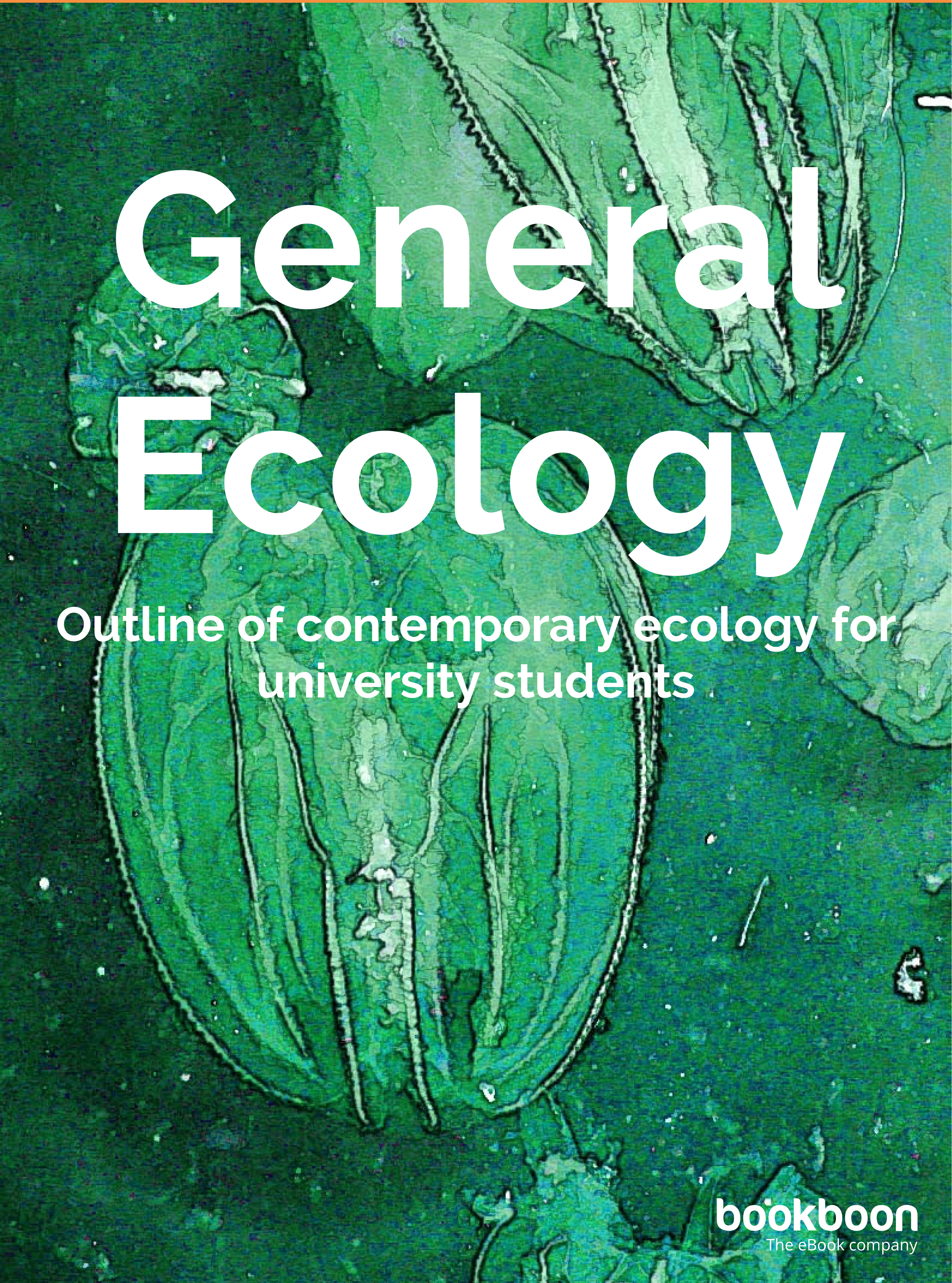
Hans Ulrik Riisgård

General Ecology

Outline of contemporary ecology for university students



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HANS ULRIK RIISGÅRD

GENERAL ECOLOGY

OUTLINE OF CONTEMPORARY ECOLOGY FOR UNIVERSITY STUDENTS

General Ecology: Outline of contemporary ecology for university students
1st edition

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Photo on front page is taken by the author and shows the invasive comb jelly, *Mnemiopsis leidyi*, which lives naturally off the US East Coast, but via ballast water from ships, it found its way to the Black Sea in the late 1980s, and to the Dutch coast in 2006.

CONTENTS

PREFACE

This book is written to meet the need for a concise textbook of ecology. The book describes the basic features of the modern ecology and is addressed to college students without special biological knowledge. The book can be used in high schools, technical colleges and other places of study where ecology forms part of the education, but where time does not permit a major review of the many ecological topics. This ecology book does not deal with 'species ecology' or autecology, i.e. single species relation to their surroundings, although these factors may be of importance for the understanding of many ecological conditions. The book deals not particularly with pollution and environmental problems, which in many people's consciousness is almost synonymous with ecology, but touches on many such topics and provides the foundation for a basic understanding of many of today's urgent environmental problems. For the sake of clarity, the number of references to textbooks, original articles, etc. is kept to a minimum, and for reasons of space references are indicated by a number in parentheses [ ] corresponding to reference number in the reference list.

Thanks are due to Tom Fenchel, Professor of Ecology, University of Copenhagen, for constructive critism of the manuscript, and to Kirstin Anderson Hansen and Josephine Goldstein for linguistic corrections and technical assistance, respectively.

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1 ECOLOGY AND ECOSYSTEMS

The word ecology is derived from the Greek word "oikos" meaning house, combined with "logy" meaning the learning of ecology and can therefore be translated to "the learning of nature's household", though the word ecology is not of ancient Greek origin. The term ecology was first used in 1869 by the German biologist Ernst Haeckel. The concept of ecology only slowly increased, and well into the 20th century it was still almost unknown outside the group of professional biologists. It was especially botanists, who first used the word ecology but later also by zoologists. It has been much debated how ecology should be defined and distinguished from related fields. Ecology has previously been defined as "the study of the distribution and amount of organisms in an area. This definition of ecology, which some people still use, is different from the one most commonly use today. In the following, there is first given a definition of the modern ecology succeeded by a brief description of what is meant by an ecosystem.

1.1 ECOLOGY AND BIOSYSTEMS

It has become customary to define ecology as "the science of biological systems above the organism level". This definition and delimitation of modern ecology is illustrated in Fig. 1, showing the different levels of organization (cell, organ, individual, population, community) and how these living (biotic) components interacts with the non-living (abiotic) components (matter and energy).

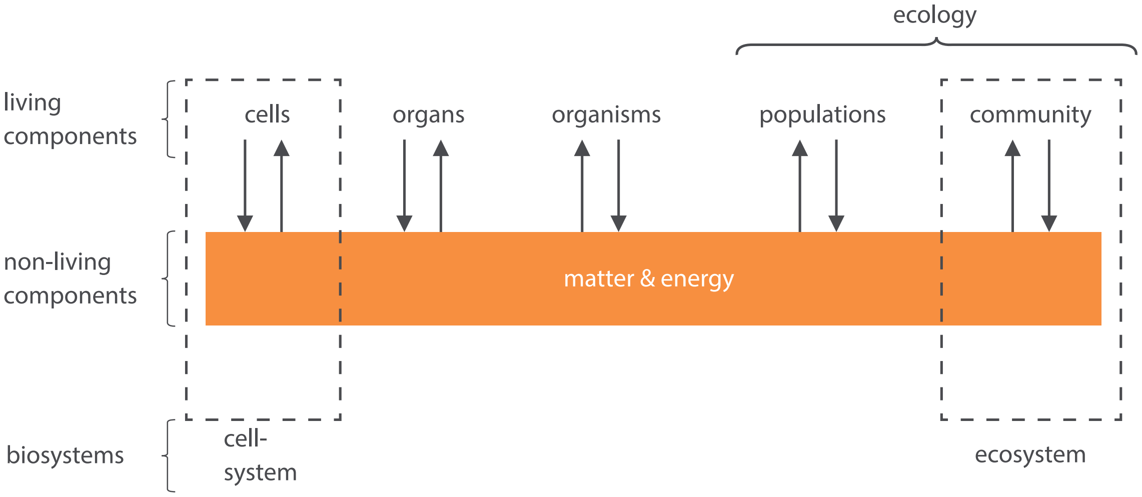


Fig. 1. Living components in interaction with the non-living (abiotic) components are called biosystems. Ecology is defined as the science of biological systems (biosystems) above the organism level [1].

The living and the nonliving components are together called for biosystems. The highest level of organization is the community, which consists of all animals, plants and microorganisms in a given area. A community that functions together with the abiotic components of a biosystem is called an ecological system or ecosystem. When moving from a biosystem to another at a higher level of organisation, characteristic properties emerge that were not present on the lower level of organization. This phenomenon is known as the "integrative level concept" or the "hierarchical control principle", which says that when biotic and biotic components are integrated to form larger functional units in a hierarchical (ranked) series, new properties emerge [1]. Thus, when moving from organism systems to population systems and further to ecosystems, new characteristic properties are developed which were not present at the previous level of organization. By recognizing the specific characteristics of a given organization, can this level can be studied without necessarily knowing everything about the neighbouring organisation levels. For example it is possible to study ecology at the ecosystem level without first studying cell biology and physiology. But how do you study a large complicated ecosystem? As with the study of any other level of organization, you begin with a description of simplified models that contains only the main components and basic functions of the biosystem in question.

1.2 ECOSYSTEM CONCEPT

An ideal ecosystem is a closed – but not isolated – biosystem with all of its biotic and abiotic components flowing through with energy. You can imagine an ideal ecosystem as an illuminated aquarium, see Fig. 2.

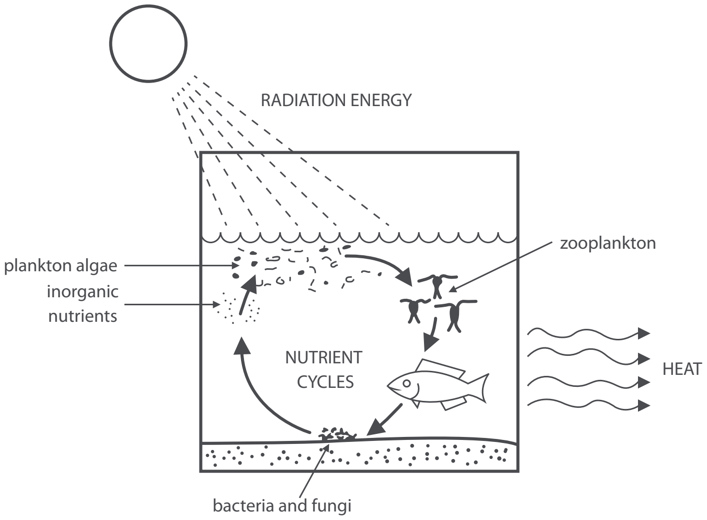


Fig. 2. Simplified model of an aquatic ecosystem. An ecosystem has a number of characteristics: 1) cyclic transformation of the chemical components, 2) a flow of energy through the system, 3) the energy flow rate determines the transformation speed of the substances.

In the aquarium there are living organisms: primary producers (phytoplankton), consumers (zooplankton, fish), decomposers (including bacteria and fungi) and abiotic components (water, oxygen, carbon dioxide, phosphate, nitrogen compounds, dead organic matter etc.). Primary producers (plankton algae) synthesizes organic matter, using light energy and inorganic nutrients. Plankton algae are "grazed" by filter-feeding zooplankton (copepods, daphnia, etc.), which in turn are eaten by fish. Dead algae, animals and faeces, which sink to the bottom, are degraded by bacteria and other organisms, releasing inorganic nutrients that primary producers can exploit. The biological activity of the ecosystem gives rise to a production of heat that is leaving the system by radiation. The system's chemical components remain on the other hand, in the system and are cyclically transformed. The velocity of this substance's transformation is determined by the flow of energy through the system. If the system is isolated so that it does not receive energy and no energy can leave, the cycling will stop and the structure of the ecosystem will disintegrate. An example of an ideal ecosystem is the biosphere, which consists of the entire Earth's surface containing life. Most natural ecosystems are, to a greater or lesser extent different from the ideal, depending on the mass and energy exchange with neighbouring ecosystems. Fairly well-defined ecosystems are lakes, forests, fjords, the sea – or a rotten tree stump in a forest, if you are interested in the turnover and interaction between microorganisms and the small animals that live here. The limits of an ecosystem is rather arbitrary and in practice, determined by an ecologist's choice of working objective.

2 ENERGY FLOW IN ECOSYSTEMS

The biosphere is dependent on solar energy that reaches the earth's surface as solar radiation. This chapter explains how sunlight reaches the Earth's surface and how the plants here utilize sunlight for new production (primary production) of organic matter that form the basis of energy for the ecosystem food chains.

2.1 SOLAR RADIATION AND GLOBAL ENERGY BALANCE

Solar radiation consists of electromagnetic waves which are created when hydrogen nuclei in the sun fusion at very high temperatures. The sunbeam spectrum is very wide, but almost all the radiation energy is in the visible light between the ultraviolet and the infrared spectrum, see Fig. 3.

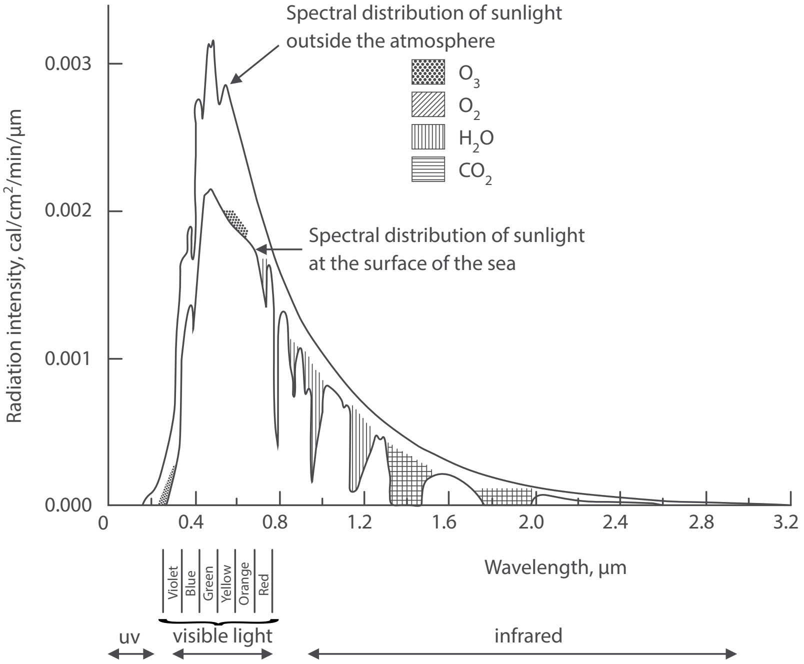


Fig. 3. The spectral distribution of the sun's electromagnetic radiation is altered by passage through the Earth's atmosphere: almost all the deadly ultraviolet radiation (UV) is absorbed by ozone (O_3) in the stratosphere, while carbon dioxide (CO_2) and water vapour (H_2O) absorb a very significant part of the infrared radiation. The figure shows the spectral distribution of the solar radiation outside the atmosphere and at sea level. Shadings indicate some of the most important gases' selective absorption of certain wavelengths [3].

