UNIT 3

Plankton and Primary Production

The drifting algae and bacteria that feed the ocean and fix half of the carbon on Earth

Image: NASA Earth Observatory image by Norman Kuring, public domain

By the end of this unit, I should be able to answer these questions:

- How can organisms that make up less than one per cent of the photosynthetic biomass on Earth fix about half of its carbon each year?
- What is the cell wall of a diatom made of, and why do most diatoms get smaller with each division?
- Below which depth does a phytoplankton cell use more energy than it gains from light, and what sets that depth?
- Why does the North Atlantic turn green in spring, and why does the bloom end within a few weeks?
- Why are the clearest blue waters of the open ocean among the least productive?
- Which nutrient limits growth where, and why did an oceanographer ask for half a tanker of iron?

Every second breath a person takes was made by cells they have never seen. The phytoplankton of the ocean, drifting algae and bacteria mostly smaller than the width of a hair, carry out close to half of all photosynthesis on Earth with less than 1 per cent of its photosynthetic biomass, and they manage this because they are eaten and replaced about once a week. This unit introduces the drifting life of the sea, the four groups of cells that do most of the work, the light and the nutrients that set their limits, the spring bloom that turns the North Atlantic green each year, and the methods by which all of this is measured, from a bottle on a rope to a satellite.

1 The drifting life

In 1887 the physiologist Victor Hensen (1835-1924), who worked in Kiel in northern Germany, needed a word for everything that is carried about by the water, and he chose the Greek word for "that which wanders". **Plankton** is defined by its way of life, so a planktonic organism is one that cannot swim against a current, whatever its size. A jellyfish with a bell of a metre across is plankton, and so is a bacterium of less than a micrometre, whereas a sardine of 15 centimetres, which can hold its position against a current, is not. Animals that swim where they choose are the **nekton**, and organisms that live on or in the seabed are the **benthos**.

Within the plankton, the first division is by diet. The **phytoplankton** are the drifting photosynthesizers, algae and photosynthetic bacteria, and they are the subject of most of this unit. The **zooplankton** are the drifting animals and the animal-like single cells that eat other plankton. The **bacterioplankton**, the bacteria and archaea that do not photosynthesize but live on dissolved organic matter (biologists call such organisms heterotrophic), outnumber both, with about a million cells in every millilitre of seawater, and the viruses that infect them number some ten million in a millilitre; what the two do with the carbon that passes through them, the so-called microbial loop, goes beyond this unit.

Plankton is also divided by life history. The **holoplankton** spend their whole lives drifting, as copepods, krill, and most phytoplankton do, whereas the **meroplankton**, the eggs and larvae of crabs, barnacles, mussels, sea urchins, and most fishes, drift for weeks and then settle or swim away (Unit 4 returns to them). A third division is by size,

and because plankton is sampled with nets and filters of a given mesh, the size classes of Table 1, proposed in 1978, are practical as well as descriptive.

Size Class	Size Range	Typical Members
femtoplankton	0.02 to 0.2 µm	viruses
picoplankton	0.2 to 2 µm	bacteria, *Prochlorococcus*, *Synechococcus*
nanoplankton	2 to 20 µm	coccolithophores, small flagellates, small diatoms
microplankton	20 to 200 µm	most diatoms and dinoflagellates, ciliates
mesoplankton	0.2 to 20 mm	copepods, fish eggs, most larvae
macroplankton	2 to 20 cm	krill, arrow worms, small jellyfish
megaplankton	more than 20 cm	large jellyfish, salp chains, siphonophores

Table 1. The size classes of plankton. Each class spans a factor of ten in length, except the mesoplankton, which spans two. The scheme follows Sieburth, Smetacek, and Lenz (1978).

Size decides almost everything else in the life of a drifting cell. A small cell has more surface for its volume, so it takes up scarce nutrients faster and sinks more slowly, which is why the smallest phytoplankton dominate the nutrient-poor open ocean; a large cell is harder for small grazers to eat and sinks faster when it dies, which is why the large diatoms dominate the rich waters of spring blooms and carry more carbon to depth.

CHECK YOUR UNDERSTANDING Question 1

A moon jellyfish with a bell of 30 centimetres drifts along a coast in the tidal current. Which statement about it is correct?

(A) It is plankton, because it cannot swim against the current, and it belongs to the megaplankton

(B) It is nekton, because any animal that moves its own body through the water counts as a swimmer

(C) It is plankton as a larva but benthos as an adult, because it lives near the bottom of the coast

(D) It is too large to be plankton, because the plankton is defined as organisms smaller than 2 millimetres

The solution is at the end of the unit.

EXCURSION ***Hensen, the word plankton, and the Plankton Expedition of 1889***

Victor Hensen turned to the sea in middle age with a question nobody had asked quantitatively: how much life does a given volume of seawater hold, and how evenly is it spread? He designed silk nets of known mouth area, hauled vertically from a known depth, so that the catch could be divided by the volume filtered, the calculation of Unit 1. In 1887 he published the method with his new word, and in 1889 he led the Plankton Expedition of the Humboldt Foundation on the steamer *National*, which sailed from Kiel to Greenland, Bermuda, and the mouth of the Amazon between July and November, hauling the same net in the same way at every station. He concluded that the open ocean was far more uniform than the coast and, to his surprise, that the cold northern waters held more plankton than the tropics. Ernst Haeckel (1834-1919) replied in 1890 that the plankton was far too unevenly spread for such counts to mean anything, and the two argued in print for years; every plankton study since has nevertheless divided a catch by a volume.

2 The phytoplankton

The phytoplankton is a collection of lineages from across the tree of life of Unit 1 that have each settled on the same way of living: a single cell, or a short chain of cells, that drifts in the sunlit layer, takes up dissolved nutrients

through its surface, and fixes carbon by photosynthesis. Four groups do most of the work of the ocean, and a marine biologist recognizes each by its cell wall and its way of moving. Figure 1 draws one member of each at the same scale.

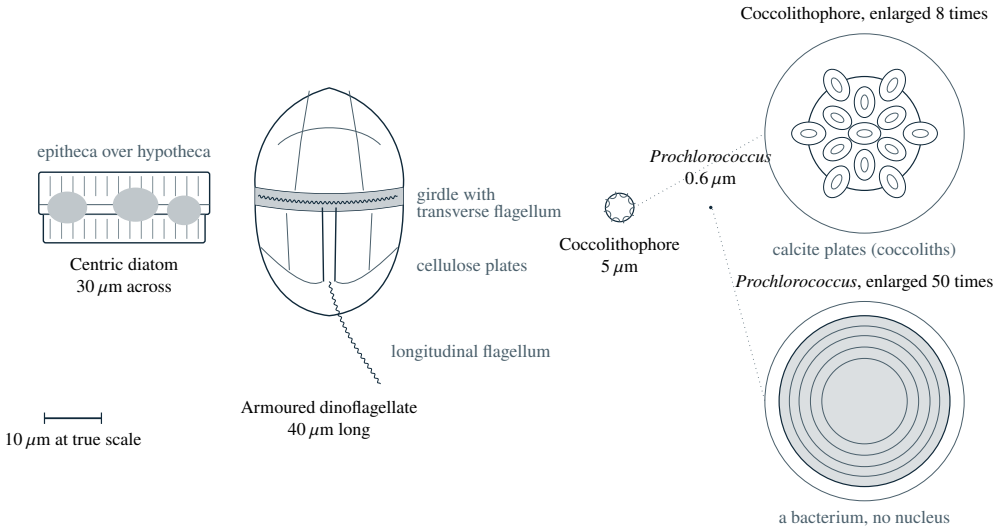


Figure 1. The four main groups of phytoplankton drawn to one scale, with a scale bar of 10 μm. From left to right: a centric diatom in side view, with its two silica valves fitting into each other like the halves of a pill box; an armoured dinoflagellate with its girdle groove and its two flagella; a coccolithophore of the size of *Gephyrocapsa huxleyi*, covered in calcite plates; and a cell of *Prochlorococcus*, which at 0.6 μm is barely a dot at this scale. The insets enlarge the two smallest cells eight and fifty times.

