Marine Biology

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Introduction

What is marine biology?

Oceanography is a group of disciplines that share the study of the ocean. Physical and chemical oceanographies are dealing with the abiotic marine environment, biological oceanography and marine biology are more focused on the living organisms. However, the latter deeply influence the chemistry of seawater.

Depending on the authors, biological oceanography and marine biology are more or less equivalent. In general, biological oceanography considers the ecosystem or biosphere levels of organization, is more global and integrated with chemical oceanography. Marine biology is more focused on the individual and population levels of organization, dedicated to the marine aspects of the biology of organisms.

It is noteworthy that marine biology is not a science on itself. It is the application of more general aspects of biology to the life in the marine environment. That means that it may include numerous aspects, namely:

- systematics and biogeography
- molecular and general biology
- physiology
- ecology
- ethology

This means that the division between marine biology and marine ecology is of low meaning and that a significant part of this course will be dedicated to so-called marine ecology.

Abiotic characteristics of the marine environment and ocean circulation

1. Abiotic characteristics of the marine environment

1.1. Composition of sea water

Due to the asymmetry of electrical charges in water molecules, water is a polar solvent able to dissolve numerous ions.

Composition of ocean water at 34.8 ‰

Ion	Concentration (g/kg SW) (modified from Segar 1998)	% w/w of ions (modified from Nybakken 1993)
H_2O	965.31	
Main constituents (>100 mg/kg)		
Cl^-	19.51	55.35
Na^+	10.81	30.61
SO_4^-	2.73	7.68
Mg^{2+}	1.29	3.69
Ca^{2+}	0.41	1.16
K^+	0.38	1.10
Sub-total		99.28
Minor constituents (1-100 mg/kg)		
HCO_3^-	0.142	0.41
Br^-	0.067	0.19
H_3BO_3	0.025	0.07
Sr^{2+}	0.008	0.04
Sub-total		0.71
Si	0.002	<0.01
F	0.0013	<0.01
Total		99.99
Trace elements (<1 mg/kg)		
N	0.0005	<0.01

Li	0.00016	<0.01
Ru	0.00012	<0.01
P	0.00006	<0.01
I	0.00006	<0.01
Mo	0.00001	<0.01
Others (Fe. Zn. etc)	<0.000001	<0.01

The general concentration in dissolved ions is expressed by:

Salinity (‰) = weight of inorganic dissolved solids* / 1000 g SW

* when all carbonates are converted in oxides and all bromides and iodides are replaced by chlorides

This is rather difficult to measure on a regular basis. For this reason a more easy relationship was derived based on the constant ratio between the most abundant elements in sea water. This constant ratio is due to the long residence time of these elements in sea water. This differs according to the considered element. For Na for instance it is 260 millions y. For Fe and Al it is in between 100 and 140 y. The constant character of the <u>relative</u> composition of SW means that the measure of the concentration of a major constituent of SW allows to infer the concentration other constituents and to calculate the salinity. The most abundant constituent and easiest to measure is Cl^-. So, the chlorinity is the concentration of Cl^- expressed in g/kg SW. As chloride ions accounts for 55% of the dissolved solids,

Salinity (‰) = 1.80655 x chlorinity

Salinity is now routinely measured by electrical conductivity of the analysed sample. Till the 80's the calibration was carried out with a standard sea water reference. Now for practical reasons (availability of the standard) salinity is expressed as the ratio between the measured conductivity of the sample and that of a standard solution of KCl chosen such as average sea water salinity is 35PSU and corresponds to 35g salts/kg SW. As a consequence, salinity is now a measure without units and is expressed in Practical Salinity Units (PSU).

Salinity in the ocean varies between 33 and 37 PSU. This depends mainly on the balance between dilution by rainwater and concentration by evaporation. This results in latitudinal variations of the mean ocean salinity (see fig.). This general trend may of course be affected by local processes like river plumes or melting ice. Marginal or semi-enclosed seas may show enhanced disbalances between evaporation and precipitation or freshwater supply by river. This is the reason why the Baltic Sea has a salinity of ca 5PSU while the Mediterranean seawater may be as high as 38PSU.

1.2. Temperature

The hydrogen bonds of water have several consequences, namely:

- a high heat capacity
- high freezing and boiling points
- a high heat of vaporization

These result in a general moderating effect of the ocean on the continental climate.

At low latitudes the sea surface shows a net uptake of heat from solar origin while at high latitude there is a net loss of heat (see fig). This results in a latitudinal gradient of sea surface temperature which average 0°C in polar seas and are ≥ 25°C in tropical waters. At medium latitude marked seasonal variations are observed. Due to the currents (see later), these differences in sea surface water temperature will result in heat transfers between different regions (see heading 2).

SW temperature is also varying according to depth. These vertical profiles will be considered in the next section.

1.3. Density

Both temperature and salinity will influence the density of sea water. Differences in density will in turn influence the movements of water masses (heading 2.2).

Due to hydrogen bonds, the spacing of water molecules in crystals is larger than that in liquid water (see fig). As a consequence, ice is floating on water (an aspect of tremendous importance in the development of life!). Furthermore, this results, in freshwater, in a maximum density before the freezing point, actually at 4°C in pure water. On the contrary in sea water whose salinity exceeds 24.7PSU, the maximum density of liquid water is at the freezing point (see fig). Thus, in liquid sea water, the lower the temperature, the higher the density.

The density of seawater is usually included between 1.02300 and 1.03000 g/cm^3 .To avoid the use of numerous non significant ciphers, the value σ_t is frequently used:

$$\sigma_t = (d_{SW}/d_{H20} - 1) \; . \; 1000$$

The mean density of sea water is 1.02567, that of σ_t is thus 25.67.

The relationship between temperature, salinity and density is not linear (see fig.): the same temperature difference has a much higher effect on density at high temperature that at low temperature. As a consequence, at low latitudes, the temperature will be the main factor affecting density, while at high latitudes salinity will have a more pronounced effect.

Vertical density profiles differ according to the latitude (see fig). They principally depend on temperature profiles except at high latitudes. At the Equator, a rather shallow layer (a few tens of meters) of low density SW tops a layer where density brutally increases, forming the so-called pycnocline. This constitutes an important barrier against the mixing of superficial and deep water masses. The pycnocline is principally due to a brutal change in temperature, the so-called thermocline and to a lesser extent to a change in salinity (halocline). In polar regions, the pycnocline is missing, the temperature being almost constant all the along the water column. This results in a less stable water column, without physical barrier, allowing small variations in salinity linked to ice melting and freezing to be the driving forces of movements of water masses (see lesson on Antarctica). This will have a tremendous importance on general water circulation (see heading 2.2).

2. Ocean circulation

2.1. Surface circulation

2.1.1. Surface currents

Surface currents are mostly wind-driven. The principal earth winds are:

- the trade winds blowing from the subtropical high pressures towards the equatorial low pressures
- the westerlies blowing from the subtropical high pressures towards the low pressures located at 60° N and S

Due to the Coriolis effect, the trade winds are blowing from the NE (Northern Hemisphere) or the SE (Southern Hemisphere) and the westerlies are blowing from the SW (N Hemisph) or the NW (S Hemisph) (see fig.). Notice that trade winds are not blowing in a narrow band (ca 400km wide) near the Equator (the so-called doldrums, feared by sailors).

The Coriolis effect: any object on the earth's surface moving horizontally through a long distance for a relatively long period of time will be observed to "turn" to the right in the N Hemisphere and to the left in the S Hemisphere. It should be noted that this is an effect seen by an immobile observer. An observer in space would not see any deflection. See: http://www.mnhn.fr/mnhn/lop/seconde/fiches/Coriolis.html
http://www.mnhn.fr/mnhn/lop/seconde/fiches/Coriolis.mov .
The Coriolis effect is due to the fact that points at different latitude are not rotating at the same linear speed: this is zero at the poles, 800km/h at 60°, 1400 at 30° and 1600 at the Equator. So, the Coriolis effect is increasing with latitude and the crucial factor is the time during which the particle is moving.

The trade winds will induce the movement of the intertropical surface water masses. This will occur due to Ekman transport: a wind blowing over a water mass for a long time over a long distance will induce the superficial water layer to move at 45° at the right (N Hemisph) from the wind direction; this will in turn induce the movement of the immediately below layer at a lower speed and in a direction deflected to the right and so on till a depth of ca. 100m (Ekman spiral; see fig). The resulting overall movement of the water mass is at 90° from the direction of the wind. The Ekman transport induced by the trade winds will cause the piling up of a water dome at the right (left) side of the wind in the Northern (Southern) Hemisphere. This piling up of water will in turn generate a pressure gradient in the opposite direction of the Ekman transport. This results in the establishment of the so-called geostrophic equilibrium. The results are that the water is flowing in the direction of the wind. Thus, the trade winds are driving the equatorial currents flowing from E to W. When encountering continental masses, the equatorial currents are deflected and taken back by the westerlies generating currents from W to E (e.g. the Gulf Stream in the N Atlantic). The combination of equatorial and westerlies driven currents results in large ocean gyres centred on 30° of latitude. These are turning clockwise in the N Hemisph and anti-clockwise in the S. Hemisph. (see figs).

The westwards movement of water caused by the equatorial currents also results in the piling up of water on the W side of the ocean basins. This induces an eastwards pressure gradient which will generate the "small" counter-equatorial currents at the level of the doldrums.

2.1.2. Up- and downwellings

Wind can also drive vertical movements of water in the surface layer (scale of a few tens to a few hundreds of meters depth).

The geostrophic equilibrium generates a dome of water that makes water layers sink in (downwelling). Two adjacent currents flowing in opposite direction will cause water to diverge due to Ekman transport. This will cause an upwelling of deeper water to compensate for the divergent water (e.g. equatorial or antarctic upwellings). If the wind is blowing parallel to a coast, Ekman transport will cause water to either diverge from the coast (upwelling) or to pile up towards the coast (downwelling). In the first case, deeper water from the continental margin, charged with nutrients, will be brought to the surface. In the latter case, offshore surface water, poor in nutrients, will move to the coast, making richer coastal waters sink (ex: Peruvian upwelling, see fig.).

