INTERUNIVERSITARY COURSE
FUNDAMENTAL AND APPLIED MARINE ECOLOGY

BIOLOGICAL OCEANOGRAPHY

CARLO HEIP

Director of Research at the Belgian National Fund for Scientific Research

Head Marine Biology Section, Zoology Institute, State University of Gent, Belgium

ACADEMIC YEAR 1985-1986

INTERUNIVERSITARY COURSE
FUNDAMENTAL AND APPLIED MARINE ECOLOGY

BIOLOGICAL OCEANOGRAPHY

CARLO HEIP

Director of Research at the Belgian National Fund for Scientific Research

Head Marine Biology Section, Zoology Institute, State University of Gent, Belgium

ACADEMIC YEAR 1985-1986

CONTENTS

Physical and chemical properties of the oceans

To the physical scientist the waters of the sea are a dilute electrolyte solution moving within a thin shell on the rotating, gravitating, spherical earth. The physical oceanographer studies the physical state and properties of the oceans, their currents and motions, and the transfer and mixing processes. The marine ecologist has to contend with the complication that the environment is moving and transporting various properties and biota. These naturally occurring, geophysical motions cover an enormous range of scales: from the capillary waves on wind-rippled water to the major currents like the Gulf Stream. The controlling mechanisms and the interactions between the various scales are extremely complex.

The planet earth is turning around its axis in one day and around the sun in one year. The air in the atmosphere and the waters in the oceans are always moving. While they are moving they are submitted to friction. The energy that drives this circulation is in last instance derived from the sun. Solar radiation is captured in the atmosphere and on the surface of the earth, largely absorbed and returned to space as thermal radiation. The earth receives less energy at the poles than at the equator and this differential heating is responsable for the movements of the atmosphere and the ocean, movements that transport heat towards the poles. This movement is modified by the rotation of the earth.

1 Radiation

The energy liberated by the nuclear reactions inside the sun is radiated as light into space.

1.1. Energy: units

The unit of energy is the Joule: it is the energy equivalent to the work produced by a force of 1 Newton applied during a displacement of 1 m in the direction of the force. The newton is the force which gives an object of mass 1 kg an acceleration of 1 $m.sec^{-2}$. Other units still widely used are the calory, the heat necessary to increase the temperature of 1 g of water by 1 °C (1 cal = 4.185 J) ; the dyne, equivalent to 10^{-5} N (c.g.s. system) and the erg = 1 dyne.cm = 10^{-7} J.

1.2. Energy-transport

With the exception of nuclear energy, all energy in the ocean-atmosphere system is under the form of heat or the result of heat -exchange. The transfer of energy can be under three forms molecular conduction convection and advection and radiation. Molecular conduction is the transport by molecular agitation without movement of material. It is the least important process. Convection and advection is the transport of heat by a vertically or horizontally moving fluid. Radiation does not imply matter: heat is part of the electro-magnetic spectrum.

1.3. Radiation

Being part of the electro-magnetic spectrum, heat can be transported at the speed of 3.10^{8} m.sec^{-1}. Every mass with a temperature over 0 °K emits radiation and the characteristics of this radiation are described by the radiation law of Planck:

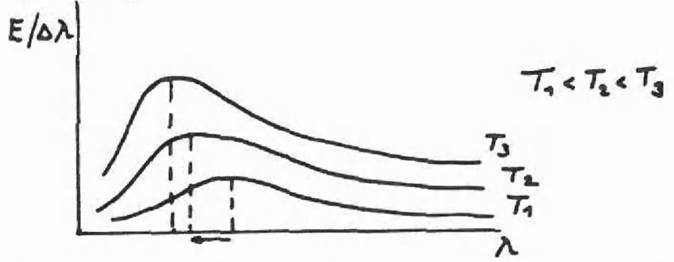
$$\frac{E}{\Delta\lambda} = \frac{\lambda^{-5}C_1}{e^{C_2/\lambda T}-1)}$$

E = energy emitted per unit time and surface

$\Delta\lambda$= a unit of wavelength

T = temperature

C_1 and C_2 = constants



When temperature increases, total energy (the surface under the curve) increase and the wavelength of maximum emission decreases. To determine them it suffices to find the first derivative and equalize to zero:

$$d(E/\Delta\lambda)/d\lambda = 0$$

On obtains the displacement law of Wien:

$$\lambda_{max} = 2897/T \quad \text{with } \lambda_{max} \text{ in } 10^{-6}\text{m and T in °K.}$$

To obtain the total energy emitted per unit time and surface we have to integrate:

$$\int (E/\Delta\lambda)d\lambda = \quad E = \sigma T^{4}$$

This is the law of Stefan-Boltzmann with the constant of Stefan-Boltzmann $\sigma = 1.36.10^{-8}$ cal.m^{-2}.deg^{-4}.sec^{-1}.

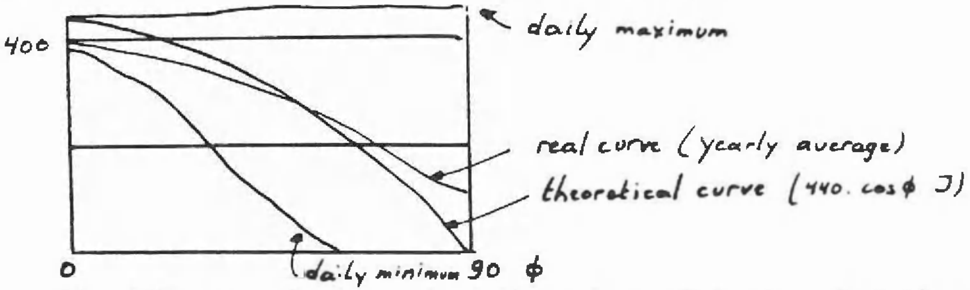
1.4. Solar radiation

The sun radiates 4.10^{26}J in all directions of space every second. The fraction of that radiation that reaches the earth is 1380 J .sec^{-1}.m^{-2}. Since the earth is not a disk but a sphere, with a surface area four times that of a circle with the same diameter, the average amount of radiation received will be less, 345 J $.m^{-2}.sec^{-1}$. This quantity diminishes from the equator to the poles. To calculate this, imagine first that the rotation axis of the earth is perpendicular on the terrestrial orbit (perpendicular on a line going from the earth to the sun). At the poles the sun will be at the horizon. At a certain latitude ø the surface of a zone of 1 m breadth as seen from the sun will be 2Rcosø (length) times cos ø (breadth). This zone will receive 1380 cos ø. 2R cos ø J $.m^{-2}.sec^{-1}$. This energy must heat the total surface of the zone, $2\pi R \cos \phi$ m^2 and the average solar radiation per m^2 over a day will be:

$$\frac{1380 \cos \phi \; 2R \cos \phi}{2\pi R \cos \phi} = 440 \cos \phi \; J \; .m^{-2}.sec^{-1}$$

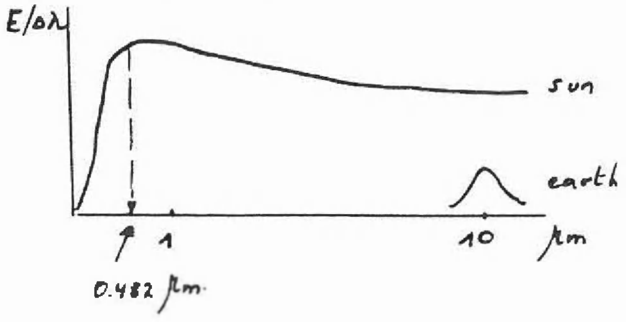
and will thus vary from 440 J at the equator to 0 J at the poles. Since however the axis of the earth is inclined with an angle of 23.5 ° the latitude at which the sun is perpendicular to the earth will vary from 23.5 °N to 23.5 °S (tropic of Cancer on 21 June and tropic of Capricorn on 21 December). This inclination of the rotation axis causes the seasons.

Moreover, the distance between the earth and the sun is not constant, the sun being closest to the earth on 3 January and farthest away on 5 July. For these reasons the latitudinal variations in radiation received from the sun are more complex than represented here.



The difference is largest at the poles. Note also that the minimum and maximum quantities received per day are not symmetrical around the equator. The maximum daily radiation is received by the earth on the south pole on 21 December.

The temperature at the surface of the sun is 6000 °K. The maximum intensity of sunlight is thus situated at a wavelength of 500 nm. Since the earth has an average temperature of only 300 °K, it radiates at a wavelength of 10 μm, in the infra red.



② The movement of fluids

2.1. Introduction

The differential heating of the surface of the earth produces movement of its fluid envelope, the oceans and the atmosphere. This movement not only transports enormous quantities of ocean water and air but is also the basis of the continual erosion of the terrestrial environment.

The basic laws governing the movement of all masses are the laws of Newton. Newton's first law says that an object that is not influenced by an external force will not change its conditions of movement or rest. At rest it will remain at rest. In movement, it will be transported with a constact velocity $v = a$. If a force acts on the body, its state of movement will change according to Newton's second law: this states that a force exerced on a body will accelerate it and the magnitude of this acceleration is equal to the product of the force and the inverse of the mass of the body: $a = f/m$ or $f = m.a$. The acceleration is expressed in $m.sec^{-2}$, the force in $kg.m.sec^{-2} = N$.

2.2. Pressure

Pressure is a force acting on a surface of 1 m^2. When a force is applied to a solid body it acts in the direction of application; on a liquid body it acts in all directions.

When we imagine a system with three dimensions and applie a force to it, this pressure will have a certain value in each point. The forces on a cube with 1 m^2 side are the six pressures acting on the walls of the cube. Moreover, the cube will be submitted to gravity along the z-axis. This force is equal to the mass of the cube times the acceleration due to gravity 9.81 $m.sec^{-2}$. A cube with length 1 dm has a mass equal to its density (mass per unit volume). The specific weigth (the weight per unit volume) is equal to the density times g. When the fluid is sea water, its density is 1.027 kg/l and the weight of a 1 l (1 dm^3) cube is $1.027 \times 9.81\ kg.m/dm^3.sec^2 = .01006$ N (this is also its weight). The specific gravity is the density of the fluid divided by the density of the same volume of pure water at 4 °C.

Apart from the force due to gravity, the other vertical forces working on the cube are a force working upwards on the lower plane and a force working downwards on the upper plane, equal to the pressures at $z = 1$ en $z = 0$ respectively. The total downward force on the cube will be: $a_g \times \rho + P_{z=0} - P_{z=1}$ and this force must be zero. The pressure increase will therefore be $P = a_g \times \rho \; m^{-1}$.

In seawater, the pressure increase with depth will be about 0.01 N per m^3, equal to about 1 bar per 10m (1 bar = 0.1 $N.cm^{-2}$) or hPa per 10m. The normal atmospheric pressure is 1.013 bar (or 76 mm Hg, the pressure exerced by a mercury column of 76 cm high).

The horizontal forces on the cube are the forces applied to the four walls. If the pressures on these walls are equal there will be no net horizontal force working on the cube. If a force b works in a certain direction there will be an acceleration in that direction equal to b/ρ $m.sec^{-2}$. If there is a pressure difference, fluids will be displaced from high to low pressures.

2.3. The Coriolis force

Once a fluid is in motion, accelerated by pressure differences, an additional force enters the game: the Coriolis force, caused by the rotation of the earth and deflecting moving objects to the right in the northern hemisphere and to the left in the southern hemisphere.

To understand the Coriolis force, consider the following example. At the north pole, the linear speed of the surface caused by the rotation of the earth is zero. At the equator it is 466 m/sec (40.000 km/24x60x60 sec). Imagine a disk at the equator and a gun at the north pole. When a shot is fired, the bullet will fly with a velocity of say 1 km/sec. It reaches the equator, at 10.000 km, after 10.000 sec. During that time the disk has already moved over 4660 km to the east. For the observer firing the gun it seems as if a force acting on the bullet has moved it to the west, to the right of its direction of movement. The disk, for the observer, has apparently not moved since they are both on the same rotating surface.

The Coriolis force is a function of the velocity of the object and of the vertical component of the rotation velocity of the earth on the place where the object is: $C = 2\Omega v \sin \phi$

$$C = 1.5 \times 10^{-4} \sin \phi .\ v \ cm/sec^{-2}$$

The acceleration due to the Coriolis force is thus small. It is of the order of 0.1 $cm.sec^{-2}$ for the wind and of 0.005 $cm.sec^{-2}$ for the oceanic currents. However, friction, which is very important at small scales, becomes negligible on the very large scales at which oceanic phenomena occur: at those scales the small pressure differences and the Coriolis force become predominating.

2.4. The influence of density

Movements of the fluid envelope of the earth are the consequence of pressure differences and the Coriolis-force. Horizontal pressure differences are causedby horizontal variatons in density, as well in the atmosphere as in the oceans. The effects of density variations can be best understood in terms of potential energy. If we consider a mass of A kg of water at a height of h m, we can calculate the force necessary to bring the mass at that heigth as A x a_g x h. The potential energy of that mass is increased by this amount. If we do not support this body of water, it will fall towards the earth, since every object has a tendency towards minimum potential energy.

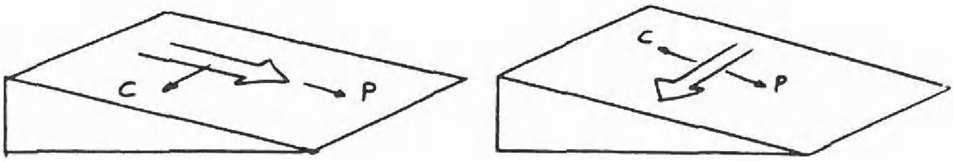
If a dm^3 of water is descended over 1 m, its potential energy is reduced by 9.81 x 1 x 1 $m.sec^{-2}.kg.m$ = 9.81 N.m = 9.81 J. If this mass of water is replaced by air, we may neglect the parallel increase in potential energy of the air, since the density of air is only 1/860 the density of water. This is not the case if one body of water is replaced by another body of water. Let us take the example of oil (density 0.8 $kg.dm^{-3}$) and water (1 $kg.dm^{-3}$). Let us take 10 g of water and 10 g of oil, thus 10 ml of water and 12 ml of oil. If the oil is on top of the water in a tube of 1cm^2 surface, the potential energy is 10 x a_g x 5 + 10 x a_g x 16 = 210 x a_g erg (J). If the water is on top , the potential energy is 10 x a_g x 6 + 10 x a_g x 17 = 230 x a_g erg (J). The system with water on top has a higher potential energy and will not be stable: after a perturbation the equilibrium (which is possible in a narrow tube) will be destroyed.

This simple relationship between density and potential energy is only valid for incompressible fluids. We have ignored the changes in density related to pressure. This is not valid for air, where we have to take into account the compressibility and internal energy. Changes in internal energy result from the work done during compression and decompression of fluids.

Horizontal variations in density will also cause movements. Less dense water will tend to flow towards the poles but the Coriolis-force will deflect this flow to the right in the northern hemisphere, thus to the east. Without rotation the warmer, less dense waters would cover the oceans and reduce even more the variations in temperature.

2.5 Geostrophic currents

Often steady state conditions are found in nature. When the velocity of a movement is constant, the different forces acting on it are in equilibrium. An important type of non-accelerated current is the geostrophic current. a movement along a straight line which exists if all forces other thanthe pressure gradient P and the Coriolis force C are negligable and when P = C. Imagine that a pressure difference makes the current flow down the gradient; once in movement the Coriolis force will deflect it to the right as a function of its speed. At the start there will be a disequilibrium and the current will turn. Since the Coriolis force is always perpendicular, it will turn as well. At equilibrium, the current will no longer flow downward (towards the region of low pressure) but along the slope. The direction of the geostrophic current is parallel to the isobars (lines of equal pressure).