2.1 Diatoms

A **diatom** is a single-celled alga that lives inside a wall of glass. The wall, called the **frustule**, is made of hydrated silica, the material of opal, and consists of two valves that fit into each other like the two halves of a pill box or a Petri dish, the slightly larger valve, called the epitheca, over the slightly smaller one, called the hypotheca. The valves are perforated by a species-specific pattern of pores that lets dissolved gases and nutrients through. Diatoms come in two shapes, the round centric diatoms and the elongated pennate diatoms, and many species of both grow in chains (Figure 2). None of the planktonic ones can swim, although many pennate species of the seabed glide over surfaces. Most species are between 20 and 200 micrometres long, which makes them the largest of the four groups, and they dominate the spring blooms of temperate and polar seas, where they divide about once a day as long as light, nitrate, and dissolved silicon last. Because every diatom must take up silicon to build its wall, the amount of silicon the ocean's diatoms use in a year gives an estimate of how much they grow; from this global silica budget, Nelson and colleagues estimated in 1995 that diatoms carry out roughly 40 per cent of all photosynthesis in the sea (the primary production of Section 6). Their glass walls make them heavy, so dead diatoms and chains sink fast, and the diatom blooms of spring are the main source of fresh organic matter for the deep seafloor, which Unit 8 follows downward.

MECHANISM IN DETAIL Why diatoms shrink, and how they recover

When a diatom divides, the two valves of the old frustule separate, and each daughter cell keeps one of them as its own epitheca and builds a new, smaller valve inside it as its hypotheca. The daughter that inherited the larger old valve is as large as the mother cell; the daughter that inherited the smaller old valve is slightly smaller, because its new valve had to fit inside the old hypotheca. Over many divisions the average size of the population therefore falls step by step, a rule described in the 1860s and 1870s and still called the MacDonald-Pfitzer rule after the two microscopists who found it.

The escape from this trap is sexual reproduction. When a cell has shrunk to about a third of the maximum size of its species, it can form gametes, and the fertilized cell grows into an **auxospore**, a cell free of the rigid frustule, which swells to the full size of the species and then builds a complete new pill box. The cycle ties the sexual reproduction of diatoms to their size, which is unlike almost any other organism.

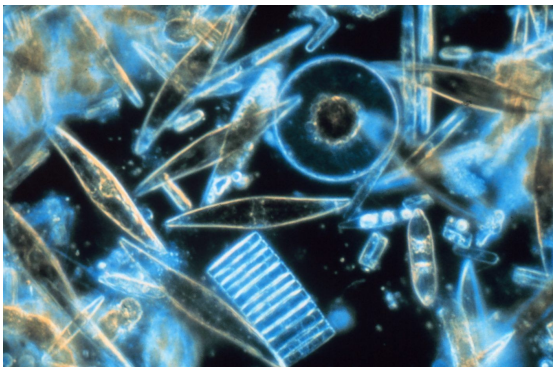


Figure 2. Diatoms photographed through a microscope from the sea ice of McMurdo Sound, Antarctica, where they live in the brine channels between the ice crystals. Chains of centric cells and single pennate cells are visible, each in its glass frustule; the largest are about 100 μm long. Credit: Gordon T. Taylor, Stony Brook University, public domain.

CHECK YOUR UNDERSTANDING Question 2

A diatom culture in a laboratory is kept dividing asexually for several months. What happens to the size of the cells?

(A) They grow larger, because each daughter cell builds its new valve on the outside of the old one

(B) The average size falls, because one daughter of each division builds its new valve inside the smaller old valve

(C) They stay the same size, because both valves of the pill box are rebuilt from scratch at every division

(D) They shed their frustules at each division and continue as naked cells of a constant size

The solution is at the end of the unit.

2.2 Dinoflagellates

A **dinoflagellate** is a single cell with two flagella, whip-like threads used for swimming, of different form. One lies in a groove around the middle of the cell, the cingulum or girdle, and makes the cell spin; the other trails behind in a second groove, the sulcus, and drives the cell forward, so that a dinoflagellate swims in a spiral fast enough to move up and down by tens of metres in a day. Many species are armoured by plates of cellulose. About 2,000 living species are known, about half of them heterotrophic, living by eating other cells, and many of the photosynthetic ones also eat, a habit called mixotrophy. Dinoflagellates divide every few days rather than daily, and they take over in summer, when the water is stratified, with warm light water lying on cold dense water as Unit 2 described, and nutrients are scarce, because they can swim down at night to the nutrients and up in the morning to the light. A few species make the most dangerous substances in the plankton; for example, the saxitoxin of *Alexandrium* species accumulates in mussels and causes paralytic shellfish poisoning, so shellfish beds are closed when the cells are counted above a threshold. Dense blooms of some species colour the water brown or red, the origin of the old name **red tide** for any harmful bloom. The dinoflagellates of the family Symbiodiniaceae, long called zooxanthellae, live inside the cells of reef corals, which lie beyond this unit.

2.3 Coccolithophores

A **coccolithophore** is a small alga, mostly between 3 and 20 micrometres across, that covers itself with plates of calcium carbonate called **coccoliths**. The plates are made inside the cell in a species-specific shape and pushed out to the surface, where they overlap like roof tiles. Between 200 and 300 living species are known. The commonest by far is *Gephyrocapsa huxleyi*, which most of the literature still calls *Emiliania huxleyi*; genetic studies have placed it in the genus *Gephyrocapsa*, and both names are in use. It is about 5 micrometres across and blooms in late spring and summer in temperate and subpolar seas, after the diatoms have used up the dissolved silicon. When the cells die and shed their plates, the water fills with billions of tiny calcite mirrors that scatter sunlight back out of the

sea, and the bloom turns the water a milky turquoise that is visible from orbit (Figure 3). Coccoliths that sink to the bottom accumulate over millions of years into chalk; the white cliffs of the English Channel are made of coccoliths that settled on the floor of a warm shelf sea in the Cretaceous period, between about 100 and 66 million years ago.