When sun's radiation passes through the atmosphere, the radiation spectrum changes considerably. At 10–50 km altitude (the stratosphere) there is an ozone layer, which absorbs almost all the ultraviolet (UV) radiation that would otherwise have a killing effect on life on land. Ultraviolet radiation has sufficient energy to break down important biological molecules and can therefore, even in minor amounts damage crops and cause skin cancer. Ozone (O_3) is formed when oxygen (O_2) by absorption of ultraviolet light. is split to the two reactive oxygen atoms (O) that soon react with intact oxygen molecules to form ozone. Ozone is a gas, which readily absorb UV light and split (dissociate) into O_2 and O. The released oxygen atom can now react with another oxygen molecule whereby ozone is regenerated. This process of splitting and regeneration can take place many times until the ozone molecule eventually collides with a free-oxygen atom, thereby forming two stable oxygen molecules. Under constant conditions, the result is a dynamic equilibrium in which the formation and degradation rates of ozone are equal. It is this balance that determines the thickness of the ozone layer.

In 1985, British scientists reported that the concentration of ozone in the atmosphere over Antarctica in the spring was reduced by 40% in the years from1977 to 1984 ("ozone hole"). Intense research quickly revealed that ozone depletion, which was also later detected in the northern hemisphere, was due to man-made chlorofluorocarbons (CFCs or "freon"), used for example in cooling liquids in refrigerators and propellants in aerosol spray cans and additives in plastic foam. The large amounts of CFCs, which over the years had been released to the atmosphere, in conjunction with long atmospheric lifetimes (up to several hundred years) for many CFC gases, puts the problem of ozone depletion into perspective. CFCs have been considered as ideal chemicals for industrial use because they are stable, unreactive and non-toxic. But when CFCs. by upward air streams are brought into the stratosphere, they are broken down by the strong ultraviolet radiation and release chlorine atoms that break down the ozone layer. CFCs have given mankind a persistent environmental problem that even extensive international agreements is difficult to reduce, over a long period of time. But there is reason for optimism. The Montreal Protocol is an international agreement to protect the ozone layer around the Earth by phasing out the production of CFCs. The historic agreement entered into force in 1989 and is one of the most successful international agreements to date. This phasing out of CFCs has in 2015, resulted in the first observation of an incipient reduction in the size of the Antarctic ozone hole [2].

In addition to ozone, oxygen, water vapour and carbon dioxide can also selectively absorb radiation at certain wavelengths [3]. Thus, carbon dioxide and water vapour absorb a large part of the incoming infrared radiation. The main part of the solar radiation that reaches the Earth's surface, is in the visible spectrum between 0.4–0.8 µm, see Fig. 3. It is this part of the spectrum (especially the red and blue light) that the green plants can utilize for photosynthesis. On average, the Earth emits a similar amount of radiation energy into space as the atmosphere and Earth's surface absorb incoming solar radiation, see Fig. 4. This energy balance determines the global average temperature, which is approximately 15 °C [4].

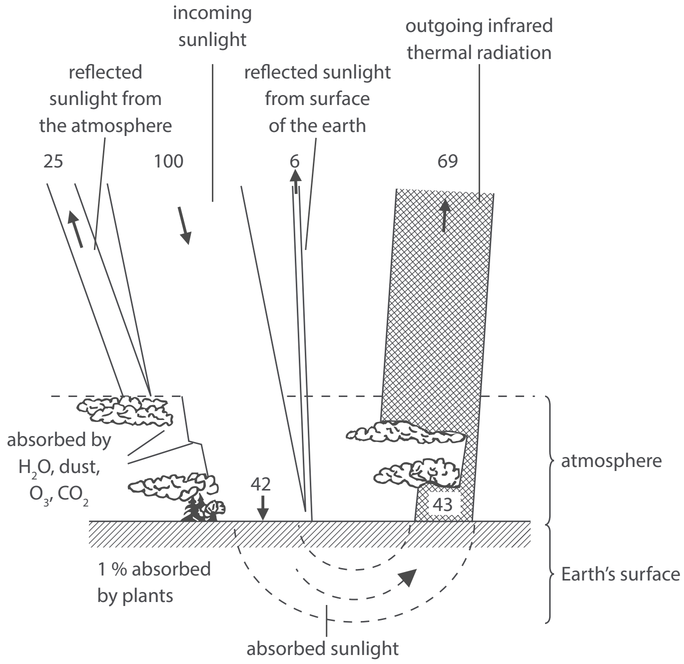


Fig. 4. The global energy balance. The energy of the incoming solar radiation is set at 100. Note that the fraction of the incoming short-wave solar radiation that is not reflected, leaves the biosphere as infrared heat radiation [4].

About 30% of the incoming solar radiation is reflected to space by clouds, dust particles and gases in the atmosphere, or snow, desert sand, etc. at ground level. The part of the incoming solar radiation reflected to space (the Earth albedo) increases if dust and soot particle concentration in the atmosphere increases (which can be caused by pollution, volcanic eruptions, and nuclear explosions). This could lead to shorter or prolonged decline in global average temperature. The part of the sun's shortwave radiation energy that is absorbed in and at ground level (40–45%) is emitted again from the ground as longwave infrared radiation ("heat radiation"). Most of this radiation is absorbed and re-emitted repeatedly by atmospheric water vapour, carbon dioxide, dust and ozone before it reaches out into space. This warms up the atmosphere, and the effect is called "greenhouse-effect" because the atmosphere – like glass in a greenhouse – is readily permeable to the short wavelength solar radiation but relatively impermeable to longwave infrared radiation. Only about 1% of the incoming solar radiation is used by the green plants for photosynthesis. The remainder of the solar energy is absorbed mainly in the earth's surface where it is converted (transformed) into heat energy, which in turn is emitted to the atmosphere as infrared heat radiation. This energy is not lost because the heat radiation makes the Earth habitable for living organisms by e.g. heating up the atmosphere, creating winds, clouds and precipitation, which is essential for life on land [5].

2.2 PRIMARY PRODUCTION AND PRODUCTIVITY

The fraction of light energy that is absorbed by the green plants is by photosynthesis converted to chemically bound energy in the produced organic matter. The photosynthesis process takes place in the chloroplasts of the plants and can be described by the following reaction:

$$CO_2 + 2H_2O^* \rightarrow (CH_2O) + O_2^* + H_2O$$

or

$$nCO_2 + 2nH_2O^* \rightarrow (C_nH_{2n}O_n) + nO_2^* + nH_2O$$

for example

$$6CO_2 + 12H_2O^* \rightarrow (C_6H_{12}O_6) + 6O_2^* + 6H_2O$$

where * indicates that the formed oxygen derives from the water; the example shows the formation of glucose.

By means of photosynthesis, land plants take up atmospheric CO_2 which is incorporated into simple carbohydrates (CH_2O) during concurrent production of O_2 being released to the surroundings. The produced carbohydrates (sugars) are used partly as energy suppliers for the plants' own metabolism (respiration), whereby the organic matter is oxidized to CO_2 and H_2O during release of energy, and partly as suppliers of energy for production of new cells and for storage. The total amount of organic matter produced by photosynthesis is called gross primary production, while the share of production that is left when the metabolism is covered is called net primary production, see Fig. 5.

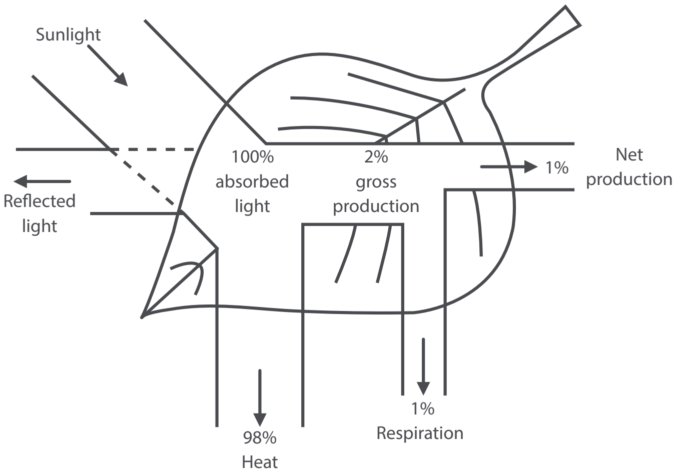


Fig. 5. The flow of energy through a land plant. Approximately 2% of the absorbed light energy goes to gross primary production, half of which goes back to the plant's own metabolism (respiration). In nature, the net primary production is about half as large as the gross primary production – which means that to about 1% of the absorbed light energy is bound as chemical energy in organic matter that can be exploited by the primary consumers in the grazing food chain or the decomposers in the detritus food chain.

About 50% of the sunlight that hits a plant is absorbed. Approximately 2% of this absorbed light is used for gross primary production. In nature, plants use around 50% of the gross primary production for their own metabolism (respiration). However, by using energy-consuming work, the consumption for metabolism may be reduced (by supplying essential trace elements, nutrients, water, or by removing competing plants), making it possible to strongly reduce the plants' own energy needs. In agriculture, it is not uncommon that the net production is up to 90% of the gross production.

2.3 FOOD CHAINS

The transfer of energy from plants to animals is done through a number of links called a food chain. Organisms located at the same step in relation to the food source are said to be on the same trophic level. The trophic classification is based on function – not on species that often can be placed on multiple trophic levels depending on the food choices.

The living organisms in an ecosystem can according to their function and place in the system, be divided into four main groups:

1) Primary producers – autotrophic (green plants convert solar energy into chemical energy bound in organic matter using photosynthesis.
2) Herbivores (lat.: herba = herb, vorare = swallow) – plant eaters or "grazers"; are also called the primary consumers.
3) Carnivores (lat.: carnis = meat) – predators. Since some predators feed on herbivores, while others feed on other predators (carnivores), we distinguish between primary carnivores that eat herbivorous animals, and secondary, tertiary etc. carnivores that eat other predators. Depending on their position relative to the primary consumers, carnivores are also called secondary, tertiary, etc. consumers. Because the herbivores' and carnivores' energy ultimately comes from the autotrophic organisms' primary production, they are also called secondary producers.
4) Decomposers or detritivores (fungi, bacteria, etc.) that can utilise the energy of dead organic material (detritus).

There are two types of food chains, "grazing food chains" and "detritus food chains". The two types of food chains are shown in Fig. 6. The grazing food chain consists of primary producers, herbivores and carnivores. The detritus food chain consists of detritivores that feed on dead organic matter from the grazing food chain, and the animals that live in part of the detritivore organisms as well as of other animals. In the detritus food chain, it is impossible to distinguish clearly between the trophic levels because there are no well-defined food chains but complicated food webs.

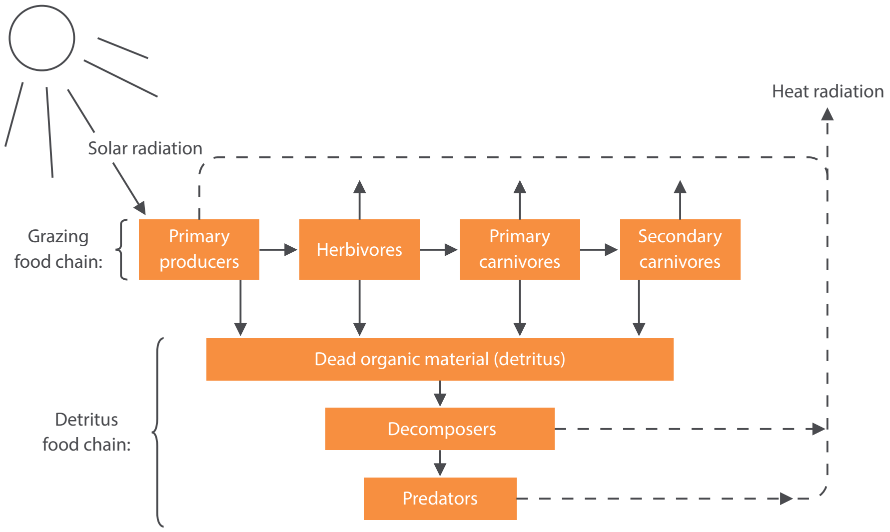


Fig. 6. As the organic matter produced by the primary producers is transported through the grazing and detritus food chains (solid arrows), it is burned off in the organisms by their metabolism, releasing energy that leaves the ecosystem as heat radiation

2.4 BIOENERGETICS

Bioenergetics is concerned with examining how the living organisms absorbs food, digests and distributes consumed or synthesized substance and energy for maintenance (metabolism = respiration) and production (new cells, storage, reproduction). The flow of energy through a population can be determined from knowledge of the individual organism's bioenergetics, with extrapolation from a single organism to all the organisms in a population. It is therefore often interesting to know how effective a given organism utilizes a given quantity of food for production because such knowledge can provide information on how much food energy that is available to the next link in the food chain. To calculate the efficiency of dietary utilization of an organism you need to know the organism's energy budget [6]. In Fig. 7 it is shown the fate of food energy in an animal consumer (e.g. a mammal or fish). It is noted that the amount of energy production (P) can be expressed as the difference between energy in assimilated food ($A = I - F$, where I = energy in ingested food, and F = energy in faeces, urin etc.) and respiration (R):

$$P = I - F - R = A - R \tag{I}$$

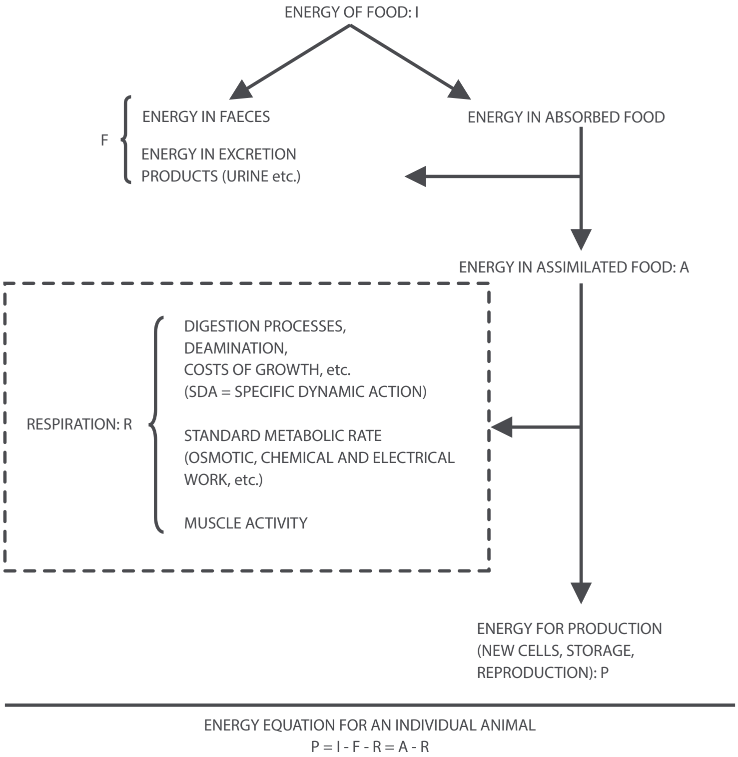


Fig. 7. The fate of food energy an animal, e.g. a mammal or a fish. It is seen that the amount of energy available for growth can be expressed as the assimilated food energy minus the energy consumption for the metabolism (often measured as the organism's oxygen consumption = respiration). It appears that the metabolism covers many ill-defined energy items which cannot be measured or are difficult to measure separately [6].

In Fig. 8 is shown a universal model of the energy flow through an organism or through a population [1].

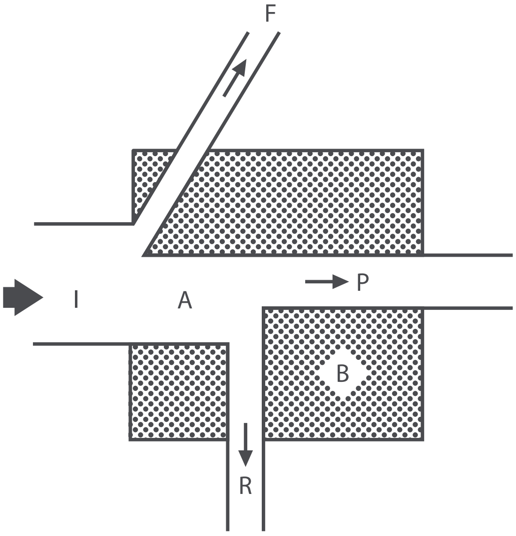


Fig. 8. Universal model of energy flow through an organism, a population, or through a trophic level. I = energy content of food consumed, F = energy content of faeces, urine and other excretory products, A = assimilated food energy, R = metabolism (respiration), P = energy to production, B = biomass.