2.1.3. Langmuir circulation

In the centre of gyres, weak , constant winds cause corkscrew motion of the upper few meters of water. This generates convection cells that result in accumulations of organic material and living organisms in convergence zones (see fig.). Notice that the scale of this phenomenon is radically different from the previous ones: we are dealing here with scales of a few meters in depth.

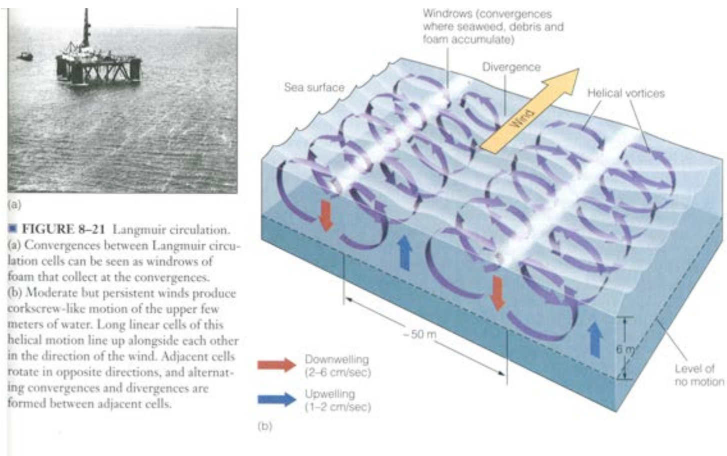


FIGURE 8–21 Langmuir circulation. (a) Convergences between Langmuir circulation cells can be seen as windrows of foam that collect at the convergences. (b) Moderate but persistent winds produce corkscrew-like motion of the upper few meters of water. Long linear cells of this helical motion line up alongside each other in the direction of the wind. Adjacent cells rotate in opposite directions, and alternating convergences and divergences are formed between adjacent cells.

(from Segar 1998)

2.1.4. Effects of modifications of the surface circulation: El Nino Southern Oscillation (ENSO)

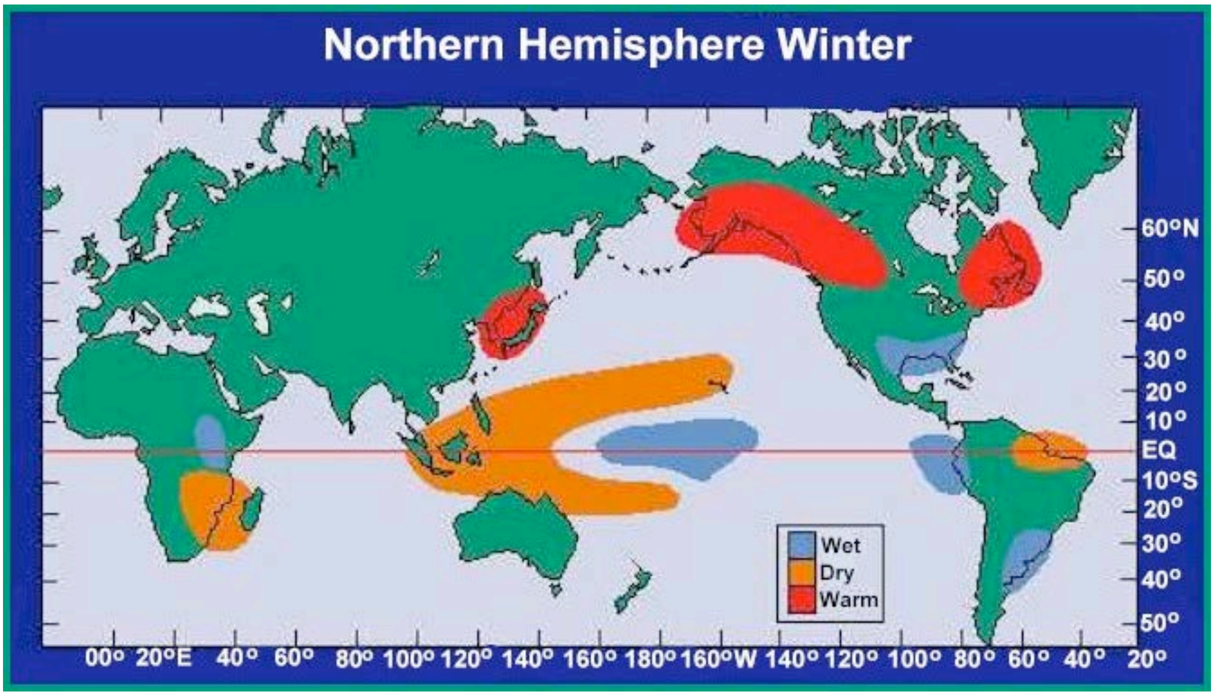
The normal climate condition in the Indo-Pacific Ocean is characterized by well-established trade winds generating a well-developed equatorial current. This pushes warm superficial waters in the Indian Ocean over Australia and Indonesia, resulting in a low pressure (due to evaporation of warm water). Concurrently, the subtropical gyre is well established, forming a northward current along the South American coasts. This current generates an upwelling along the Peruvian coast, bringing up cold water to the surface. This results in a high pressure (due to the cold air) in the Eastern subtropical Pacific (see fig.).

Every 2 to 10 years, the trade winds relax, causing a weakening of the equatorial current. The equatorial counter-current becomes dominant and the warm water masses (and the accompanying low pressure) are pushed from the Indo-Pacific eastwards to South America (see fig.). This phenomenon usually occurs around Christmas from which is name is derived (el Nino in Spanish means the Christ). The oscillation refers to the changing value of the difference in atmospheric pressure between the Indo-Pacific Ocean and South-America.

The consequences of El Nino are dramatic (see fig.):

- due to the weakening of the equatorial current and dominance of the counter-current, the coastal current along South America is flowing southwards, causing a downwelling which brings warm water to the Peruvian coast, killing many cold water organisms, and tremendously reducing primary production (due to the lack of nutrients) which results in a crash of the Peruvian anchovy fisheries;
- the low pressure on South America causes storms and massive rains generating floodings over the W coast of S America and the S of the USA.
- the high pressure over the Indian Ocean causes severe droughts in Indonesia, Australia and the Philippines but also in S Africa and Zimbabwe. Sometimes, these droughts are inducing huge forest fires affecting the health of millions of people in SE Asia (this was the case in 1998).

The cost of El Nino in 1982 was assessed to 8 billions US $.



An El Niño can have impacts on weather at various locations around the globe. Off the east coast of southern Africa, drought conditions often occur while El Niño is in progress. In countries such as Zimbabwe, whose economy is critically tied to maize production, the effects of drought can be devastating. In western South America, farmers can benefit by planting more rice rather than a normal crop of cotton during an El Niño as they are likely to experience heavier than normal rainfall. (from http://nsipp.gsfc.nasa.gov/)

2.2. Thermohaline circulation

2.2.1 Mechanisms and conveyor belt

Thermohaline circulation is principally taking place below the pycnocline. It takes its origin in differences of density of water masses. These differences result in the water masses going up or down. In turn, this creates horizontal gradients of pressure (for instance when a sinking mass encounters a denser water mass and is deflected horizontally). The thermohaline circulation originates at high latitudes where the pycnocline is virtually absent. At these latitudes, the surface water is cooled by the atmosphere that is making it denser and therefore sinking (examples of these mechanisms will be studied in the lesson on Antarctica). The main zones where deep water is forming are:

- the Weddell Sea where Bottom Antarctic Water forms
- the Norway Sea and Iceland Sea where North Atlantic Deep Water (NADW) forms

No deep water is formed in the North Pacific because a rather shallow sill, blocking the movement of deep water, borders the arctic basin of the Pacific.

The NADW is flowing southwards till 50°S where it mixing with Deep Antarctic Water and turning towards the Indian Ocean and the Pacific Ocean. In both oceans the water masses then flow northwards and towards the surface where they mix with local water masses and warm up. Then, they enter the wind-driven circulation and the oceanic gyres, going back to the N Atlantic. This huge "conveyor belt" results in a net transfer of heat from low latitudes to high latitudes in the N Atlantic. In particular the Gulf Stream is bringing part of this heat towards the NE (Europe) which is the reason why the N European climate is milder than the East coast N American climate at the same latitudes.