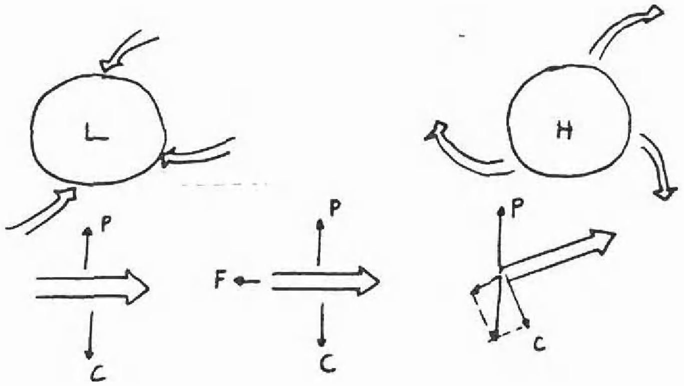


2.6. Gradient currents and friction currents

When the geostrophic current flows along the slope, one has to take into account centrifugal forces, given by $S = v^2/r$, with v the velocity and r the radius of the movement. If pressure, Coriolis force and centrifugal force are the only important forces, the resulting movement is called a gradient current. As in the case of the geostrophic current the movement is parallel to the isobars.

When one then introduces friction, always directed in a sense opposite to the movement and function of the velocity, the velocity will decrease. The direction will also change and also the magnitude of the Coriolis force and the current will turn more the left. The result will be a slower current to the left of the geostrophic current.

A region of low pressure is a region of convergence, since the fluid will flow to the centre; a region of high pressure is a zone of divergence.



3. The atmospheric circulation

To understand the atmospheric circulation, we consider first a fixed immobile earth with a uniform surface. The intense heat received at the equator will make the air rise there. The vacuum created by that rising air will be filled in by air coming over the surface from the poles.

To see what happens to the rising air, consider Boyle's law:

$$\boxed{PV = nRT}$$

with R the gaz constant, equal to 83 bars.cm^{-3}.deg^{-1}.mol^{-1}.

n the number of moles (mass divided by molecular weight)

Since the molecular weight of air is 28.8 g, 1 g of air has a specific volume of 83 x T/28.8 P; for a pressure of 1 bar and T = 300 °K (30 °C) the specific volume of air is 83x300/28.8x1 = 870 cm^3/g. The density of air is thus 1/870 = 0.00115 g/cm^3 at P = 1 bar. In general, the density of air is

$$\frac{P}{2.89\ T} \quad \text{g.cm}^{-3}$$

and the pressure variation, equal to the product of density and the acceleration of gravity, is

$$\frac{dP}{dh} = \frac{a_g\ P}{2.89\ T} \quad \text{dyne cm}^{-3}$$

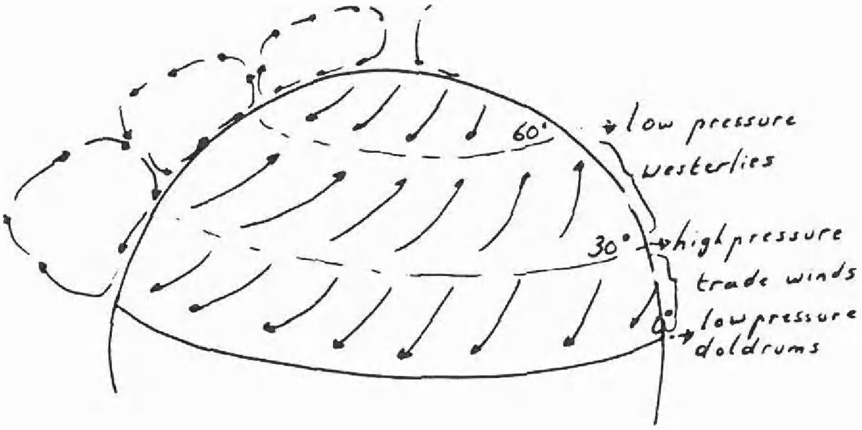
$$P_h = e^{(a_g/2.89T).h}$$

Temperature does not remain constant during the rising of the air. Since the pressure decreases, the volume of air increases. The air thus delivers work which is equal to the product of pressure and the change in volume: 86 bar.cm^3 2 cal.g^{-1}. If this heat is not provided from outside, the air must get colder. If during a mechanical process work is done without adding or substracting heat, the process is called adiabatic.

The ancient theory of Hadley predicts three convection cells in the atmosphere. The air rising at the equator descends again at 30 °. This is a region of high pressure and dry air (desert region). This descending air then flows over the earth towards the equator or towards the poles. When it flows towards the poles it meets the very cold air from the poles at about 60 ° and converges with it, rising again and producing the two other convection cells.

Applying the Coriolis force to this movement, on obtains the main direction of the winds. The region between the equator and 30 ° is characterized by the trade winds, from south-west. The equatorial region itself is the region of the doldrums, very weak winds. The high pressure zone at 30 ° is called the horse latitudes.

The tricellular theory has become impopular recently and has been replaced by the eddy theory, based upon the principle of conservation of angular moment instead of on convection (product of mass, velocity and radius of the movement). When the earth turns, its atmosphere turns with it and stays immobile relative to it. Every parcel of air has its own angular moment that is conserved. Every change in velocity must entrain a change in angular moment. When one compares a parcel of air at the equator, with a velocity of around 1800 km/h to a parcel of air in the region of the trade winds, there will be a deficit in angular moment between the equator and 30 ° and this moment has been transferred elsewhere. This is done by turbulent systems of high and low pressure.



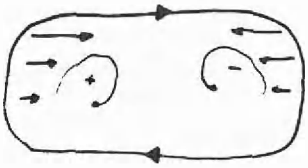
4.The oceanic circulation

The major oceanic current systems move water masses over enormous distances over the surface of the oceans. This movement is due to inequal heating but the effect is considerably modified by the wind and the fact that oceans are contained in basins.

When the wind blows over the ocean it produces waves that travel in the direction of the wind. If the earth would be competely covered by water the circulation of the ocean water would be similar to that of the atmosphere. How the two major oceans, the Atlantic and Pacific Oceans are limited at their eastern and western sides. The movement in these basins is caused by the general circulation of the air. The movement of the water will be from east to west at the poles, from west to east in the region of the westerlies, from east to west in the region of the trade winds. The margins of the basin will deflect the currents and produce a series of gyres.

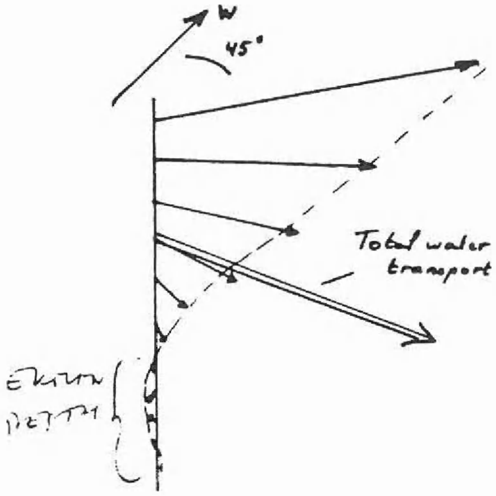
The most important gyre is the subtropical gyre. Towards the poles one finds subpolar gyres and at both sides of the equator, the equatorial gyres. This simple model predicts six gyres, three at each side of the equator. The actual situation is different: subtropical gyres are indeed present in each ocean and the equatorial gyres are found back principally as the equatorial counter-currents. The subpolar gyres consist of several gyres in the north and encircle the Antarctic continent in the south. In the Indian ocean the situation is complicated due to its limited extension to the North. The influence of the wind is different in summmer, when it blows from the ocean to the continents, and in winter, when a cold and dry wind blows from Asia towards the ocean and reverses its circulation.

The simple model gives a symmetrical current. Actually the currents are much stronger at their western border in the northern hemisphere. This is due to the Coriolis force which increases when a current goes to the north in the western part of the bassin.



Surface ocean circulation

The circulation at the surface of the oceans is closely linked to the atmospheric circulation. When the wind blows across an open ocean far from any boundaries, the resulting movement of the water will be greatest at the surface and decrease in magnitude with depth. Because of the rotation of the earth a deflection will occur to the right in the northern hemisphere: the water will move at 45 ° to the wind direction, this angle increasing gradually and the current velocity decreasing with depth. At a depth called the Ekman depth the current is opposite to that on the surface and is very small. The spiral of current beneath the wind is called the Ekman spiral with the property that the depth integrated transport of water is at right angles to the wind direction. Only when the movement of water is restricted by land the direction of the current will be that of the wind.



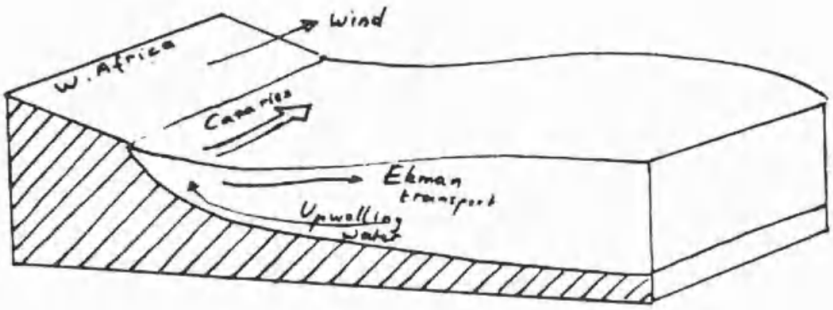
Due to the wind system the water acquires a clockwise rotation tendency in the northern hemisphere. The Coriolis force increases this tendency, depending on latitude. A balance is achieved by friction, which is proportional to the square of the velocity. Currents are much stronger on their western boundary. Where the warmer central portions of the gyres meet the eastward flowing limbs at 30-40 ° latitude, the Subtropical Convergences are formed. The Subpolar Convergences, where the warmer water meets the colder polar waters are generally well defined.

The Gulf Stream

The Gulf Stream is formed from the Florida Current an the Antilles Current which join north of the Bahama Islands. The landward side of the Gulf Stream is well defined both in terms of temperature and salinity. There is little difference between the Gulf Stream and the oceanic water to the east. The Gulf Stream only extends to a few hundred meters depth and is not a continuous stream in a fixed path. The current meanders over a wide area, occupying at any time only one third of a 150 km wide zone. The meanders sometimes become detached and large masses of cold water become surrounded by warmer sub-tropical water. These structures are known as cold-core-rings. They have a cyclonic, anti-clockwise rotation and wander slowly south-westwards at about 2 km per day, remaining recognizable for up to 2 years. They are 150 to 300 km in diameter, have peak tangential velocities of 1 m/sec and reach depths of 3000 m. Consequently they raise the thermocline by 500 m or so and have considerable potential and kinetic energy. The rings have a biomass considerably higher than that in the surrounding sea. Anticyclonic or warm core rings also form on the coastal side of the Gulf Stream.

Upwelling

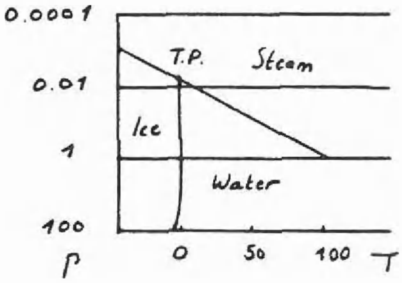
When the current and the winds are in the same direction, parallel to a coast on the left-hand side in the northern hemisphere and the right-hand side on the southern hemisphere, upwelling of deeper water may occur. An example is the Canaries Current. It flows southward in the area of the North-east Trade Winds, with the African coast on the left-hand side. The Coriolis force associated with this current balances the effect of the sea surface slope and the density gradients. The effect of the Ekman transport beneath the wind is to move the surface water towards the right. Because of the presence of the coast this water is then replaced by water occurring at 100 - 200 m depth further offshore, by a slow overturning. These waters are relatively nutrient-rich and highly productive when coming into the euphotic zone. Upwelling areas support some of the world's most important fisheries. The water is also relatively cold.

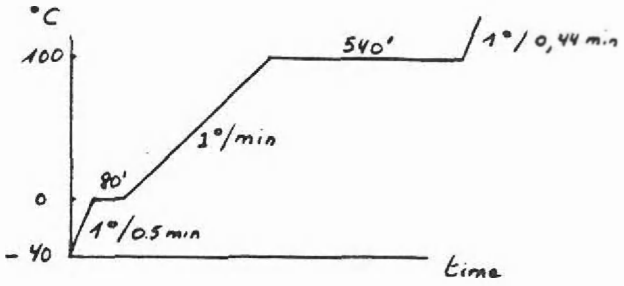


The characteristics of water

Life, as we know it, would be impossible without water. Nevertheless, water has some peculiar characteristics. It has the highest surface tension of all liquids, except mercury. If we compare water to molecules with a similar composition we expect it to boil at -80 °C and to freeze at -95 °C. The reason for its exceptional behaviour is the structure of the water molecule. The two hydrogen atoms form an angle of 105 ° with the oxygen atom. This gives the water molecule a polarity, an orientation of its electric charges. Other, adjacent molecules are attracted, and form groups of several molecules held together by hydrogen bridges. Water molecules are dipoles and subject to polymerisation.

As all matter, water exists in three phases. Temperature and pressure determine in which phase it will be. The phase diagram gives the boiling curve, the freezing curve and the sublimation curve which meet in the triple point.





To pass from one phase to another one has to add heat. If we add one calory per minute, we obtain a curve as drawn above. We need 0.5 cal.g^{-1}.deg^{-1} for ice, 1 cal.g^{-1}.deg^{-1} for liquid water and 0.44 cal.g^{-1}.deg^{-1} for vapour. This is the heat capacity. To melt 1 g of ice, we need 80 cal, to vaporize 1 g of liquid water we need 540 cal. These are the heats of phase transformation. The heat capacity of water is the largest known for all solids and liquids except NH_3. For this reason water has been chosen as the reference of the specific heat (number of calories necessary to increase temperature of 1 g of substance with 1 °C). The specific heat of water is thus 1 cal.g^{-1}.deg^{-1}.

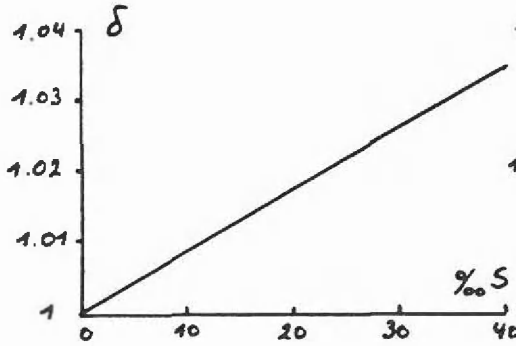
Also the latent vaporisation heat of water is the largest of all substances known. This is of extreme importance since it permits the exchange of enormous quantities of heat at the earth surface. Every gram of water that changes phase takes up this quantity of heat.

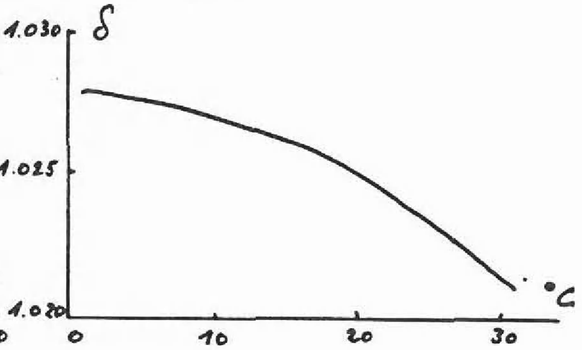
5.2. The density of water

Water is also unique in the fact that it is more dense as a liquid than as a solid. This implies that ice restson top of liquid water, with evident consequences for life on earth. The erosion of rocks is another consequence of this, since the specific volume of ice is greater than of water.