A parameter of great ecological interest is the assimilation efficiency (AE), defined as:

$$AE = A/I \qquad \text{(II)}$$

where $A = I - F$ or $A = P + R$.

The assimilation efficiency vary widely among different organisms depending on type of food. The assimilation efficiency of predators is often close to 100%, while the herbivores and detrivores have lower efficiencies (often less than 10%). Another efficiency of ecological interest is the net growth efficiency (NGE), which expresses how much of the assimilated food energy (A) that can be used for production:

$$NGE = P/A \qquad \text{(III)}$$

If a blue mussel, for example, has a net growth efficiency of 67% this means that ⅔ of the assimilated food energy can be used for production of animal material, which is available to the next link in the food chain.

The production of a population is the amount of energy stored as organic matter per unit of time, regardless whether this substance is lost for the population along the way due to death, lost skin cells etc. A population may therefore have a production even if you cannot detect any differences in population weight (biomass). The production of natural populations can be determined using various methods. Three methods are mentioned in the following:

1) An often used method is based on determination of the population's energy budget. With knowledge of the parameters of the energy equation for individuals belonging to the different size classes of the population you can, when the population size and age structure is known, determine production of the population as the difference between the total amounts of food assimilated by the population and the total respiration of the population.
2) The production of a population can be determined from knowledge of the individual growth curve and with regular determination of the size and age structure of the population. A particularly simple situation exists when one wishes to determine the production of a population comprising a single generation (e.g. annual insects) or a single brood. To determine the production of such a population a survival curve is required. This is determined by counting the population at various times (t) and an individual growth curve, see Fig. 9.

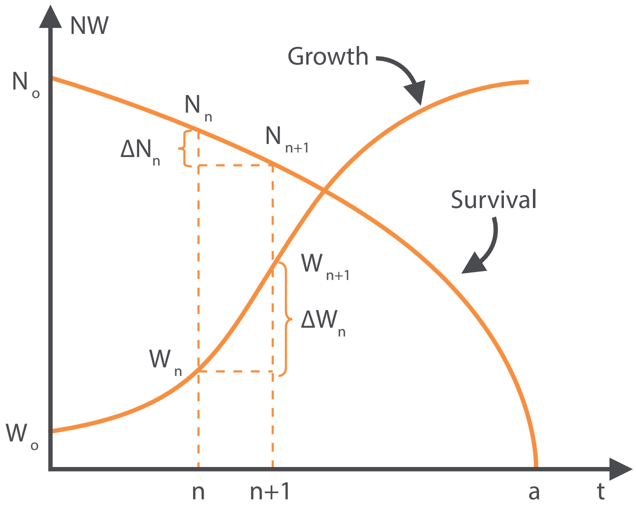


Fig. 9. Based on knowledge of the individual growth-curve and survival-curve for a population of one litter or a single generation (e.g. annual insects), it is possible to calculate the production of the population over a given period of time. Explanation of all terms, see the text.

If ΔN_n is the number of individuals that have died in the period $t_n - t_{n+1}$ and ΔW_n is the individual growth during the same period, the production of the died individuals in this period approximately = $(\Delta N_n \times \Delta W_n)/2$, as individuals on average die midway through the period. The production of the surviving individuals is = $N_{n+1} \times \Delta W_n$. The whole production ($P_n$) in the period $t_n - t_{n+1}$ then becomes: $P_n = N_{n+1} \times \Delta W_n + (\Delta N_n \times \Delta W_n)/2$, and the entire population production (P) is determined as:

$$P = \sum_{n=0}^{n=a} P_n$$

where a is the maximum life expectancy.

3) If the biomass of a population is called B and the biomass eliminated from the population in a given period is denoted E, then during this time there has been a production $P = \Delta B + E$, as illustrated in Fig. 10.

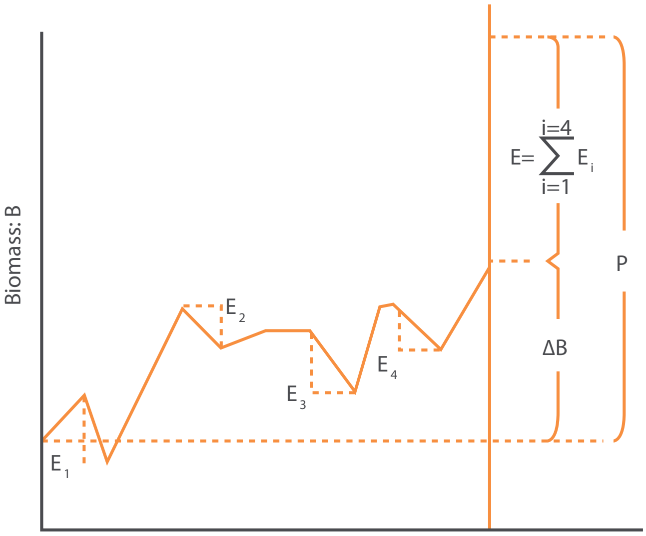


Fig. 10. The production of a population (P) can be determined by summing the changes in biomass (ΔB) and the total biomass eliminated (E) over a given period of time (t). The eliminated biomass may represent dead individuals, casted skin, etc., and can be found by determining the biomass of the population at appropriately frequent time intervals, so that any decrease in biomass (E_1, E_2, E_3 … E_i) is recorded resulting in the sum of these being equal to E.

2.5 ECOLOGICAL EFFICIENCIES

Figure 11 shows with realistic figures the flow of energy through three trophic levels in a theoretical grazing food chain. The simplified diagram shows how energy (as heat and detritus) is lost in and between each link in the food chain. The relationships between energy flows both within and between trophic levels have significant ecological interest. Such relationships are called "ecological efficiencies" and are expressed as percentages. Table 1 lists and defines some of the most frequently used ecological efficiencies. Experience shows that the various efficiencies are often confused with misunderstandings as a result. There is no agreed standard use of symbols; but the notation used in Fig. 11 is frequently seen.

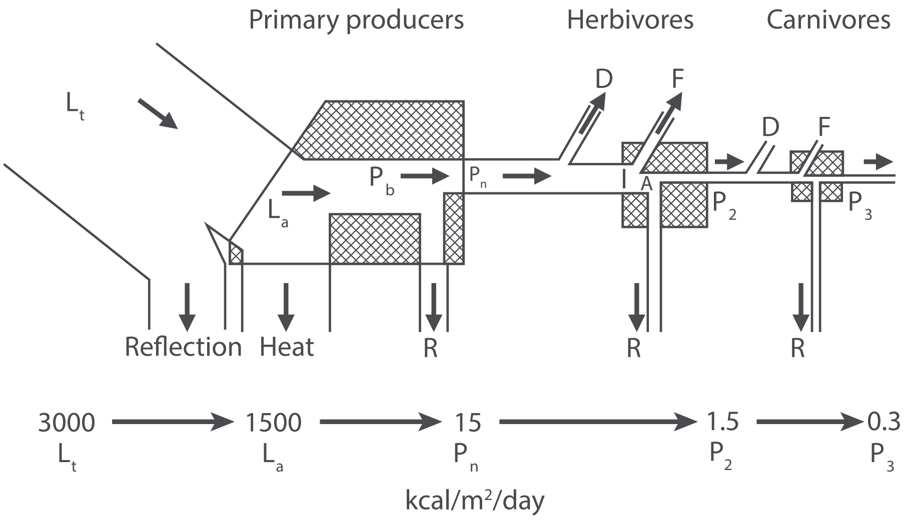


Fig. 11. The flow of energy through three trophic levels in a theoretical grazing food chain consisting of primary producers, herbivores and carnivores. L_t = total light energy L_a = absorbed light energy, P_b = gross primary production, P_n = primary production, R = respiration, I = ingested food energy, A = assimilated food energy, F = not assimilated food energy (feces, urine, etc.), D = detritus, P_2 and P_3 = secondary and tertiary production [1].

The more simple notation used in Fig. 12, which does not pay special regard to the primary producers, provides a quick overview and facilitate the definition of the ecological efficiencies in Table 1. As shown, it is important to accurately define the relationship that should be expressed when using ecological efficiencies. The trophic level production efficiencies in Fig. 11 is thus in the order of 10% ($P_2/P_1 = P_2/P_n = 1.5/15 = 0.1$) for the second, and about 20% ($P_3/P_2 = 0.3/1.5 = 0.2$) for the third food chain link. As can be seen, it is limited how many links there can be in a food chain. In practice, food chains have rarely more than 3–4 links.

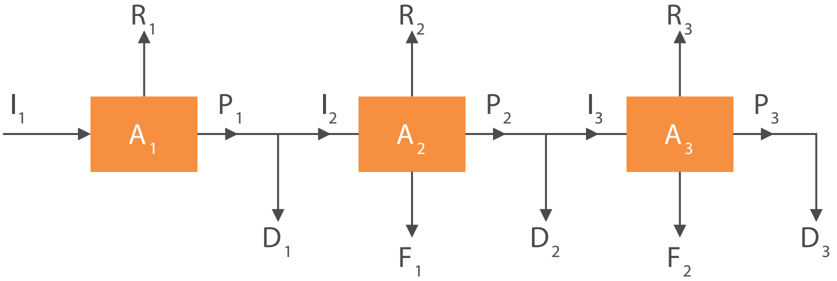


Fig. 12. Linear grazing food chain consisting of three trophic levels: 1: primary producers (plants), 2: herbivores, 3: carnivores. I: consumed energy; A: assimilated energy; R: respiration; P: production; D: loss from the food chain (detritus); F: not assimilated food energy (faeces, urine, etc.). Both D and F supply the decomposers (i.e. the detritus food chain).

Relationship between trophic levels:

I_t/I_{t-1}: efficiency of trophic level energy intake

A_t/A_{t-1}: trophic level assimilation efficiency

P_t/ P_{t-1}: trophic level production efficiency

I_t/P_{t-1}: utilization efficiency

Relationships within trophic levels:

P_t/A_t: production efficiency

P_t/I_t: ecological growth efficiency

A_t/I_t: assimilation efficiency

Tabel 1. Definitions of ecological efficiencies for relationships between and within trophic levels. For explanation of symbols used, see Fig. 12.

Figure 13 shows a natural ecosystem, namely the Silver Springs which is a popular tourist attraction in Florida. It is seen that the primary producers' ecological net-production-efficiency is 2% ($P_1/ I_1 = P_n/L_a = 8833 /410{,}000 = 0.02$). The herbivores' trophic level assimilation efficiency is 16%. ($A_2/A_1 = A_2/P_b = 3{,}368/20{,}810 = 0.16$), whereas the primary carnivores' trophic level assimilation efficiency is 11% ($383/3{,}368 = 0.11$). Moreover, the majority of the primary production goes through the detritus food chain, and that $(4.600/5.060)\times100 = 91\%$ of this energy is released from the ecosystem as heat. A large export relative to the import (mostly bread that tourists throw out to the fish) shows that the ecosystem produces more organic material than it uses for respiration. Such an ecosystem in which the production (P) is greater than the respiration (R) is called an autotrophic ecosystem.

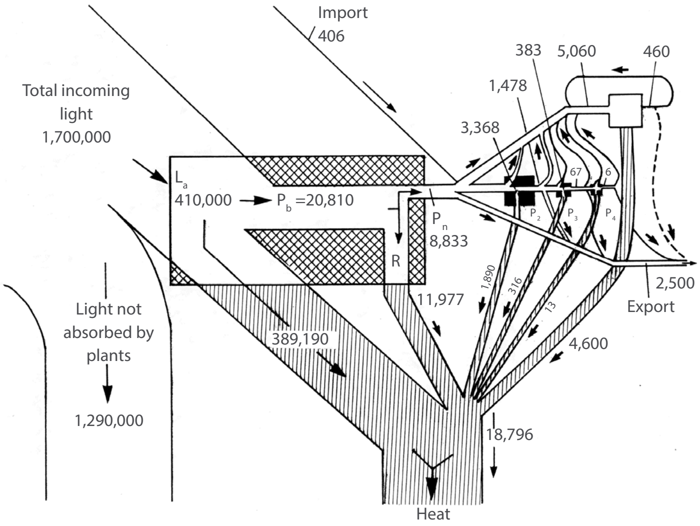


Fig. 13. The flow of energy through an aquatic ecosystem, "Silver Springs", Florida. L_a = absorbed light energy, P_b = gross primary production, P_n = primary production, R = respiration, P_2 = herbivores, P_3 = primary carnivores, P_4 = secondary carnivores, D = detrivores ("decomposers"). It is noted that the largest part of net primary production goes through the detritus food chain [1, 7]. All figures are in kcal/m²/year.

An ecosystem where P is less than R is called heterotrophic. An often used graphical way to show how the chemically bound energy in a grazing food chain decreases is to build an "energy pyramid" where the width of each step of the pyramid, which represents a trophic level, is a measure of the assimilated energy in the organisms belonging to that trophic level, see Fig. 14.

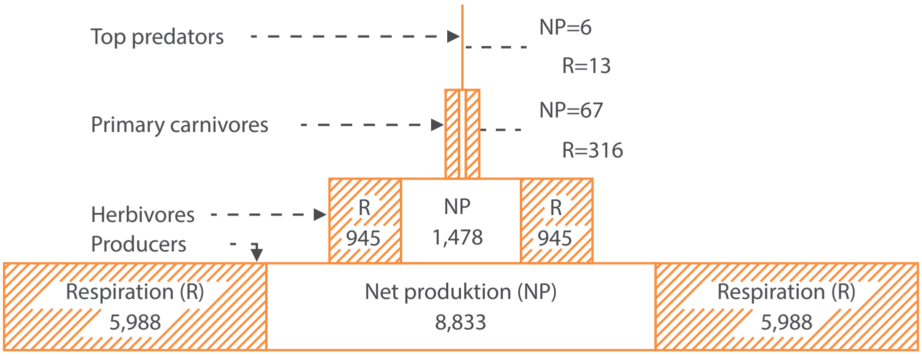


Fig. 14. Energy pyramid, based on data from the grazing food chain in "Silver Springs", see fig. 13. The energy pyramid shows how the assimilated energy is used for respiration (R) and net production (NP) at each trophic level [7].

2.6 BIOMAGNIFICATION OF POLLUTANTS

Chemical substances (pollutants) that are difficult to decompose (persistent) and at the same time fat-soluble, tend to accumulate (biomagnify) in the food chains because these substances may effectively be transferred from link to link in the food chain. At the same time there is a combustion of biomass which becomes smaller and smaller, while the concentration of pollutants become correspondingly higher in each link of the food chain. The insect poison DDT, now banned in most industrialized countries, is an example of a substance that can be biomagnified and thereby cause damage in the higher links of food chains. DDT and its breakdown products are believed to be primarily responsible for the observation that since 1945, North American and English peregrines as well as Swedish ospreys have laid eggs with thinner shells [8, 9]. For a time the population of these predatory birds in Sweden was directly threatened, because the thin-shelled eggs broke during incubation. Since the use of DDT was banned in Sweden and neighboring countries in the 1960s, eggshells have become thicker and the population of ospreys is now re-establishing itself. Another example of a substance that can biomagnify is the insecticide DDD, which was much used in the U.S.A. after World War II, to eradicate mosquito larvae in Clear Lake near San Francisco. Deaths among fish-eating birds in 1957 led to investigations, which showed that DDD was biomagnified in the lake's food chains. The concentration compared to the lake water was 265 times in the plankton, 500 times in small fish, 85,000 times in carnivorous fish, and 80–125,000 times in fish-eating birds [9].