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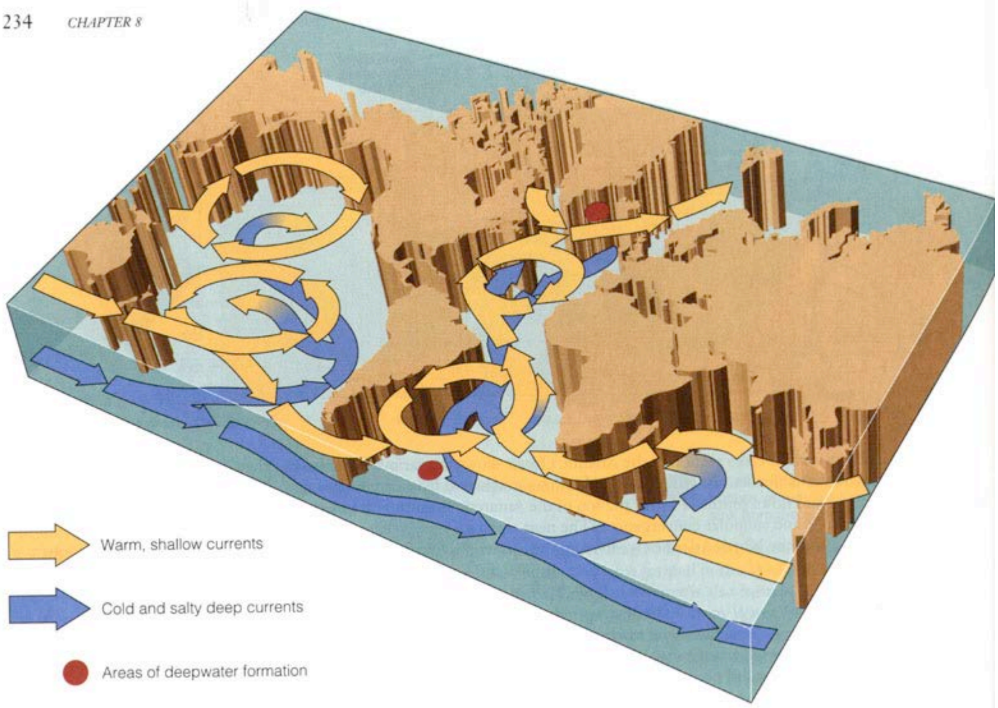
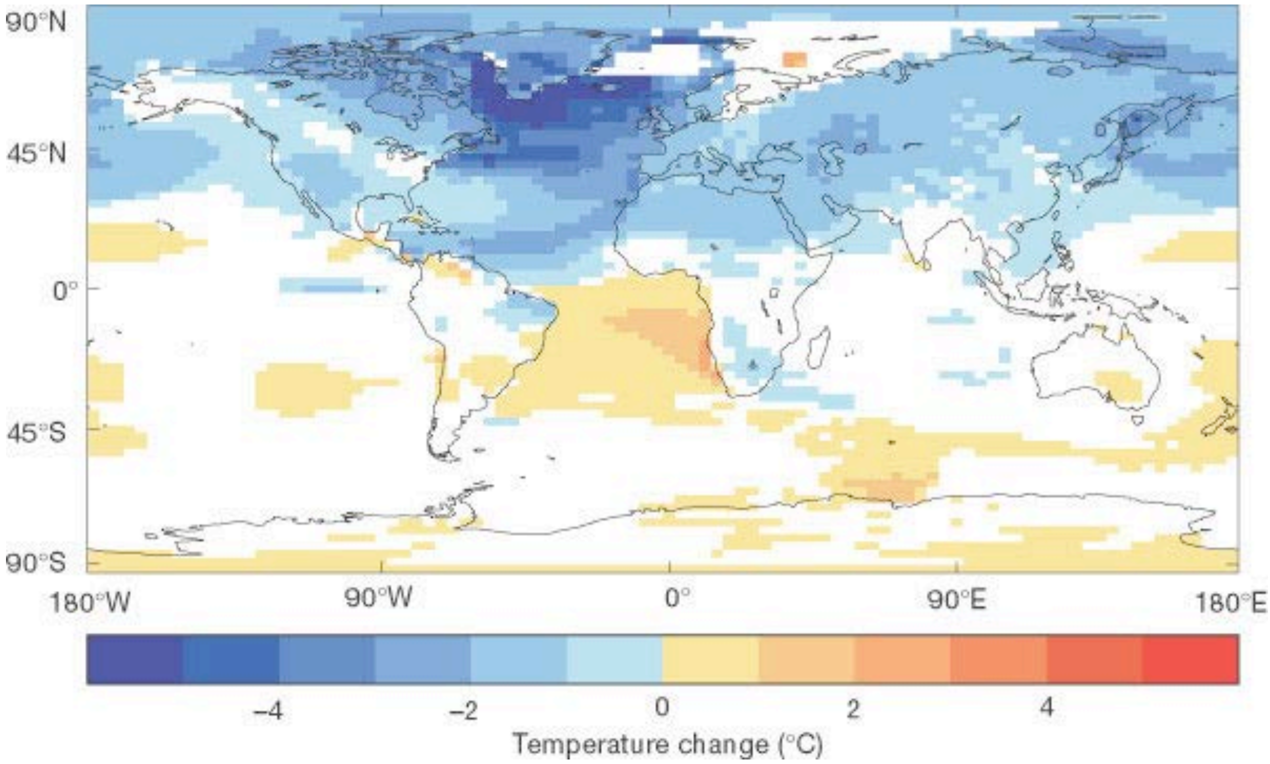


■ **FIGURE 8–29** A simplified depiction of the "conveyor belt" circulation that starts with the formation of North Atlantic Deep Water near Greenland. This water mass flows south through the Atlantic, flows over and mixes with the deep water formed near Antarctica and is transported around Antarctica and then north into the Indian and Pacific Oceans. This deep water is gradually warmed and mixed upwards and is returned to the North Atlantic in a complex and not yet well understood surface and near surface circulation. This system is instrumental in transporting heat from low latitudes to high latitudes of the North Atlantic Ocean.

(from Segar 1998)

2.2.2. Consequences of disruptions of the thermohaline circulation

Models show that if the formation of NADW stops, the air temperature in W Europe would be reduced by 6°C (see fig). This already occurred in the past (13500 years BP) when the last Ice Age abruptly stopped in ca. 100y. This caused a brutal thawing of ice shields and mountains whose freshwater, flowing down the St Laurent River (presently in Canada), covered the NW Atlantic with a much lighter layer preventing the formation of NADW. In an apparent paradox, this corresponded in N Europe with a cold period (despite the end of the Ice Age) due to the disruption of the conveyor belt, which lasted for several hundreds of years (the Younger Dryas). During the 20th century, in the 80's, the formation of NADW off Greenland decreased by 90%. The cause is currently not well understood but could be linked to global warming due to the increased concentration of greenhouse gas. If this is correct, global warming could result in lower temperatures in NW Europe.



Changes in surface air temperature caused by a shutdown of North Atlantic Deep Water (NADW) formation in a current ocean–atmosphere circulation model.

Note the hemispheric see-saw (Northern Hemisphere cools while the Southern Hemisphere warms) and the maximum cooling over the northern Atlantic. In this particular model (HadCM3)7, the surface cooling resulting from switching off NADW formation is up to 6 °C. It is further to the west compared with most models, which tend to put the maximum cooling near Scandinavia. This probably depends on the exact location of deep-water formation (an aspect not well represented in current coarse-resolution models) and on the sea-ice distribution in the models, as ice-margin shifts act to amplify the cooling. The largest air temperature cooling is thus greater than the largest sea surface temperature (SST) cooling. The latter is typically around 5 °C and roughly corresponds to the observed SST difference between the northern Atlantic and Pacific at a given latitude. In most models, maximum air temperature cooling ranges from 6 °C to 11 °C in annual mean; the effect is generally stronger in winter. (from Rahmstorf 2002)

Pelagic biological processes

1. Divisions of the pelagic environment

The pelagic domain is spited in neritic (above the continental shelf) and ocean provinces (above the shelf slope and abyssal plains).

It is also divided in zones according to available light and depth.

Depth (m)	Zone	Characteristics
0		
	Epipelagic	- euphotic (available light is able to support photosynthesis - mixing zone - surface water masses - nutrient concentrations are low - O_2 concentration high
200		
	Mesopelagic	- disphotic (available light is unable to support photosynthesis - pycnocline zone - intermediate water masses - O_2 conc decreases towards a minimum at 700-1000m due to bacterial activity - nutrient conc. increase
1000		- base of pycnocline
	Bathypelagic	- aphotic - deep water masses - O_2 conc increases (deep water is usually originating from rapidly sinking surface water, cf NADW and diffusion from bottom water of similar origin) - high nutrient conc.
4000		
	Abyssopelagic	- aphotic - bottom water masses (originating at high latitude) - high O_2 conc. - high nutrient conc.

2. Biological processes in the pelagic domain

2.1. Definitions

Pelagos: Organisms living in the water column without any contact with the bottom and which do not depend on the benthos for feeding

Plankton: pelagic organisms unable to swim against the currents

Nekton: pelagic organisms able to swim against the currents

Tripton: Particulate Organic Matter (POM)

Seston: plankton + tripton (i.e. material retained on a 0.45 or 0.22μm membrane filter)

Functional classification of the plankton

Classically the plankton is divided in phyto- and zooplankton, i.e. in autotroph and heterotroph planktonts. However, there is no clear-cut barrier between these two groups for several reasons:

- mixoplankton: these are planktonts that are principally autotroph but can be heterotroph or vice versa. Autotrophs (like some dinoflagellates) can be phagotrophic (mainly by ingestion of bacteria) or osmotrophic (absorption of dissolved compounds to get extra nutrients or vitamins). Heterotrophs (e.g. ciliates and amoeba) may either trap functional chloroplasts from their preys or include endosymbiotic algae

- importance of the bacterioplankton: this can be the main heterotrophic component in some communities but it also includes several autotrophic groups (e.g. cyanobacteria).

- there is no systematic divide between the phyto- and the zooplankton: most groups include autotroph and heterotroph planktonts

Classification of the plankton according to size

Ultraplankton	< 2 μm
Nanoplankton	2 – 20 μm
Microplankton	20 – 200 μm
Macroplankton	200 – 2000 μm
Megaloplankton	> 2000 μm
Mesoplankton	*200 – 20000 μm* *1000 – 5000 μm* *(according to authors)*

2.2. Primary production

2.2.1. Limiting factors

Light and mixing

Photosynthesis is related to light intensity (see fig). This relationship is characterized by a first linear increasing phase corresponding to limiting light intensities. This phase is possibly followed by a plateau that corresponds to the saturating light intensity. The latter is followed by a decreasing phase due to the deleterious effects of high light intensities (especially UV), increased respiration (inducing a reduced net production), and increased leakage of organic molecules by the cell (also reducing the net production).

This relationship between light intensity and photosynthesis is qualitatively the same for most planktonts but quantitatively differs according to the considered group or species (see fig); therefore, according to light regime, different groups will be favoured (e.g. diatoms against flagellates).

As water absorbs light, light intensity across the water column follows an inverse exponential profile with depth (see fig):

$$I_z = I_o\, e^{-kz}$$

where k is the extinction coefficient and z depth.

This will induce a very general relationship between photosynthesis and depth:

- photoinhibition will occur at the very surface (a few meters; inhibition threshold is usually 170Wm^{-2})

- except in this superficial layer, light is limiting (saturation level: 120Wm^{-2}) and photosynthesis follows an inverse exponential relationship with depth.

This allows to use a very general formula to calculate the net primary production per surface unit of the ocean:

$$\Sigma_i P = n_i \, Pmax_i \, d$$

where $\Sigma_i P$ is the net primary production of the population of the i^{th} organism, n_i is the density of this population, $Pmax_i$ is the photosynthetic saturation rate of the i^{th} organism and d is the depth at which the intensity of the most penetrating radiation is reduced to 10% of the surface value. This relation makes it usual to express the plankton primary production per surface unit.