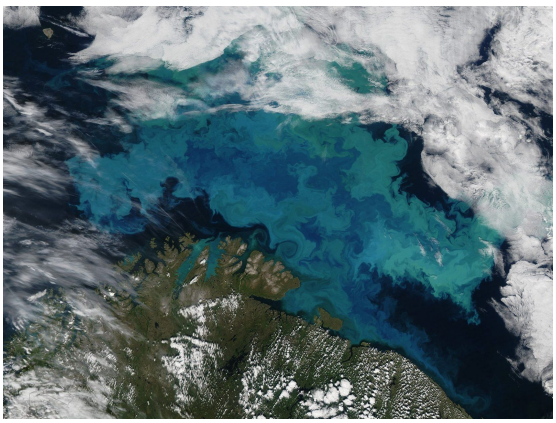


Figure 3. A bloom of coccolithophores in the Barents Sea, north of Norway, photographed by the MODIS instrument on NASA's Aqua satellite on 14 August 2011. The milky blue colour comes from sunlight scattered by calcite plates in the water; the bloom spans several hundred kilometres. Credit: Jeff Schmaltz, NASA Earth Observatory, public domain.

2.4 Cyanobacteria

The fourth group belongs to the bacteria rather than to the algae. **Cyanobacteria** are the bacteria that photosynthesize with chlorophyll and release oxygen, as plants do, and two genera of them dominate the picoplankton of the warm ocean. *Synechococcus*, a cell of about 1 micrometre, was recognized as a major component of the open ocean in 1979. *Prochlorococcus*, with cells of 0.5 to 0.7 micrometres, was discovered only in 1988 by Sallie Chisholm and her colleagues, who found it with a flow cytometer, the laser cell counter of Unit 1, because the cells were too small and dim for a microscope. A global count from more than 35,000 samples, published by Flombaum and colleagues in 2013, gave about 3×10^{27} *Prochlorococcus* cells in the ocean, a 3 followed by 27 zeros and far more than there are grains of sand on Earth, and about 7×10^{26} *Synechococcus* cells, and together the two genera are estimated to carry out about a quarter of all marine photosynthesis. *Prochlorococcus* lives in the warm belt between about 40 degrees north and south, and its whole strategy is its size, because the surface of a sphere grows with the square of its diameter and its volume with the cube, so the surface per unit of volume is inversely proportional to the diameter, and a sphere of 0.6 micrometres therefore has $30/0.6 = 50$ times more surface for its volume than a diatom of 30 micrometres. It can therefore live on nutrient concentrations that would starve any larger cell.

The four groups divide the ocean by this logic. The fast-growing, heavy diatoms win where nutrients arrive in pulses, as in the spring of temperate seas and in upwelling regions. The tiny cyanobacteria win where the water is permanently stratified and poor, and dinoflagellates and coccolithophores take the seasons in between. Section 4 explains what sets the supply.

3 Light and photosynthesis in the sea

A phytoplankton cell gains carbon by photosynthesis and loses it by respiration, and both rates can be measured. Photosynthesis depends on light, which Unit 2 showed to fade exponentially with depth according to the Beer-Lambert law, $E(z) = E_0\, e^{-K_d z}$, with E_0 the irradiance just below the surface and K_d the attenuation coefficient. The quantity that matters to the cell is the **photosynthetically active radiation**, or PAR, the light between 400 and 700 nanometres that chlorophyll and its helper pigments can absorb, counted as photons arriving on a square metre each second, in μmol photons $\mathrm{m}^{-2}\,\mathrm{s}^{-1}$. A micromole of photons is about 6×10^{17} of them, and full sunlight at noon delivers about 2,000 μmol photons $\mathrm{m}^{-2}\,\mathrm{s}^{-1}$ to the sea surface. When the light of a whole day is added up, it is given in moles of photons per square metre per day instead; one mole per day is about 12 micromoles per second

averaged over the 24 hours, and a clear summer day delivers a few tens of moles to each square metre of sea. Both units appear in this section, the first for measurements that take minutes, the second for the balance of a day.

3.1 The photosynthesis-irradiance curve

When the photosynthesis of a sample of phytoplankton is measured at a series of light levels, the result is the **photosynthesis-irradiance curve**, usually called the P-I curve, and Figure 4 shows its form. At low light the rate rises in proportion to the light, because every photon absorbed is used, and the slope of this part, written α, measures how efficiently the cells use dim light. At high light the rate levels off at a maximum, $P_{\max}$, because the enzymes that fix carbon are working as fast as they can and additional photons are wasted. The irradiance at which the initial slope, if continued, would reach the maximum is the saturation irradiance $E_k = P_{\max}/\alpha$. In very bright light the curve often turns down again, because the light damages the photosynthetic machinery faster than the cell can repair it, which is called photoinhibition.

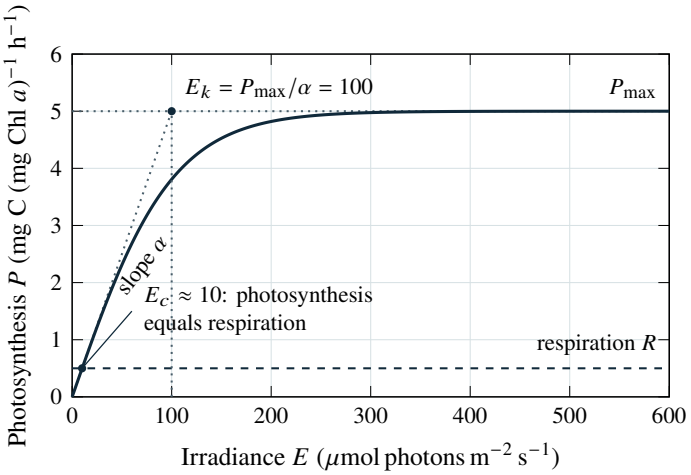


Figure 4. A photosynthesis-irradiance curve computed from the hyperbolic tangent form with $P_{\max} = 5$ and $\alpha = 0.05$ milligrams of carbon per milligram of chlorophyll a per hour, per μmol photons m^{-2} s^{-1}, values typical of temperate phytoplankton. The dotted line continues the initial slope to the saturation irradiance $E_k = 100\,\mu$mol photons m^{-2} s^{-1}. The dashed line is a respiration rate of 10 per cent of $P_{\max}$; where the curve crosses it, at the compensation irradiance E_c of about 10 μmol photons m^{-2} s^{-1}, the cell gains exactly as much carbon as it loses.

KEY RESULT The photosynthesis-irradiance curve

The rate of photosynthesis P rises in proportion to the irradiance E at low light, with the initial slope α, and saturates at a maximum $P_{\max}$ at high light. The two regimes meet at the saturation irradiance $E_k = P_{\max}/\alpha$, typically 50 to 300 μmol photons m^{-2} s^{-1}. A common mathematical form is $P = P_{\max}\tanh(\alpha E/P_{\max})$, proposed by Jassby and Platt; the hyperbolic tangent tanh is a function that rises in a straight line from zero and then flattens out towards 1, which is exactly the shape of the curve. The rates are given per milligram of chlorophyll a, in milligrams of carbon per milligram of chlorophyll a per hour, because the chlorophyll of a sample is far easier to measure than the number or mass of its cells.

3.2 Compensation depth and critical depth

Light is a function of depth, so the P-I curve can be read as a profile, that is, as a plot of the photosynthesis rate against depth. Respiration, by contrast, hardly depends on light, and to a first approximation a cell respires at the same rate at every depth, day and night. There is therefore an irradiance at which photosynthesis equals respiration, the **compensation irradiance** E_c, and a depth at which the light has fallen to that value, the **compensation depth** z_c. A cell above the compensation depth gains carbon over a day; a cell below it loses carbon and will, in time, starve. Textbooks often place it close to the 1 per cent light depth, the bottom of the euphotic zone of Unit 2, but

the compensation irradiance measured for different species and communities varies by a factor of ten, and the depth varies with it.