Monomethyl mercury (CH_3Hg^+) can be mentioned as a final example of a chemical substance that is biomagnified. Severe cases of polluting of lakes and rivers with mercury in Sweden in the late 1950s, and the deaths of several hundred people in Japan in the mid-1960s, as well as an extensive mercury pollution of the waters around Harboøre Tange in Denmark, caused by a chemical factory [10] has led to intensified research in the ecotoxicology of mercury (dispersion, circulation and biological effects in nature). Thus it was discovered that phenylmercuric acetate, earlier used to control fungi in the wood-pulp industry and for staining seed, can be converted by microorganisms to monomethyl mercury which in contrast to inorganic mercury (Hg^{++}), is fat-soluble, highly toxic, and persistent. These properties make monomethyl mercury able to biomagnify in food chains. It must be added that the "classical" description of biomagnification of monomethyl mercury seems to be too simplified because the effectiveness of the degree to which this mercury compound is transferred from link to link in the food chain, is also very much determined by the physiology of the different organisms and their capabilities to detoxify and excrete the toxic substance [11]. Thus, there are major physiological differences (blood circulation, liver and kidney function, etc.) between filter-feeders (mussels, zooplankton) and fish that constitute the important part of aquatic "grazing food chains". Biomagnification of monomethyl mercury cannot be exclusively assumed to be a simple consequence of the ability of the substance to be "burned in the energy pyramid".

3 BIOGEOCHEMICAL CYCLES

All nutrients have their own characteristic biogeochemical cycle. This chapter deals with macro- and micronutrients, as well as short reviews of four major biogeochemical cycles are given.

3.1 SEDIMENTARY AND GASEOUS NUTRIENT CYCLES

In the biological evolution, only certain elements have been used as the atomic building blocks in the living cell. Of the 92 naturally occurring elements, it is now believed that only about 24 are involved in the life processes. The molecular building blocks of the cell, namely proteins, carbohydrates and fats are made up of six relatively light elements: C, H, N, O, P and S.

Five elements, which are also in the light-weight end of the periodic table, help to maintain electroneutrality in body fluids or are used to maintain the electrochemical potential gradients across the cell membrane. The latter is important, for example the impulse conductivity of nerve cells, and for the ability of cells to maintain a constant volume. The elements, which are all found on ion form are: Na, K, Ca, Mg and Cl. A third group of elements, the essential trace elements (Zn, Cu, Co, Mn, Fe, Mo) are only found in the body in very small quantities. These trace elements are necessary for particular the function of many enzymes. All these elements are called nutrients because they are vital (essential) for the living organism. Substances, which are required in large quantity, are called macronutrients (C, H, N, O, P, S, Na, K, Ca, Mg, Cl), while the elements required in small quantities are called micronutrients (especially Zn, Cu, Co, Mn, Fe, Mo, but also Va, In, Se, Si, F, Ba are necessary in some species). All micro- and macronutrients are circulated between the living organisms and the surrounding abiotic environment. Such cycles of nutrients are called biogeochemical cycles. Fig. 15 shows a biogeochemical cycling incorporated in a simple energy flow diagram. This is to show the interaction between energy and material cycling. Energy is required to drive a nutrient cycle.

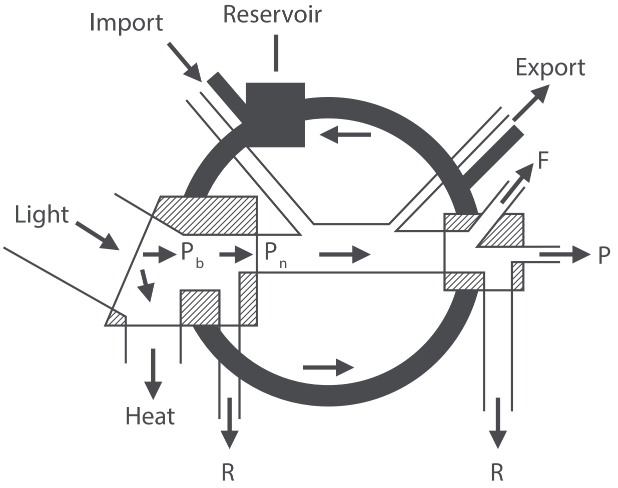


Fig. 15. Biogeochemical cycle built into a simple energy-flow diagram. The circulating material is represented by a circle extending from the primary producers to the consumers and back again. The large reservoir of non-biologically bound substances is shown by a rectangle. P_b = gross primary production, P_n = primary production, P = heterotrophic production, R = respiration, F = not assimilated food energy. Hatched = biomass [1].

It is convenient to distinguish between a large, slow moving non-biological pool and a smaller but more active pool of substances that are exchanged quickly between organisms and the environment. Fig. 15 demonstrates the circulating material represented by a circle extending from the primary producers to the consumers and back again. The large reservoir of non-biologically bound substances is shown by a rectangle. All micro- and macronutrients have their own distinctive cycles, which are divided into two main types:

1) Sedimentary types of cycles where the largest reservoir is found in sediments (e.g. S, P, Ca).
2) Gaseous types of cycles in which the atmosphere is the largest reservoir (e.g. N, C, O).

In the following sections, an outline of some important biogeochemical cycles is given.

3.2 CARBON CYCLE

The carbon compounds in the biosphere are all the time being formed, transformed and decomposed, see Fig. 16 [12, 13]. This dynamic state is maintained by the autotrophic and heterotrophic organisms. The autotrophic organisms (i. e. the green plants and the chemo- and photoautotrophic bacteria) produce organic carbon compounds by reducing CO_2 using energy coming from the sun or from inorganic chemical compounds. The primary producers use a portion of the produced organic material for their own metabolism whereby CO_2 is produced and emitted into the surroundings. The heterotrophic organisms (animals, fungi and decay-bacteria) are powered by breaking down organic matter that is ultimately derived from the autotrophic organisms. As the energy is used up in the food chains, organically bound carbon is released as CO_2 to the atmosphere. On land, the larger plants take up CO_2 (with a concentration of 0.3%)from the atmosphere. From the free air and through the stomata, the CO_2 diffuses into the leaf where the photosynthesis takes place.

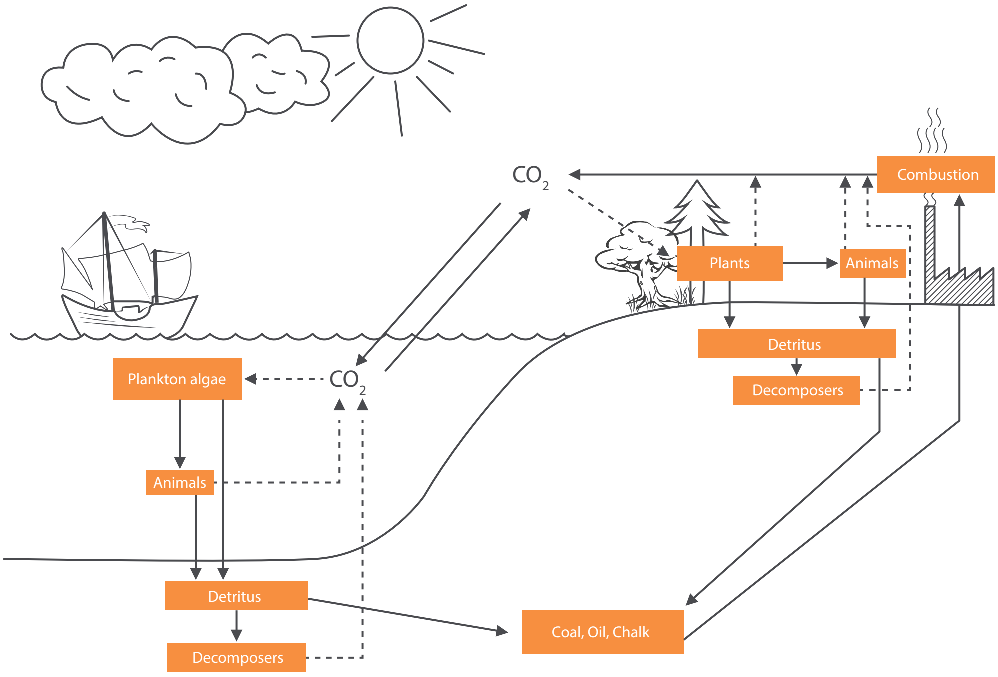


Fig. 16. The biogeochemical cycle of carbon [13].

The uptake of CO_2 by land plants is sometimes so pronounced that it can be detected as a concentration drop in the atmosphere. In the height of a forest canopy on a sunny summer day, a pronounced minimum can be recorded around noon where the photosynthetic activity is at its peak. Variations can also be seen between the seasons, see Fig. 17. In the summer, the CO_2 concentration in the atmosphere is lower than in the winter when the photosynthesis process comes to a standstill or is greatly reduced. Thus, variations in atmospheric CO_2 content can be recorded during day and night, vertically and seasonally.

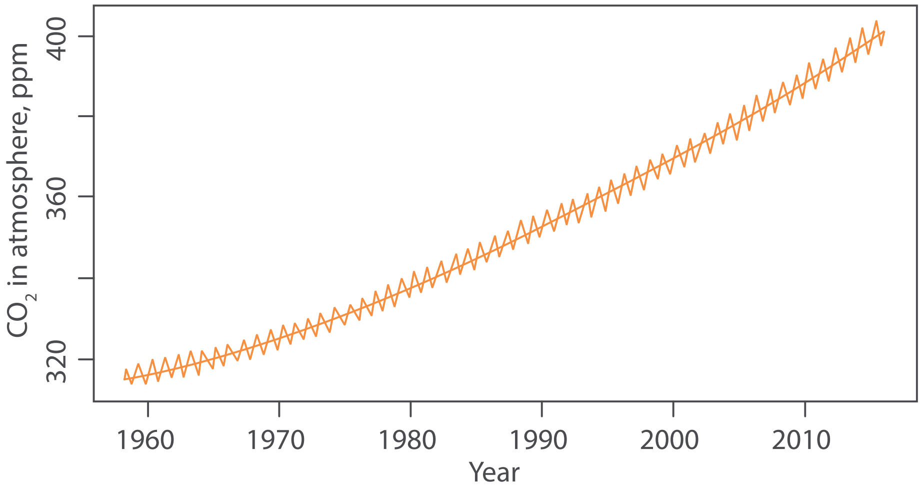


Fig. 17. The concentration (ppm = parts per million = µl/l) of carbon dioxide (CO_2) in the atmosphere has been measured in Hawaii since 1958. Over the 58 years that the figure illustrates, measurements demonstrate a drastic increase in the atmospheric content of carbon dioxide, from about 290 ppm in 1850 to 400 ppm in 2016. Other measurements taken around the world confirm this development of which consequences for the world's climate is unknown. The dashed curve shows the seasonal variation in atmospheric CO_2 content, which is lowest in summer when the plants' photosynthesis and thus CO_2 consumption is highest [12].

In the aquatic environment, conditions are different. Here there are only a few plants that can survive with the limited CO_2 which is dissolved in the water. This is because the diffusion rate of CO_2 in water is only a fraction of the diffusion rate in air. Only the smallest single-celled planktonic algae and mosses with thin leafs can adequately absorb CO_2, by passive diffusion across the outer surfaces. However, the diffusion distances in larger planktonic algae (more than about 30 µm in diameter) and in macroplants are so long that the CO_2 concentration is too low to ensure sufficient photosynthesis. These plants therefore take up CO_2 through the carbonic acid system occurring in water:

$$CO_2 + H_2O \leftrightharpoons H_2CO_3 \leftrightharpoons H^+ + HCO_3^- \leftrightharpoons 2H^+ + CO_3^{--}$$

Aquatic plants that cannot cope with the passive uptake of CO_2 from the surrounding water, actively take up HCO_3^-. In the plants' chloroplasts the enzyme carbonic anhydrase catalyzes the process: $2HCO_3^- \rightarrow CO_2 + H_2O + CO_3^{--}$. The CO_2 that is split off is then used for photosynthesis. The "carbonic acid system" in water implies that the photosynthesis gives rise to a shift to a higher pH in the water, while the supply of CO_2 caused by respiration processes has the opposite effect. Thus, it is well known that the pH increases during the day in the upper layers of water penetrated with light, while it drops during the night. It is well known that pH can drop significantly due to CO_2 production in the bottom sediments, or in the water below light exposed water masses (photic zone), where settling organic materials are being broken down by bacteria. The carbon circulation in the biosphere has two distinct circuits, one on land and one at sea. The total amount of CO_2 that marine phytoplankton take up per year is of the same magnitude as the amount of CO_2 that land plants bind by their gross primary production. The carbon cycle in the ocean is practically self-maintained. However, there is a lively exchange of CO_2 between the atmosphere and the ocean caused by winds and waves, which ensure that the amount of dissolved CO_2 in the oceans' surface layer is in equilibrium with the concentration of CO_2 in the atmosphere. Because the oceans tend to be stratificated (due to thermocline), there is only a limited circulation between the surface water masses and the bottom water. Thus, it takes about 1,000 years to replace the water in the deepest parts of the ocean. In contrast, the CO_2 in the atmosphere is much more quickly circulated. Measurement of radioactive carbon-14 after the nuclear bomb-blasting tests in the early 1960s has shown that the residence time of the CO_2 in the atmosphere before it is dissolved in the sea is about 7 years. The carbon that land plants bind by their photosynthesis is sooner or later returned to the atmosphere when organic matter decomposes in the food chains. The decomposition of the organic matter takes place quickly in the tropics (10–30 years) while the process is much slower in the northern regions (several hundred years).

The photosynthesis by land plants removes annually about 100 billion tons of carbon from the atmosphere in the form of carbon dioxide. Land plant and soil respiration (i.e. total decomposition of organic matter) releases carbon dioxide equivalent to 2 × 50 billion tons per year. Burning of coal and oil (fossil fuel) and the burning of tropical rainforests releases 5 and 2 billion tons of carbon, respectively. Physical and chemical processes at sea level release about 100 billion tons of carbon into the atmosphere while around 104 billion tons are taken up in the oceans. The annual net addition of carbon dioxide to the atmosphere is equivalent to about 3 billion tons of carbon, see Fig. 18. This increase in atmospheric carbon dioxide, which absorbs infrared radiation, results in increasing "greenhouse effect" and thus an increased global temperature. In earlier geological periods the breakdown was less than the amount of carbon fixed, and therefore large amounts of carbon accumulated as coal and oil. But since the beginning of the Industrial Revolution in the mid-1800s, mankind has performed a large-scale global geochemical experiment by burning large quantities of fossil fuels. Since 1850, the atmospheric CO_2 concentration has increased from approximately 290 ppm to nearly 350 ppm in 1990, with about 50% of the increase occurring since the mid-1960s. In 2016, the CO_2 concentration had further increased to 400 ppm for the first time in the last 800,000 years [12].

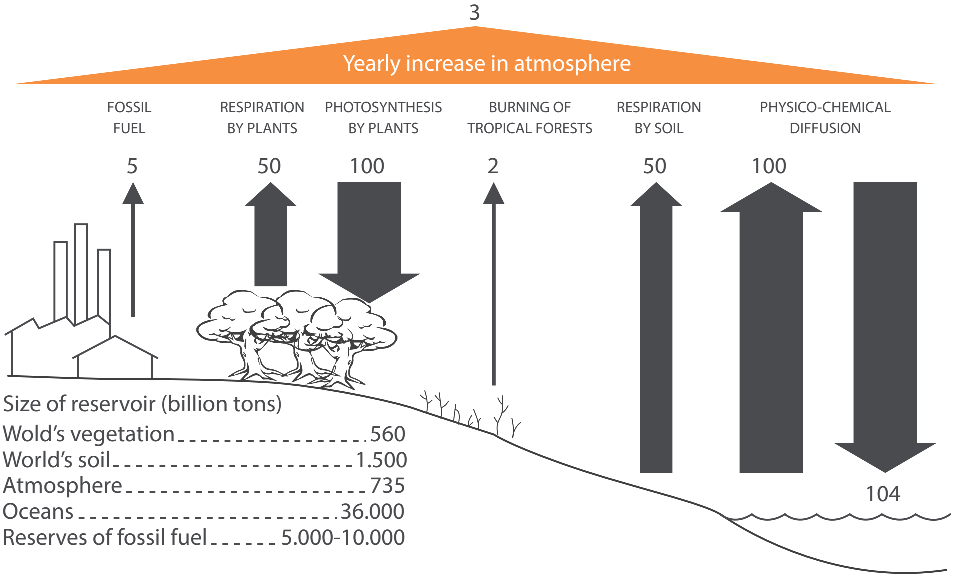


Fig. 18. The global cycle of carbon. All rates are given in billion tons per year [15].