Respiration is independent of depth. Therefore, there is a depth at which the respiration of the considered primary producer is equal to its gross photosynthesis. This depth is the compensation depth. Of course, it varies according to the considered organism. When the primary producer is above its compensation depth, its net primary production is positive. When it is below, it needs to use stocked energy to survive.

Now, according to mixing conditions determined by hydrodynamism and wind, the primary producer community is spending different amounts of time above and below the respective compensation depths of the different species. The depth at which the gross primary production of the whole community is equal to the total respiration of this community is called the critical depth. If the mixing depth (i.e. the depth above which the water column is mixed) is shallower than the critical depth, the net primary production of the community will be positive. If it is deeper, the net primary production will be negative and the primary producer community will be reduced.

Nutrients

Three types of nutrients can be recognized:

- Major nutrients (building blocks of the phytoplanktonts): C, N, P, O, Si, Mg, K, Ca
- Trace nutrients: Fe, Cu, V, (Cd)
- Organic nutrients: vitamins

The uptake of nutrients may be described by a Michaelis-Menten type equation (notice that this is just a mathematical description, it is not implying that the uptake of nutrients is depending on enzyme kinetics following Michaelis-Menten processes) (see fig):

$$V = Vmax . C / Ks + C$$

Where Vmax is the velocity at saturation, C is the concentration of the nutrient in SW and Ks is a constant corresponding to the concentration of nutrient at which V = Vmax/2.

Thus Ks is a measure of the nutrient concentration necessary to reach half the maximum uptake rate. Primary producers with a low Ks will be favoured in oligotrophic waters (because they reach high uptake rate at lower nutrient concentrations) while those with a high Ks will be more efficient in eutrophic waters (because they will take up higher concentrations of nutrients).

Ks is varying according to the species and groups. As a very general rule (with several exceptions!), flagellates show lower Ks than diatoms. This is in part due to their higher surface/volume ratio: smaller cells are taking up (on a weight basis) nutrients faster because their absorption surface is proportionally higher (see fig.).

For all these reasons, nutrient availability will be a major factor controlling the composition of the primary producer community.

Four nutrients have been demonstrated to be possibly limiting for the marine primary producers: nitrogen, phosphorus, silicon, and iron.

<u>Nitrogen and phosphorus</u> were demonstrated by enrichment experiments to be limiting in numerous locations (see figs). Usually, N is the primary limiting factor while P is only secondarily limiting (once N limitation is removed; like for instance in eutrophicated waters as in the Southern North Sea).

<u>Nitrogen</u> is necessary for protein synthesis. It occurs in the sea under 3 principal inorganic forms: NH_4^+, NO_3^-, NO_2^-.The ammonium ion is the most favourable for primary producers because it does not need reduction prior to its incorporation in proteins. Nitrate and nitrite need a previous reduction by nitrate reductase. However, most dissolved N in the sea is nitrate, at concentrations usually around 1μM, rarely >25μM. It is noteworthy that N is much less concentrated in SW than in freshwater (see fig.) where P is usually the limiting nutrient for primary producers. There are three main sources of N in the marine environment:

(1) sediments and deep waters: usually as nitrate; the primary production based on these sources is called "new production" because it is based on N coming from outside the considered water mass

(2) excretion and decomposition from or by consumers: usually producing ammonium; the primary production based on these sources is called "regenerated production" because it is based on N coming from inside the considered water mass
(3) fixation of atmospheric N_2: carried out by yeasts and principally by cyanobacteria, some of them being symbionts of diatoms in oligotrophic waters; fixation of gaseous nitrogen may account for up to 20% of N supply in some zones

Phosphorus is necessary in energy transfer processes (ATP), in the phosphorylation of enzymes, and in the synthesis of nucleic acids. In the ocean it is present as dissolved inorganic phosphate, dissolved organic phosphate, and particulate phosphorous. Phosphate is the most favourable. It is usually very quickly recycled.
Most primary producers require a rather constant ratio C/N/P of 106/16/1 that is called the Redfield ratio (according to the name of Redfield who described it for the first time). Departures from this ratio often indicate the limitation by a nutrient.
Silicate is the main building block of diatom shells. Its depletion may terminate diatom blooms although limitation by other factors is often involved.
Iron is a prominent part of ferredoxin, which is involved in electron transfer from photosystem I to $NADP^+$). Its concentration in oceanic waters is usually below 1nM but it is enriched (1-3nM) in neritic waters because its main sources are continental either from river or airborne. Iron is limiting in some oceanic waters where high concentrations of other nutrients are present. These zones were called High Nitrate Low Chlorophyll (HNLC) zones. Limitation by Fe in these zones was demonstrated by elegant mesoscale enrichment experiments in the Equatorial Pacific and in the Southern Ocean. In all these experiments, the Fe enrichment induced an important increase in production and biomass (up to 27 times for chlorophyll a, a measure of biomass) going together with a depletion of nitrate (see figs). This clearly indicates that Fe is the factor limiting the use of N by primary producers. The principal group that respond to the enrichment was diatoms. Limitation by Fe is further evidenced by measures up- and downstream islands (Galapagos) or capes (Drake passage). Around the Galapagos for instance, Fe and chlorophyll a concentrations up- and downstream the islands are, respectively 0.06nM Fe, 0.25μg chla/l and 1.3 to 3nM Fe, 0.7μg chla/l.
HNLC ecosystems were recognized in offshore upwelling zones(Equatorial Pacific, Antarctic circumpolar current -see lesson on the Antarctic Ocean- but also in coastal Southern

California where supply of Fe is very low due to the very dry climate resulting in very low river discharges.

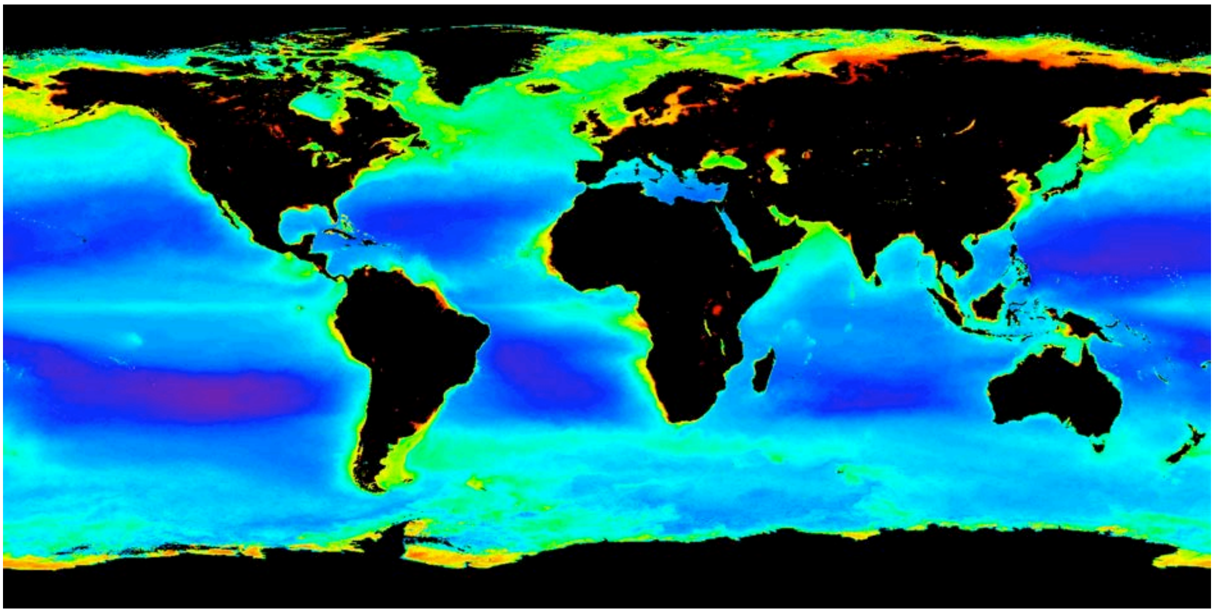
Grazing

Grazing is able to control primary production as evidenced by respective spatial distributions of producers and grazers (see fig.). However, this control may be of very different magnitudes (see table). This is due to differences in generation times between primary producers (hours, days) and grazers (weeks). Food preferences of grazers depending on size or chemical composition of producers are also important. In particular they may modify the producer community by systematically eliminating a given size class. It is noteworthy that the interaction between primary producers and grazers is for a part mutualistic. Indeed, grazing is bringing back nutrients in the environment, which are the base for regenerated primary production. This is particularly important in regions where nutrient supply is poor.

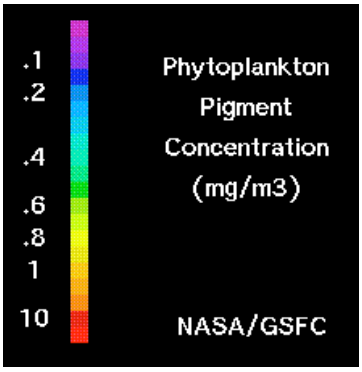
2.2.2. Variations of primary production in space and time

Spatial variations

Large scale variations in primary productions (see fig.) are principally linked to hydrographic processes. High production is recorded in coastal upwellings where nutrient-rich waters are brought to the surface (Peru, NW and SW Africa, E India, W coast of N America). Coastal zones with large nutrient supply of land origin and with high mixing conditions also support high productions (e.g. the Southern North Sea). Offshore upwellings (equatorial and antarctic divergences) bring superficial waters to the surface, allowing the recycling of nutrients and support medium productions; however, these are often limited by iron. Eddies ensure mixing of the water column, supporting a medium to low regenerated production. On the contrary, the centre of oceanic gyres is the place of a downwelling with a permanent pycnocline so that recycling of nutrients is very low and primary production is among the lowest of the oceans. Finally, the primary production in the Arctic Ocean is limited by the low light experienced by this region of the world. Actually this is the only region, on a global scale, where production is limited by light. In all other regions large scale primary production is limited by nutrient supply depending on hydrographic conditions.



The map displays the composite of all Nimbus-7 Coastal Zone Color Scanner data acquired between November 1978 and June 1986. Approximately 66,000 individual 2 minutes scenes were processed to produce this image.
(From http://seawifs.gsfc.nasa.gov/SEAWIFS/CZCS_DATA/global_full.html)



At small scale a patchy distribution of primary production is evidenced due to local phenomenons like Langmuir circulation, grazing (see above) or reproduction (daughter cells are necessarily close to each other, so blooms are localized).