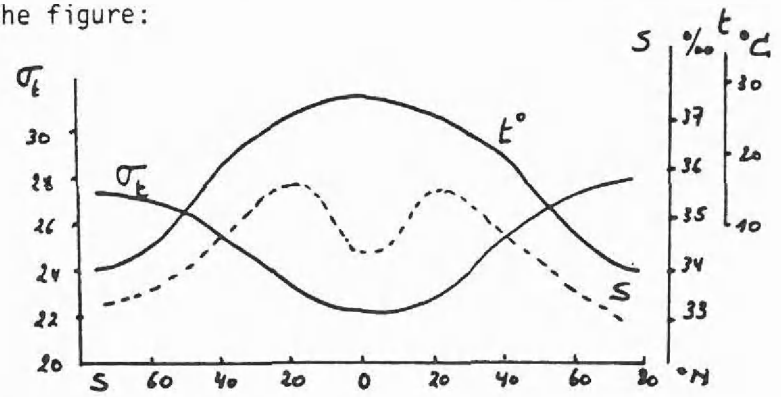
Pure water has its greatest density at 4 °C, its specific volume is then equal to 1 cm^3/g and its specific gravity is one. In sea-water the presence of salt makes that the maximum density is reached at 0 °C.

Every increase of 1 ‰ of salt increases density with 0.8 ‰. Seawater with a salinity of 35 g/l has a density of 1.028 at 0 °C. This is usually expressed as $\sigma_T = 28$.





The influence of temperature on density of seawater is somewhat more complex. Density decreases when temperature increases. The combined effect of temperature and salinity on density are shown in the figure:



5.3. Salinity

If the total mass of salts in the sea can change considerably from place to place, the relative proportion of the principal salts remains constant. Most salts are present as ions. Eight ions form the great majority of dissolved salts:

Cl^-	55.0 %
SO_4^{--}	7.7 %
HCO_3^-	0.4 %
Br^-	0.2 %
Na^+	30.6 %
Mg^{++}	3.7 %
Ca^{++}	1.2 %
K^+	1.1 %

All other substances are present as traces only, but on the other hand sea-water contains nearly all known elements.

Definition

Salinity is the total amount of salts dissolved in 1 kg of sea-water. Because the relative proportion of the ions is constant, one can determine only one of them. The chloride ion is easily determinable. One defines chlorinity as the mass in grams of halogens contained in 1 kg of sea-water. The relationship between salinity and chlorinity is

$$S = 1.80655\ Cl.$$

The distribution of salinity in the oceans

The salinity of the surface waters in the oceans is a function of evaporation and precipitation which concentrate or dilute the surface waters, and of mixing between superficial and deeper waters. Fluvial transport may influence coastal regions and the melting of ice plays a role in the polar regions.

The salinity is minimal in certain zones such as equatorial regions with very high precipitation (Gulf of Guinea, Gulf of Bengalen, South-East Asia), zones influenced by large rivers (rio de la Plata, Amazone Saint Laurence, Baltic Sea, Black Sea) and the Arctic Ocean. Maximum salinities are reached in the Mediterranean, the Red Sea and subtropical parts of the Indian Ocean and Atlantic. The surface waters of the Pacific have a lower salinity. Salinity variations are small, usually lower than 0.5 ‰. Diurnal variations are negligable: even during heavy precipitation the normal values are restored after a few hours.

5.4. Temperature

Temperature is with salinity the most important characteristic of ocean water. It is a conservative property, since it can only be changed by mixing after the waters have left the surface. Indeed: temperature is a function of solar radiation, thermal exchange between ocean and atmosphere and mixing between different oceanic water layers.

Water absorbs solar radiation within the first few meters. At latitudes lower than 20 ° the oceans accumulate heat, at higher latitudes they render it. The surface isotherms are zonal, with a maximum of about 28 °C slightly north of the equator and a minimum of -2 °C in the polar regions. The annual variations in temperature follow the seasonal variations in solar radiation, but also depend on currents and dominant winds. In the northern hemisphere, the annual variations are much larger than in the southern hemisphere. Diurnal variations are generally very small, in the order of 0.2 to 0.4 °C.

The vertical distribution of temperature is profoundly influenced by differences in radiation and thermal exchange with the atmosphere. The oceanic circulation patterns govern the vertical profile of temperature, except in the surface layers. At latitudes lower than 50 ° one can distinguish three layers: a) a thin superficial layer, with a depth of less than 100 m, under the direct influence of solar radiation with exchange with the atmosphere and mixing due to the wind. This layer is more or less homogeneous in winter and has a seasonal thermocline in summer; b) a transition layer where temperature decreases rapidly from more than 20 °C to about 5 °C. This is the permanent thermocline. In the equatorial regions the maximum value of the vertical gradient may be more than 0.4 °C per meter. A higher latitudes the value may drop to 0.05 °C per meter and the depth of the layer is between 100-200 m. At 50 ° latitude the permanent thermocline reaches the surface: c) a deep layer, with temperatures decreasing from about 5 °C to less than 2 °C. These deep waters, originating from the polar regions, constitute the major part of the oceans.

The seasonal thermocline

The establishment of a thermocline in summer is of great importance to understand biological processes in the superficial layers. The slope of the thermocline is larger when the heating of the water is more rapid and when the sea is calmer. The superficial layers become less dense and a stable stratification is established. During summer this continues and the stability of the stratification is increased by more heating. Mixing with deeper layers is reduced, till at the end of the summer the thermocline is a real barrier which effectively stops all exchange.

5.5. Temperature, salinity and density

Variations in density of oceanic water are mostly dictated by temperature changes, especially in the vertical direction. Thermoclines are therefore also pycnoclines, zones where density changes rapidly with depth.

Since temperature and salinity are in principle two completely independent parameters: each one of them can change without the other. In the oceans this independence in reality does not exist and if a diagram is made with both parameters, a T-S diagram, one has a tool to distinguish different water masses. Since temperature and salinity are conservative properties, they reflect the origin and the age of ocean waters once they have left the surface as well as the mixing that has occurred since.

Since temperature and salinity determine density (at atmospheric pressure) isopycnes may be drawn in the T-S diagram, which gives an idea of the stability of the vertical distribution of the water masses. Stability is maximum when the T-S curve is perpendicular to the isopycne.

5.6. Deep circulation

One distinguishes several deep water masses: a) the central water, between the subtropical convergence at the surface to the permanent thermocline; b) intermediary water, directly underneath the central water and formed in the regions of the arctic and antarctic convergencies. Several intermediary waters exist: the North-Atlantic (3-5 °C, 34.7-34.9), Antarctic (2-7 °C, σ_T = 34.1 - 34.7), North Pacific (6-10 °C, σ_T = 34.0-34.1. c) the deep water: originating from the Labrador- Irminger area, with a temperature of 3 °C and a σ_T = 34.9. d) the bottom water, orginating from the Antarctic.

The Chemical Environment

1. The geochemical balance of the oceans

The actual composition of sea water results from an equilibrium between the rate at which dissolved matter enters the oceans from land or the atmosphere and the rate at which matter disappears into the sediments or the atmosphere.

When one compares the composition of sea water with the fresh water in rivers important differences are seen (in meq.kg^{-1}):

	Sea Water	River water	Cyclic salts
Na^+	468	0.27	0.19
K^+	10	0.06	0.00
Mg^{++}	107	0.34	0.04
Ca^{++}	20	0.75	0.01
Cl^-	546.5	0.22	0.22
HCO_3^-	2.3	0.96	0.00
SO_4^{--}	56.2	0.24	0.02

Sea water is not simply concentrated river water. Fresh water is mostly a solution of calcium bicarbonate, whereas the principal salt in the sea is sodium chloride. There are mechanisms that change the relative proportion of salts.

Evaporating sea water is not purely H_2O. Important quantities of salt cristals are brought into the atmosphere and transported by the wind; around these cristals water condensates. When rain is formed, these (cyclic) salts are brought back to earth. Substraction of the quantity of cyclic salts, calculated by supposing that all chloride is cyclic, shows the contribution of erosion of rocks to the salt concentration in rivers.

The oceans contain about 1.4×10^{21} kg of water and the rivers add to this about 10^9 kg per second. It takes thus 4.4×10^4 years to add to the oceans their own volume. This is the residence time of water, the average time during which an element is in the ocean. Rivers contain about 1.2 meq.kg^{-1} of non-cyclic salts, the sea about 600 meq.kg^{-1}. The residence time of salt is thus 2.2×10^7 years ($600/1.2 \times 4.4 \times 10^4$).

In general, if A is the concentration of the substance and dA/dt the rate of import, the residence time is given by:

$$\tau = \frac{A}{dA/dt}$$

For the individual substances, the values are (in 10^6 years)

Water: 0.044
HCO_3^-: 0.11
Ca^{++}: 1.2
K^+: 7.5
SO_4^{--} : 11
Mg^{++}: 16
Na^+: 260
Cl^-: ∞

The residence time of most substances is much smaller than the age of the oceans. The oceans are not simple accumulators of salts put into them by the rivers. The concentration of major and many minor elements are regulated by equilibria between dissolved cations and aluminum silicates either in suspension or in the sediments. Clay minerals are important to maintain an equilibrium because they are ion exchangers and reconstitute degraded minerals by incorporating K and Mg. For trace minerals the geochemical balance is maintained by autogenic mineral absorbtion or by biological processes.

For anions the mechanisms implied in the geochemical balance are quite different. Chlorid and bromid are inert but important quantities of sulphate reach the sea due to erosion on land of rocks containing sulphide. The geochemical balance is probably maintained by deposition of sulphides and sulphur in the sediment due to bacterial reduction.

The residence time of metals such as Fe, Al, Cr, Ti, Be are in the order of only 100 to 1000 years. These ions are rapidly hydrolysed at the pH of sea water and incorporated in autogenic minerals, such as manganese nodules. The relatively short residence times of Cu, Ni, Co and Mn (7000-50000 years) are indicative of the efficiency with which they are incorporated in manganese nodules.

2. The dissociation of water

Pure water contains some dissociated molecules: $H_2O \rightleftharpoons H^+ + OH^-$. The dissociation constant is 10^{-14} $mol^2 kg^{-2}$, and the concentrations of H^+ and OH^- are equal to 10^{-7} $mol.kg^{-1}$ (pH : $-\log H^+ = 7$).

Most ions in sea water do not react with H^+. The most important which does is CO_2. This gaz thus plays an important role in the regulation of the acidity of sea water.

Variations in temperature and pression change the pH of sea water because of their influence on the dissociation constant of carbonic acid. An increase in temperature of 1 °C decreases pH with 0.01. pH decreases nearly proportional to pression, the proportionality varying from -0.035 for an initial pH of 7.5 to 0.020 for an initial pH of 8.3.

In surface waters the pH will normally vary between 8.0 and 8.3. Higher values may be found when photosynthesis is strong. Below the euphotic zone, pH evolves somewhat like oxygen. When oxygen is consumed, pH will decrease to 7.5.

3. The CO_2-system and alcalinity

When carbon dioxide dissolves in water, it will combine with a water molecule and form carbonic acid:

$$CO_2 + H_2O \rightleftharpoons H_2CO_3$$

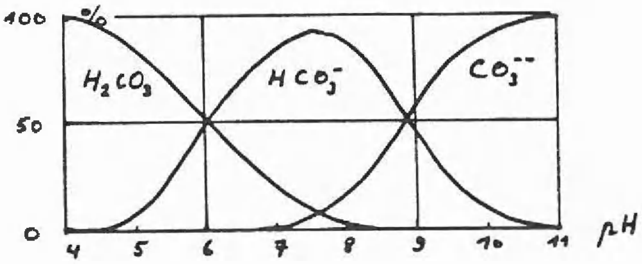
The carbon atom contains six electrons. In the CO_2 molecule, the carbon atom shares two electrons with each of the oxygen atoms. When CO_2 combines with water, the oxygen of the water molecule will also share two electrons with the carbon atom. The result is that H^+ is only weakly bound to H_2CO_3. When an ion H^+ is lost, bicarbonate is formed:

$$H_2CO_3 \rightleftharpoons H^+ + HCO_3^-$$

The bicarbonate ion can also lose a proton H^+ and form the carbonate ion:

$$HCO_3^- \rightleftharpoons H^+ + CO_3^{2-}$$

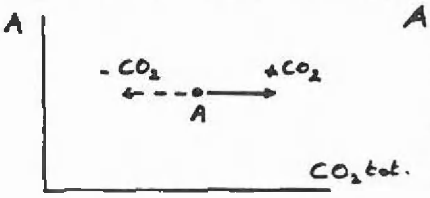
When carbonate and bicarbonate ions are formed, they will attract hydrogen ions to reduce their charge. There will thus be a continuous exchange of hydrogen ions between the different forms of carbonate and the solution and the relative concentration of the different species will depend on the pH:

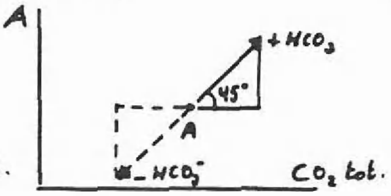


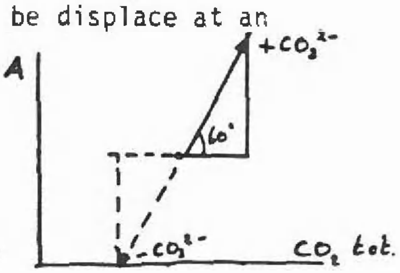
Besides the ions of the carbonate system, there are other ions that can react with H^+: OH^- and $H_2BO_3^-$. The total charge of all ions reacting with H^+ is the alcalinity, expressed in meq/kg. In sea water the alcalinity is due principally to HCO_3^-, but small quantities of carbonate and different forms of boric acid are also present.

$$[A] = [HCO_3^-] + 2\,[CO_3^{2-}] + [H_2BO_3^-] + [OH^-] - [H^+]$$

The Deffeyes diagram shows the total concentration of CO_2 as a function of alcalinity. If we consider a mass of sea-water with an alcalinity A and we add CO_2, the concentration of CO_2 will increase but alcalinity will remain the same since CO_2 is not charged. In the diagram the point will go to the right. If we add 1 mmole of HCO_3^- to 1 kg of sea water the total concentration of CO_2 and alcalinity will increase by 1: the point will move over an angle of 45 ° with the horizontal axis. Finally, if we add carbonate at the rate of 1 mmole/kg, the concentration of CO_2 will increase with one and alcalinity with two, and the point will be displace at an angle of 60 ° with the horizontal.



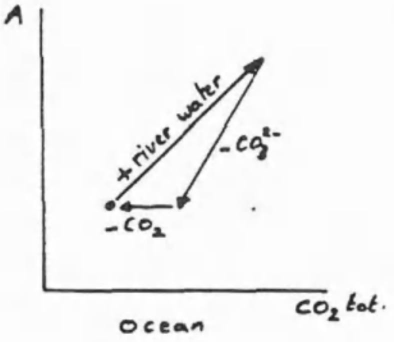


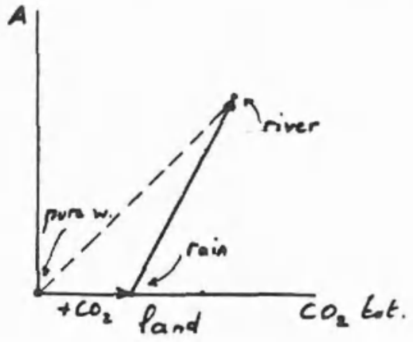


Consider now the influx of fresh water. Since water evaporates, the net effect will be an increase of HCO_3^-. In the diagramme, the composition will change. The process which counters this is the precipitation of calcium carbonate by organisms. However, the cycle can not be completed since alcalinity decreases with a 2:1 rate. When the initial alcalinity is reached, there will be an excess of CO_2. To complete the cycle this excess of CO_2 has to be returned to the atmosphere, where it dissolves in rain water, without alcalinity change. When this rain falls on earth, the CO_2-charged water will react with rocks forming bicarbonates

$$CO_2 + H_2O \rightleftharpoons H_2CO_3$$

$$H_2CO_3 + CaCO_3 \rightleftharpoons Ca^{2+} + 2HCO_3^-$$





Under the surface of the sea and far from land, there is no influx of bicarbonate from rivers and no exchange of CO_2 with the atmosphere. ⊕ Marine organisms interact with the carbonate system in two ways: plants utilize CO_2 for the synthesis of organic matter and animals respire organic matter to form CO_2. Respiration continues at all depths and will increase the CO_2 concentration. $CaCO_3$ precipitates in the cells and skeletons of marine organisms.