The total increase in the atmospheric content can account for about one third of the total 200 billion tonnes of CO_2, which has so far been released from fossil fuels. Part of the remaining CO_2, have probably been taken up in the oceans, resulting in acidification of the water. Thus, the pH of ocean surface waters has decreased from 8.25 in 1751 to 8.14 in 2004, and the pH may further decline to around 7.85 in 2100, which will result in incalculable damage effects on marine life [14]. But a significant portion of the CO_2 that is not absorbed in the oceans, may very likely result in an increase of the vegetation on land. Studies have shown that plants grow faster when the ambient atmosphere is enriched with CO_2. It is therefore possible that the burning of oil and gas causes a “fertilization” of forests and agricultural areas. However, there is no evidence for this fertilization effect.

3.2.1 INCREASED GREENHOUSE EFFECT

Since 1958 reliable measurements have been made of the atmospheric carbon dioxide content. Fig. 17 shows that the content of carbon dioxide is increasing. It is not currently known to what extent this increase in atmospheric carbon dioxide content will be able to change the world's climate. But there is reason for concern. Calculations have given some evidence that a doubling of atmospheric carbon dioxide content (from 300 ppm to 600 ppm) could raise the Earth's average temperature by 2.5 °C which is enough to melt some of the huge amounts of polar ice and put large areas of land under water, as has been the case in previous warm geological periods. The term "global warming", used in the climate debate, refers to the increase in global average temperature, which has been measured since 1900 and more intensively after 1975. Since 1915 the global temperature has increased by about 0.8 °C. There is evidence that the increase in temperature has already resulted in increased depth to the permafrost in Alaska, smaller maximum spread of ice around Antarctica, and increased withdrawal of European glaciers. If the trend continues, there will be less rainfall at the lower latitudes and more precipitation at higher latitudes. Signs of such a trend have been observed already in the late 1980s [12, 15]. The so-called "greenhouse gases" consist in addition to CO_2 of methane (CH_4), nitrous oxide (N_2O) and chlorofluorocarbons (CFCs). Possible future climatic changes can be assessed by studying the correlation between the atmospheric content of "greenhouse gases" and climatic changes in the past geological periods. Analyses of air bubbles in Antarctic ice cores have been used to study the conditions 160,000 years back. It has been found that there is a "positive feedback" (i.e. an increased effect) between the temperature and the greenhouse gases carbon dioxide and methane. When the temperature goes up (as the last interglacial period) the microbial decomposition of organic matter increases, releasing carbon dioxide. Under anaerobic conditions (swamps, bogs, moist soil) the bacterial decomposition of organic matter takes place by fermentation whereby methane ("swamp gas") is produced. Methane is 20 times more effective than carbon dioxide in absorbing longwave heat radiation from the Earth. An increasing temperature leads to an increased release of "greenhouse gases" and thus an increased temperature. This self-reinforcing warming effect has been called "the respiratory feedback mechanism".

3.3 NITROGEN CYCLE

Nitrogen (N_2) constitutes 79% of the atmosphere, but only few living organisms can utilize this nitrogen directly [16, 60]. Plants and animals can only take advantage of "fixed" nitrogen in form of nitrate (NO_3^-) or ammonia (NH_3). A few species of prokaryotes (characterized by not having a cell nucleus) comprising bacteria, cyanobacteria and actinobacteria are able to fix atmospheric nitrogen. Usually a distinction is made between symbiotic nitrogen collectors (e.g. nodule bacteria on legume plants, *Rhizobium*, and actinomycetes in symbiosis with plants, such as alder, sweet gale, sea buckthorn) and free-living nitrogen collectors (cyanobacteria: *Anabaena*, *Nostoc* and others, and bacteria: *Azotobacter* (aerobic), *Clostridium* (anaerobic)), see Figs. 19 & 20.

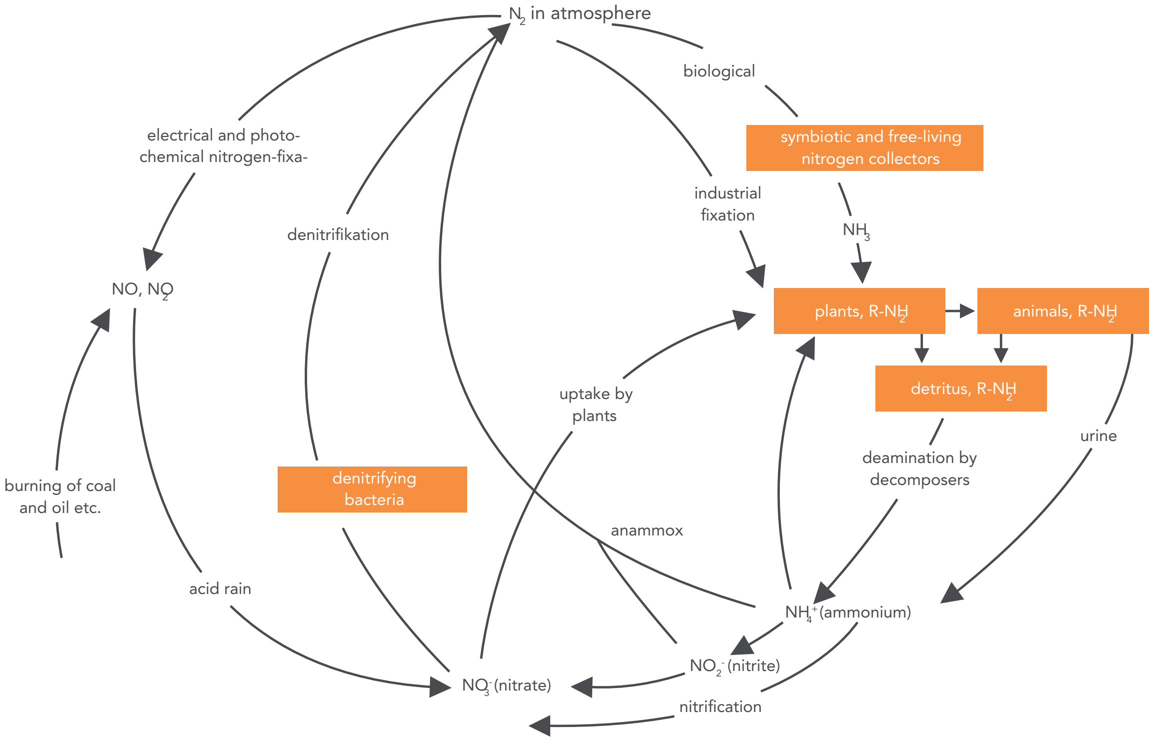


Fig. 19. The biogeochemical cycle of nitrogen [14]. Four types of processes operate the nitrogen cycle: 1) nitrogen-fixation and incorporation of nitrogen as amino groups (R = NH_2) in the living organisms, 2) deamination, whereby the organically bound nitrogen is released as ammonia, 3) nitrification, whereby bacteria convert ammonium (NH_4^+) to nitrite (NO_2^-) and nitrate (NO_3^-), and 4) denitrification (nitrate respiration), whereby bacteria under anaerobic conditions convert nitrate to free nitrogen in the presence of easily degradable organic matter, or sulphur, see table 2. In addition, certain bacteria under anaerobic conditions perform a denitrification process called anammox (= anaerobic ammonium oxidation): $NH_4^+ + NO_2^- \rightarrow N_2 + H_2O$ [18].

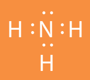
Step	Compound	Formula	Dot formula
+5	Nitrate ion	NO_3^-	
+3	Nitrite ion	NO_2^-	
0	Nitrogen	N_2	:N:::N:
-3	Ammonia	NH_3	

Fig. 20. When two elements chemically combine, their atoms share one or more electrons in the atoms' outer electron shell, which is particularly stable when 8 electrons are present. Atoms of nitrogen and oxygen, lacking only a few electrons in having filled the outer electron shell, try to cover the missing electrons by taking up electrons from other atoms that bind less to them. This principle explains why nitrogen (N) can have several oxidation steps, depending on whether the nitrogen is part of the hydrogen (H) or oxygen (O) under formation of nitrate (NO_3^-), nitrite (NO_2^-) or ammonia (NH_3). In the oxidized states (+) the electrons of the nitrogen atom fill the outer electron shell of the oxygen atom. In the reduced (-) state the outer electron shell of the nitrogen atom is filled with the electrons of the hydrogen atoms.

Plant roots easily absorb ammonia and nitrate, in the soil, and the absorbed nitrogen compounds are incorporated into amino acids, which in turn are incorporated into proteins. When the plants die and decompose, or are eaten by animals and the proteins are transported through the food chains, the amino groups ($-NH_2$) of the amino acids are split off and released to the surroundings as ammonia (NH_3), or excreted in the urine as urea. This process is called deamination. Ammonia and ammonium (NH_4^+) is a corresponding acid-base pair. At pH 7, the concentration of ammonium is about 200 × higher than the concentration of ammonia. Ammonium does not leach out very easy because the positive charge allows it to bind to the negatively charged particles of clay and humus in the soil. Nevertheless, the nitrogen compounds leach because the ammonium ions can be oxidized to nitrite (NO_2^-) of chemoautotrophic bacteria (*Nitrosomonas*). Nitrite can be further converted to nitrate (NO_3^-) by other bacteria (*Nitrobacter*). The conversion of ammonia to nitrite and further to nitrate is called nitrification. Under anaerobic conditions, nitrate is reduced to free nitrogen by a process known as denitrification, which is performed by the bacterium *Pseudomonas denitrificans*: glucose + $NO_3^- \rightarrow CO_2 + N_2$ + 2387 kJ. The process with O_2 per mol glucose would have given an energy output of 2872 kJ. Thus, there is almost as much energy gain by anerobic denitrification as by combustion with oxygen, see Table 2. Since it was learned to fix free atmospheric nitrogen through industrial processes, the consumption of nitrogen fertilizers has increased dramatically. The natural biological fixation of nitrogen on land is of the order of 44 million tonnes per year, but the industrial fixation is almost as large (30 million tons per year). This in combination with a strong increase in the use of nitrogen fixing legumes, has given rise to increased nitrate concentrations in ground- and surface water. The result is nitrate polluted groundwater and eutrophicated rivers, lakes and coastal waters. Changed cultivation practices and use of excess manure at the wrong times of the year have also been an important factor for the worsened situation in many industrialised countries. In particular, sandy soils cannot retain nitrate, which leaks down into the groundwater when the vegetation is insufficient to take it up. Globally, it is estimated that today more nitrogen is fixed biologically, industrially and atmospherically (92 million tons per year) than denitrified (83 million tons per year). This means that we have significantly gained influence on the global nitrogen balance. Until now plant growth both on land and in the sea has been limited by nitrogen, and therefore it is clear that an increased fixation of nitrogen not being matched by a corresponding denitrification will result in ecological disorders.

Finally it should be mentioned that the photo chemical and electrical processes in the atmosphere can oxidize N_2 to nitrogen oxides (NO and NO_2), which can also be formed by burning of oil and coal and brought to the soil by rain as nitric acid – on weight basis, this nitrogen contribution is about 1/10 of the biological fixation. It is a thoughtful consideration that without denitrifying bacteria, the oceans would be a nitric acid solution. Denitrification must therefore have been developed soon after the emergence of O_2 in the atmosphere. In 1999, the scientific world was surprised when a previously unknown denitrification process was identified. It turned out that some bacteria under anaerobic conditions can perform denitrification by a process called anammox (= anaerobic ammonium oxidation), where ammonium and nitrite are converted to free nitrogen and water: $NH_4^+ + NO_2^- \rightarrow N_2 + H_2O$. Globally, this process is responsible for 30–50% of the free nitrogen produced in the oceans. Anammox is the main sink of fixed nitrogen and thus directly contributing to the limitation of the primary production in the oceans [17, 18].

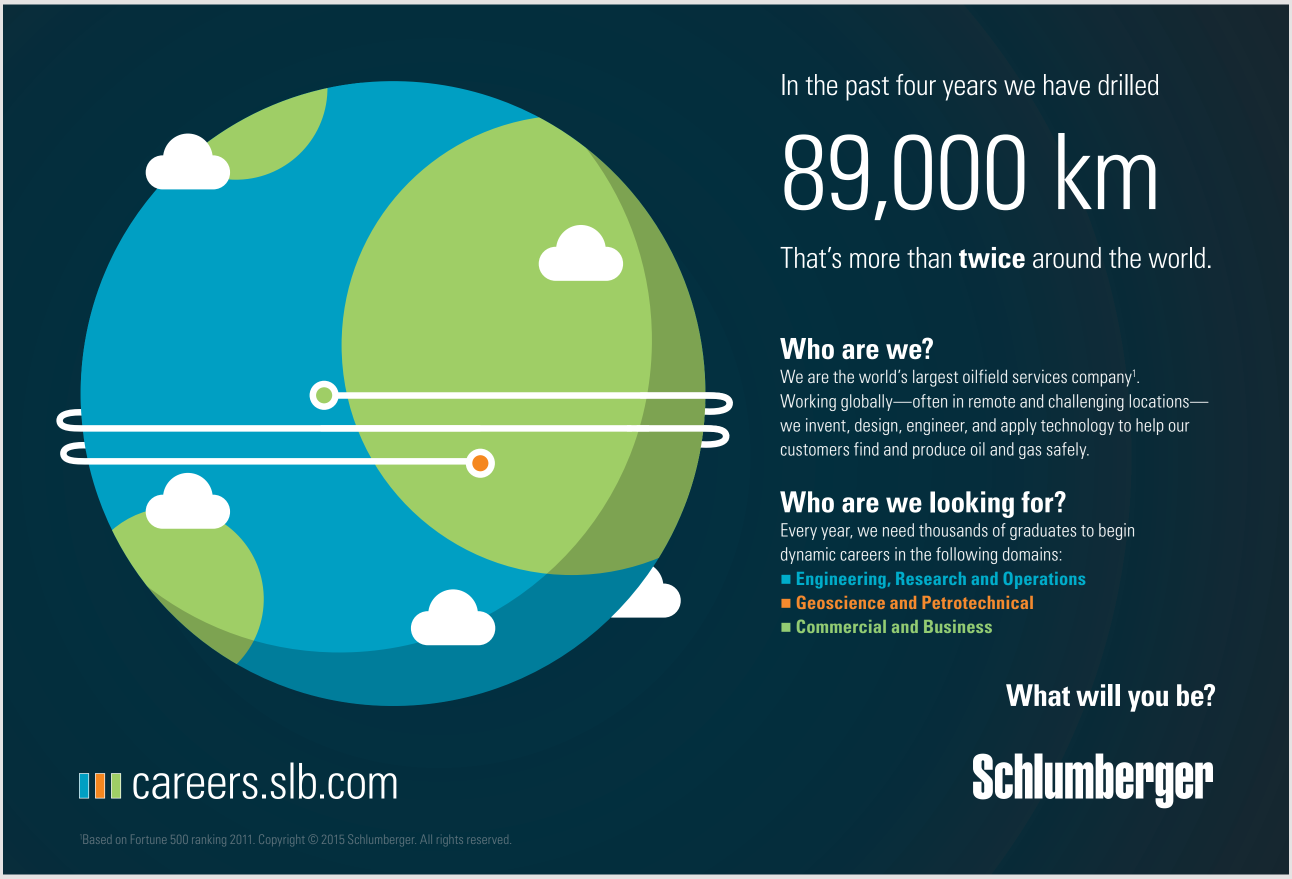
Very large quantities of nitrogen are bonded in the oceans' sediments and rocks in the Earth's crust, but since the turnover of this nitrogen is very slow, unlike the atmospheric nitrogen, the nitrogen cycle is of the gaseous biogeochemical type.