Seasonal variations

Seasonal variations of primary production differ according to latitude and oceans.

In the boreo-temperate North-Atlantic, the seasonal succession is particularly outstanding (see fig.). In winter, the water column is not stratified and the mixing depth is deeper than the critical depth. Primary production is limited by light and nutrient concentrations in water are high. In spring, temperature increases and the water column becomes stratified. Mixing depth becomes shallower and light increases. As a consequence, the primary production increases exponentially and a spring bloom, usually of diatoms develops. As a result, nutrient concentrations (mainly nitrate and silicate) dramatically decrease which eventually terminates the bloom. Due to their heavy shell, dead diatoms rapidly sink and are exported below the thermocline. Simultaneously, the consumer biomass increases, being limited by the termination of the bloom. In summer, the water column is totally stratified and the water layer above the thermocline is poor in nutrients (which were exported below the latter by sinking diatoms). Primary production is based on nutrients recycled by heterotrophs (regenerated production). Primary producers are principally nanoflagellates controlled by grazers. The system is limited by nutrients. At the end of the summer and in the fall, the storms break the stratification allowing a mixing of the water column bringing up nutrients. A small bloom develops, immediately controlled by grazers. Due to a rather low concentration in silicate and still reduced nutrient concentrations, this bloom is dominated by flagellates. The decreasing light eventually terminates this bloom.

In polar regions, a single short bloom develops in summer, followed by a peak in consumer biomass. The system is principally limited by light. In tropical regions, no seasonality occurs; primary production is low all around the year due to a permanent thermocline and controlled by grazers. In boreo-temperate North Pacific, seasonality is, surprisingly, not the dominant factor. The dominant grazers (copepods of the genus *Neocalanus*) "anticipate" the bloom: they reproduce before the bloom using food reserves and prevents the development of the bloom.

2.3. Consumers

2.3.1. The microbial loop

Until the mid-70's, the typical pelagic food chain was considered to be:

Dinoflagellates + diatoms -> copepods ->herring -> mackerel ->tuna.

(the so-called "linear chain")

That means that considered primary producers were only those retained on plankton nets (therefore called "net plankton"). The development of membrane filters (Millipore) allowing to filter much smaller organisms in the mid-70's allowed to realize that more than half of the world primary production was actually the fact of nanoflagellates (2-10μm in diameter) and cyanobacteria. At the same period, the marketing of DAPI, a fluorescent dye of DNA allowed to directly count bacteria in sea water instead of tedious culturing on Agar plates which only reveal 1-10% of the bacteria present in the sample. This reveals bacteria concentrations of 1million/ml, accounting for 200μgC/l, meaning that bacterial biomass may equal the biomass of primary producers. Eighty to ninety % of these bacteria are free in the water column. Their secondary production was measured to range between 0-500 μgC/l. day in coastal waters and 0.5 – 5 μg C /l day in oceanic waters. This corresponds to 5-30% of the primary production in the same waters. Taking into account a maximum efficiency of 0.5 for bacteria, this means that 10 to 60% of the primary production may be consumed by bacteria. These consumed dissolved organic matter leaked by primary producers (this may account for as much as 30% of the primary production) as well as fragments (particulate organic matter) of dead or preyed primary producers (generated by sloppy feeding of macrograzers).

Bacteria populations are limited by several factors: availability of food (in spring, when nutrients are available), nutrients (bacteria are limited in summer by N and P; see fig.) and predation, mainly by heterotrophic nanoflagellates. The latter was evidenced in incubations of pelagic microbial communities where micro- and macroplankton components were removed (to avoid control by higher levels). In these incubations, oscillations of bacteria and heterotrophic nanoplankton population sizes, typical of predator-prey interactions were observed (see fig). When the nanoplankton was also removed, bacteria showed first an exponential increase in population size, which later reached a plateau due to limitation in food and/or nutrients. These oscillations are at a short-term scale for two reasons. First the generation time of the nanoplankton is of the same order of magnitude as that of bacteria (3-24h vs. 6h for bacteria). Second, the heterotrophic nanoplankton has a very high clearing rate. It is able to clear bacteria of 10^5 times their volume every hour. In coastal waters, one considers that the heterotrophic nanoplankton filters the whole water column every day.

Nanoflagellates are in turn controlled by ciliates, which usually prevents the occurrence in the field of the oscillations in population sizes observed during incubation experiments.

These different discoveries led to a new view of the pelagic food chain including bacteria and the nanoplankton (see fig). This added a whole network to the linear chain, called the "microbial loop".

The occurrence of the microbial loop has several implications in our understanding of pelagic food networks.

(1) Much more trophic levels are involved than previously assumed; this means that the energy that was believed to be available for the linear food was overestimated. Indeed the energy available for the next trophic level is equal to:

$$P = B\ E^n$$

where P is the production of trophic level n, B is the annual primary production of the ecosystem, E is the ecological efficiency, i.e. the ratio between the energy effectively incorporated in growth by level n and the energy ingested by level n, and n is the number of trophic levels calculated from primary producers.

Usually E equals 10-50%, meaning that the highest n the lowest P. Actually, in most pelagic ecosystems, the main part of chemical energy and carbon is dissipated in the microbial loop (this is the reason why it is called a loop, as carbon and energy are cycling inside this compartment of the ecosystem). Therefore, the transfer of C between the microbial loop and the linear food chain is pretty low or even not significant in some cases. Only the primary production from microplankton (mainly diatoms) is available in significant amount to the linear food chain.

(2) Bacteria were, for a long time, considered as the main recyclers of nutrients. Actually the bacterial biomass is a sink for nutrients (as illustrated by their C:N ratio; see table). However, they are very important in the modification of nutrient redox potential, being involved in their reduction. Now, protozoans and other nano and microconsumers are considered as the main actors of nutrient regeneration. Zooplanktonts excrete 2-10% of their N charge and 5-25% of their P charge every day, ensuring a rapid recycling of nutrients in the water column (turnover of phosphate in temperate waters is 1.5 day, a little bit more fro N).

(3) In the microbial loop, organisms of different size classes (up to three orders of magnitude) occur at the same trophic level. This means that the classical separation of trophic levels according to size is no more valid, making calculation of the energy available for the next trophic level difficult. This also implies that there is no simple trophic chain but that a trophic network has to be considered.

The importance of the microbial loop was further emphasized by the assessment, in the 90's, of the importance of virus in the water column. Surface waters count 10^6-10^7 up to 10^8 (in coastal waters) virus particles/ml. These are responsible for 8-26% of bacterial mortality and may terminate some blooms like those of coccolithophorids.

2.3.2 Linear food chain

Plankton

Pelagic food webs are relatively "unstructured" (if compared with benthic ecosystems) due to several factors:

- the complexity of trophic relationships in the water column (see above)
- most predaceous species are themselves controlled by their predators; so, no predator may become dominant
- "gelatinous" species (jellyfishes and salps –planktonic tunicates-) may control in some ecosystems but not in other most zooplankton preys, consuming 10-59% of the zooplankton daily (Nova Scotia)
- some planktonts show a density-dependent control of abundance in some instances but not in other (see fig.).

It results from these factors that large differences occur between ecosystems in the prevalence of carnivorous or herbivorous species (see table).

Nekton

Most data deal with fishes, cetaceans, and birds.

Teleostean fishes are the more studied due to the economical importance of fisheries. Most Teleosteans are opportunist species that follow an r strategy. They produce huge numbers of small-sized planktonic larvae (≤ 1 mm). These larvae are submitted to heavy predation by numerous trophic levels during their development and are dependent on currents. The survival till maturity is very low (10/million). This survival is generally density-dependent, indicating food limitation in larvae (bottom-up control) (see fig). This is combined with very variable recruitments into the adult population according to years (in most cases this is controlled by hydrodynamic factors). Interestingly, both the recruitment success and the growth rate of juveniles are independent of adult population density indicating that there is probably no food-limitation in adult populations (see fig.). This also indicates a disconnection between larval and adult ecologies. Actually, teleostean fishes are mainly controlled by predators (top-down control) among which man is the most important for numerous species.

Birds and mammals

Contrary to teleosteans, birds and mammals follow a K strategy. They produce few offspring, take care of youngsters, in some case for protracted periods of time, which reduces juvenile mortality, age at first reproduction is delayed, and life is usually long. Their role in the structure of pelagic communities is rather poorly known. However, the effects of whaling in the Antarctic Ocean provide a full-scale experiment. Industrial whaling lasted from 1920 till 1970, until most whale populations crashed. This resulted, in Antarctica in a reduction of prey (mainly krill) consumption by whales of 75%. Interestingly, the four krill-eating penguin species increased in parallel to the reduction of whale populations (see table). Similarly, the population of two seal species also increased. This strongly suggests that these species were limited by food through competition with whales (bottom-up control).

Further evidence indicates that whale themselves were competing for food. The modal size of fin whales landed just after the Second World War was smaller than those catched later (see fig). The arrest of whaling during the war allowed an increase in the fin whale population, which induced an increased competition for food and a reduced growth.

These data show that pelagic mammals and birds are controlled by bottom-up mechanisms. This suggests that they have a strong influence on the structure of the communities to which belong their preys. As they are K species, they are particularly prone to overexploitation by predators, in this case mainly man. This anthropic overexploitation is so important that it is, from the ecological point of view, very difficult to separate the impact of fisheries from other control mechanisms.

Case study: the Antarctic Ocean

1. Physico-chemical environment

1.1. Water masses and circulation

The Antarctic continent has a surface of 14 millions km^2. It is surrounded by a continental shelf which is four times deeper (500-900m) than usual, due to isostasic subsidence caused by the weight of the ice that caps most of the continent (24.10^{15} T).This shelf is also narrower (30-200 km) than usual (with the exception of Ross and Weddell Seas). These characteristics favour water exchange between offshore and coastal zones. The basins are also usually deeper (≥ 3000m).