Sea water contains about 20 meq/kg of Ca^{++} and 2.3 meq/kg of HCO_3^- . In deep water, there is a limit below which $CaCO_3$ disappears. This limit is the snow line, because at this depth (4.2 km in the Pacific and 4.7 km in the Atlantic) the skeletons of marine organisms no longer cover the sediments. Because of higher CO_2-concentrations in deeper water, due to animal respiration, pH is lower, and higher pressure and lower temperature increase the solubility of calcium carbonate as well.

4. The redox potential

Besides the concentrations and nature of the principal ions and the acidity of sea water, the redox potential is also a fundamental characteristic of the chemical state of the oceans.

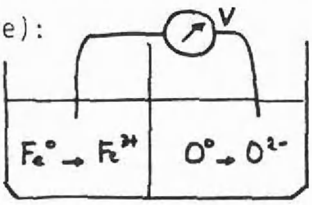
All chemical reactions implying change in the oxydation-reduction state of an element can be considered as the result of two half-reactions. As an example:

$$2\ Fe^0 + 3/2\ O_2 \rightleftharpoons Fe_2O_3$$

$$\text{Oxydation: } 2\ Fe^0 \rightarrow 2\ Fe^{3+} + 6e^-$$

$$\text{Reduction: } 3/2\ O_2 + 6e^- \rightarrow 3\ O^{2-}$$

Since every oxydation-reduction reaction implies the transport of electrons, one can imagine that the reaction creates an electric tension (a potential difference):



In general one can write:

$$Ox + ne^- \rightleftharpoons Red$$

$$K = \frac{[Red]}{[Ox][ne]}$$

$$\log K = \log [Red] - \log [Ox] + npE$$

$$pE = \frac{1}{n} \log K + \frac{1}{n} \log \frac{[Ox]}{[Red]}$$

$$pE = pE^{o} + \frac{1}{n} \log \frac{[Ox]}{[Red]}$$

This quantity is related to the redox potential as:

$$pE = \frac{Eh}{0.05915} \text{ at } 25\ ^{\circ}C \quad \left(\frac{Eh}{2.3\ RT/F}\right)$$

The redox-potential for sea-water is determined by the concentration of oxygen. The half-reaction to consider is:

$$O_2 + 4\ H^+ + 4e^- \rightleftharpoons 2\ H_2O$$

with log K = 83.1

All reactions in sea-water that involve a transport of electrons are controlled by this half-cell and the Eh (or pE) is fixed since the conentrations of oxygen and the pH are determined:

$$\log K = 2 \log [H_2O] - \log P_{O_2} - 4 \log [H^+] - 4 \log [e]$$

$$83.1 = -.0.01 \times 2 + 0.69 + 8.1 \times 4 + 4\ pE$$

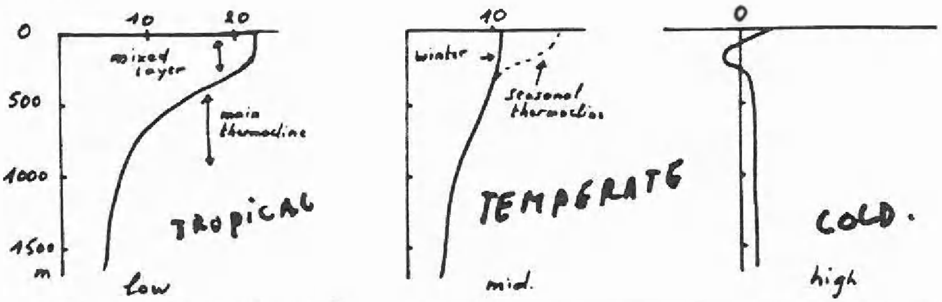
$$pE = 12.5$$

Sea-water is a very oxydizing solution and many elements exist in sea-water in their maximum oxydation state. In anoxic basins or in sediments the Eh may decrease however.

Vertical zonation in the ocean

Light is absorbed in the first few to at most several hundred meters of the water column. The restriction of photosynthetic processes to the thin surface layer of the ocean and the subsequent depletion of this layer in nutrients create a first important vertical zonation. All life beneath the euphotic zone is heterotrophic and depends on organic matter formed in the surface layer (with the exception of life depending on chemosynthesic primary production). The input of organic matter in deeper parts of the ocean clearly depends on surface productivity and on depth since the organic material is constantly being used as it rains down.

Another important gradient is that of temperature. An upper layer of warm water floats on a cold ocean. Water with a temperature above 10 °C occupies only 10 % of the total ocean volume. The mean temperature of the entire ocean is 3.5 °C (the average salinity is 34.7 ‰). Typical temperature profiles for low, mid and high latitudes are shown below:



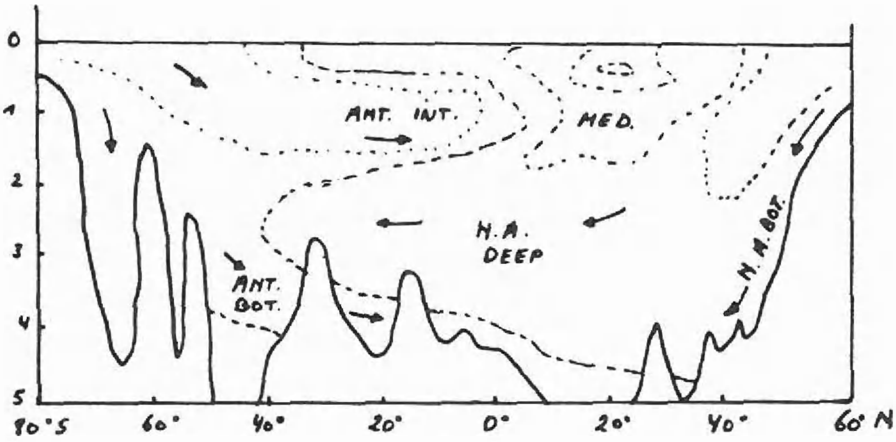
In the tropics there is an isothermal surface layer ranging from 10 to 200 m in thickness. Temperature in this zone ranges between 15 and 30 °C depending on season and latitude. In a zone below this extending between 300 and 1000 m depth, temperatures fall rapidly to values near 5 °C, then in the rest of the water column the temperature decreases slowly to levels between 1 and 2 °C at 4000 m depth, the mean depth of the oceans.

The surface layer which is mixed by the wind becomes thicker in winter, especially in middle latitudes. The mixed layer is separated from cooler waters by the seasonal thermocline, which may persist through most of the year in subtropical regions. The zone between 300 and 1000 m is knowns as the permanent thermocline. In temperate waters the thermocline beneath the mixed layer develops only in summer. In the polar regions there is no longer development of thermoclines and there is little change in temperature from top to bottom.

Density of sea water depends on pressure, salinity and temperature. The pressure increases with about 1 atm per 10 m (see p.) but since marine animals have nearly the same compressibility as the sea they will change in density at the same rate as the sea. Gases are highly compressible and animals that depend on a gas-filled float for neutral buoyancy have evolved means of regulating their density against changes of pressure. Changes in pressure have effects on the activities and enzymes systems of marine organisms and some deep-sea organisms appear to be sensitive to pressure changes because of this.

Differences in salinity, temperature and density characterize different water masses occupying characteristic depth zones in the oceans. The deepest water is formed in the Antarctic. During the winter the surface waters around Antarctica become colder and saltier; over the shelf of the Weddell Sea the temperature may go down to -1.9 °C and the formation of sea ice leads to a relatively high salinity of 34.6 ‰. This water has a high density of 1.0279 and, after mixing with circumpolar water, it sinks down the continental slope and flows away form Antarctica over deeper reaches of the ocean floor. This is the Antarctic Bottom Water and it moves northward and eastward into the basins of the three oceans. In the Atlantic this water has been traced as far north as 40 °N, about the latitude of Spain.

Surface waters off Antarctica are driven clockwise round the continent as a broad west wind drift. Due to the coriolis force this water is deflected to the north. Over southerly reaches the properties of Antarctic Surface Water, which has a thickness of 100 to 250 m, vary with the seasons, but during their drift north these waters absorb summer heat and at latitudes between 60 ° and 50 °S temperatures are close to 2 °C and salinities below 34 ‰S. Between these latitudes and along a narrow circumpolar front called the Antarctic Convergence, Antarctic Surface Water meets Subantarctic water of higher temperature and begins to sink. On the way down it mixes strongly with deeper and warmer waters that are rising above Antarctic Bottom Water, and, after finding its level at about 1000 m, continues north as Antarctic Intermediate Water. In the Atlantic this water mass crosses the equator in the west. North of the equator a smaller intermediate water mass is formed by the sinking of Mediterranean water to 1000 m or more as it flows into the Atlantic. The warm deep water is not formed in the Southern Ocean but far to the north in the surface waters of the North Atlantic. South of Greenland at about 60 °N relatively saline waters that are chilled in winter sink and the flow south between 1500 and 4000 m as the very voluminous North Atlantic Deep Water Mass.



North of the Antarctic Convergence at about 40 °S there is a second circumpolar front, the Subtropical Convergence, where cool Subantarctic Water meets a warmer mass of water. Over a broad front water sinks to levels between Antarctic Intermediate Water and the surface mixed layer to form South Atlantic Central Water. North Atlantic Central Water is forped along another broad front at about 40 °N in the northwestern Atlantic. These Atlantic Central Waters, which extend to depths of 300m on either side of the equator and deepen to 600-900 m at mid-latitudes have temperatures between 17 and 7 °C and salinities from 36.5 to 34.5 ‰.

The Southern Subtropical Convergence is also the southern boundary of the Atlantic, Indian and Pacific Oceans. The rest of the ocean is formed of seas. Antarctic Bottom Water and Antarctic Intermediate Water also penetrate into the Pacific and Indian Oceans. In the northwestern Indian Ocean there is an intermediate water that flows out of the Red Sea. There are also two deep-water masses formed in the Indian Ocean: North Indian Deep Water forms in the Arabian Sea from Red Sea water; after mixing with Antarctic Intermediate Water and Bottom Water it is transformed into South Indian Deep Water. The Central Water Masses of the South Pacific and South Indian Ocean arise at the Southern Subtropical Convergence. Between the Central Water Masses of the Pacific and north of the Central Water of the Indian Ocean there is a vast Equatorial Water Mass which has no counterpart in the Atlantic Ocean.

With the different water masses pelagic organisms are disposed in horizontal strata in the ocean. Pelagic organisms may range in size from bacteria to the largest whales. Plankton consists of diverse organisms that are non-motile or have limited powers of movement and drift with the sea. Bacterioplankton and phytoplankton are microscopic forms, whereas the zooplankton may range from the millimetre-long copepods to large jellyfishes over a metre in diameter. The most ubiquitous forms are copepod crustaceans: other important groups are cnidarians, ostracod crustaceans, pteropod molluscs, arrow worms and pelagic tunicates.

Members of the nekton have sufficient powers of locomotion to make their way against currents. Cetaceans, seals, turtles, fishes and squid are classic forms of nektonic animals. There is of course some overlap with the plankton: the commonest deep-sea fishes belong to the genus *Cyclothone* and the smallest species range from 25 mm to 50 mm in length. Several species of euphausiid shrimps fall within this size range or even exceed it, yet they are considered planktonic animals.

Animals that move or float on the sea surface have the collective name of pleuston. The movers are water striders (*Halobates*) of the insect order Hemiptera. The floaters have some kind of gas-filled buoyancy chamber and include cnidarians (*Physalia*, *Velella*, *Porpita*) and nudibranch mollusks (*Glaucus*). Organisms that live in the uppermost few centimeters of the sea form the neuston. There are bacteria, tiny species of phytoplankton (nanoplankton) and diverse planktonic animals. In subtropical and tropical regions many members of the neuston are suffused with blue or purple pigments.

The uppermost waters of the open ocean are known as the epipelagic zone, which extends to about 150m depth, and is roughly equal to the euphotic zone. In very clear ocean water blue-green rays may penetrate to 1200 m depth and this limits the mesopelagic zone (or disphotic zone). In subtropical and tropical waters the mesopelagic zone zone contains the main thermocline but everywhere below this zone temperatures at a given level are virtually uniform and range between 5 °C and negative values. The bathypelagic zone is thus uniformly cold and dark (except for bioluminescence). At depths below 1000 m there is a distinct bathypelagic fauna of calanoid copepods. Lantern-fishes, most of which migrate daily between daytime-levels and the surface at night, are classis mesopelagic fishes. The mesopelagic zone is full of luminous animals. Below 1000 m bioluminescence is much less frequent and the diversity and biomass of pelagic life are much reduced in the bathypelagic compared to the mesopelagic zone.

In the deeper parts of the bathypelagic zone, below 4000 m, there seems to be a distinct abyssopelagic fauna, with members of the copepod family Spinocalanidae. Species of this family also live near the sea-bottom as part of a bentho-pelagic fauna (hyperbenthos).

About 98 % of all marine species are benthic. The benthic domain is also stratified according to depth and zones may be distinguished according to the typical features of the ocean floor. Benthos may be distinguished into the infauna, animals living in the sediments, and the epifauna, consisting of animals living and moving on the sediments or hard substrates of the sea bottom.

Primary Production in the Sea

1. Autotrophic processes

In the open ocean there are algae and some bacteria which can synthesize high-energy organic compounds from low-energy inorganic compounds such as water and carbon dioxide. The source of energy for these organisms is either light or chemical energy derived from the oxidation of inorganic compounds. Such organisms are called autotrophic, since they do not require organic material as a source of energy.

Besides algae and bacteria, vascular plants may be important producers of organic material in coastal areas (sea grasses, mangroves).

The amount of organic material produced by these organisms is called primary production; primary production per unit time and unit volume (or surface) is called primary productivity.

1.1. Photosynthesis

The fundamental relationship governing the photosynthetic process can be summarized in the following equation:

$$CO_2 + 2\ H_2A \longrightarrow CH_2O + 2\ A + H_2O$$

Reduced compounds such as H_2O, H_2, H_2S, $H_2S_2O_3$ and some organic compounds may be used as the H-donor in H_2A, but only light is used as an energy source.

The photosynthetic process can further be described by three different steps: 1) capturing light energy and transferring the energy into chemical forms; 2) changing the chemical forms into another suitable chemical form for biochemical reactions (ATP and NADPH); 3) fixing CO_2 using ATP and NADPH produced in the former steps.

Photosynthetic algae require H_2O as the H-donor and the previous equation can be rewritten as:

$$CO_2 + 2\ H_2O \longrightarrow CH_2O + O_2 + H_2O$$

This process requires ca. 112 kcal per mole of carbohydrate formed. The energy is derived through the absorption of light by photosynthetic pigments, which absorb the light mainly in the visible region from 300 to

720 nm. Each photosynthetic pigment has a distinctive photon or quanta absorption characteristic depending on their molecular structure. Each group of organisms contain chlorophyll a and several accessory pigments in the thylakoid membranes in the chloroplasts in the cell. In bacteria, including the cyanobacteria or blue-green algae, there are no intracellular organelles and thylakoid membranes are suspended directly in the cell. The light-absorption spectra are different for each algal group depending on the pigment systems present.