Reaction	Energy yield (kJ)
Denitrification	
1 $C_6H_{12}O_6 + 6KNO_3 \rightarrow 6CO_2 + 3H_2O + 6KOH + 3N_2O$ glucose potassium potassium nitrogen nitrate hydroxide oxide	2282
2 $5C_6H_{12}O_6 + 24KNO_3 \rightarrow 30CO_2 + 18H_2O + 24KOH + 12N_2$ Nitrogen	2387 (per mol glucose)
3 $5S + 6KNO_3 + 2CaCO_3 \rightarrow 3K_2SO_4 + 2CaSO_4 + 2CO_2 + 3N_2$ potassium calcium sulphate sulphate	553 (per mol sulphur)
Respiration	
4 $C_6H_{12}O_6 + 6O_2 \rightarrow 6CO_2 + 6H_2O$ carbon water dioxide	2872
Deamination (ammonification)	
5 $CH_2NH_2COOH + 1.5O_2 \rightarrow 2CO_2 + H_2O + NH_3$ glycine oxygen ammonia	737
Nitrification	
6 $NH_3 + 1.5O_2 \rightarrow HNO_2 + H_2O$ nitric acid	276
7 $KNO_2 + 0.5O_2 \rightarrow KNO_3$ potassium nitrite	73
Nitrogen fixation	
8 $N_2 \rightarrow 2N$ “activation” of nitrogen	-670
9 $2N + 3H_2 \rightarrow 2NH_3$	54

Table 2. The energy yield of various chemical reactions of interest to the nitrogen cycle (14).

3.4 SULPHUR CYCLE

All living organisms contain sulphur (about 1.2% on dry weight basis). The most common form of sulphur (S) is sulphydryl (-SH) groups in organic molecules. The heterotrophic organisms cover their individual requirements by consuming sulphur-containing amino acids (cysteine and methionine) which the plants have build by incorporating sulphur absorbed through the roots as inorganic sulphate (SO_4^{--}) or through the leaves as sulphur dioxide (SO_2). By aerobic bacterial decomposition, sulphate is released from the dead organic matter, but under anaerobic conditions, for example in the deeper sediment layers, decomposition of organic matter results in formation of hydrogen sulphide (H_2S). Hydrogen sulphide that is emitted to the atmosphere by spontaneous oxidation can be converted into SO_2. But SO_2 is also produced by combustion of coal, oil and gas, etc., see Fig. 21.



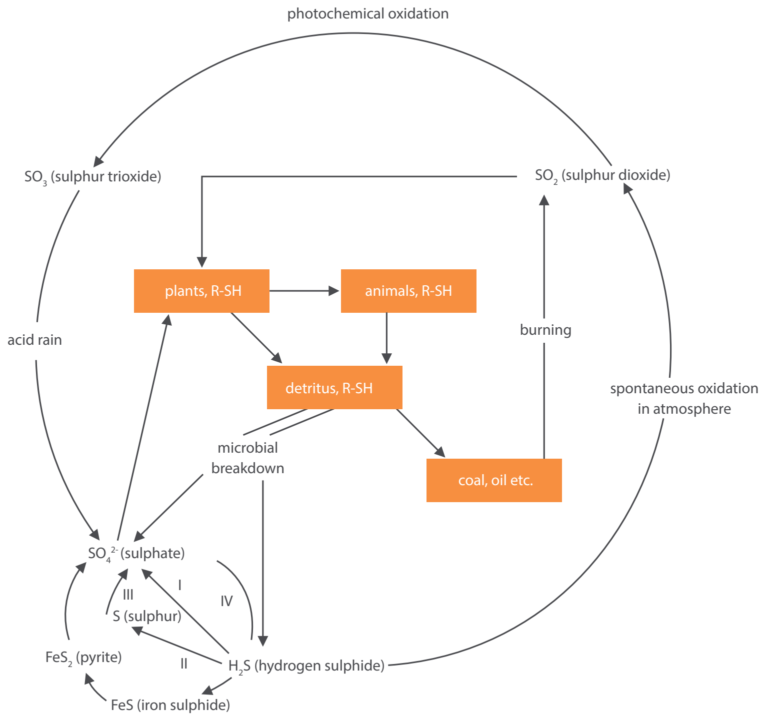


Fig. 21. The biogeochemical cycle of sulphur [3, 16]. The Roman numerals close to the arrows, showing the turnover of sulphate, hydrogen sulphide and sulphur, refer to:

I: a) spontaneous chemical reaction in an oxygen-rich environment
b) photoautotrophic sulphur bacteria:
$2nCO_2 + 4nH_2O + nH_2S \rightarrow$ (infrared light) $\rightarrow 2(CH_2O)_n + 2nH_2O + 2nH^+ + nSO_4^{--}$
c) chemoautotropic sulphur bacteria (*Thiobacillus*): chemical energy and no light power the process, thereby forming organic material and sulphate.

II: a) chemoautotropic bacteria (*Beggiatoa* = “white sulphur bacteria”):
$2nH_2S + nCO_2 \rightarrow$ (chemical energy) $\rightarrow (CH_2O)_n + 2nS + nH_2O$
b) photoautotrophic sulphur bacteria:
$nCO_2 + 2nH_2S \rightarrow$ (infrared light) $\rightarrow (CH_2O)_n + nH_2O + 2nS$

III: denitrifying bacteria:
$5S + 6KNO_3 + 2CaCO_3 \rightarrow 3K_2SO_4 + 2CaSO_4 + 2CO_2 + 3N_2 +$ energy.

IV: sulphate-reducing bacteria (*Desulfovibrio*): in the absence of oxygen, these bacteria respire by using SO_4^{--} (instead of O_2), leading to the formation of CO_2 and H_2S (and not H_2O, as in the respiratory process in an oxygen-rich environment). This causes the sulphur to be in a gaseous form, which may be released to the atmosphere.

In small amounts SO_2 may fertilise plants, but in larger quantities the compound is harmful. By photochemical oxidation in the atmosphere, SO_2 can be converted to SO_3, which reacts with water to form sulphuric acid (H_2SO_4), which together with nitric acid formed by air pollution with nitrogen oxides, falls to the ground as “acid rain” (16). Acid rain can cause forest decline and acidification of specially decalcified lakes [19]. In recent years in Norway and Sweden, acid rain has wiped out fish stocks in many hundreds of lakes. But “acid rain”, defined as rain with pH below 5.65, can give rise to other injuries. Sandstone, containing calcium carbonate ($CaCO_3$), decays much faster in sulphur contaminated air. Striking examples are the historic monuments of Greece and Italy that have stood up to several thousand years without major changes, but over the last decades, have suffered much damage. This is because acid rain or dry sulphur (e.g. from local car exhausts) deposited on the monuments, react with the calcium carbonate forming soluble calcium sulphate (plaster), which is easily washed away by rainwater.

Under anaerobic conditions in aqueous environments SO_4^{--} can be converted to hydrogen sulphide (H_2S), by for example *Desulfovibrio* bacteria that are sulphate reducing. With the aid of these bacteria, SO_4^{--} is used for oxidizing organic matter, forming H_2S, which in the anaerobic (anoxic) sediments can react with iron (Fe^{+++}) to form FeS (iron sulphide) whereby the colour of the sediment becomes black. After some time, the iron sulphide is eventually converted to pyrite (FeS_2), which gives the deeper zone in the sediment a greyish colour. Deposits of plant residues in oxygen-poor water where the breakdown is incomplete, can lead to the formation of peat and brown coal with a high content of pyrite. When pyrite by drainage or peat digging comes into contact with atmospheric oxygen, it can be oxidized into sulphuric acid (H_2SO_4) and ochre ($Fe(OH)_3$) in water. Brown coal digging in Denmark during the two World Wars, resulted in formation of extremely acidic lakes in the former lignite excavation areas. Thus, a creek that drains a former digging area is extremely acidic with pH = 2–3. At such a low pH, pyrite is not spontaneously oxidized in an oxygenated environment, but some chemoautotropic bacteria (*Thiobacillus ferrooxidans*) may instead oxidize the pyrite to sulphate and ferric ions (Fe^{+++}). When the pH rises, the dissolved oxidized iron precipitates as ochre. Ochre pollution is the consequence which is a problem seen not only in relation to peat and brown coal digging, but is also frequently seen when the groundwater level is lowered by drainage of fields and straightening of rivers. In aquatic environments with abundant organic matter, so much hydrogen sulphide may be produced that it penetrates right up to the sediment surface, where photosynthetic sulphur bacteria (green and purple sulphur bacteria) utilise the hydrogen sulphide, if enough infrared light is penetrating down to the bottom. If no light is present, chemoautotropic "white sulphur bacteria" can exploit the chemical energy in the H_2S, producing organic matter by consumption of CO_2 and formation of SO_4^{--} (*Thiobacillus*) or elemental sulphur (*Beggiatoa*). Finally, hydrogen sulfide released into the oxygen-rich water can be spontaneously converted to SO_4^{--}.

The importance of sulphate breathing bacteria for the turnover in marine sediments is great. About 50% of the decomposition of organic matter (mineralization) at the bottom of a temperate marine area (Limfjorden in Denmark) is performed by sulphate breathing bacteria – which also means that 50% of the oxygen consumption at the bottom is used for oxidation of H_2S. This acts as a carrier of energy from the deeper anoxic to the overlying aerated (aerobic) zone near the sediment surface [20].

If the oxygen concentration at the bottom is very low (less than 2 mg $O_2 1^{-1}$) and if at the same time an abundance of hydrogen sulphide is produced, the “white sulphur bacteria”, which are often seen as excessive white films on the bottom, may no longer be able to absorb and transform the hydrogen sulphide, which is a powerful environmental poison. Hydrogen sulphide can then penetrate the sediment and come up into the overlying water, which kills the benthic fauna. This phenomenon caused by oxygen depletion has, since the 1970s, become an increasingly widespread and more frequent phenomenon in the many marine coastal and shallow areas, due to increasing eutrophication (nutrient overloading from domestic waste and agriculture). Although sulphur has a gas phase in the atmosphere, this is not a large reservoir (though the turnover rate of sulphur in the atmosphere is poorly known). The large reservoir is found in sediment. The sulphur cycle is therefore of the sedimentary biogeochemical cycle type.

3.5 PHOSPHORUS CYCLE

Most biologically important elements – apart from the already mentioned (C, N, S) – have only a small or no reservoir in the atmosphere. An example is phosphorus (P) present in the environment as a phosphate (PO_4^{---}) or one of its analogues (HPO_4^{--}, $H_2PO_4^{-}$). The importance of phosphorus for living organisms appears from the fact that it is for example part of the ATP molecules that control the biochemical transfer of energy in the cells.

Free phosphate ions are taken up across the outer surfaces of the phytoplankton cells or through the roots of larger plants and incorporated into the living tissues. Phosphorus passes through the grazing food chain in the same way as nitrogen and sulphur, and excess phosphorus is predominantly excreted in faeces. Inorganic phosphate is released into the abiotic environment when the decomposers in the detritus food chain break down the phosphorus-containing organic material in faeces or dead plants and animals. The organic phase of the biogeochemical cycling of phosphorus is very simple. The inorganic phase of the phosphorus cycle is more complex and less well known, especially in terms of its turnover in sediments [3, 7]. Sediments take up or release phosphate, depending on the chemical conditions. Under aerobic conditions, there are often found large quantities of phosphate bound to oxidized iron compounds (Fe^{+++}) in the upper sediment layers ($FePO_4$). In summer, where there may be oxygen depletion at the bottom, sulphide can penetrate up to the sediment surface and reduce the iron compounds producing iron sulfide, resulting in the release of phosphate. The widespread and frequent incidents of oxygen depletion in certain eutrophicated shallow marine areas, therefore leading to significantly higher phosphate concentrations in the water during summer than during winter when the sediment surface is oxidized (and light brown, due to iron hydroxides = “rust”). The first case of oxygen depletion during summer starts an “evil circle” where the released phosphate (which is the limiting nutrient factor in early summer) causes an increase in the phytoplankton production, which during the summer and early fall triggers new incidents of oxygen depletion [20].

Phosphate is only to a lesser extent washed out of the ground. The reason is that phosphate reacts chemically with the aluminium, calcium, manganese and iron ions, and form poorly soluble compounds. The plants cannot absorb phosphate bound in these compounds, and thus the amount of biologically available phosphate is not only determined by the absolute amount of phosphate in an ecosystem, but rather the speed at which it is recycled. Especially in many freshwater lakes, where the "mobile pool" of phosphate is very small. Thus, it is the phosphate that is the limiting factor for the growth of phytoplankton in many lakes. They receive larger or smaller amounts of nitrate leached from surrounding agricultural areas, but because phosphate, not being leached from the soil, is the limiting factor, the nitrate does not cause immediate problems with growth of plankton algae. But if domestic sewage, containing relatively high amounts of bioavailable phosphorous is discharged at the same time (often being the case), causing rapid growth ("bloom") of phytoplankton then this can result in a series of environmental problems [21]. If a lake during a number of years, has received phosphate containing wastewater, a large pool of phosphate may have been bound in the mud at the bottom of the lake. This phosphate will be released ("mobilized") due to eutrophication and deposition of organic matter, if anoxic conditions develop at the bottom. Therefore, a stop for further discharge of phosphate will only have an effect many years later.

3.6 WATER CYCLE

Solar energy drives the water cycle [1, 7]. The sun heats the ocean surface, and large amounts of water evapourates and rise into the air. The lower temperature at higher altitudes makes the water vapour condense into clouds, which consists of very small water droplets. Winds, which are also driven by solar energy, blow clouds into areas of land where they are cooled to form precipitation in the form of rain, snow and hail. Rainfall can accumulate as ice caps and glaciers, which can store frozen water for thousands of years; but a large part of the water, which hits the ground surface, evapourates again. Only a small proportion of the precipitation is taken up by plants, but most of the water evapourates quickly from the leaves. A portion of the precipitation, which does not evapourate, flows through the ground or runs through drain pipes to lakes and streams, and then back to the sea. But the remainder of the precipitation seeps into the ground through the topsoil and becomes groundwater. In the upper part of the soil where there is air present in the small cavities, the water moves vertically downwards. This part of the soil is called the unsaturated zone. If the soil is sandy, the water moves down with a speed of about 4 m per year; but if the soil is clayey, the movement is only 0.5 m per year. At a certain depth is the groundwater zone where all pores and small cavities are filled with water. The top of the groundwater zone is called the water table. In the groundwater zone, water moves more or less horizontally to areas where the water table is lower. Much of the uppermost water in the groundwater zone flows with a slight inclination towards rivers, lakes and the sea. From here, the water evapourates again and the cycle is closed. In this great cycle, the water moves at very different speeds. Water moves very slowly in the groundwater zone, and a drop of water that has fallen on a field far inland, can spend several thousand years to reach the sea. Some orders of magnitude for how long time water stays in the individual stages are: clouds 10 days, streams 20 days, lakes 10 years, unsaturated groundwater zone 5 years, saturated zone with sand 500 years, saturated zone with moraine clay 10,000 years, the sea 3000 years. The oceans contain 97% of all water in the biosphere, about 2% is bound in ice caps and glaciers, 1% is found in lakes, rivers and groundwater; only a negligible amount is in the atmosphere.