A cell in the ocean does not sit still. In winter, storms and the cooling of the surface mix the upper water column to depths of a hundred metres and more, and a phytoplankton cell is carried through the whole of the **mixed layer**, spending part of its time in the light near the surface and part in the dark far below the compensation depth, so what matters for it is the balance over the whole layer. The Norwegian oceanographer Harald Sverdrup (1888-1957), who had led the Scripps Institution of Oceanography in California for twelve years before returning to Norway, put this into a clear criterion in 1953, using measurements from a weather ship in the Norwegian Sea.

PRINCIPLE The critical depth model of Sverdrup

The **critical depth** z_{cr} is the depth of a mixed layer in which the photosynthesis of the phytoplankton, summed over the layer, exactly equals their respiration summed over the layer. If the mixed layer is shallower than the critical depth, the phytoplankton of the layer gain more carbon than they lose and their population can grow; if it is deeper, they cannot grow, whatever the light at the surface. Sverdrup proposed the criterion in 1953 to explain why the spring bloom of the North Atlantic begins when the winter mixed layer becomes shallow. The model assumes a uniformly mixed layer, a photosynthesis rate proportional to light, a respiration rate independent of depth, and enough nutrients.

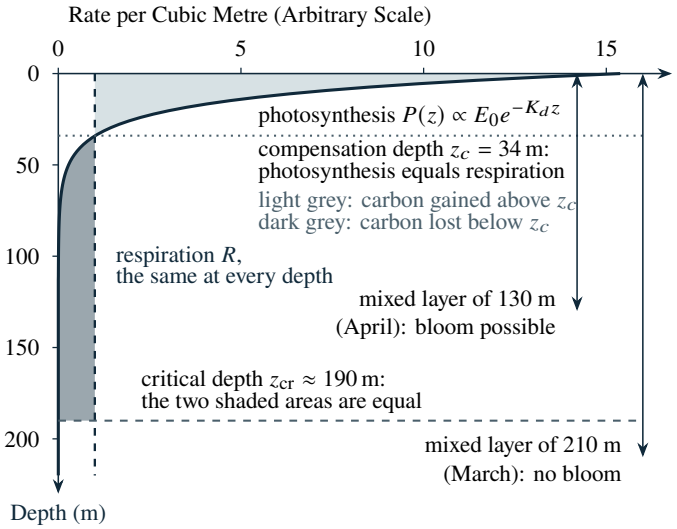


Figure 5. The compensation depth and the critical depth for a surface irradiance of 20 and a compensation irradiance of 1.3 moles of photons per square metre per day and an attenuation coefficient of 0.08 m^{-1}, the numbers of Worked Example 1. The photosynthesis rate (solid curve) falls exponentially with depth, following the light; the respiration rate (dashed line) is the same at every depth. They cross at the compensation depth of 34 metres. Above it the cells gain carbon (light grey) and below it they lose carbon (darker grey); the two areas become equal at the critical depth of about 190 metres.

In Figure 5 the critical depth is far deeper than the compensation depth, because the surplus gained in the bright water near the surface pays for a long stretch of slight losses below; the following mechanism turns the picture into a formula.

MECHANISM IN DETAIL The critical depth from the attenuation law

Let E_0 be the daily irradiance just below the surface and $E_0 e^{-K_d z}$ the light at depth z. Sverdrup assumed that the daily photosynthesis at depth z is proportional to the light there, $P(z) = a\, E_0 e^{-K_d z}$ with a constant a, and that respiration is a constant R at every depth. The compensation irradiance is the light at which the two are equal, $E_c = R/a$, and the

compensation depth follows from $E_0 e^{-K_d z_c} = E_c$ as

$$z_c = \frac{1}{K_d} \ln \frac{E_0}{E_c}.$$

Over a mixed layer of depth z_m, the total photosynthesis is the area under the exponential curve between the surface and z_m. For an exponential curve that area has a simple value, $\frac{aE_0}{K_d}\left(1 - e^{-K_d z_m}\right)$ (readers who know calculus will recognize the integral of $e^{-K_d z}$), and the total respiration is the area of a rectangle, $R\, z_m$. The critical depth is the value of z_m at which they are equal, and dividing both sides by a gives Sverdrup's condition,

$$\frac{E_0}{K_d}\left(1 - e^{-K_d z_{\mathrm{cr}}}\right) = E_c\, z_{\mathrm{cr}}.$$

This equation cannot be solved for z_{cr} by rearranging it, because z_{cr} appears both inside and outside the exponential. Whenever the critical depth is much deeper than the 1 per cent light depth, however, which is the usual case, the exponential term is negligible (at the 1 per cent depth it has already fallen to 0.01, and it keeps falling below that), and the condition becomes

$$z_{\mathrm{cr}} \approx \frac{E_0}{K_d\, E_c}.$$

Compared with the compensation depth, the logarithm of E_0/E_c has been replaced by the ratio itself, which is why the critical depth is so much deeper.

KEY RESULT Compensation depth and critical depth

$$z_c = \frac{1}{K_d} \ln \frac{E_0}{E_c}, \qquad z_{\mathrm{cr}} \approx \frac{E_0}{K_d\, E_c}$$

At the compensation depth z_c a single cell gains as much carbon by photosynthesis as it loses by respiration. At the critical depth z_{cr} the gains and losses of a whole mixed layer balance. E_0 is the daily irradiance just below the surface, E_c the compensation irradiance, and K_d the attenuation coefficient. Phytoplankton can bloom when the mixed layer is shallower than z_{cr}, provided nutrients are available.

WORKED EXAMPLE A critical depth for the North Atlantic in April

A research vessel in the subpolar North Atlantic at 50 degrees north measures, on an overcast April day, a daily irradiance just below the surface of $E_0 = 20\,\mathrm{mol\ photons\,m^{-2}\,d^{-1}}$ and an attenuation coefficient of $K_d = 0.08\,\mathrm{m^{-1}}$. For the compensation irradiance it takes the value that Siegel, Doney, and Yoder derived from satellite and ship data for the whole North Atlantic in 2002, $E_c = 1.3\,\mathrm{mol\ photons\,m^{-2}\,d^{-1}}$, which includes the losses to the grazers and bacteria of the whole community and not only the respiration of the phytoplankton. Where are the compensation depth and the critical depth, and can the phytoplankton bloom?

The compensation depth is

$$z_c = \frac{1}{0.08\,\mathrm{m^{-1}}} \ln \frac{20}{1.3} = \frac{2.73}{0.08\,\mathrm{m^{-1}}} = 34\,\mathrm{m},$$

and the critical depth, from the approximate formula, is

$$z_{\mathrm{cr}} \approx \frac{20}{0.08\,\mathrm{m^{-1}} \times 1.3} = 192\,\mathrm{m}.$$

The long-term monthly averages measured by the Argo floats of Unit 2 give, for this part of the ocean, a mean mixed layer depth of about 210 metres in March and 130 metres in April, so the layer is deeper than the critical depth in March and shallower in April, and Sverdrup's criterion predicts that the bloom can start in April. The critical depth is about 190 metres, five times the compensation depth.