Two separate photochemical reactions occur with chlorophyll a, based on light absorption at two wavelengths, 670 and 680 nm. The energy absorbed at the longer wavelength is used directly for photochemical reactions or emitted as fluorescence (at 730 nm). Energy absorbed at the shorter wavelength is transferred by the accessory pigments to chlorophyll a before being used or emitted as fluorescence (at 684 and 695 nm). The energy accepted by both types of chlorophyll a is used for photochemical reactions in two photosynthetic systems, I and II. These two systems are conjugated by a series of electron transfers, involving quinone and cytochrome. System I is mainly involved in electron transfers. The photosynthetical reaction catalysed by pigment system II liberates oxygen from water and transfers electrons to plastoquinone. The energy transferred for the two photochemical reactions is used for the reduction of NADP and the photophosphorylation of ADP. These reactions are carried out in the light and they are referred to as the light reaction.

The reducing power of NADPH and the energy of ATP promote the reduction of CO_2 and produce carbohydrate as well as synthesizing proteins and fats. These reactions are carried out in the dark and are referred to collectively as the dark reaction. The metabolic processes of the dark reaction are known as the Calvin-Benson cycle. In this cycle the first product of CO_2 assimilation is the three-carbon compound 3-phosphoglyceric acid. Recently another pathway has been found, the Hatch-Slack pathway, in which the first product of CO_2-assimilation is the four-carbon compound oxaloacetic acid. Plants with the Hatck-Slack pathway are called C4-plants, plants with the Calvin-Benson pathway C3-plants.

The basic photochemical reaction of photosynthesis is carried out by photons: four photons (quantum energy) are required to produce one mole of ATP and NADPH. Since the quantum energy E is a function of the wave length ($E = hv = hc/\lambda$ with $h = 6.63.10^{-34}$ J/sec, v = frequency and λ = wavelength) the shorter wavelength photon has more energy. The actual energy requirements° will be much greater in the reaction with the short

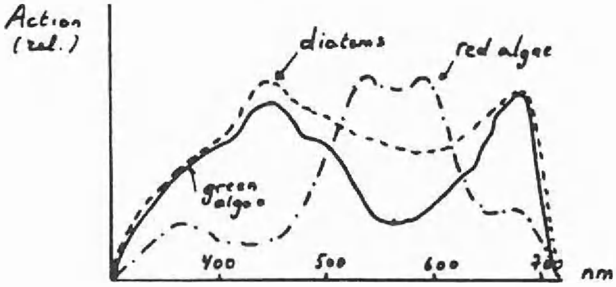
---

°) of a reaction requiring four photons

wavelength than with long wavelength light. The efficiency of quantum energy transfer from pigments to photosynthetic systems is not always the same. The transfer efficiency can be estimated from the quantum yield: the number of moles of CO_2 fixed by one photon of light absorbed by the pigments.

The actual light utilization spectra of algae can be obtained by combining the light absorption of intact cells with the quantum yield: one then obtains the action spectrum. The action spectrum is considered to show the photosynthetic light utilization efficiency of a cell and is one of the important characteristics of a species since it determines the ability of phytoplankton to adapt to different light regimes in the ocean.

Marine algal groups have been classified into three pigment types: 1) chlorophyll a and b type for green and euglenoid algae; 2) chlorophyll a, c and carotenoid type for diatoms, dinoflagellates and brown algae and 3) chlorophyll a and phycobilin type for red algae and cyanobacteria. The relative action spectra of the three types are shown below:



- The chlorophyll a,b type shows active photosynthesis around 435 and 765 nm.
- The chlorophyll a,c and carotenoid type has a similar action spectrum but the minimum occurs around 580 nm instead of 550 nm. The chlorophyll a, phycobilin type has a rather low photosynthetic rate in blue and red light and three distinctive peaks between 500 and 560 nm due to the phycobilins.

The final product of photosynthesis is carbohydrate. This means that the photosynthetic quotient expressed as the ratio of evolved O_2 to absorbed CO_2 is close to unity (for proteins it is 1.25 and for lipids 1.43). Photosynthetic products are partly consumed by basic respiration in the mitochondria. Respiration takes place both in the light and in the dark but can only be detected in the dark. Measurement of phytoplankton respiration in the open ocean is practically impossible. An average figure for respiration will be around 10 % of maximum photosynthesis P_{max}. When flagellates are abundant, somewhat higher figures have been found in cultures, between 35 and 60 % of P_{max}.

Respiration increases in light due to additional basic respiration in the mitochondria and to photorespiration, which is the light-dependent O_2-uptake that occurs in photosynthetic cells. Oxygen competes with CO_2 to combine with ribulose biphosphate. When this succeeds, the ribulose biphosphate splits to form one molecule of phosphoglyceric acid and one of a two carbon compound, phosphoglycollic acid (glycollate). Glycollate can be broken down to form CO_2 again, and some glycollate produced is lost from cells by exudation. In most cases glycollate is the major photosynthetic product exudated by marine algae and it is also the major source of protein synthesis. High O_2 concentrations and temperature, pH and light intensity favour increased photorespiration.

1.2. The light environment in the oceans

The quantity and quality of light in the sea fluctuates, sometimes greatly, depending on time, space, weather conditions, angular distribution. The visible light, between 300 and 760 nm wavelength, is the most important fraction for many biological aspects of the sunlight reaching the earth. The energy required by algae is restricted between 300 and 720 nm. The total radiation at this wavelength is called photosynthetically available radiation (PAR).

The quantitative assessment of light is done by intensity measurements in three different ways: 1) illumination, 2) energy and 3) quanta. Illumination is the indicator of brightness which only includes the visible portion of the energy spectrum and is defined as flux per unit area. The basic unit is the candle, which is the intensity of a standard light detected by a standard observer who has a distinctive sensitivity for different wavelength luminosity factors; highest sensitivity is at 555 nm and becomes less sensitive towards the longer and shorter wavelengths, over the total spectrum. The luminous flux per unit area is defined for illumination as 1 international candle on 1 m^2 is 1 lux. The illumination measure is a convenient measure for biological problems in the sea, but one should remember that precise comparison of illumination units is only valid for the same type of light source used.

Energy units for light-intensity measurements apply for the whole energy spectrum, including UV and IR, and are expressed by units such as watts.sec or Joule (1 J = 4.185 cal = 4.185 watt.sec). The energy flux with dimensions of units time and area is most useful for biological purposes (cal/cm^2= langley). The measurement of light is entirely dependent on the quality (spectral differences). When an energy unit is used for biological events, the light source should always be specified as well as environmental conditions, such as the thickness of the water. Only a rough conversion from an illumination unit to an energy unit can be made: 1 lux is approximately 6.10^{-6} ly/min for the sunlight at the sea surface, approximately 86.10^{-6} ly/min for a tungsten lamp and approximately 5.10^{-6} ly/min for a white fluorescent lamp.

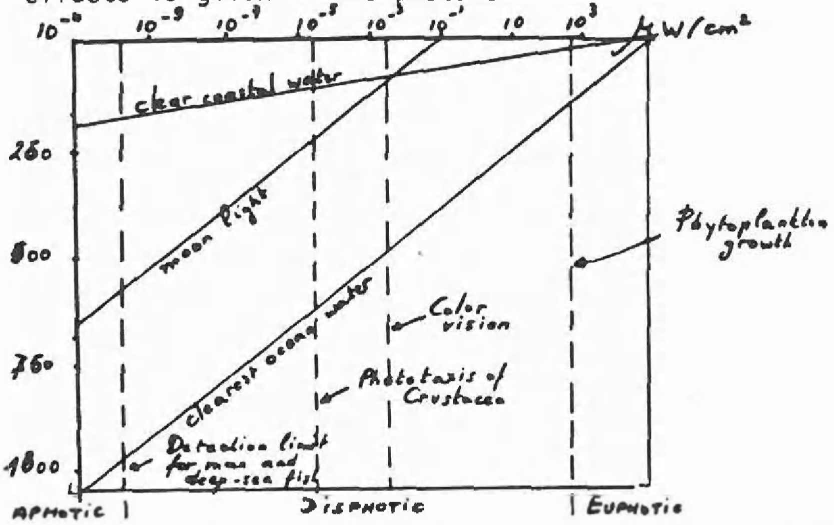
The measurement of light in quanta measures the number of photons of a particular energy which is related to the wavelength: 1 cal = $2.11.10^{15}.\mathring{A}$ quanta = 3.50×10^{-9} Å einsteins with Å the wavelength in 10^{-10} m. In the range of visible light, between 4000 and 7500 Å, the average energy of each photon at the average wavelength of visible light, 5500 Å, is 1 einstein = $(2.86 \times 10^{8})/5500 = 52.10^{3}$ cal.

Changes of the incoming light in the atmosphere have already been described (see radiation). Some solar energy is lost by true reflection and by scattering from particles (including foam) at the sea surface. The actual value for surface varies considerably with conditions of sea surface and sun angle: on a fine day in the summer, with a sun angle of 30 °, the surface loss would be only a few percent under conditions of complete calm. This value increases to 5-17 % with light winds and to over 30 % for moderate to strong winds. As the sun angle decreases to 10 %, reflection increases rapidly to 30 % and more. A mean value of 15 % for total surface losses may be used.

Light penetrating the water is reduced by selective absorption and scattering due to the seawater itself and dissolved and suspended matter in the water. The reduction of light in the water column can be expressed in terms of the vertical extinction coefficient k (also called attenuation coefficient) given by $I_d = I_o e^{-kd}$ with I_o the incoming light intensity and I_d the light intensity at depth d. The value of k varies with the wavelength being large for ultraviolet and infrared light (0.033 m^{-1} at 425 nm, 0.018 m^{-1} at 475 nm and 0.288 m^{-1} at 650 nm for pure water). In clear oceanic water blue-green light (maximum around 480 nm) can only penetrate to any appreciable depth. However, under turbid conditions due to particulate material, blue light is selectively scattered and the spectral peak of transmitted light is moved towards the red (maximum at ca. 550 nm).

The extinction coefficient in the water column can be defined as $k = k_w + k_p + k_s$ where the k's are possible diffusion and scattering due to suspended particles, water and dissolved matter. For biological purposes the average extinction coefficient k' in the wavelength of PAR is probably the most practical.

A summary of the conditions of ligth in the sea and its critical limiting effects is given in the picture:



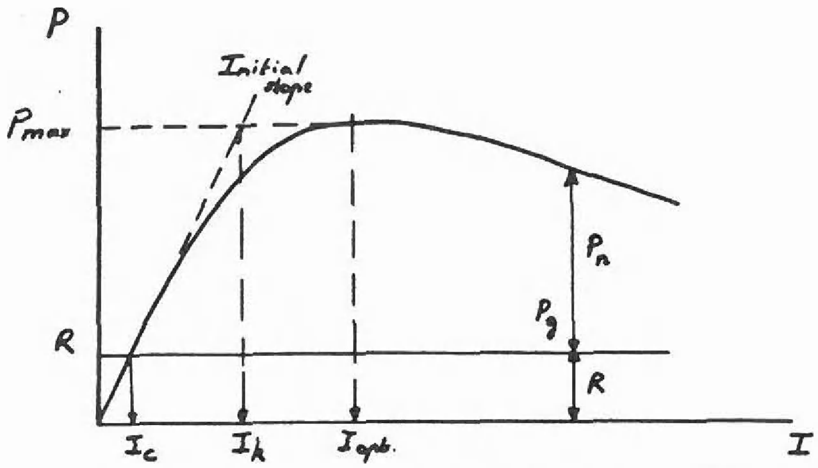
Terms used in deep bodies of water for zones based on the light factor are: the euphotic zone, where sufficient light for photosynthesis occurs; the disphotic zone, with insufficient light for photosynthesis but sufficient light for animal responses and the aphotic zone with no light of biological significance from the surface. The actual depth limits of these zones vary widely according to transparency.

Measurement of solar radiation at the sea surface is done with different instruments (pyranometers, photometers). Instruments to determine underwater radiation also exist. A very early but still widely used method is the Secchi disk reading, which is related to extinction as $k' = 1.7/D_s$, with D_s the depth at which the Secchi disk becomes invisible.

1.3. The effects of light on photosynthesis

Light intensity strongly affects the rate of photosynthesis (usually expressed as mg C/mg Chl a/h). Methods for measurement either involve measurement of the carbon dioxide taken up or the oxygen produced per unit time. The ^{14}C-method is usually used for the measurement of CO_2 uptake but some doubts exist as to its interpretation. If the loss of dissolved organic carbon is small, the ^{14}C-method will approach net photosynthesis. Production estimates based on O_2 production can be made with an oxygen electrode or the Winkler titration technique.

The photosynthesis versus light-intensity curve is usually of the following form:



Photosynthesis increases with increasing light intensity up to some asymptotic value P_{max} where the system becomes light saturated. The two most important properties are the slope ($\Delta P/\Delta I$) and P_{max} (also called the assimilation number). The initial slope is a function of the light reaction and not usually affected by other factors. It has been defined as the quantum yield: the number of moles of oxygen evolved (or carbon incorporated) per unit light intensity (in einsteins). The maximum value for the quantum yield is about 0.125 mole oxygen per einstein absorbed. The minimum quantum requirement in order to produce 1 mole of oxygen is 8 einsteins. Considering 112 kcal per mole of organic carbon and 570 kcal of 8 einsteins at 400 nm, the efficiency of photosynthesis is about 20 %.

The quantum yield in nature will be usually lower because accessory pigments sensitize photosynthesis less efficiently than chlorophyll and because the quantum yield depends on the physiological and growth stage of the plant. A yield of 0.06 mole CO_2 per einstein has been suggested for natural healthy populations.

P_{max} is a function of the dark reaction provided no environmental factors are causing photosynthetic inhibition. If other environmental factors are operative P_{max} becomes a function of the inhibitor. As a combination of the initial slope and P_{max} we can use I_k, the light intensity of an extension form the initial slope and P_{max}.

The figure above also shows the difference between total or gross photosynthesis P_g and net photosynthesis P_n, equal to P_g minus respiration. An approximate P_n can be estimated directly by the oxygen method because oxygen is consumed by respiration at the same time as it is produced through photosynthesis. When $P_g = R$, $P_n = 0$ and the system is at the compensation point, with light intensity equal to the compensation light intensity I_c. The compensation point is best determined on a 24 h basis and is in the range of 0.002 to 0.009 ly/min over 24h.

In field work the compensation depth can be approximated from the depth of 1 % of surface radiation, which can itself be approximated as three times the depth of Secchi disc visibility. Compensation depths may vary from a few meters in turbid coastal waters to over 150m in tropical areas.

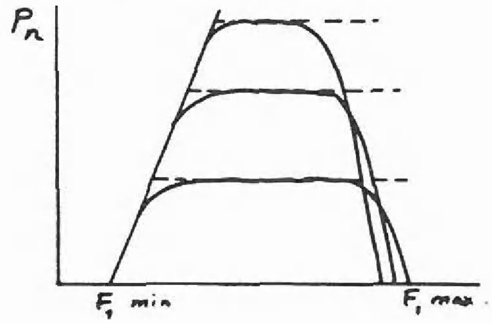
Algal respiration can be expressed as $R = rP_{max}$ where r is a proportionality factor called the loss factor, which is around 0.1 for phytoplankton.

If light intensity increases above the point where saturation occurs, the P-I curve may show a depression in photosynthetic rate. This phenomenon is called light inhibition or photoinhibition.

Values of the initial slope vary between 0.33 and 2.2 mgC/mg Chl a/ly in cultures and between 0.14 and 2.2 (average 1.1) mg C/mg Chl a/ly in natural populations. Some species are adapted to high and other to low intensities. Values of P_{max} range from between 1.1 to 6.2 mgC/mg Chl a/h for cultures and 0.1 to 6.0 mgC/mgChla/h in natural populations.