4 POPULATION ECOLOGY

A population is defined as all individuals of the same species in a given area. A population has a number of features that are characteristic of this organization level, and not found on the organizational level below (individual) or above (community). A population has, for example, an age structure, a distribution, and a density, see Fig. 22. This chapter describes how populations are regulated by means of a complex interplay with the ambient environment.

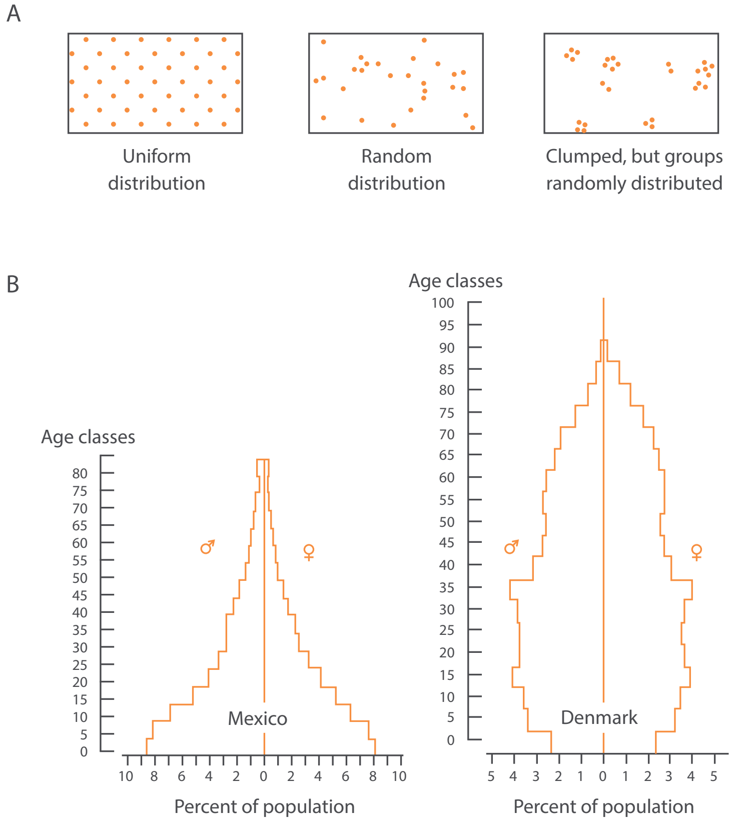


Fig. 22. Populations have a number of features not found in the individual (cf. "the hierarchical control principle"). For example, a population has a distribution, a density, an age structure, and a birth- and death rate. The figure illustrates (A) the possible distributions and densities of a population in an area, and (B) the age structure of males and females in the population of people in the two countries, Mexico and Denmark, with different population growth rates.

4.1 REGULATION OF POPULATION DENSITY

A population's size, density, age structure and growth is regulated by a complex interplay of impacts from: 1) the abiotic surroundings, 2) populations of other species (interspecific factors), and 3) impacts from the population itself (intraspecific factors), see Fig. 23.

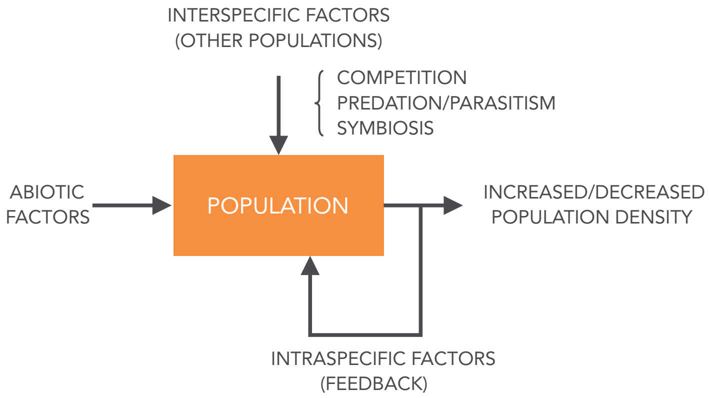


Fig. 23. Factors which affect the density of a population.

Some populations are regulated mainly by abiotic factors. Other populations are regulated to a high degree by predators that pursue the individuals of the population. Still other populations are regulated mainly through competition with other populations' species, which partially exploit the same food resources. Finally, there are also populations, which are largely self-regulating and do not grow larger than the area can feed over a long period of time [60].

In the following, some examples are given of interaction between populations and their abiotic- and biotic surroundings, with emphasis on explaining how abiotic, inter- and intraspecific factors can regulate populations' growth and thus their size and distribution.

4.1.1 NICHE CONCEPT AND IMPORTANCE OF ABIOTIC FACTORS FOR REGULATION OF POPULATIONS

It has been proposed to define the ecological niche of a species that the niche can only contain one species in a given ecosystem. But this definition is not entirely satisfactory. A more precise definition of an organism's niche can be derived as follows: Plot linearly on an x-axis an environmental factor (e.g. temperature) for a species S_1, see Fig. 24. On the axis is marked the interval x'- x" ("tolerance width") within which the species can survive. Out along a y-axis is marked the interval y' – y" of another environmental factor (e.g. pH) within which the species can survive. The resulting area containing the points with respect to the two environmental factors x and y indicates S_1's ability to maintain a population. A third factor z can be treated in the same way, which generates a volume that contains points that describe S_2's environmental requirements in relation to three factors. If n -environmental factors are treated in the same way, then an n-dimensional hyper-volume, $N_{1,}$ can be created. The points contained in N_1 correspond to all the environmental combinations where S_1 can maintain a population and N_1 is called species S_1's "fundamental niche". The fundamental niche thus describes the physiological tolerance limits.

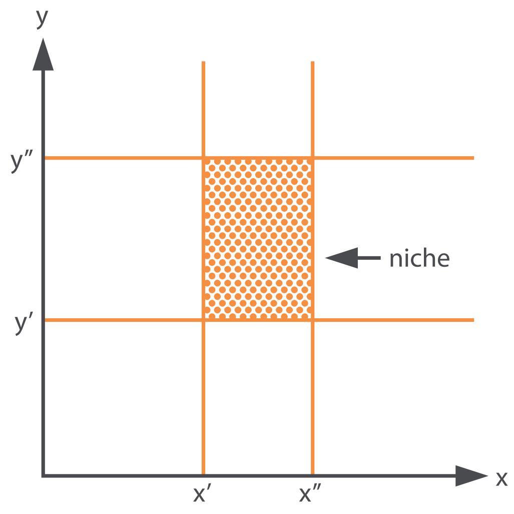


Fig. 24. Two dimensions of the fundamental niche of a species with regard to the environmental factors x and y.

The above model for the description of a species' niche is more accurate and comprehensive than the commonly used definition of a niche as a species' "profession" in the ecosystem (as opposed to the species' habitat). One must be aware that the n-dimensional niche model does not take into account that any tolerance range for a given environmental factor has an optimum where the species thrives, and that the "graphic" mode of expression does not allow a description of, for example, that certain environmental factors can mutually influence each other's tolerance width. As an example, the growth of diatoms in a lake can be used to demonstrate how abiotic factors can be dominating in the regulation of a population's size. When light and temperature conditions are favourable in the spring, the diatoms begin to grow fast due to the ample amounts of nutrients in the water at this time of year. Because the zooplankton is only represented by a few individuals in the early spring, the algae grow unimpeded until the nutrient silicon (Si) is exhausted and thereby limiting further growth. The diatom bloom in early spring and the subsequent reduction is governed exclusively by the abiotic factors (light and silicon). When the diatom growth ceases due to silicon shortage, other algal species get a chance to grow. The growth of these algae can in turn be strongly regulated by zooplankton, which by their "grazing" can reduce the concentration of phytoplankton. Regulation of the zooplankton, which tends to graze the algae down, takes place through fish predation of the zooplankton. This creates balance in the ecosystem so that the size of the various populations fluctuates (oscillates) around a more or less constant value.

4.1.2 IMPORTANCE OF INTERSPECIFIC FACTORS FOR REGULATION OF POPULATIONS

There are many kinds of interactions between populations. The interspecific factors can be subdivided into a number of types, between which, there can be gradual transitions. Interspecific factors can be classified as: 1) competition, 2) predation or parasitism, 3) symbiosis. In the following, these phenomena are described with some examples.

4.1.2.1 Competition

When the fundamental niches of two species completely or partly overlap one another, there will be competition for food and/or space (see Figs. 25 & 26). This kind of competition is called *interspecific competition*. The following sections describe four types of observations that illustrate or demonstrate interspecific competition, which is very important for the distribution of animals and plants in nature.

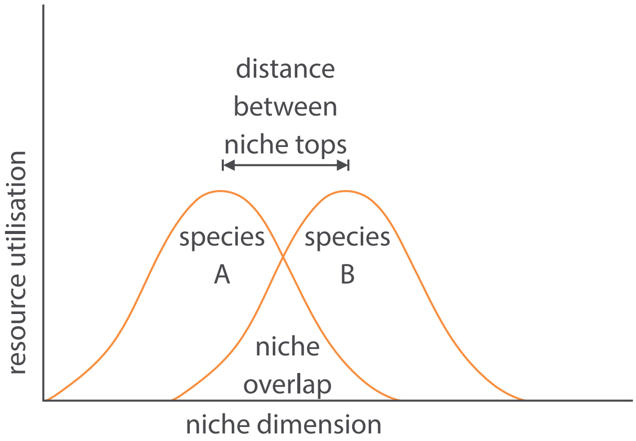


Fig. 25. A dimension of an ecological niche. The two bell-shaped curves represent resource utilization of two species in a community. The niche dimension may represent the temperature, pH, or, for example, the size of food particles, which are eaten by the two species. The competition is most intense where there is niche overlap, resulting in restrictions in the two species distribution. Such interspecific competition results in selection of individuals that do not have overlap. This leads eventually to a separation of the two species with completely separated niches (i.e. diversification niche).

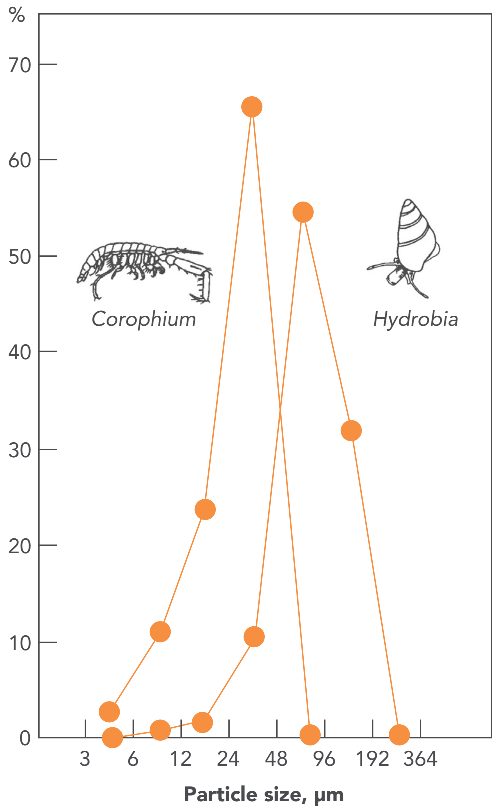


Fig. 26. The size distribution of mineral particles found in the intestine of the deposit-feeding amphipod crustacean *Corophium volutator* and the deposit-feeding mud snail *Hydrobia ulvae* [22]. The two species are often living together on sandy tidal flats, where they utilise the micro-organisms that sit on the particles. The two species have "shared" the food resources by swallowing particles of different size. Interspecific competition occurs where there is "niche overlap" of the coexisting deposit-feeders, which implies that the realized niche of both species is narrower than it would have been if the competitor was not present.

1) Displacement of a species from another species

In the 1930s, the Russian biologist Georgy Gause conducted a large number of laboratory experiments on competition between different species of single-celled ciliates of the genus *Paramecium* fed with bacteria or yeast cells. In some of the experiments, two species were cultivated separately with the amount of feed offered (bacteria) kept constant. After some time the *Paramecium* populations grew up to the size that was allowed by the food supply, see Fig. 27. Subsequently, the two species of *Paramecium* were grown in the same culture chamber at the same constant amount of food. Up to about the fourth day, both species populations grew. But when the food resources were fully utilized, one of the species decreased in number while the other (more efficient) species still increased in number. After about 16 days, the less effective species was extinct while the effective species approximately attained a population size similar to that achieved when it was cultured alone.

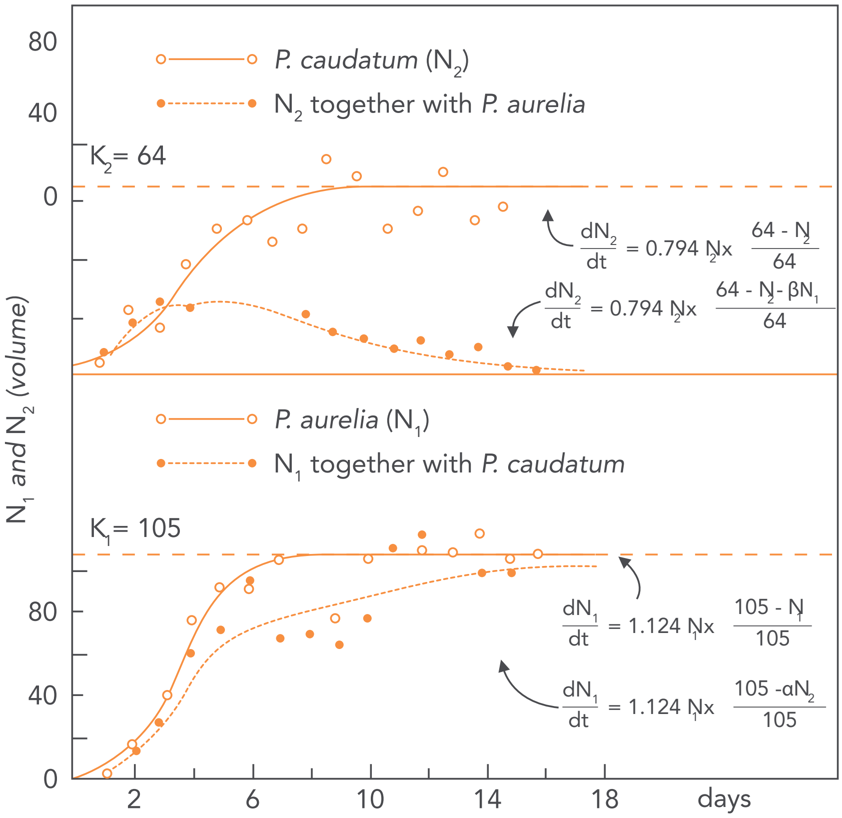


Fig. 27. Growth of two ciliates (*Paramecium aurelia* and *P. caudatum*) that have "the same niche". The figure shows the growth of the two ciliates when cultured separately, or in a mixed culture. It is seen that *P. caudatum* is competed by *P. aurelia* [23]. The mathematical expressions for the growth of the two ciliates are explained in section 4.2.

Environment	Percentage of experiments that won	
hot-humid	Y (100)	X (0)
hot-dry	X (90)	Y (10)
temperate-moist	Y (86)	X (14)
temperate-dry	X (87)	Y (13)
cold-humid	X (71)	Y (29)
cold-dry	X (100)	Y (0)

Table 3. The results of the competition experiments started with the same number of the two species of flour beetles (X) and (Y), respectively, under different climatic conditions [24].

Another example of interspecific competition between two closely related species can be retrieved from American biologist Thomas Park's experiments from the 1950-60s with flour beetles. In a series of experiments conducted at various combinations of temperature and humidity, Park examined the competition between the two species of flour beetles. It was found that one species always completely suppressed the other species. One species (*Tribolium castaneum*) always won in a hot-humid environment while the second species (*Tribolium confusum*) always won in a cold-dry environment, see Table 3. However, in an environment with temperature-humidity lying between the two extremes, there was – depending on the initial number of individuals at the onset of the experiment – a certain randomness in the outcome of which of the two species won, see Fig. 28. Elimination of a species due to interspecific competition with another species has been known as "the competitive exclusion principle" or "Gause's principle" that says that "two species with the same ecological niche can not coexist".