The Antarctic Ocean totally encircles the continent, which ensures some homogeneity. Two main currents flow around Antarctica (see fig.). The East Wind Drift is located between the continent and 60°S; it is generated by polar east winds and flows anti-clockwise around the continent. The east Wind Drift is not continuous: it is mainly developed east from the Weddell Sea and at the level of the Ross Sea. The West Wind Drift or Antarctic Circumpolar Current (ACC) is located between 60 and 40°S. It is generated by westerlies and flows clockwise. ACC is the main circulation system of Antarctic water masses and the largest current in the world (flow rate is 130 millions m^3/sec). The two currents flowing in opposite directions generate a divergence, the so-called Antarctic divergence that results in an oceanic upwelling. Upwelled water is the Circumpolar Deep Water (CDP) that arises from the North Atlantic deep water through the conveyor belt. CDP has a high salinity (>34.7PSU, a rather high temperature (1.6 – 2.5°C) and is poor in oxygen (4-5ml/l). CDW will mix with Ice Shelf Water (ISW) on the one hand and with Antarctic Surface Water (ASW). ISW is a coastal cold water mass which, once mixed with CDW, will sink and form the Antarctic Bottom Water (ABW), whose salinity is 34.65PSU and temperature –0.9°C. This is one of the main sources of bottom water in the global ocean. Its signature can be recognized as far as 5°S (see fig). Winter ASW, formed during the freezing of ice has a rather low salinity (34.2 – 34.5 PSU) and a very low temperature (-1.8°C). Summer ASW, formed during ice melting has, therefore, a lower salinity (<34 PSU). As a consequence, winter ASW flows below summer ASW, at depths between 50 and 300m.

Between 50 and 60°S, "warm" Subantarctic Surface Water (SSW) meets ASW. The latter, 2 to 4°C colder sinks and forms the Antarctic Intermediate Water (AIW) of rather low salinity (34.2PSU) and rich in oxygen (5-7ml/l). AIW can be recognized until 20°N. The zone where the two water masses (SSW and ASW) meet is the so-called Antarctic convergence or polar front. This corresponds to the northern limit of the Antarctic Ocean. The area between the Antarctic and Subtropical (40°S) convergences is the Subantarctic zone. The Southern Ocean extends from the Subtropical convergence to the Antarctic continent. (Notice that English-speaking authors no more speak o the Antarctic ocean but only of the Southern Ocean despite the fact that the polar front is a true hydrological and biological barrier, especially for plankton.

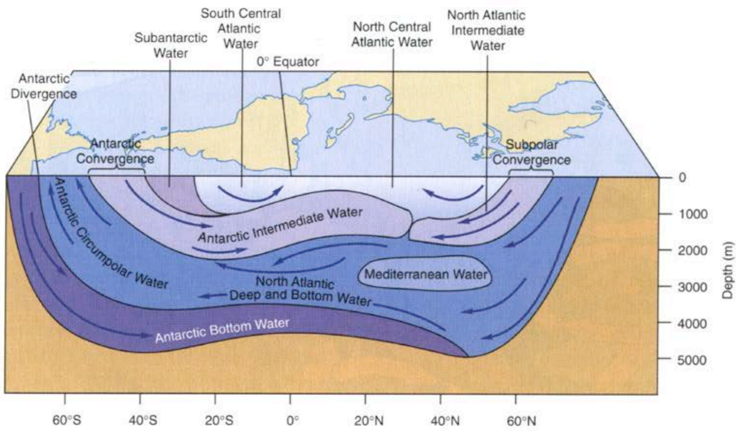


FIGURE 8–27 A vertical cross section of the Atlantic Ocean shows the various water masses that form layers at different depths. Antarctic Bottom Water is the densest water mass and it flows northward from around Antarctica. North Atlantic Bottom Water sinks near Greenland and flows southward over the top of the Antarctic Bottom Water. Intermediate depth water masses are formed and sink at the Antarctic and subpolar convergences. The near surface layers are more complex. Note the tongue of Mediterranean Water that spreads across the North Atlantic Ocean from the Straits of Gibraltar at about 2-3,000 m depth between 20°N and 55°N.

1.2. Light

Antarctica experiences a particularly marked day length cycle. At 75°S for instance, there are 100 days of continuous night (see fig). A second characteristic very influential on light availability in the water column is the extent of sae ice. This is maximum from June to September, covering 56% of he Southern Ocean and minimum from January to March (covering 17.5% of the Southern Ocean) (see fig). Of course, it directly influences available photosynthetic active radiations (PAR) (see fig.).

2. Primary production

2.1. Producers

The main primary producers of the Antarctic Ocean of the nanophytoplankton are flagellates (Prasinophyceae, Cryptophyceae, Prymnesiophyceae, Cryptomonas being the most abundant genus). Among microphytoplanktonts, centric diatoms (Bacillariophyceae) of the genus Corethron, Thalassiosira, Rhizosolenia, and Fragilariopsis are the most frequent together with Phaeocystis colonies (Prymnesiophyceae) (see figs).

2.2. Factors controlling primary production

2.2.1. Light

Due to the photoperiod and ice cover, primary production only occurs in the spring and summer with a single peak of production (see fig.). If ice cover is higher than 20%, no bloom occurs and nanophytoplanktonic communities develop.

2.2.2. Wind

Strong winds are frequent over the Antarctic Ocean due to its continuity (winds may "turn" around Antarctica without continent to stop them). They are also fluctuating a lot over time scales of weeks. They directly influence the mixing depth (see fig.). If wind speed is higher than 8m/sec no bloom develops and nanophytoplanktonic communities are favoured.

2.2.3. Nutrients

Macronutrients
Due to the Antarctic divergence, the Antarctic Ocean surface waters are rich in nitrate (32.5μM), phosphate (2.5μM) and silicate (100μM) (see fig for comparison with other regions of the world).

Micronutrients
On the contrary, iron is generally present at low concentration (<1nM) except in neritic zones (Weddell and Ross Seas), in the plume of Drake passage, and in the marginal ice zones (see table). This prevents diatom blooming in most regions of the Antarctic Ocean: these microphytoplanktonts require 2nM dissolved Fe to bloom (see fig). The shortage in Fe is the reason for the offshore Antarctic Ocean being a HNLC ecosystem. This was clearly demonstrated by mesoscale enrichment experiments (over 200km^2) that brought dissolved Fe to concentrations of 1-3nM for a transient period. This enrichment resulted in a first response of the system (increased photosynthetic competency) after 24h and in increases of biomass (x6) and primary production (x3) after 3 to 4 days (see fig). Picoeucaryotes and prymnesiophytes were the first to increase but a shift in the community occurred after 6 days when the diatom *Fragilariopsis kerguelensis* bloomed.
Due to this limitation in iron, primary production in the Antarctic Ocean is usually below 1gC/m^2.day (mean: 0.3 gC/m^2.day). In comparison the Peruvian upwelling shows production of 2.7 gC/m^2.day. Based on available nitrate and without Fe limitation, primary production in the Antarctic Ocean could reach 2.2 gC/m^2.day.

3. Consumers

3.1. The microbial loop

The microbial loop is, as usual, initiated by autotrophic nanoflagellates consumed by microflagellates and whose dissolved and particulate organic material is used by bacteria, themselves consumed by heterotrophic nanoflagellates which are also consumed by microflagellates (see fig). The microflagellates control the production of autotrophic nanoflagellates preventing them to bloom.
The budget of the marginal ice zone (integrated on the 70 days of biological activity) show that 88% of the net primary production (29 gC/m^2) is assimilated by the microbial loop (see fig). The net secondary production of the microbial loop is 8 gC/m^2 (which corresponds to an efficiency of 25%) and the primary production not ingested by the microbial loop is 4 gC/m^2. So, a maximum of 12 gC/m^2 is available for the linear food chain. This means that the possible export of this system is low. This is even more pronounced in offshore waters where production available for the linear food chain does not exceed 8.5 gC/m^2.

Thus, conditions favouring the nanophytoplanktonic communities will favour the microbial loop which in turn control these communities, preventing their blooming.

3.2. The linear food chain

The linear food chain is initiated by microphytoplankton blooms whose main consumer is krill (see fig.).