CHECK YOUR UNDERSTANDING Question 3

In March a research vessel finds the mixed layer at 250 metres and calculates a critical depth of 190 metres for the light and water clarity of that bright day. What does Sverdrup's model predict for the phytoplankton of the mixed layer?

(A) They can bloom, because the surface light is far above the compensation irradiance

(B) They can bloom, because the mixed layer is much deeper than the compensation depth

(C) They cannot bloom, because the layer as a whole respires more carbon than it fixes

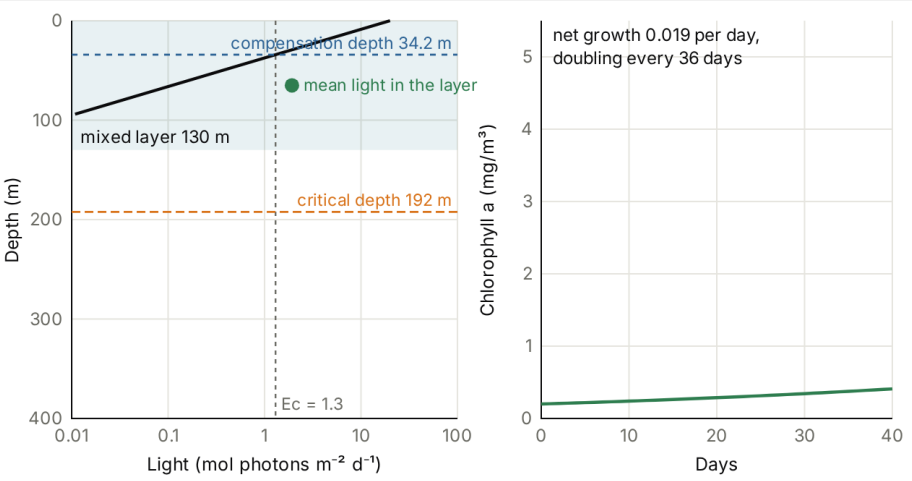
(D) They cannot bloom, because no light at all reaches the bottom of the mixed layer

The solution is at the end of the unit.

3.3 The North Atlantic spring bloom and what starts it

Each spring, the North Atlantic between about 40 and 65 degrees north turns from blue to green over a few weeks, one of the largest seasonal events of the living ocean and the subject of the picture at the head of this unit. In winter the mixed layer of its subpolar part is 200 to 400 metres deep and the surface chlorophyll is low, around 0.2 mg m^{-3}. From April onward the surface warms, the mixed layer shrinks to tens of metres, and the chlorophyll rises within a month to several milligrams per cubic metre as diatoms divide once a day on the nitrate, phosphate, and silicate that the winter mixing brought up from below. By June the silicate and then the nitrate of the surface layer are used up, the diatoms sink or are eaten, and the bloom ends as quickly as it began. Figure 6 shows this cycle in the monthly means at one site in the eastern North Atlantic.

INTERACTIVE The critical depth and the spring bloom



Set the mixed layer depth, the daily light below the surface, and the water clarity, or pick a month of the subpolar North Atlantic, and watch the compensation depth and the critical depth move on the light profile. When the shaded mixed layer is shallower than the critical depth, the mean light in it exceeds the compensation irradiance of 1.3 moles of photons per square metre per day, and the chlorophyll curve on the right grows. Its net growth rate is 0.04 per day for every multiple by which the mean light exceeds the compensation irradiance, so a mean light of twice that value gives 0.04 per day and three times gives 0.08 per day. Notice that a bright surface does not help while the layer is deep.

Click the picture or this link to try it in the online version of this unit.

WORKED EXAMPLE The growth rate of a bloom from a satellite record

Suppose that a satellite measures the surface chlorophyll of one patch of the subpolar North Atlantic at $0.3\,\mathrm{mg\,m^{-3}}$ on 20 April and at $3.0\,\mathrm{mg\,m^{-3}}$ on 10 May, twenty days later, values typical of a strong spring bloom. What is the net growth rate of the population, and what is its doubling time?

If the chlorophyll grows exponentially, $C(t) = C_0 e^{rt}$ as in Unit 1, the rate follows from the ratio of the two values:

$$r = \frac{1}{t}\ln\frac{C(t)}{C_0} = \frac{1}{20\,\mathrm{d}}\ln\frac{3.0}{0.3} = \frac{2.30}{20\,\mathrm{d}} = 0.115\,\mathrm{d^{-1}},$$

and the doubling time is $\ln 2/r = 0.693/0.115 = 6.0$ days. The net growth rate is therefore $0.115\,\mathrm{d^{-1}}$, a doubling every 6 days. This is a net rate, the difference between the division rate of the cells and their losses to grazing, sinking, and viruses. Diatoms in such a bloom divide about once a day, so a division rate of about $0.7\,\mathrm{d^{-1}}$ is being offset by losses of about $0.6\,\mathrm{d^{-1}}$, and the bloom is the small difference between two large numbers. The monthly means of Figure 6 rise more slowly, because the average over five years combines blooms that fell in different weeks and so spreads the rise over several months.

Sverdrup's model was the accepted explanation of the spring bloom for half a century, and the satellite record then raised a difficulty. When Michael Behrenfeld examined nine years of SeaWiFS data for the subarctic Atlantic in 2010, he found that the total amount of phytoplankton under a square metre begins to increase in midwinter, when the mixed layer is still deepening and far deeper than any critical depth. His explanation, first called the dilution-recoupling hypothesis and later the disturbance-recovery hypothesis, moves the attention from the plants to their predators. A bloom, in this view, is any period in which the division rate of the phytoplankton exceeds their loss rate, which is mostly grazing. When winter mixing dilutes the plankton, the grazers meet their prey less often and the balance tips in favour of the phytoplankton, even though light and division rate are at their lowest; in spring the division rate accelerates and stays ahead of the grazers for a while, which is the visible bloom, until the grazers catch up. The dispute is not settled, and the research spotlight describes the field programme designed to settle it.

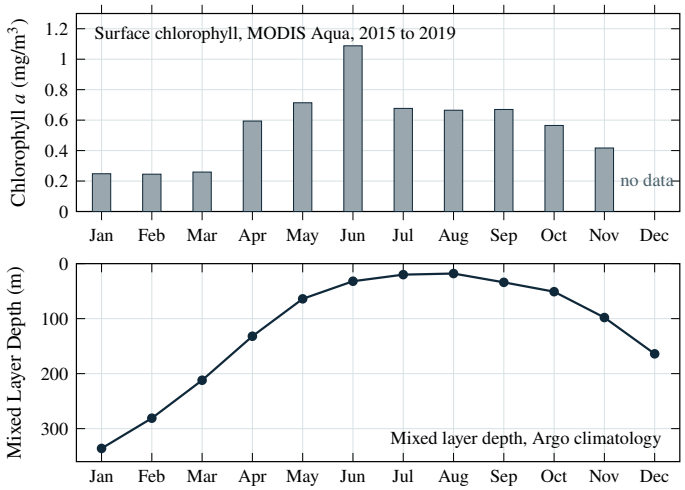


Figure 6. The seasonal cycle at the Porcupine Abyssal Plain, about 49 degrees north and 16.5 degrees west. Upper panel: the monthly mean surface chlorophyll *a* from the MODIS instrument on NASA's Aqua satellite, averaged over 2015 to 2019 and over one degree of latitude and longitude around the site (NASA Ocean Color data, read through the NOAA CoastWatch ERDDAP server); in December the sun stands too low over this latitude for the ocean colour measurement. Lower panel: the monthly mean mixed layer depth from the long-term Argo float averages of Holte, Talley, Gilson, and Roemmich (2017) for the same square. The chlorophyll rises when the mixed layer shallows in April and May and peaks in June.