1.4. Nutrient and temperature effects

According to Liebig's law of the minimum, the rate of photosynthesis is determined by a single limiting factor, the one of which supply is minimal. The principle is shown in the figure below:



Algae require C,H,O,N,Si,P,Mg,K and Ca in large amounts (macro-nutrients) and Fe, Mn, Cu, Zn, B, Na, Mo, Cl, V and Co in small amounts (micro-nutrients). Nitrogen and phosphorus may often limit plant growth during the summer or throughout the year in tropical and subtropical waters. The uptake of carbon, nitrogen and phosphorus by marine phytoplankton is generally found to be in the ratio 106:16:1, the Redfield number.

In the oceans, nitrogen exists mainly as molecular nitrogen and as inorganic salts nitrate, nitrite and ammonia, and some organic nitrogen in amino acids and urea. The usual range of concentration of these compounds is 0.01-50 µgat/l for nitrate, 0.01-5 µgat/l for nitrite and 0.1 -5 µgat/l for ammonia, 0.2-2 µgat N/l for amino acids and 0.1-5.0 µgat N/l for urea. Saturation concentrations of dissolved nitrogen gas are in the range of 370-800 μgat/l, depending upon salinity. Molecular nitrogen is fixed by cyanobacteria, especially Trichodesmium spp. in tropical waters, and by bacteria, but most algae have no ability to fix it and must utilize inorganic nitrogen salts and organic forms. Algae generally prefer ammonia over nitrate or urea.

The processes involved in the uptake of nitrate by phytoplankton involve two steps. The active uptake of NO_3^- from the water and the translocation across the cell membrane is done by a first enzyme system. Within the cell, nitrate is reduced to nitrite by nitrate reductase and to ammonium by nitrite reductase. Ammonium is incorporated into the amino acid pool via glutamate synthetase from glutamate.

Phosphorus occurs in sea water in three principal phases: dissolved inorganic phosphorus, dissolved organic phosphorus and particulate phosphorus. Phytoplankton normally satisfy their requirement by direct assimilation of dissolved inorganic phosphorus (orthophosphate ion) and sometimes by using dissolved organic phosphorus. Some coastal algae may use polyphosphates in presence of excess nitrate. Phosphorus absorbed into a cell becomes part of the structural component of a cell (e.g. in poly-P-RNA) and is in part continually turned over in the energetic processes of organisms e.g. as ATP.

Diatoms and dinoflagellates take up a great amount of dissolved silicon and deposit it as hydrated silica to form their valves. The concentrations of dissolved silicon are generally high in coastal and deep pelagic waters and low in surface waters away from estuaries.

Nutrient uptake can generally be described by Michaelis-Menten kinetics as:

$$v = \frac{V_m S}{K_s + S}$$

in which v is the rate of nutrient uptake, V_m is the maximum rate of nutrient uptake, K_s is the substrate concentration at which $v = V_m/2$ and S is the nutrient concentration. By plotting S/v versus S a straight line is obtained with an intercept on the abcissa equal to $-K_s$. The constant K_s reflects the ability of a species to take up low concentrations of a nutrient. K_s-values are temperature dependent. Since K_s is also strongly dependent on V_m, the ratio of V_m/K_s is used as an indicator of uptake efficiency.

In the case of silicon the Si uptake does not start from zero concentrations and the equation has to be modified to:

$$v = \frac{V_m (S - S_0)}{K_S + (S - S_0)}$$

Under conditions of no nutrient stress, nutrient uptake rate shows a hyperbolic relation with light intensity, similar to the response commonly observed in photosynthesis/light relations. Nutrient/light relations can also be described by Michaelis-Menten kinetics but quite often there is a positive value for nutrient uptake even at zero light intensity because some nutrients are taken up in the dark, and nutrient uptake may be depressed at bright light intensities.

Nutrient uptake can take place without cell division but there are indications that the half-saturation constants for nitrate uptake and for growth are very similar. Growth can then be written as:

$$\mu = \mu_{max} \frac{S}{K_s + S}$$

1.5. Chemosynthesis

Some micro-organisms can satisfy their primary energy requirements by utilizing simple inorganic compounds, such as ammonia, nitrite or methane, or elements such as ferrous iron, hydrogen gas or even water-insoluble amorphous sulfur. Since this process, chemosynthesis, usually involves carbon dioxide fixation and the primary formation of new particulate material, it may be considered as a special form of primary production.

In general terms the chemosynthetic process can be expressed in three stages: 1) as the result of dehydrogenation, high reducing power is produced as follows:

$$AH_2 + H_2O \xrightarrow{\text{dehydrogenase}} AO + \underset{\text{reducing power}}{4(H^+ + e^-)}$$

2) a proportion of the reducing power is utilized for energy production (ATP) by being transferred through the cytochrome system to molecular oxygen. A second part of the reducing power is transferred to NAD to reduce it to $NADH_2$.

$$4(H^+ + e^-) + ADP + P + O_2 \longrightarrow 2H_2O + ATP$$

$$2(H^+ + e^-) + NAD \longrightarrow NADH_2$$

3) the ATP and $NADH_2$ are then used for the assimilation of carbon dioxide:

$$12\ NADH_2 + 18\ ATP + 6\ CO_2 \longrightarrow C_6H_{12}O_6 + 6\ H_2O + 18\ ADP + 18\ P + 12\ NAD.$$

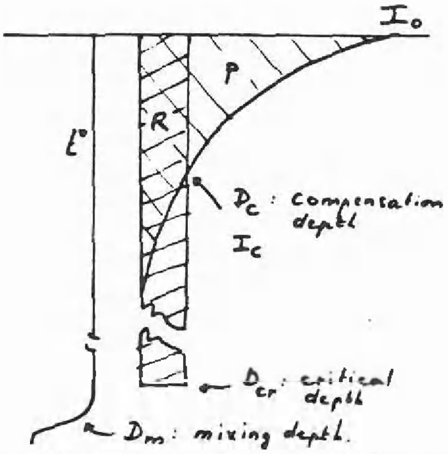
The different inorganic substances used by chemosynthetic bacteria are the sole source of energy and of reducing power.

Depending on the different inorganic substrates chemosynthetic bacteria are classified into several groups such as nitrifying, sulfur, hydrogen, methane, iron and carbon monoxide bacteria. Most require free oxygen as the electron acceptor but facultative or obligate anaerobes can use bound oxygen derived from sulfate or nitrate. Among the inorganic substrates available, nitrogen and sulfur compounds are relatively abundant and widely distributed in the pelagic environment. Reduced sulfur compounds are present at levels from 0 to 100 µgat/l (thiosulphate and polythionates). Sulphides are usually not detectable in the open ocean but abundant in sediments.

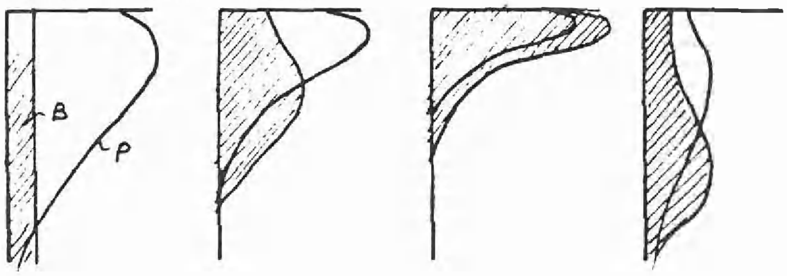
Reduced inorganic substances are mainly produced through anaerobic metabolic processes. Anaerobic environments, such as sediments, fjords and estuaries, create favourable habitats for chemosynthetical bacteria. Chemosynthetic activity in the open ocean can be estimated from carbon dioxide uptake in the dark.

2. Primary production and depth

Since light is rapidly attenuated in the sea, production over the world ocean is due mostly to the phytoplankton populations inhabiting the surface and near-surface layer. Phytoplankton cells are mixed above and below the compensation depth (where production is equal to respiration), and experience an average light intensity. The depth at which the average light intensity for the water column equals the compensation light intensity is called the critical depth, i.e. the depth at which photosynthesis for the water column equals respiration for the water column.



If the critical depth is less than the depth of mixing, no net production can take place. Phytoplankton growth in a stratified water column is shown diagrammatically below:



Just after mixing, phytoplankton is distributed homogeneously in the water column, but the photosynthesis per unit biomass is different at each depth, with a subsurface maximum. As the biomass increases the extinction coefficient will increase and self-shading will occur. The compensation depth and the growth maximum will become shallower and a bloom at the surface will occur. Then as nutrient become exhausted the depth of the maxima in phytoplankton biomass will deepen.

In very shallow areas sufficient light for photosynthesis may reach the bottom and also plants in intertidal areas may contribute to production. On muddy shores the salt marsh type of environment may add significantly to marine production and in tropical regions the mangrove swamps are very extensive and highly productive.

The more seaward areas of mud flats have flowering plants restricted to a few genera which live completely submerged in shallow waters. These include Zostera, Ruppia, Posidonia, Cymodocea and Thalassia . Though tidal flats and shallow water appear to be dominated by eel and turtle grasses, certain algal species may be present in considerable abundance. Green algae and cyanobacteria are often abundant. Other major contributors to production in shallow water areas are microbenthic algae, mostly diatoms.

Coastal shallow areas characterized by a hard substratum may have an extensive flora of macroscopic seaweeds, which reach their maximum abundance in temperate and boreal regions of the world. They can also be plentiful in association with coral reefs, especially the calcareous red algae. Many species of red and green algae may be found, but the most obvious are brown algae. The vast majority of seaweeds are fixed to a substratum, but Sargassum may be found floating free in the North Atlantic.

Benthic seaweeds, submerged sea grasses and benthic micro-algae contribute to the enormous productivity of shallow coastal waters but the overwhelmingly important agent of primary production on the global scale is the phytoplankton. Different plant groups occur in the phytoplankton. Coccolithophorids or calcareous flagellates derive their name from the minute calcareous plates (coccoliths) that form around them and which vary in size from 1 to 35 µm. They are known from Jurassic times onwards and are the main constituent of chalk deposits of the Cretaceous. Even smaller than the calcareous flagellates, which range between 5 to 25 µm, are the micro-flagellates which belong to several classes of algae. They have one or more flagellae and many species contain green or yellow-brown pigments. They may be only 1-2 µm large.

Dinoflagellates are considerably larger: most species fall in the range 10 to 1000 µm. There are two main groups, armoured and unarmoured. Armoured species form a transparent wall of cellulose that soon divides into platelets pierced by minute holes. The cell wall of unarmoured species is thin and undivided. There are two flagella and in many species one of them is housed in a groove around the cell: the other one is attached so that it trails backward. The grooved flagellum rotates the cell, while the other drives it forward. Plant-like dinoflagellates contain yellow, brown or greenish photosynthetic bodies. Forms of photosynthetic species (zooxanthellae) are symbiotic in diverse invertebrates and in the open ocean occur in various radiolarians. There are also heterotrophic forms.

Many dinoflagellates are luminescent. The light is produced in cellular organelles called scintillons.

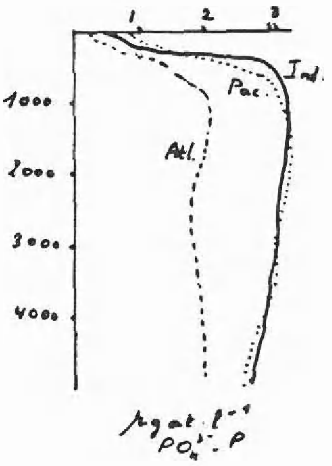
Diatoms are known since Triassic times. They are transparent but have rather thick cell walls of hydrated amorphous silica. Just inside the cell wall is a thin layer of cytoplasm that holds the greenish or brownish photosynthetic bodies. The cell wall is formed in two halves part of one fitting closely inside a corresponding part of the other. When the cell divides in two, each new cell is enclosed in one half of the old cell wall and a new cell wall is formed inside the old half. As one vegetative division follwos another, diatoms gradually decrease in size. This decrease stops at a fixed cell size when the vegetative cells form male and female cell in the auxospore stage. During unfavourable times diatoms form resting cells which settle on the bottom in shallow water. There are two main groups of diatoms. The Pennales are bilaterally symmetrical, the Centrales are radially symmetrical.

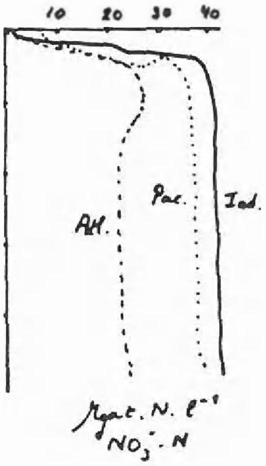
Besides the eukaryotic algae presented above, the Cyanobacteria or blue-green algae are often important members of the phytoplankton. The well-known tropical species Trichodesmium erythraeum often gives blooms which give the sea a rusty appearance (it gave the Red Sea its name).

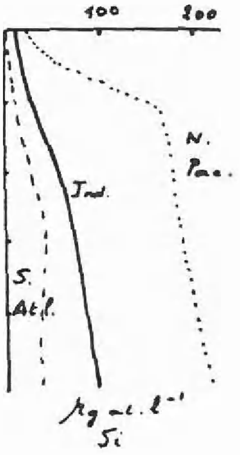
3. Nutrient cycles

The primary nutrients phosphorus, nitrogen and, for some organisms, silicon are present in inorganic form in sea water mostly as phosphate, nitrate and silicate ions respectively. The major exogenous source of phosphorus and silicon is land drainage. Nitrogen is also introduced into the sea by land runoff, but the larger proportion comes from the atmosphere and is a result of the evaporation of ammonia from the land surface and in situ fixation. Nutrients are removed by the phytoplankton from the euphotic zone, resulting in a thin nutrient-depleted layer at the surface over large regions of the world ocean. The surface nutrient content is replenished by mixing from the nutrient-bearing deeper layers and local regeneration processes.

Representative vertical distributions of phosphate, nitrate and silicate are given below:







Considerable variation occurs between oceans, although nitrate and phosphate tend to vary together; silicate is the most variable, depending heavily on river input. The nutrient budget is as follows: (in million tons)

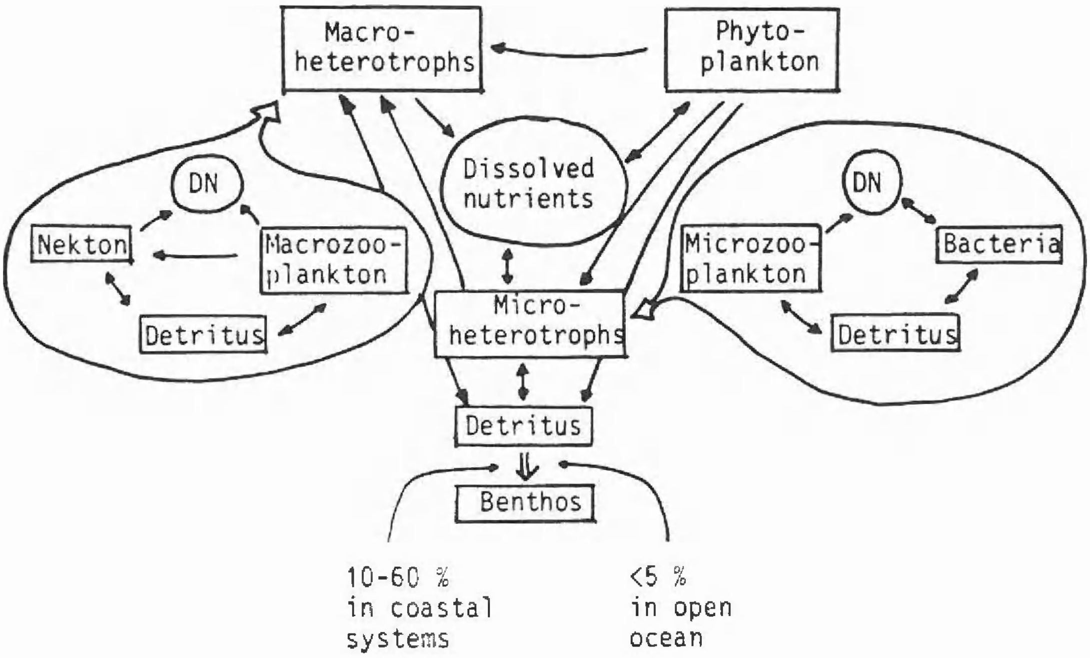
	Nitrogen	Phosphorus	Silicon
Reserve in ocean	920,000	120,000	4,000,000
Annual use by phytoplankton	9,600	1,300	
Annual contribution by rivers	19	14	4,300
Dissolved	19	2	150
Suspended	0	12	4,150
Annual contribution by rain	59	0	0
Annual loss to sediments	9	13	3,800

The amount of carbon in plankton tends to be in constant proportion to nitrogen and phosphorus and is approximately C:N:P = 106:16:1 (Redfield ratio). The concept of a constant proportionality of uptake between carbon, nitrogen and phosphorus can be used to study the cycles of nutrients in the sea.