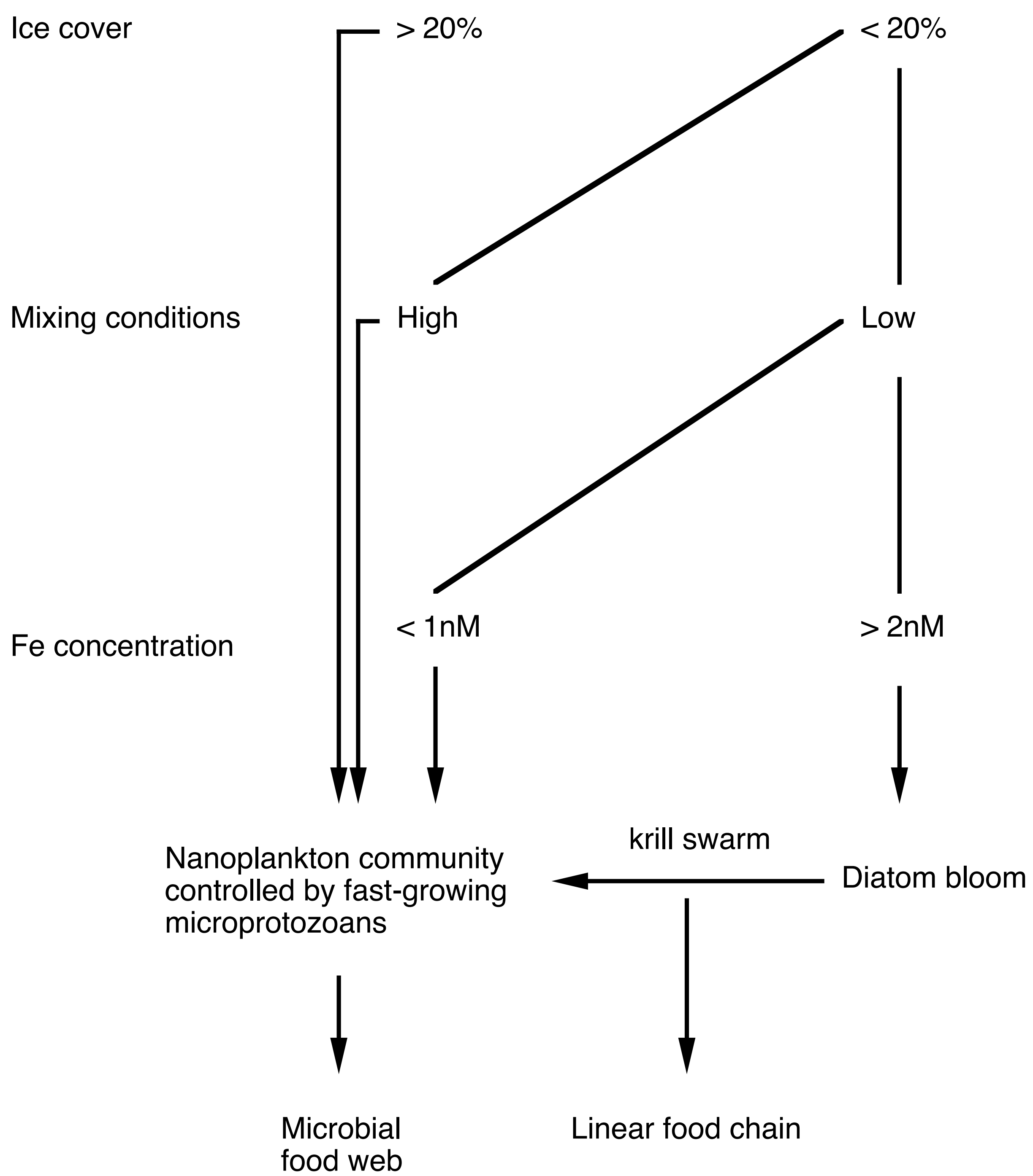
3.2.1. Krill

The most abundant species is *Euphausia superba*. It belongs to the class Malacostraceans, order Euphausiacea. Adults are 6.5 cm long and weight ca. 1gFW. Its life span is 4 to 7 years. *E.superba* is able to swim at ca 1km/h, which makes it able of autonomous movements in the water column. Krill is thus at the limit between plankton and nekton. They form swarms which may reach several millions tons. Krill shows an aggregative distribution that corresponds to zones of microphytoplankton blooms (see fig.) This distribution makes it difficult to establish budgets for this species. Knox tentatively estimated total krill biomass in the Antarctic Ocean to be in the order of 10^8 T. Taking 500 10^6 T as mean estimate, and a supposed production-biomass ratio between 0.8 and 2.77, he reached an estimated secondary production for krill of 400 to 1385 10^6 T/year.

The gregarious behaviour of krill allows them to consume rapidly microphytoplankton blooms and to actually terminate them (see fig). As a consequence, these blooms are most often short-lived. Swarm grazing eradicates the whole microplankton community. Microphytoplankton does not recover as iron is exported together with the grazed algae. Microplanktonic heterotrophs are also seriously depleted by krill. Therefore, the nanophytoplankton is able to bloom before being progressively controlled by the slowly recovering microprotozoans (see fig.).

Thus, microphytoplankton may bloom in iron-rich zones if light and mixing conditions are appropriate. These blooms are usually short-lived due to grazing by krill swarms. After such grazing, a nanophytoplankton bloom may develop until it is eventually controlled by grazing microplanktonts.

Controls on primary production in the Antarctic Ocean



3.2.2. Higher rank consumers

Krill is the main prey of most higher rank consumers. Therefore, it is the principal link between primary producers and other consumers, playing a pivotal role in the Antarctic Ocean ecosystem. Krill consumers include cetaceans, seals, cephalopods, birds, and fishes.

Taxa	Krill consumption (10^6 T/year)	
	Lower estimate	Higher estimate
Cetaceans (baleen whales)	34	43
Seals (crabeater seal *Lobodon carcinophagus)*	64	129
Cephalopods (principally squids of the order Oegopsidea)	30	50
Birds (penguins accounting for 90% of the biomass of and 86% of the food consumed by Antarctic birds)	25	50
Fishes (*Champsocephalus gunnari Notothenia rossii*)	10 ?	20 ?
Total	**163**	**292**

Using Knox's minimum and maximum estimates of krill production (see 3.2.1), consumption of krill ranges between 11. 8% (163/1385) and 73% (292/400) of the annual krill production. This indicates that these consumers are possibly food-limited (bottom-up control). This is further emphasized by the estimated krill consumption by baleen whales before industrial whaling: 190 10^6 T/year, meaning 13.7 to 47.5% of the krill production.

Benthic biological processes

1. Divisions of the benthic environment

The benthic environment is divided into zones according to their position on the shore (intertidal zones), available light and depth.

Tide level or depth	Zone	Characteristics
	Supralittoral	Saline moistening Continuous emersion except at extreme high waters of spring tide
Mean high water of spring tide		
	Mesolittoral	Daily cycles of immersion and emersion
Mean low water of neap tide		
	Infralittoral	Continuous immersion except at low waters of spring tide
Compensation depth of seagrasses or photophilic algae 15-20m at high latitudes 30-40 m Mediterranean 80 m intertropical regions		
	Circalittoral	
Compensation depth of the algae tolerating the lowest light intensities (150-200m)		
	Bathyal	Continental slope and its foothills
2500-3000m		
	Abyssal	Abyssal plains Hydrothermal vents
6000-6500m		
	Hadal	Deep trenches

2. Primary producers

2.1. Main taxa

Domain Bacteria
Cyanobacteria make multicellular assemblages. They are able to fix atmospheric nitrogen if they are in anaerobic conditions. Therefore, they build multicellular mats, often on mudflats (but these also occur on rocky substrates) whose interstitial water is anoxic. They can be symbionts of marine angiosperm rhizomes (which benefit from the N_2 fixed by the bacteria. Main pigments include chlorophyll a (absorbs red), phycocyanin (absorbs blue) and phycoerythrin (absorbs green).
Chemosynthetic bacteria do not obtain their energy from light but from reduced substrates, originally fixed by photosynthesis; therefore this is usually regarded as regenerated production. It is noteworthy that these bacteria need both reduced compounds and oxygen for their metabolism. For this reason they often live at the boundary between oxic and anoxic zones. A particular case is the chemosynthetic bacteria from hydrothermal vents that are using reduced sulphur compounds of geothermal origin; this results in true new production.

Domain Eukarya
Reign Chromista (chlorophyll a and c)
The *microphytobenthos* principally includes pennate diatoms (Ph Heterokonta, Cl Bacillariophyceae) that are often mixotrophic. They form algal mats on mudflats.
The *Phaeophyceae* (Ph Heterokonta; brown algae) contain fucoxanthi, xantophyll and carotene (the last two groups of pigments being responsible for their colour). They absorb green and yellow. They are the dominant algae of intertidal zones and rocky infralittoral, whatever the latitude.

Reign Protozoa (chlorophyll a and c)
Coral reefs include endosymbiotic zooxanthellae (Ph Dinophyta, genus *Symbiodinium*) that make them important primary producers.

Reign Plantae (chlorophyll a and b)

The *Chlorophyta* (green algae) absorb red and blue. They generally have a low capacity for storing nutrients. For this reason, they mainly occur in nutrient-rich habitats, in particular eutrophicated areas.

The *Rhodophyta* (red algae) contain chlorophyll d, phycoerythrin (responsible for their red colour, absorbs green), and phycocyanin (absorbs blue)

The *marine angiosperms* (Ph. Spermatophyta; flowering plants) (see fig.) are generally encountered on soft substrates. They include seagrasses which are living submerged most of the time (genus *Zostera, Posidonia, Thalassia*), saltmarsh plants (*Spartina, Salicornia*) and mangrove trees that replace saltmarsh plants in sheltered habitat with soft substrate in tropical environments (*Avicennia, Rhizophora*).

Notice that macroalgae belong to very different taxonomic groups!

2.2. Factors controlling benthic primary production

2.2.1. Light

As for pelagic primary producers, the production of benthic primary producers is a function of light intensity (see fig.), including photoinhibition at high intensities. However, the latter is less pronounced that for pelagic producers due to shading by fronds or leaf tissues. Due to light absorption by water (and possibly particles), benthic autotrophs are limited in depth as pelagic producers. However, due to their sessile character, their compensation depth is the same as the critical depth.

Different light wavelengths are not absorbed by water in the same way (see fig.). As different taxa do not contain the same pigments, their vertical distribution will differ. Seagrasses and green algae will be limited to shallow depths. On the contrary, red algae that are able to absorb blue and green lights and will be the deepest encountered algae. Moreover, their pigments are adapted to low light intensities.

2.2.2. Nutrients

Algae are limited by nutrients, especially nitrogen, when these are low in the water column as demonstrated by enrichment experiments(see figs). Angiosperms have roots and are therefore able to take up nutrients from the interstitial water of sediments where their concentrations are usually high. However in some periods of the year uptake of nutrients by competing primary producers (microphytobenthos, epiphytes) may render these limiting (see course on the Posidonia ecosystem). Also, if sediments are anoxic, transport mechanisms are inhibited by sulphide and nutrients may become unavailable and therefore limiting.

2.2.3. Emersion

In the intertidal zone, emersion results in desiccation, warming and salinity fluctuations, all factors that affect production and vertical zonation. These aspects will not be addressed in the present course.

2.2.4. Substrate

The nature of substrate (soft vs. rocky) will influence the primary producers that will develop. Macroalgae are more frequent on rocky substrates on which they settle thanks to holdfasts while most angiosperms are rooted in soft substrates.

Notice that there is no clear-cut difference between soft and rocky substrates. The functional limit is linked to the mobility of particles. This will depend on their size and weight but also on hydrodynamism in the considered zone. In general particles larger than 2cm and richly colonized by sessile organisms will be considered as a rocky substrate.

2.2.5. Exposure

Hydrodynamic forces will influence the composition of communities and/or the growth of the primary producers. Different species or morphologies will be encountered on exposed or sheltered shores.

2.2.6. Biotic interactions

The structure of communities is deeply influenced by biotic interactions. These include intra- and interspecific competition and grazing. Two classical examples are the tide pools on rocky shores of New England and the kelp forests of the NE Pacific.