RESEARCH SPOTLIGHT
Michael J. Behrenfeld *Oregon State University*

Four seasons at sea to find out what starts the North Atlantic bloom

The North Atlantic Aerosol and Marine Ecosystem Study, NAAMES, was a NASA field programme led by Michael Behrenfeld that observed the whole annual cycle of the subarctic Atlantic plankton rather than only its spring climax. The overview paper of 2019, which he wrote with 44 co-authors, describes the cycle in the disturbance-recovery view as four phases: a winter transition, when deep mixing dilutes the plankton and the stock first begins to grow, an accumulation phase in early spring, a climax transition in late spring, when division rates peak and the grazers catch up, and a depletion phase in summer and autumn. The programme sent the research vessel *Atlantis* and a NASA C-130 aircraft to the western subarctic Atlantic once for each phase, in November 2015, May and June 2016, August and September 2017, and March and April 2018. The ship measured division and grazing rates directly, with species, light, nutrients, and the mixed layer depth, and the aircraft measured the aerosols and clouds above it. The authors write that many of their initial expectations proved incorrect or incomplete, among them the expected dominance of diatoms at the climax, and that the data of all four campaigns are open to anyone.

Read the paper: Behrenfeld, Moore, Hostetler, and 42 co-authors (2019), The North Atlantic Aerosol and Marine Ecosystem Study (NAAMES): Science Motive and Mission Overview, Frontiers in Marine Science 6, 122

4 Nutrients and what limits growth

Light decides where photosynthesis can take place, and the supply of nutrients decides how much of it there is. A phytoplankton cell builds itself from carbon, which seawater holds in abundance as dissolved carbon dioxide and bicarbonate, and from elements that seawater holds in short supply. The three that run out first are nitrogen, taken up mostly as nitrate (NO_3^-) and ammonium (NH_4^+), phosphorus as phosphate (PO_4^{3-}), and, for diatoms only, silicon as dissolved silicic acid, called silicate. Behind these comes iron, which the enzymes of photosynthesis and of nitrate uptake need in tiny amounts. Surface water in the subtropical gyres holds nitrate below $0.1\,\mu\text{mol}\,\text{L}^{-1}$, whereas the deep water below a thousand metres holds some 20 to $40\,\mu\text{mol}\,\text{L}^{-1}$, because that is where the sinking remains of the plankton are decomposed. How fast this deep store returns to the light, by winter mixing and by the upwelling of Unit 2, sets the productivity of the sea.

4.1 The Redfield ratio

In 1934 Alfred Redfield (1890-1983) of the Woods Hole Oceanographic Institution noticed that the ratio of nitrate to phosphate in deep seawater from every ocean was nearly constant, about 20 atoms of nitrogen for every atom of phosphorus by his first estimate, and that the plankton collected at the surface had, on average, the same ratio in their tissues. He concluded that the composition of the deep water is set by the decay of the plankton. Richard Fleming revised the plankton analyses to 16 atoms of nitrogen per atom of phosphorus and added carbon in 1940, and Redfield gave the ratio its modern form in 1958.

PRINCIPLE The Redfield ratio

Marine plankton contain carbon, nitrogen, and phosphorus in the average atomic proportions

$$\text{C} : \text{N} : \text{P} = 106 : 16 : 1,$$

and the nitrate and phosphate released when their remains decay in deep water appear in the same proportion of 16 to 1. The ratio is an average over the whole ocean; single species and samples depart from it, with nitrogen-to-phosphorus ratios between about 5 and 30.

WORKED EXAMPLE From nitrate consumed to carbon fixed

At the end of winter the mixed layer of a subpolar sea, 50 metres deep, holds 16 μmol of nitrate in every litre, a value measured in parts of the subpolar North Atlantic and the subarctic Pacific. By early summer the nitrate at the surface has fallen to almost zero. How much carbon did the phytoplankton fix from this nitrate, per litre and under each square metre of sea?

By the Redfield ratio, 16 micromoles of nitrogen go with $16 \times 106/16 = 106$ μmol of carbon. One mole of carbon has a mass of 12.0 g, so 106 μmol is $106 \times 12.0\,\mu\text{g} = 1{,}270\,\mu\text{g} = 1.27$ mg of carbon per litre, which is 1.27 g m^{-3}, because a cubic metre holds 1,000 litres. The mixed layer is 50 metres deep, so under each square metre the bloom fixed

$$1.27\,\text{g C m}^{-3} \times 50\,\text{m} = 64\,\text{g C m}^{-2}.$$

The winter nitrate of the mixed layer therefore supports about 64 grams of carbon per square metre, which is close to half of the yearly average production per square metre of ocean given in Section 6. Production fed by nitrate from below is called **new production**, the part that can sink out of the surface without draining it (Unit 8 uses the distinction); the year's total is larger, because the same nitrogen is used several times over as the grazers excrete ammonium and the cells take it up again.

4.2 Liebig's law and the limiting nutrient

Which nutrient runs out first is decided by a principle from agricultural chemistry. In 1840 Justus von Liebig (1803-1873) stated, building on the soil studies of Carl Sprengel (1787-1859), that the yield of a crop is set by the nutrient that is scarcest in relation to the plant's needs and not by the total amount of all nutrients.

PRINCIPLE Liebig's law of the minimum

The growth of an organism or a population is limited by the single resource that is in shortest supply relative to the organism's requirement. Adding any other resource does not increase growth until the limiting one is supplied. In the sea the requirement is measured against the Redfield ratio: water with a nitrogen-to-phosphorus ratio well below 16 runs out of nitrogen first, and water with a ratio well above 16 runs out of phosphorus first.

Over most of the low-latitude ocean the limiting nutrient is nitrogen, because the ratio of nitrate to phosphate in the surface water is a little below 16 and because nitrogen is lost from the sea by bacteria that turn nitrate back into nitrogen gas, a cycle that goes beyond this unit. For diatoms the first nutrient to run out in spring is often silicate, which is why diatom blooms end before the nitrate is gone and hand over to groups that need no silica, such as the coccolithophores. The most surprising case concerns the three regions where nitrate and phosphate remain high all year and the phytoplankton still fail to grow, the Southern Ocean, the equatorial Pacific, and the subarctic North Pacific, together roughly a quarter of the ocean's surface, known as the **high-nutrient, low-chlorophyll** regions. The missing element there is iron, which reaches the open sea mainly as dust blown from deserts, and these three regions lie far from any desert.

CHECK YOUR UNDERSTANDING Question 4

Surface water at the end of winter holds 2.0 micromoles of nitrate and 0.4 micromoles of phosphate per litre. Which nutrient will phytoplankton that grow in the Redfield ratio run out of first?

(A) Phosphate, because its concentration of 0.4 micromoles per litre is the lower of the two numbers

(B) Nitrate, because the ratio of 2.0 to 0.4 is 5 to 1, far below the 16 to 1 that the cells take up

(C) Both at the same moment, because a ratio of 5 to 1 is close enough to the Redfield ratio

(D) Neither of them, because in surface water the diatoms always exhaust the silicate first

The solution is at the end of the unit.