2. Nutrient regeneration

Estimates of global nutrient cycles show that external nutrient input in the oceans can account for less than 1 % of the annual requirements of phytoplankton only. Almost all required nutrients come from internal recycling, which can be in situ regeneration and allochthonous inputs from deep ocean reserves by upwelling and eddy diffusion. It is estimated that about 80 % of requirements come from internal regeneration.

The principal components in nutrient regeneration are drawn in the following picture:



2.1. Decomposition

Organic decomposition is primarily a biological process. Particulate organic matter decomposition after death of an organism typically proceeds in three stages. The first is characterized by cellular lvsis (autolysis) brought about by action of endogenous enzymes. Twenty to fifty percent of the initial particulate biomass as carbon and nitrogen may go into solution during this stage and as much as 75 % of cellular phosphorus. The second stage is characterized by microbial colonization of the remaining particulate matter. During this phase decomposition proceeds as an apparent first-order reaction:

$$\frac{-dS}{dt} = k\ S$$

with k the decomposition rate and S the substrate concentration. Microbial decomposition is further subdivided into two additional stages: a fast phase where labile compounds are mineralized and a second slower phase where more resistant compounds are broken down. Initial fast-phase constants for plankton and detritus may be on the order of 5-10 % per day, rate constants for the more resistant compounds are an order of magnitude smaller. A significant portion of the organic matter appears to be refractory.

Mineralization of dissolved organic matter also proceeds as a first-order reaction, with constants dependent on temperature and the source of organic matter. There is a relatively consistent pattern in nutrient rations during organic mineralization, with initial low N:P ratios associated with the selective phosphorus release during autolysis. Following this, the ratios stabilize at 16:1.

2.2 The distribution of organic matter

P.O.M.: In near-surface waters, POM concentrations decrease by an order of magnitude or more between productive inshore (upwelling) waters and the oligotrophic open ocean. This gradient is primarily a consequence of differences in productivity. Strong vertical gradients also exist in the upper 200-400 m , but below this depth the concentrations are relatively invarient. This implies that all or nearly all of the POM produced in the surface waters is recycled in the upper 400 m. RILEY proposed that 75-80 % of the POM produced at the sea surface is consumed in the upper and mid-oceanic depths, about 20 % is consumed within the meso- and bathypelagic zones and only 5 % at most reaches the deep-sea benthos. More recent studies showed that over 90 % of the surface production is recycled in the first 400 m and the highest recycling efficiences are found in the least productive waters. These studies also indicate that most of the transport of POM to the deep ocean is through fast-sinking, large particles, predominantly zooplankton fecal pellets. Only in shallow water is benthic regeneration important. Within coastal and oceanic water columns, grazing by herbivorous zooplankton is considered the most important mechanism for nutrient recycling, but direct microbial degradation may also be important.

D.O.M.: Dissolved organic matter also generally decreases offshore and with depth although concentration gradients are slight compared with POM. Typically, concentrations are 30-50 % higher in near-surface waters than in the deep ocean. Concentrations decrease to about 300 m depth, beyond which no measurable change occurs. The bulk of the dissolved constituents are refractory, particularly in the deep ocean, and the concentrations are about 20 times higher than those of DOM. A small component of DOM (simple sugars, amino acids etc.) is biologically very reactive and there is a rapid turnover (more than 100 % per day in inshore surface waters to 1-10 % per day in the open ocean).

2.3 The sources of regenerated nutrients

Benthos: nutrients released through benthic community metabolism are an important source for primary production in coastal waters, to a depth of about 200 m. Sediment nutrient fluxes are a function of abundance and metabolic activity of benthic organisms, organic loading and turbulence associated with the sediment-water interface.

Macroheterotrophs: a significant fraction of the organic material ingested by macrozooplankton will be mineralized through respiration and excretion. Both nitrogen and phosphorus are excreted in molar ratios of 10:1, lower than phytoplankton requirements (16:1). 75 % of the nitrogen is ammonia, 50 % of the phosphorus is orthophosphate. The excretion rates depend on food availability and decrease rapidly when feeding stops, and on temperature (Q_{10} 1.5). In inshore waters zooplankton excretions only contributes for a small fraction of requirements; in oligotrophic open ocean waters, macrozooplankton excretion may account for 40-60 % of the N-requirements of phytoplankton and over 100 % of the P-requirements, but some estimates are much lower.

Microheterotrophs: tintinnids, radiolarians, nauplii, rotifers, bacteria etc. may be responsable for the bulk of planktonic respiration, grazing and nutrient regeneration. Their excretion rate is much higher than in macrozooplankton. As an example, a ciliate may excrete its body equivalence of phosphorus in less than an hour. In oligotrophic waters 30-75 % of the planktonic nitrogen excretion may be due to microzooplankton. The role of bacteria is still not well known. They may compete with phytoplankton for phosphorus: they convert DOM into bacterial biomass that is then taken up by protozoans.

Algal excretion: phytoplankton excrete about 10-20 % of their production as DOM. Carbohydrates are the largest fraction, but as much as 10 % of the assimilated inorganic N may be excreted as DON. Also significant excretion of DOP occurs.

Bacterial production in the ocean

1. Bacterial production and biomass

Early attempts to determined the abundance of bacteria in the sea used culture techniques and appear to have given numbers low by two or three orders of magnitude. Direct staining techniques using fluorescence stains such as acridine orange have been adopted as standards. In coastal waters bacterial biomass is in the range of 5-10 μg C.l^{-1}, in oligotrophic ocean waters this falls to 1-3 μg C.l^{-1}. The number of bacterial cells corresponding to this biomass is between 0.5 and 5.10^{9} cells.l^{-1} in coastal and shelf waters, between 0.02 and 1.10^{9} cells.l^{-1} in open ocean water. Only between 10 and 50 % of these cells appear to be active. Rates of production in open ocean and shelf water appear to fall between 1 and 50 μg C.l^{-1}.d^{-1}.

2. Bacteria in the ocean ecosystem

The biomass of single celled heterotrophic organisms is comparable to that of the metazoa. Their contribution to overall metabolism must be substantial, unless most cells would be dormant. Over half of the plankton respiration may be due to organisms of bacterial to microflagellate size.

Only a small part of bacterial production passes onto the metazoa. The principal aspect of marine microbial metabolism is mineralization, at least in the pelagic food chain.

Plankton feeding and production

Among the zooplankton, methods of feeding may be broadly defined into filter feeding and raptorial feeding. We will briefly review the different taxonomic groups important in the zooplankton and their mode of feeding.

Among the planktonic Protozoa the feeding of foraminifera and radiolaria is generally accomplished through the extrusion of pseudopodia. The size of particles captured efficiently varies from 1 to < 20 µm diameter. Microflagellates are important as heterotrophic feeders of bacteria. Ctenophores become very abundant in many temperate waters in summer. They are entirely carnivorous and feed largely on small crustaceans (Tentaculata) or other ctenophores (Nuda). They may consume up to ten times their body weight per day and double population numbers every day. Chaetognaths become abundant at the same time as the ctenophores. They are succesful predators on copepods at densities below those required by ctenophores, but also feed on larval fish. Urochordates or tunicates consist of three classes of which two are pelagic; the Thaliaceans or salps, most abundant in sub-tropical and tropical seas, and the Larvaceans. Both are extremely abundant in some tropical areas and are fine filter feeders that consume phytoplankton and bacteria. Theygive rise to accumulations of flocculant fecal material and detritus. Among the coelenterates, two classes, the Hydrozoa and the Scyphozoa, are important in the plankton. Nearly all feed as carnivores using nematocysts on their tentacles to paralyze their prey. Some species may reach 1 m and more in diameter and have tentacles of 10 m length, and these animals can capture small fish and nekton. The mollusca consist of several classes of which the cephalopods are important among the nekton and the Prosobranchia and Opisthobranchia have important species in the plankton. The prosobranchs include the pelagic heteropods which are exclusively carnivorous, locating prey by sight and capturing it with the large grasping teeth of the radula located at the tip of a proboscis. Among the opisthobranch molluscs, two orders are often abundant among the plankton. The thecosomatous or shelled pteropods feed primarily on phytoplankton. Food particles are collected on mucus produced in the mantle cavity or on the foot. The specialized pseudothecosomes capture small particles in very large (up to 2 m diameter) external mucus webs produced by special glands on the wings. Most gymnosomatous pteropods feed on thecosomes.

By far the largest group of suspension feeders in the zooplankton are the Crustacea. The major groups are planktonic crustaceans are the calanoid copepods, the amphipods and euphausiids. In some areas ostracods and cladocerans may be abundant while in coastal regions mysids, isopods, cumaceans and harpacticoid copepods also occur in great numbers.

Crustacean appendages are adapted either for filtering or raptorial feeding or a combination of both. Recent studies seem to show however that real filtering does not occur, at least not in copepods, because of the viscous forces at work: the setae of the appendages appear as rakes but work as paddles.

1.1 Rate of filtering

In microcrustaceans the rate of filtering is broadly related to body size and also depends on food concentration and temperature. It can be measured over a given time period t as the decrease in phytoplankton cell concentration at the beginning and the end of the experiment:

$$F = \frac{v(\log C_o - \log C_t)\ 2.303}{t}$$

with v the volume of water per animal. F is however only constant for small values of C_o-C_t.

1.2 Prey selection

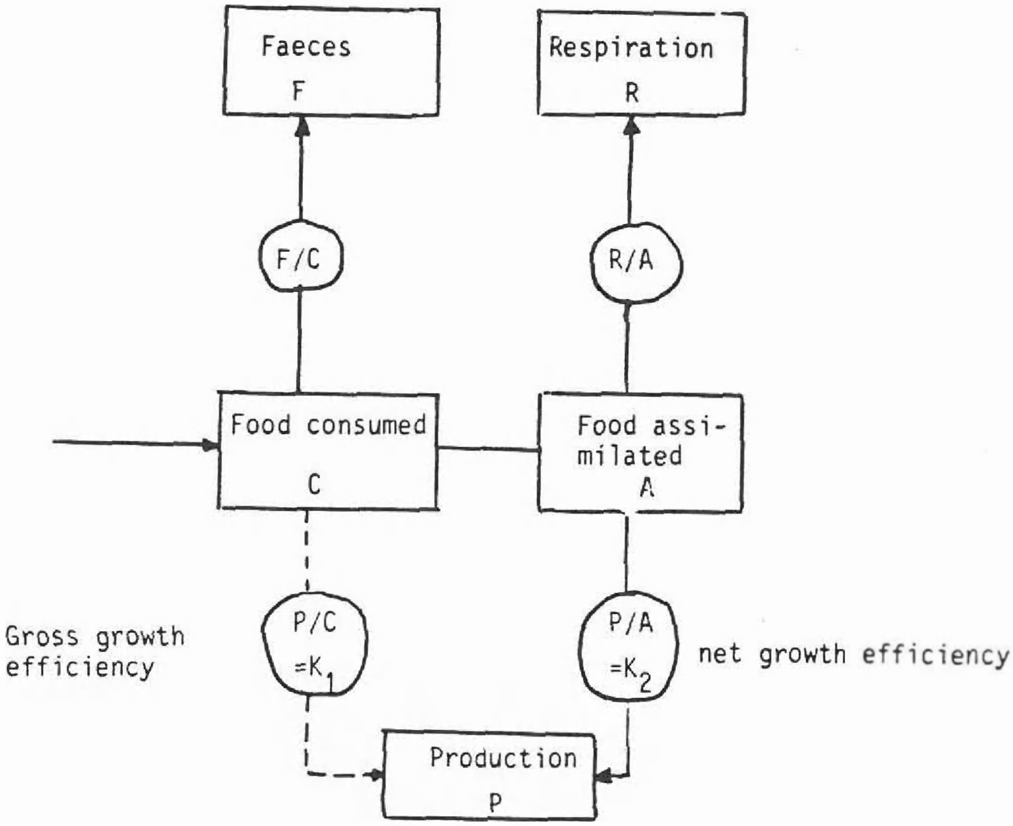
The size of the prey item is probably the single most important factor governing prey selection among various organisms in the marine zooplankton. This is true for herbivorous and for carnivorous feeding. Additional factors are numerous: e.g. for some carnivores prey must be alive and moving; bioluminescence has been reported to discourage copepods feeding on dinoflagellates. The role of chemosensory mechanisms in deciding the prey of some predators has become recognized among zooplankton as well as in nekton, e.g. copepod activity is sensitive to dicarboxylic amino acids.

2. The energy budget

The energy present in the ration consumed is distributed into the various life requirements of the animal. The food requirement for a zooplankter can be expressed as the sum of the major requirements for growth, metabolism and feces:

$$C = P + R + \underbrace{U + F}_{E}$$

The consumption can be used for different physiological requirements or being egested as feces in the following ways:



It is of course impracticable to measure all components of the carbon-budget equation in routine estimations of production. One usually determines coefficients for growth efficiency which can be applied either to ingestion (gross growth efficiency) or to assimilation (net growth efficiency) to estimate production as $P = K_1C$ or $P = K_2A$. Estimates are based mainly on consumption (or ingestion) C, assimilation efficiency A/C and growth efficiency K_1 or K_2.

2.1. Food intake

Food intake is a function of the filtration rate or predation rate and the food concentration in the water. The grazing rate per unit biomass may be constant for certain concentrations of food. However, there normally is a lower threshold below which herbivores do not feed and an upper limit beyond which their feeding is constant. IVLEV found that in fish the quantity of food eaten increases with the quantity of food offered up to some maximum ration C_{max}. The relation between the actual consumption C and the concentration of prey p must be proportional to the difference between the actual and maximum consumption such that:

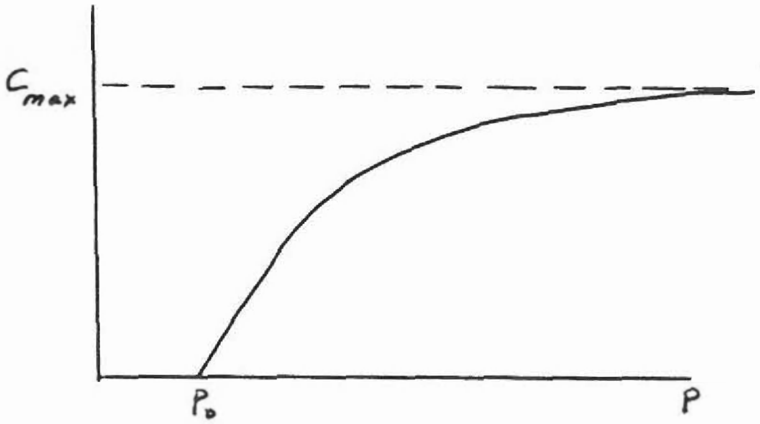
$$\frac{dC}{dt} = k(C_{max}-C)$$

Integration gives:

$$C = C_{max}(1 - e^{-kp})$$

This can be further modified by considering that feeding only starts at a minimum concentration of food p_o :

$$C = C_{max}(1 - e^{-k(p_o-p)})$$



Threshold values for p_o have been reported to range between 40 to 130 µg C/l; maximum ration for herbivorous copepods is above 300 µg C/l and for euphausiids above 1 mg C/l. The amount of food ingested ranges from a few to nearly 100 % of body weight per day, with lower average values of 10-20 % for the larger crustacean zooplankton and 40-60 % for the smaller crustaceans.