In tide pools of New England, available algae are *Enteromorpha intestinalis* (a green alga) and *Chondrus crispus* (a red alga). The main grazer is the common periwinkle *Littorina littorea* whose preferred food is *E.intestinalis*. The latter is abundant in tide pools where there are few periwinkles and *Chondrus* is the dominant specie sin pools with numerous snails. To determine if differences in seaweed species composition were caused by the different grazer abundances, experimental alterations were carried out by Lubchenco. All periwinkles were removed from a pool where *Chondrus* was dominant. This caused *Enteromorpha* to quickly settle on *Chondrus* (together with ephemeral algae) and to outgrow the latter that disappeared after one summer (see fig.). In another pool dominated by *Enteromorpha*, *Littorina* were added. This severely reduced the abundance of the green alga and some ephemeral became abundant in winter, when snails were less active. *Chondrus* did not recover due to the low recruitment rate of this species. In an untreated control pool, the abundance of *Chondrus* remained high trough the 1.5 year of the study. These experiments show that the grazer controls the composition of the producer community, allowing the less competitive species to become dominant. The latter is then determined by other factors like light and nutrients.

Kelp forests off California consist in the canopy-forming giant kelp *Macrocystis pyrifera* and two understory kelp species *Laminaria dentigera* and *Pterygophora californica*. The main grazer is the sea urchin *Strongylocentrotus franciscanus* whose preferred food is the giant kelp, then other kelps and, if those are not available, detritus and algal turf. In 1976, a disease decimated the population of sea urchins. Soon after, the density of *Macrocystis* increased markedly (see fig.) and by 1977 only about 1% of the light at the surface reached the bottom. This caused intraspecific competition for light due to self-shading by the giant kelp and eventually resulted in a decline in the numbers of *Macrocystis*. However, the number of fronds on the surviving kelp increased, so that the total biomass of giant kelp remained significantly higher after the mass mortality of sea urchins. The two understory kelp species increased rapidly after sea urchins died but they decreased in abundance to almost zero in subsequent years due to shading by *Macrocystis*. Here we have an example of control of the producer by grazing with subsequent competition for light between primary producers. In some documented cases this control may go as far as to graze out the kelp bed. In this case, it is rather difficult for the kelp community to re-establish, since the urchins remain, feeding on detritus, algae and benthic fauna. This results in a new totally different equilibrium (barren grounds) that may persist for many years.

In both examples, the food preference of the grazer (due to the absence of efficient phytochemical defence of some producer) results in the overgrazing of this producer, the less favoured producer species being controlled by competitive interactions. In both cases, the control process is top-down.

3. Benthic consumers

3.1. Classification

3.1.1. According to localization

- epifauna: the whole organism or most of it are localized above the water-substrate interface
- endofauna: organisms living below this interface; these can be burrowers, perforators (in rocky substrates) or interstitial (living and moving in interstitial water between sediment particles.

3.1.2. According to size

Size limits (depending on authors)	
	Macrofauna
2 – 0.5 mm	
	Meiofauna
100 – 40 μm	
	Microfauna

3.1.3. According to diet

- suspensivorous: feeding on particles caught in the water column
- depositivorous: feeding on sediment
- herbivorous: feeding on primary producers
- carnivorous: feeding on consumers
- detritivorous: feeding detritus

Notice that the different categories are not all mutually exclusive.

3.2. Factors controlling benthic consumers

3.2.1. Emersion

The factors affecting primary producers in the intertidal zone are also controlling the consumer communities that are also presenting a zonation depending on physiological adaptations of the members of the community. This is particularly obvious on rocky shores.

3.2.2. Substrate

On *rocky shores*, the main problem for consumers is to resist to hydrodynamic constraints that will depend on the exposure mode, the slope of the substrate and microtopography (cracks, caves etc.)

Physical and chemical characteristics of *sediments* will affect their associated fauna. Physical characteristics include the particle size distribution and porosity. Particle size will directly influence the benthic life habits. For instance, very fine sediments will be too unstable for large size organism that will be unable to maintain their position. Gravels will contain very few organic fine particles and will therefore be unsuitable for depositivorous organisms. Sediments may also be homogenous ("well-sorted") or inhomogeneous ("poorly sorted"). The porosity is the ratio between interstitial volume and total volume. It will directly control the oxygenation of the sediment through diffusion rate. It will also influence the meiofauna living in the interstitial volume.

Chemical characteristics are dependent on oxygen that is diffusing from the water-sediment interface and on the action of bacteria. Aerobic bacteria consume oxygen in the upper layers of the sediment. Therefore, oxygen concentration in interstitial water progressively decreases with depth in the sediment. This causes a modification of the redox potential that is usually brutal (see fig.), the so-called redox potential discontinuity (RPD). The RPD zone is the interface between oxic and anoxic layers of the sediment. The depth of the RPD will depend on water motion above the sediment (favouring oxygen diffusion) and the porosity of the sediment. This gradient in redox potential induces a vertical zonation of sediment microorganisms. In the oxic layer, aerobic microorganisms, possibly photosynthetic occur. The RPD zone is occupied by chemosynthetic sulphur bacteria that need both H_2S and oxygen. Below the RPD zone the general vertical succession is as follows. Fermenting bacteria, which use organic compounds and produce fatty acids and alcohol are the first encountered. Then, come sulphate-reducing bacteria that reduce sulphate to H_2S (which will diffuse upwards and be used by sulphur bacteria). Methanogenic bacteria are the deepest; they break down organic substrates and produce methane.

Eukaryotes will be mainly restricted to the oxic zone. However, some ciliates (Odontostomatida) containing endosymbiotic anaerobic bacteria are able to live permanently below the RPD. Some Metazoa are also found below the RPD, namely nematodes, turbellarians, gnathostomulida, rotifera, and gastrotriches (see fig.). However, it is not clear if they are living permanently below the RPD and if they are able to live only on an anaerobic metabolism. The whole community found below the RPD was called by Fenchel and Riedl the thiobios.

It is noteworthy that the RPD is not always horizontal due to the activity of bioturbators (see fig.). These will not only affect the oxygen distribution in the sediment but they will also increase the heterogeneity of the sediment due to, for instance, selective feeding on some particle sizes. They will also structure the sediment (tube building) and take part in the transfer of particulate organic matter to deeper layer through burying or mixing (see fig.).

3.2.3. Biotic interactions

Rocky substrates

In heading 2.2.6 we considered the role of sea urchins in the control of kelp forests. The main predator of sea urchins was the sea otter (*Enhydra lutris*) that was distributed from Japan and Aleutian Islands to Southern California. The species was quasi extirpated by hunting for fur in the 19th and first half of the 20th centuries. At present, the sea otter occurs mainly in certain islands off Alaska and as a remnant population in Central California. On average, an otter weighs 23kg and consumes 20 to 30% of its body weight in food every day (sea otters have no blubber and need to have a very high metabolism to maintain their temperature). In the Aleutian islands some islands still have a sea otter population (Amchitka) while others do not (Shemya). In Amchitka, the population is dense (20-30 individuals/km^2). Algae almost completely cover the substratum, density of sea urchins is low with small size classes being dominant and found in cracks (see fig.). In Shemya, on the contrary, there is no subtidal algal cover and the density of sea urchins is high (up to >400ind/m^2) with large size classes being well developed (see fig.). This study was extended to many other locations in Alaska, clearly showing that the absence of otters is always highly correlated with a low cover of kelp (see fig.). Follows up of the recolonization of some islands also showed shifts from low to high algal covers with some variability due to the frequency of sea urchin recruitment.

These studies clearly demonstrated that sea otters do control sea urchin populations by predation and, therefore, indirectly, the primary production. This system is actually one of the best studied examples of trophic cascade in the benthic domain. Otter, in this case, is a so-called "keystone-species" (*sensu* Paine), that means a species whose impact on the ecosystem is not proportional to its biomass. Notice that this is different from a "dominant species" whose importance is immediately proportional to its biomass (kelp are dominant species of the kelp forests).

In the tide pools of New England (heading 2.2.6), the main predators are the dog whelk (*Nucella lapillus*) and the starfish *Asterias forbesi*. Their main preys are the barnacle *Balanus balanoides* and the blue mussel *Mytilus edulis*. The two latter compete for space with the red alga *Chondrus crispus*. To understand the interactions between these species, Lubchenco and Menge carried out different experiments. In a first set of experiments, plots were cleared of all sessile organisms (see fig.). In cleared areas with no further manipulations ("control" in the fig), the mussel settled but did not survive predation for very long, and *Chondrus* became the dominant species. Where stainless-steel cages excluding the dog whelk and starfish were installed on cleared plots, *Mytilu*s survived and was able to outcompete the barnacle in a short time. In other cleared plots with cages, the mussels were removed; this allowed *Balanus* to settle and eventually to grow into the most abundant species. In cages where mussels were removed and barnacles reduced in density, *Chondrus*, after some initial coexistence with *Balanus*, became dominant. Thus, at least as colonizers of bare substrates, the competitive hierarchy is (1) *Mytilus*, (2) *Balanus*, (3) *Chondrus*. In places where predators are naturally absent, such as in sites exposed to severe wave action, *Mytilus* is the most abundant species. In protected sites, predators are not swept away or damaged by waves, and their presence prevents their preferred preys from monopolizing space. *Chondrus* can then colonize.

Another set of experiments was carried out in plots where stands of *Chondrus* were already established (see fig.).Cages excluding predators allowed the recruitment of *Mytilus* and growth of these eventually resulted in the exclusion of *Chondrus* from the plot.

So, in both experiment series, if predators are present (as on sheltered shores), they control the abundance of the dominant competitors and colonization by algae is possible. This corresponds to a top-down control. If predators are absent (as on exposed shores), the dominant competitor occupies the space available.

Soft bottoms

On soft bottoms, the main predators are usually fishes and crabs. If these are prevented to enter plots by cages, the biomass of macroinvertebrates in the cage remains high during all the growing season while in the absence of cage, it rapidly decreases (see fig.). Contrary to the situation on rocky shores, exclusion of the predators on soft bottoms does not have much impact on the competition between preys probably due to the fact that these are not sessile.