EXCURSION *John Martin and half a tanker of iron*

The idea that iron could limit the phytoplankton was old, but nobody could measure iron in seawater at concentrations of a few billionths of a gram per litre without contaminating the sample. John Martin (1935-1993) of the Moss Landing Marine Laboratories in California spent the 1980s building clean sampling systems, and with them he found that the high-nutrient, low-chlorophyll waters of the subarctic Pacific and the Southern Ocean held almost no iron, and that a few tens of billionths of a gram of iron added to a litre of such water set off a bloom. Because ice cores, in which bubbles of old air are trapped between the layers of snow of each year, showed dustier air and less carbon dioxide during the ice ages, Martin proposed that more iron had meant more phytoplankton, more carbon sinking into the deep sea, and less carbon dioxide in the air; at a lecture in Woods Hole in 1988 he put it, half in jest, as "give me half a tanker of iron, and I will give you an ice age". The sceptics argued that a bottle changes the community inside it, so Martin planned an experiment on the ocean itself. He died in June 1993, four months before his team spread about 450 kilograms of dissolved iron over 64 square kilometres, a square of 8 by 8 kilometres, of the equatorial Pacific near the Galápagos Islands in the first IronEx experiment, which doubled the plant biomass. IronEx II in 1995 added the iron in three doses and produced what the published account called a massive bloom, with chlorophyll rising by a factor of about 30 and the carbon dioxide of the surface water falling sharply. Later experiments confirmed the result but found that little of the extra carbon sinks to depth, so the tanker was never a practical proposal.

5 The grazers

More than half of what the phytoplankton produce is eaten within a few days. Measured over the whole ocean, the greater part of it, about two thirds, goes to single-celled grazers of the microplankton, the ciliates, which are cells that swim and feed with rows of tiny hairs, and the heterotrophic dinoflagellates, and both divide as fast as their prey; the rest goes to three groups of animals. The **copepods** are small crustaceans, most of them 1 to 5 millimetres long, that filter or catch single phytoplankton cells with their feeding limbs, and they are probably the most numerous animals on Earth. For example, *Calanus finmarchicus*, a copepod of 2 to 4 millimetres, is the main grazer of the North Atlantic spring bloom and the main food of herring, mackerel, and the right whale. The **krill** are shrimp-like crustaceans of a few centimetres; the Antarctic krill (*Euphausia superba*) forms swarms of thousands of animals per cubic metre and has a total biomass of a few hundred million tonnes (379 million tonnes in the most cited estimate, by Atkinson and colleagues in 2009), which is about the combined weight of all the people on Earth, and this biomass feeds the whales, seals, and penguins of the Southern Ocean. The **gelatinous zooplankton**, the jellyfish, comb jellies, and salps, are mostly water, multiply fast when food is plentiful, and pack what they filter into dense faecal pellets that sink hundreds of metres a day. Unit 4 describes the anatomy of these animals, and the fate of the pellets and the uneaten cells, the biological pump that carries carbon to the deep sea, is the subject of Unit 8.

6 Measuring production and the global picture

6.1 Three ways to measure primary production

Primary production is the rate at which the phytoplankton fix carbon by photosynthesis, measured in milligrams of carbon per cubic metre per day or, summed over the sunlit layer, per square metre per day or per year. Gross primary production is the total carbon fixed, net primary production is what remains after the respiration of the phytoplankton themselves, and only the second is available to the rest of the food web. Three methods measure it, the oldest with bottles and dissolved oxygen, the second with a radioactive tracer, and the third from orbit.

The oldest method, introduced in 1927 by the Norwegian scientists Torbjørn Gaarder and Haaken Hasberg Gran, uses pairs of glass bottles filled with seawater and its plankton and hung at a series of depths for a day. In the clear bottle the oxygen rises by photosynthesis and falls by respiration; in the bottle painted black it can only fall. The dark bottle therefore gives the respiration, the light bottle the net production, and their sum the gross production, all in oxygen, which is converted into carbon with the photosynthetic quotient, the moles of oxygen released per mole of carbon fixed, between about 1.0 and 1.4 depending on whether the cells grow on ammonium or on nitrate, because a cell that takes up nitrate must first reduce it and releases extra oxygen in doing so.

The method that made the global map possible came in 1952 from the Danish botanist Einer Steemann Nielsen (1907-1989) on the Danish *Galathea* expedition round the world. A small amount of bicarbonate labelled with the radioactive isotope carbon-14 is added to a bottle of seawater, the bottle is incubated in the light, and at the end the cells are filtered out and their radioactivity is measured. Because the labelled carbon mixes evenly with the ordinary dissolved carbon, the cells take up the same fraction of both, so the fraction of the added label found in the cells, multiplied by the dissolved inorganic carbon of the water, is the carbon fixed. The method detects production about a hundred times smaller than the oxygen bottles can and is the standard against which the others are calibrated; its weaknesses are that the result lies between gross and net production, because some labelled carbon is respired again during the incubation, and that a bottle is a cage, in which the community changes during a long incubation.

WORKED EXAMPLE A carbon-14 bottle at the 10 per cent light depth

On a cruise in temperate waters in May, a water sample from 29 metres, where 10 per cent of the surface light remains with $K_d = 0.08\,\mathrm{m^{-1}}$ (because $e^{-0.08\times29} = 0.10$), is spiked with labelled bicarbonate and incubated for the 12 hours of daylight in a tank on deck, under a screen that lets through 10 per cent of the sunlight. At the end, the cells on the filter hold 0.10 per cent of the radioactivity that was added. The dissolved inorganic carbon of the water is $2{,}100\,\mu\mathrm{mol\,L^{-1}}$. What was the production at that depth?

A litre of the water holds $2{,}100\,\mu\mathrm{mol} \times 12.0\,\mu\mathrm{g\,\mu mol^{-1}} = 25{,}200\,\mu\mathrm{g} = 25.2\,\mathrm{mg}$ of inorganic carbon. The cells fixed 0.10 per cent of it, $25.2\,\mathrm{mg} \times 0.0010 = 0.0252\,\mathrm{mg\,C\,L^{-1}}$, and because cells take up the heavy isotope about 5 per cent more slowly than ordinary carbon, the true value is 5 per cent higher, $0.0265\,\mathrm{mg\,C\,L^{-1}}$ or $26.5\,\mathrm{mg\,C\,m^{-3}}$. The daily production at 29 metres is therefore about $26\,\mathrm{mg\,C\,m^{-3}\,d^{-1}}$. The bottle gives the production at that depth although it stood on deck, because photosynthesis is a function of the light and the screen reproduced the light of 29 metres; bottles at 100, 50, 25, 10, and 1 per cent of the surface light give the whole profile, and the area under it is the production per square metre of sea.