There is also evidence that plankton herbivores can adapt their grazing rate to the type of food available.

The food intake of crustacea appears to be a function of body weigth, the relationship being of the form $C = aW^b$.

2.2 Assimilation efficiency

The assimilation efficiency A/C may be estimated from the ratio of total weight to ash-free dry weight in food and faeces when we assume that only the organic fraction of the food is assimilated:

$$A = \frac{(J-L)}{(A-L)J} \times 100$$

in which J is the ratio of ash-free dry weight to dry weight in the ingested food and L this ratio in the feces. The assimilation efficiency is largely independent of temperature, the amount of food offered of consumed and may be given as:

$$A = 87.8 - 0.73\ X$$

an empirical relationship found by CONOVER in which X is the percentage ash per unit dry weight of food.

Although this method is useful to determine organic carbon assimilation it appears that the assimilation efficiency of elements such as nitrogen and phosphorus can not be determined with this method.

Herbivorous zooplankton assimilates food with an efficiency of 60-95 %. At high food intake this may decrease to 10-20 %. For carnivorous plankton the assimilation is generally higher.

2.3. Respiration

The food used for metabolism within an animal can be expressed as a function of the animal's body weight:

$$R = aW^b$$

R can be measured as $\mu l\ O_2$/animal/hr. The factor b is relatively constant and reflects internal metabolism. Values of b differ for tropical, temperate and boreal species:

$$\log R = -0.169 \log W + 0.023 \quad \text{(boreal)}$$
$$\log R = -0.309 \log W + 0.357 \quad \text{(temperate)}$$
$$\log R = -0.464 \log W + 0.874 \quad \text{(tropical)}$$

with W in mg dry weight per animal and R in $\mu l\ O_2$/mg dry weight/hr.

The conversion of respiration to biomass is made by the following equations:

$$\text{mg C} = \text{mg } O_2 \times \frac{12}{32} \times RQ$$
$$= \text{ml } O_2 \times \frac{12}{22.4} \times RQ$$

with RQ the respiratory quotient $+\Delta CO_2/-\Delta O_2$. The RQ may range between 0.7 and 1.0 depending on whether fats or carbohydrates are being utilized.

2.4 Growth efficiencies

A great deal of the food assimilated by zooplankton is used in respiration, in the order of 40-85 %. The net growth efficiency $K_2 = P/A$ is therefore in the order of 20-60 %, but values varie with temperature, food and stage of development.

In approximate terms, zooplankton assimilate about half of their daily ration, the remainder being voided as feces. Of the assimilated, about half is used in metabolism , frequently more than is available for growth. The gross growth efficiency is of the order of 20 %. Secondary production in the plankton differs from that of other grazing systems in that most of the available food is ingested, the subsequent flux to detritus is relatively high and the stock of herbivores is small relative to their production.

Since $A = aC$, with a the percentage of food assimilated, we may write $P + R = aC$ or $P = aC - R$. If a is constant and for a constant basal metabolism R is appears that production can be increased by increasing the ingested ration C. In fish the increase of C results in a decreased efficiency of food utilization and the relationship between gross growth efficiency K_1 and ration is log-linear, according to PALOHEIMO and DICKIE:

$$\ln K_1 = -a - bC$$

Gross and net growth efficiency (or production efficiency if all production is due to growth and reproductive production is not considered) are:

$$K_1 = \frac{\Delta W}{C \Delta t}$$

$$K_2 = \frac{\Delta W}{aC \Delta t}$$

in which $\Delta W / \Delta t$ represents growth per unit time. It follows that:

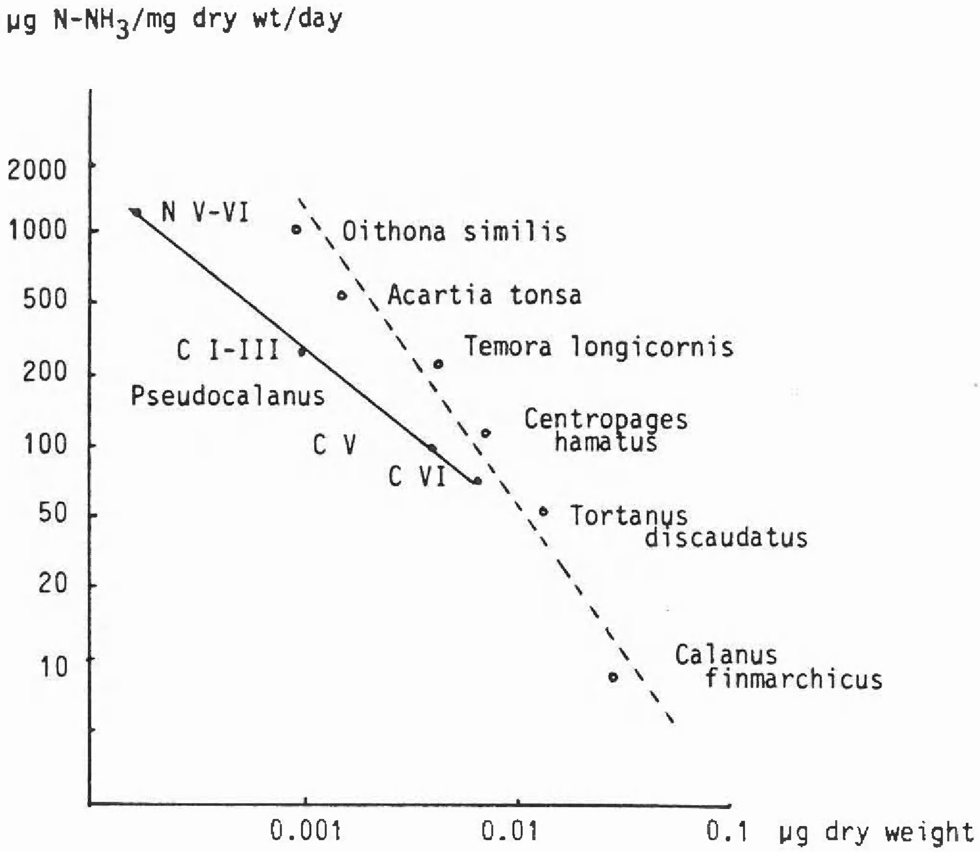
$$\frac{\Delta W}{C \Delta t} = e^{-a-bC}$$

$$\frac{\Delta W}{\Delta t} = Ce^{-a-bC}$$

which expresses growth as a function of consumption or ration.

2.5 Excretion

The principal excretion product of crustacean zooplankton is ammonia. Data on different copepods are shown in the figure (next page):



2.6 Conversion factors

Food can be expressed in terms of energy and the following conversion factors are used for zooplankton:

1 ml O_2 consumed = 5 cal (with RQ 1)

1 mg dry weight of food = 5.5 cal

assuming an average dry weight composition of 50 % protein, 20 % fat and 20 % carbohydrate (plus 10 % ash). The caloric equivalents are 5.65 cal/mg for protein, 4.10 cal/mg for carbohydrate and 9.45 cal/mg for fat. In the SI system the equivalents are 23.65 J/mg, 17.16 J/mg and 39.55 J/mg respectively.

2.7 Effect of temperature

Temperature affects such overall processes as growth, reproduction, respiration and the size of organisms. In general there is a 2-3 fold increase in rate of biological reactions with each 10 °C temperature increase (Q_{10} = 2-3). A good empiral equation is the formula of BELEHRADEK:

$$V = a(t + \alpha)^b$$

in which a,b and α are constants. This formula describes development rate, metabolic rate and size. The constant α is the scale correction factor and is known as the biological zero since it expresses the temperature at which $V = 0$. α is positively correlated to environmental temperature and varies with latitude, being lowest in northernly regions. The constant b reflects the degree of curvature and represents the general dependence on temperature of all metabolic processes leading to changes in the measured parameter V. The value of a depends on units used but is also related to size.

2.8. Production

A zooplankter can be seen as a living machine transforming plant material into animal tissue. The total mass of herbivore tissue formed within a given time is the herbivore production. It is therefore equal to the sum of the growth of all individual members of the population during a certain time interval.

The growth of an individual may be written as:

$$\frac{dW}{dt} = GW$$

with $G = \frac{1}{W}\frac{dW}{dt}$ the weight-specific growth rate

$$dW = GWdt$$

$$W = \int_0^t GWdt$$

For all individuals in the population:

$$P = \int_1^N \int_0^t G_i W_i dt$$

which may be approximated as

$$P = \sum_1^N \sum_0^t G_i w_i \Delta t$$

Over a small interval one may consider G_i to be constant:

$$G_i = \frac{\Delta w_i}{\Delta t} \cdot \frac{1}{w_i}$$

so that $P = \sum_1^N \sum_0^t \Delta w_i$

$$P = \sum_0^t N \Delta w$$

which is equivalent to $P = \int^{t} N\,dW$

One can arrive at this formula also be considering that:

$$P = \int_{0}^{N}\int_{0}^{t} dW$$
$$= \int_{0}^{t} NdW$$
$$= \int_{0}^{t} dB$$

Production can thus be calculated as the surface under a curve relating density N and average individual weight $\bar{W}$ at each time interval (Allen-curve).

A second approach to biomass production is to consider the fate of the biomass produced during a certain time interval Δt. We may write:

$$P = B_t - B_o + E$$
$$P = \Delta B + E$$

in which E is the biomass eliminated during Δt. We get an estimate for E by multiplying the number of individuals eliminated N_E by the average weigth of an eliminated individual $\bar{W}_E$. If there are not births or migration during Δt we may write $N_E = N_o - N_t = \Delta N$, and $\bar{W}_E = (W_o+W_t)/2$

Therefore:

$$P = N_t\bar{W}_t - N_o\bar{W}_o + (N_o-N_t)\left(\frac{\bar{W}_o+\bar{W}_t}{2}\right)$$

$$P = (N_o+N_t)\left(\frac{\bar{W}_t-\bar{W}_o}{2}\right)$$

$$P = \bar{N}\Delta\bar{W}$$

which is in general $P = \int N\,dW$, as above.

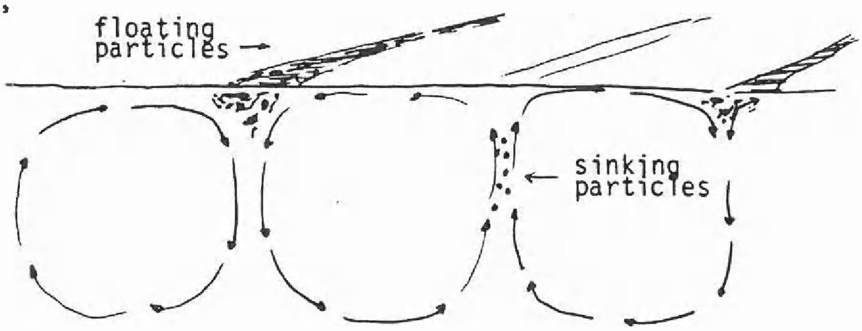
A third method consists of calculating the turnover rate P/B or the time needed for the herbivore biomass to be replaced by fresh production B/P. If the turnover rate is known it is possible to calculate production from the biomass of the stock. A good approximation to B/P is mean age, given as:

$$\frac{1}{\int N_t dt}\int t\,N_t\,dt$$

Grazing

Algal cells may disappear from the euphotic zone by sinking but in most marine regions the great majority is consumed by the grazing of the herbivorous zooplankton. Problems of grazing are made more complex by patchiness (spatial heterogeneity) of plankton, which applies to both phyto- and zooplankton and occurs on scales from a few metres to hundreds of kilometers.

Long, narrow patches of phytoplankton, a few metres wide and some hundred of metres long, exist which are related to Langmuir-circulation, as shown below;



Larger scale patches of plankton are frequently roughly elliptical with a diameter in terms of kilometers and length of the order of tens of kilometers. Such patchiness occurs usually without obvious physical boundary. While a small plankton patch might tend to be smoothed out by turbulence, one a patch of sufficient size has developed, algal growth can more than compensate for diffusions losses and lead to large-scale spatial heterogeneity. A critical diameter for a patch would be:

$$l_c = 4.8 \sqrt{k/a}$$

where k is the diffusion coefficient and a the algal growth rate. Patch size is controlled primarily by turbulence for scales less than about 100 m.

Denser patches of phytoplankton and zooplankton tend to alternate with each other, but in general areas rich in phytoplankton are also rich in zooplankton, and the importance of grazing in reducing algal crops throughout the world's oceans is clear.

The effect of grazing was first expressed mathematically by FLEMING in 1939. He wrote:

$$\frac{dP}{dt} = P(a-b-ct)$$

dP/dt is the rate of change of a phytoplankton population, a is the division rate of phytoplankton cells, b is the initial grazing rate and c the increase of grazing rate which is assumed to be linear.

RILEY developed a mathematical model in 1946 for the rate of increase of a phytoplankton population, introducing loss by algal respiration as affected by temperature, the effect of incident illumination and reduction of light energy with depth and limitation due to nutrient depletion. He estimated that 60-80 % of the phytoplankton variation on Georges Bank (Eastern USA) could be accounted for in terms of depth and illumination, temperature, nutrients and zooplankton density. The initial relationship may be expressed as:

$$\frac{dP}{dt} = P(P_h - R - G)$$

with P the phytoplankton population, P_h the photosynthetic coefficient, R the coefficient of phytoplankton respiration and G the grazing coefficient. RILEY proceeded to look for expressions for these different coefficients, which were to be regarded as ecological variables rather than constants. For the photosynthetic coefficient, a constant p was found so that

$$P_h = pI$$

with p ca. 2.5 if I is measured in ly/min. Since the illumination at depth z is given by $I_o e^{-kz}$ an average photosynthetic rate for the whole euphotic zone can be found by integrating the illumination from the compensation depth to the surface and dividing by depth. Thus:

$$P_h = \frac{pI_o}{kz}(1 - e^{-kz})$$

The effect of nutrient depeletion on the photosynthetic rate was designed as N and calculated in terms of the phosphate concentration as (P)/0.55. RILREY further introduced the critical depth concept by the factor V = (depth of euphotic zone)/(depth of mixed layer). Thus:

$$P_h = \frac{pI_o}{kz}(1 - e^{-kz}NV)$$

Algal respiration would reduce photosynthetic production and would be temperature dependent:

$$R_T = R_o e^{rT}$$

the constant r was determined as 0.069 per 10 °C increase.
Grazing rate may be expressed as:

$$G = gZ$$

with g the rate of reduction of phytoplankton per unit of animals and Z the quantity of zooplankton. RILEY supposed a daily food intake of from 1.2 % in winter to 7.1 % in summer of the body weight.
Finally:

$$\frac{dP}{dt} = P\ (\frac{pI_o}{kz}\ (1 - e^{-kz}NV) - R_o e^{rT} - gZ)$$

The rate of change of phytoplankton is thus expressed as a function of six ecological parameters: solar radiation, nutrients, transparancy of the water, depth of the mixed layer, temperature and zooplankton quantity.