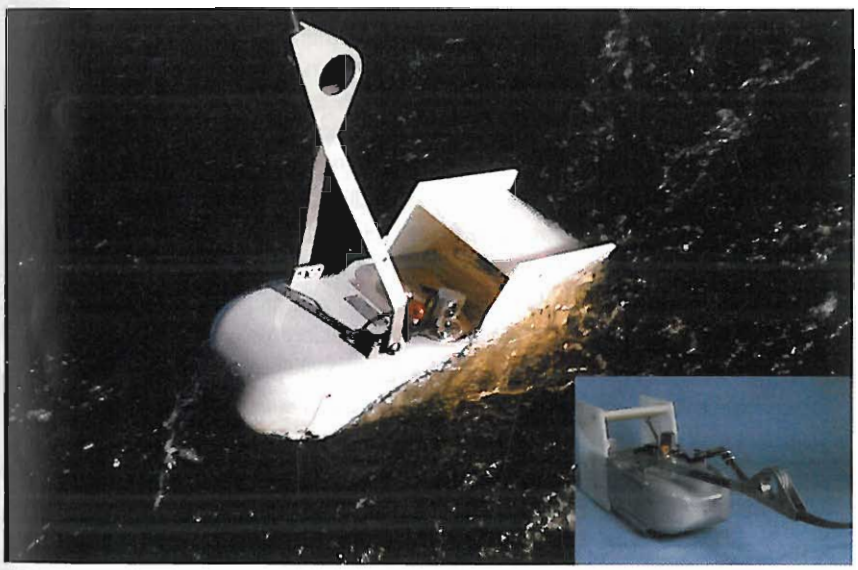


Fig. 2.34 Various profilers are now available that can be towed from a ship. They are designed to undulate over a water column profiling a range of parameters using a range of sensors (insert) carried on the vehicle. Data can either be logged on the profiler or, more normally, be sent back through cables so that scientists get real-time data on board the ship. (Photographs: Chelsea Technologies Group, **www.chelsea.co.uk**.)

chlorophyll sensors, light sensors, salinity, temperature, pressure, nitrate and nitrite, and particle concentration sensors. The data from the sensors can be sent to the operators by the connecting cable, giving the scientists on board 'real time' data about a whole suite of information.

These technologies are still restricted to the places that ships travel, and therefore large part of the worlds' oceans will be visited only infrequently, if at all. What is needed is roaming platforms that are able to measure physical, biological, and chemical parameters across depths and for long transects. A whole range of Autonomous Underwater Vehicles (AUV), gliders, and floaters have been under development since the late 1990s. These battery-powered devices are designed to 'roam' pre-programmed tracks over large regions of the ocean, collecting data. Periodically these devices surface to send the collated data to satellites, which then transfer the data to base stations from where scientists can download the information. To date, many of these devices carry sensors for salinity, temperature, and pressure among others. However, as technology progresses fluorescent and nutrient sensors will be routinely deployed on such platforms.

● In the future Autonomous Underwater Vehicles will be used to roam the oceans sending information about primary production and chemistry to satellites and back to researchers at their desks.

CHAPTER SUMMARY

- About half of the global primary production takes place in marine systems. Most of the primary production in the world's oceans is due to microscopic phytoplankton, since macroalgae are restricted to a rather narrow band on coastlines.
- Photosynthetic algae can vary in size from just a few μm to giant macroalgae 50 m long. Growth of primary producers is the difference between the gains from photosynthesis and losses to respiration, excretion and the construction of skeletal material and storage products.
- Rates of primary production are mainly controlled by light and inorganic nutrient supply. The amount of light available for photosynthesis depends upon water depth, and the amount of light-scattering particles that occur in the water.
- The main limiting inorganic nutrients are nitrogen and phosphorus, while in certain marine systems trace elements such as iron are limiting.
- Seasonal dynamics of algal growth are controlled by a complicated suite of interactions between irradiance and nutrient supply, ultimately driven by the physical dynamics of the system.
- Eutrophication of a water body is a reversible process and can be caused by factors other than solely increased inorganic nutrient loading of a system.
- Frontal systems, gyres, river plumes and coastal upwelling all influence the rate of primary production, as they influence the transport of nutrient-rich waters to the sea surface.
- Primary production in Polar oceans is restricted to a short summer season, in contrast to temperate waters where two peaks in production are often observed. Primary production of tropical waters is generally consistently low.

- The measurement of small-scale primary production can be made using oxygen and carbon dioxide tracers, or electrodes and various fluorometric techniques. On a global scale primary production is measured using satellite-borne colour sensors that are used to estimate the concentrations of plankton in the water.

FURTHER READING

A classic introduction to phytoplankton dynamics and constraints on growth is presented by Fogg (1991) as well as short essays by Smetacek (1999, 2000, 2001). The evolution of modern phytoplankton is discussed by Falkowski et al. (2004).

Both Falkowski and Raven (1997) and Williams et al. (2002) give comprehensive overviews of primary production in aquatic systems, whereas del Giorgio and Williams (2004) deal specifically with respiration. However, these primarily deal with phytoplankton, while Lobban and Harrison (1997), Lee (1999), and Graham and Wilcox (2000) give good overviews of factors influencing primary production of macroalgae. Microbial processes and the underlying biochemistry of photosynthesis, respiration, and associated metabolism is given by Madigan et al. (2002), who also give a good overview of microbial physiology and ecology. Bacterial metabolism and ecology is comprehensively covered by Dyer (2003); as is general marine microbial dynamics by Kirchmann (2000).

The influence of physical processes on primary production is dealt with by Mann and Lazier (1996). Bigg (2003) summarizes many of the large-scale ocean processes that influence primary production.

It is important to set the topics covered by this chapter into a wider context of biological oceanography, and Lalli and Parsons (2004), Libes (1993), Mann and Lazier (1996), and Millar (2004) comprehensively link aspects of physics, chemistry, and biology. There are three excellent books published by The Open University (1989, 1995, 2000), that together make a superb companion text to discussions about issues related to marine primary production.

For a more global consideration of primary production and its role in global biogeochemical cycles, comprehensive overviews are given by Andrews et al. (1996), Black and Shimmield (2003), Longhurst (1998), and Schulz and Zabel (2000).

Arrigo (2005) gives a comprehensive overview on the role of microorganisms, nutrient cycles and biogeochemical cycling in marine systems.

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