The third method does not touch the water. Chlorophyll *a* absorbs blue and red light and leaves the green, so the colour of the sea, measured from orbit, gives the concentration of chlorophyll in the uppermost layer, roughly the top $1/K_d$ metres, which is a few tens of metres in clear water and a few metres in turbid water. The first instrument to do this was the Coastal Zone Color Scanner on the Nimbus-7 satellite, from 1978 to 1986, followed by SeaWiFS from 1997 to 2010, MODIS on the Aqua satellite since 2002, and the PACE mission launched in 2024. A satellite sees the whole ocean every few days, and Figure 7 shows a year of its view. The step from chlorophyll to production needs a model built on the P-I curve, the light, the temperature, and the depth of the sunlit layer, calibrated against thousands of carbon-14 measurements. The leading models agree on the global total to within about 20 per cent, but a comparison of two dozen models by Carr and colleagues in 2006 found totals that differed by a factor of two, so the number is less certain than the map suggests.

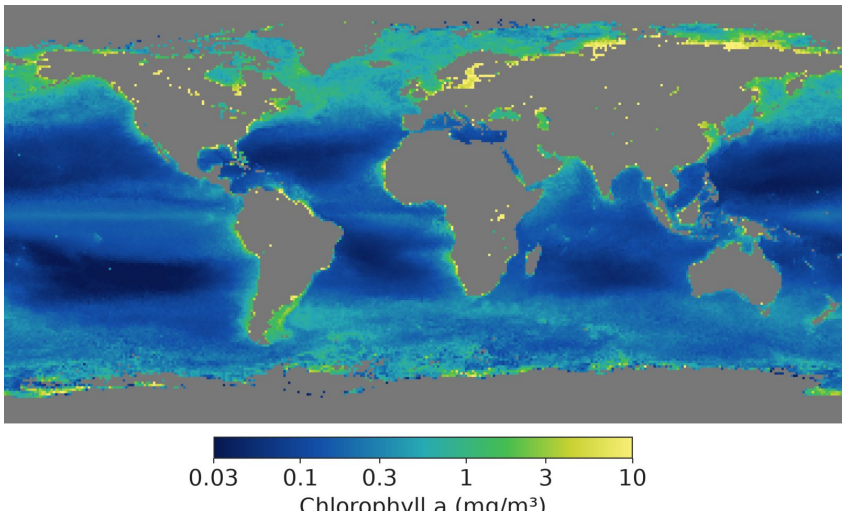


Figure 7. The chlorophyll *a* concentration at the sea surface in 2021, the geometric mean of the twelve monthly maps (the average taken on the logarithmic scale of the colour bar) from the MODIS instrument on NASA's Aqua satellite on a grid of one degree, on a logarithmic colour scale from 0.03 to 10 mg m^{-3} (NASA Ocean Color data, read through the NOAA CoastWatch ERDDAP server). Grey marks land and water without data, including the polar seas in their dark months. The subtropical gyres hold less than 0.1 mg m^{-3}; the equatorial Pacific holds two to three times more, and the coasts, the upwelling regions off Peru, California, and south-west Africa, and the high latitudes hold ten times more.

6.2 The global numbers

Figure 7 answers one of the opening questions by inspection. The clearest and bluest water of the ocean, in the five subtropical gyres, holds the least chlorophyll, below 0.1 mg m^{-3}, because the water there is warm and permanently stratified, so that the nutrients released in the deep are never mixed back to the light. The coasts, the upwelling regions, and the high latitudes hold ten to a hundred times more, because rivers, upwelling, or winter mixing supply nutrients there.

Summed over the ocean, the satellite models give a net primary production of about 50 Pg C per year, where one petagram is 10^{15} grams, a billion tonnes, also written as one gigatonne. The most cited estimate, by Field and colleagues in 1998, was 48.5 petagrams of carbon for the ocean against 104.9 for the whole planet, so the sea fixes close to half of the carbon fixed on Earth each year. Spread over the 361 million square kilometres of the ocean, the average is about 140 g C m^{-2} yr^{-1}, below 50 in the gyres and above 300 in the upwelling regions and the shelf seas. The key result below sums this up, and the example compares it with the land.

KEY RESULT Marine primary production and its turnover

The phytoplankton of the ocean fix about 50 Pg C per year, close to half of the global total of about 105 Pg C per year, with a standing biomass of only about 1 Pg C, under 1 per cent of the photosynthetic biomass on Earth, so the stock turns over in about one week; the global figure is a model result uncertain by at least 20 per cent.

WORKED EXAMPLE The turnover time of the phytoplankton

The biomass of the phytoplankton of the whole ocean is estimated at about 1 Pg C, and their net production at about 50 Pg C yr^{-1}. How long does it take them to produce their own mass, and how does this compare with the plants on land, which hold about 450 Pg C and produce about 56 Pg C yr^{-1}?

The biomass divided by the production rate is the turnover time. For the ocean,

$$\frac{1\ \text{Pg C}}{50\ \text{Pg C yr}^{-1}} = 0.02\ \text{yr} = 7.3\ \text{d},$$

and for the land, 450/56 = 8.0 years. The phytoplankton of the ocean replace themselves in about one week, roughly 400 times faster than the vegetation on land, which is how 1 per cent of the photosynthetic biomass can carry out half of the photosynthesis.

The seasonal cycle behind the map differs with latitude in a way that follows from everything in this unit. In temperate and subpolar seas winter mixing recharges the nutrients, the spring bloom follows the shallowing of the mixed layer, and the first autumn storms often mix enough nutrient into still well-lit water for a second, smaller bloom. In polar seas light is the stronger limit, and there is a single short bloom in summer, often at the edge of the retreating sea ice, where melt water forms a shallow, stable layer. In the tropics and subtropics the water is stratified all year and the surface chlorophyll stays low and nearly constant. The largest concentration of cells there sits in a thin layer near the bottom of the sunlit zone, where light from above and nutrients from below just overlap, and this layer is called the **deep chlorophyll maximum**. The upwelling regions, where the seasons follow the winds rather than the sun, are the exception.

KEY POINTS

- Plankton is defined by its way of life, drifting, whatever its size, and is divided by diet into phytoplankton, zooplankton, and bacterioplankton, by life history into holoplankton and meroplankton, and by size into classes a factor of ten apart.
- Four groups do most of the photosynthesis of the sea: diatoms in walls of silica, which dominate blooms and sink; swimming dinoflagellates with two flagella; coccolithophores covered in calcite plates; and the cyanobacteria *Prochlorococcus* and *Synechococcus*, about 3×10^{27} and 7×10^{26} cells in the warm, nutrient-poor ocean.
- A cell breaks even at the compensation depth, $z_c = \ln(E_0/E_c)/K_d$, and a mixed layer at the much deeper critical depth, $z_{\mathrm{cr}} \approx E_0/(K_d E_c)$. By Sverdrup's criterion a bloom can start when the mixed layer becomes shallower than the critical depth; the disturbance-recovery hypothesis puts the start in winter, when dilution frees the cells from their grazers.
- Plankton are built in the Redfield ratio of 106 carbon to 16 nitrogen to 1 phosphorus, and Liebig's law says that the nutrient in shortest supply relative to this ratio limits growth: nitrogen in most of the warm ocean, silicate for diatoms, iron in the high-nutrient, low-chlorophyll regions.
- Primary production is measured with oxygen bottles, with carbon-14, and from the colour of the sea seen from orbit; the ocean fixes about 50 petagrams of carbon a year, close to half of the global total, with a biomass of about 1 petagram that turns over in about a week.

Solutions to the questions in the text: 1-A, 2-B, 3-C, 4-B. The online version of this unit explains each answer.