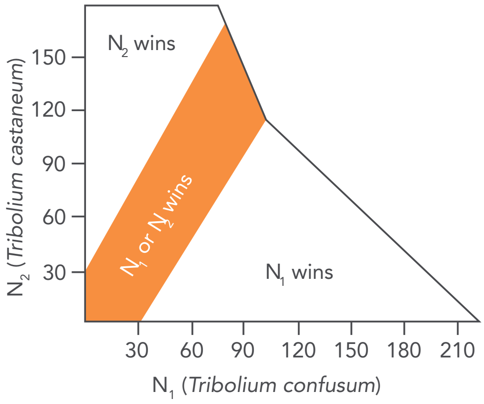


Fig. 28. Competition experiments with two species of flour beetles (33N$_1$ and N$_2$) of the genus *Tribolium*. Either N$_1$ or N$_2$ eventually wins, depending on the initial population sizes, but in certain combinations there is an "unstable balance", which implies that either N$_1$ or N$_2$ eventually winds – i.e. the result is random [33].

2) Fundamental and realized niche is not identical

If two species are not equally well adapted to all the habitats in "the fundamental niche", but otherwise exploit the same food resources, they can often co-exist by sharing the niche between them. The part of "the fundamental niche" which is utilized when there is an interaction (interspecific competition) with other species organisms is called the "realized niche". Based on the patterns of distribution, it has in many cases been documented that the organisms in nature do not exploit (realize) their entire fundamental niche. A classic example is the turbellarian worms *Planaria montenegrina* and *Planaria gonocephala* that live in brooks. No individual species live in the whole extent of a brook, but when the two species occur in the same brook, they share it between themselves: one species occurs below 14 °C, the second species above this temperature [25].

Another classic example is the distribution of two species of acorn barnacles on Scottish rocky coasts [26]. One of the barnacle species (*Chthamalus*) can live from the high-tide line and downwards, but because of competition from the other barnacle species (*Semibalanus*) which do not tolerate drying out at low tide, live usually only in that part of its fundamental niche which lies in the tidal zone, see Fig. 29.

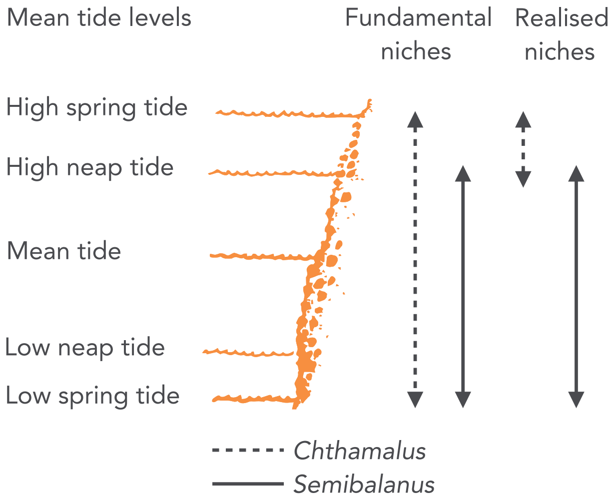


Fig. 29. Interspecific competition between two species of barnacles, *Chthamalus* and *Semibalanus*, that live on rocky shores where they feed on zooplankton and suspended food particles filtered from the water. The free-swimming larvae of both species settle over a wide range, but the adults live in a very precisely defined belt. The limit for *Semibalanus*' upper limit is determined by physical factors, including drying. *Chthamalus* is not prevented from living in *Semibalanus*' area due to physical factors, but because of *Semibalanus* which grows faster and either push away or overgrow *Chthamalus*. If *Semibalanus* is removed (it has been done by biologists scraping them off), *Chthamalus* will spread further down the rock side, i.e. it occupies a larger part of its fundamental niche [26].

In a series of experiments dealing with competition between the two ciliate species *Paramesium bursaria* and *Paramesium aurelia* grown in centrifuge glass tubes with yeast as food, Gause demonstrated in 1935, that the ciliates divided the "niche" (centrifuge tubes with yeast cells) between them, because *Paramesium bursaria* was found at the bottom of the centrifuge tubes in which the were living off sedimented yeast cells, while the other ciliate species swimming in the liquid fed on suspended yeast cells [27]. The culture of yeast cells were part of both species "fundamental niche", but each of the species could only realize a part of this when the other species was present.

3) Niche diversification

By niche diversification it is meant that related species living in the same area exhibits a specialization so as to avoid competing for the same limited resources – i.e. they avoid niche overlap. Only two examples are cited from the abundant literature on the subject.

A study of the food choices of the great black cormorant (*Phalacrocorax carbo*) and the closely related common shag (*Phalacrocorax aristotelis*) has shown that the two species have specialized in catching different kinds of fish [28]: the great black cormorant eats preferably sand eel and herring fish while the common shag eats a mixed feed of flatfish, shrimps, gobies and other things, see Fig. 30.

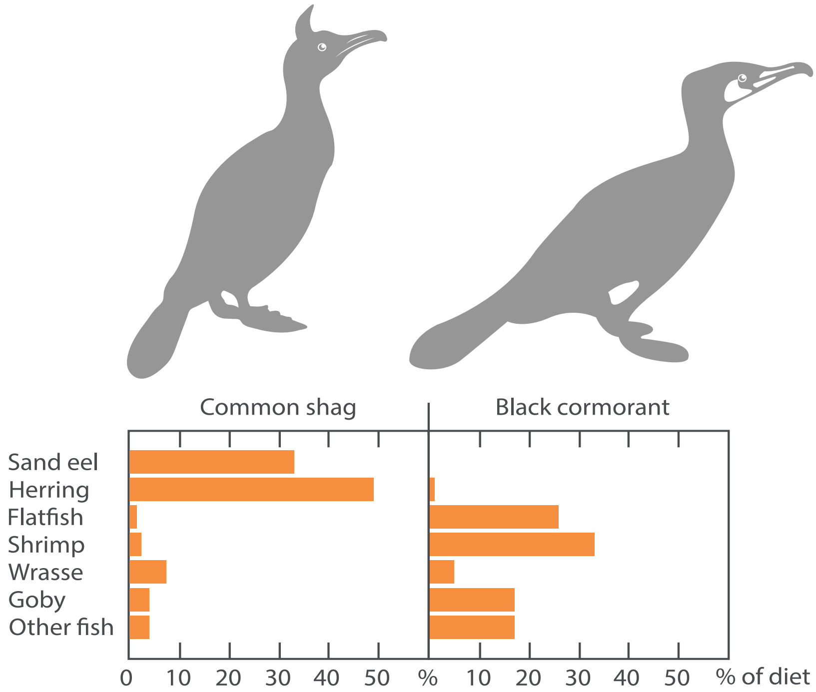


Fig. 30. The food choice of two cormorant species: the common shag (*Phalacrocorax aristotelis*, left) and the great black cormorant (*Phalacrocorax carbo*). The two related cormorant species are often observed at the same sites during the breeding season, but even if the habitat is the same, the food choice is differently. Hence the two species have different niches, and the two cormorant species do not directly compete with one another [28].

Three species that belong to the same genus of parasitic wasps live in the same area where their larvae feed parasitically on the same wood boring larval species that can only lay eggs in the "host" when their organ used for laying eggs (ovipositor) is fully inserted. Because the wood-boring larvae are found at different depths in the tree trunks, the parasitic wasps have specialized in boring larvae that live at different depths. The three parasitic wasp species have developed significantly different length of ovipositors to avoid direct competition [29].

4) Character displacement

When two related species geographically overlap each other, they tend to deviate from each other in their form and construction (morphological) and there is less variation within the species than in those cases where the species live apart from each other. This phenomenon is called character displacement and can be considered as an illustration of the phenomenon when interspecific competition has forced the species to niche diversification, i.e. to share the niche between them.

A known example is Darwin's finches on the Galapagos Islands. On islands where the species occur together, the height of their beaks significantly deviates from each other while on islands where the finches occur separately, the beak height can overlap [30], see Fig. 31.

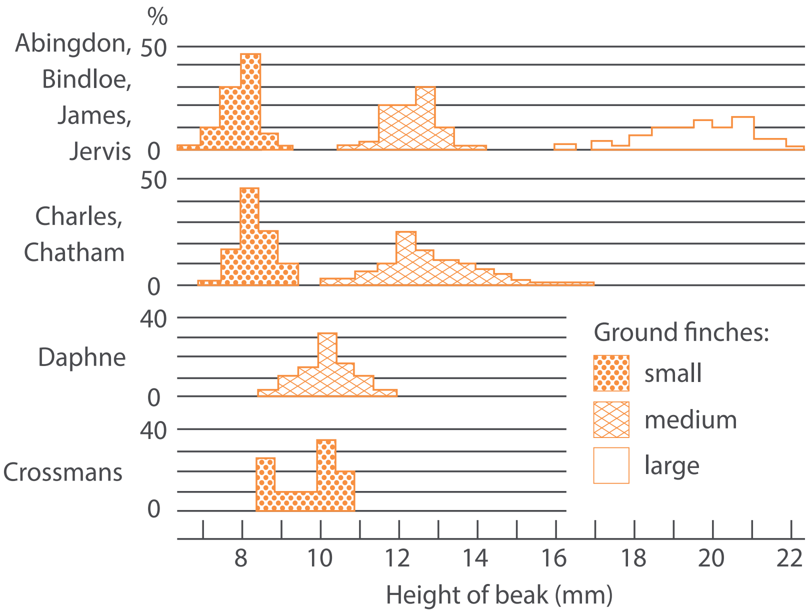


Fig. 31. Height of beak in three species of ground-finches (*Geospiza* sp.) on the Galapagos Islands. The measurements of the beak-height are depicted horizontally and the percentage of individuals of each species is shown vertically. At Daphne and Crossmans, both of which are very small islands, there is only one species of finches. These species have beak-heights that lie between those found in small and medium sized finches on the larger islands. It is assumed that the finches have descended from a single species, which at one time or another came to the outlying islands from South America. As there was no other closely related species, the finches specialized, and when Darwin visited the islands in 1835, he was captivated by seeing how the finches had exploited ecological niches that were normally filled by other types of birds.

4.1.2.2 Predation

There is a gradual transition of possibilities for interaction between a predator and its prey: 1) the predator limits the prey so much that the population of prey becomes extinct or nearly eradicated, 2) the predator regulates the stock so that the prey population does not become so large that the food resources are destroyed (overgrazed), 3) the predator is neither highly regulating or limiting. An example of predator being highly limiting for a prey population can be found in Canada, where the snowshoe hare is pursued by the lynx. If the population of snowshoe hare is growing because of particularly favourable conditions, this subsequently leads to such a strong increase in the population of lynxes that it can reduce the population of snowshoe hare to near extinction [31]. This gives rise to violent fluctuations of both species populations, see Fig. 32.

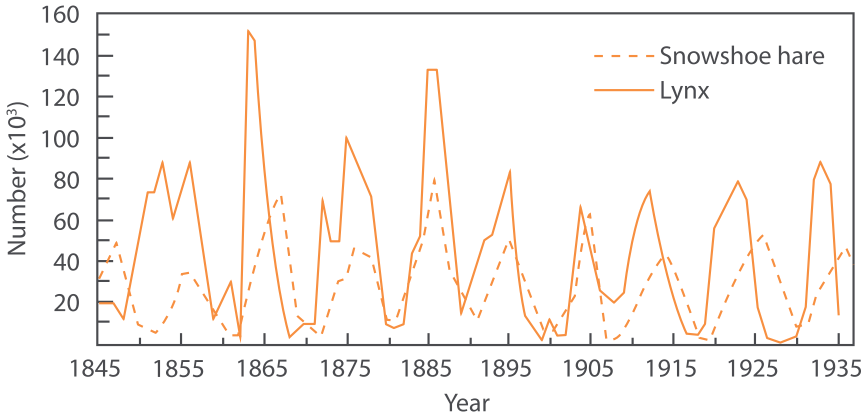


Fig. 32. Changes in the number of snowshoe hare (prey) and lynx (predator) in the years 1845 to 1935, determined as the number of furs received by the Hudson's Bay Company [31].

A predator has often a positive regulatory influence on a prey population by maintaining it at a level that does not exceed the area's carrying capacity. A classic example should be mentioned [32]: In Kaibab National Forest, Arizona, a campaign was started in 1907 to eliminate predators (mountain lions, wolves) because they pursued the deer. After 1910 the deer population began to grow rapidly, which had otherwise remained constant at around 4,000 animals. Eight years later, the deer population burst and grew to about 30,000 individuals. In the mid-summer of 1924 the population was estimated at 100,000 individuals. But the winter in Kaibab National Park was long and hard in both 1924 and 1925 with a lot of snow and low temperatures. During the two long winters 50,000 deer starved to death. As a result of the overpopulation and the destruction of grazing opportunities, the deer population continued to decline in the following years. The area could now only carry a deer population smaller than when the population was kept down by the predators.

In nature, it is rare that a predator (or parasite) exploits its prey so much that the existence of the population is threatened. It is usually only when two species that are not adapted to each other are brought together, that you see examples of extinction, cf. Fig. 33.

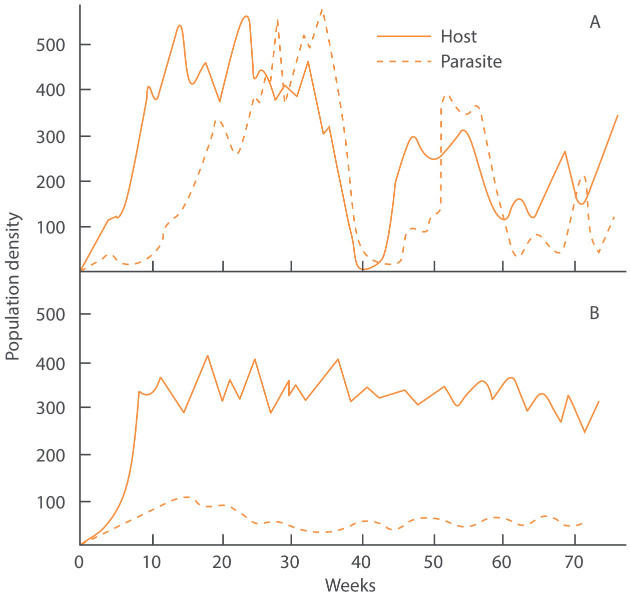


Fig. 33. "Host-parasite relationship" between the house fly and a parasitoid wasp under laboratory conditions in newly established conditions (A) and in a two-year-old host-parasite relationship (B) [1]. In the newly established conditions, the parasite is nearly eliminating the "host" after 40 weeks and the population densities fluctuate strongly, in contrast to the small fluctuations in population densities in the two year old host-parasite relationship, where the species have adapted to each other.

However, it is worth noting that predation is not a one-way interaction. The existence of predation results in the selective development of an often effective prey defence mechanism. Many defence mechanisms are behavioural. Some herd animals defend themselves from attack by a predator, for example, by lumping together with the largest and strongest males forming in front, against the attacker. Other defences are camouflage (e.g. fish, which adjusts the colour on the surroundings, and butterflies where the colour coincides with tree bark or leaves), toxic compounds (many insects and plants avoid being eaten because they are toxic) and physical defences (many animals and plants have prickly needles, etc.). Finally, it can be mentioned that many "harmless" animals use other poisonous species' "warning colouring" (mimicry).

4.1.2.3 Keystone species

Keystone species are in contrast to the dominant species not necessarily abundant in a community. They exert strong control over the community structure, not by number but by their key ecological niches. One way to identify a keystone species is to experimentally remove or eliminate the species so that its importance becomes enhanced. Here are a couple of examples on how a keystone species can help to increase diversity.

In a classic experiment, Robert Paine removed the starfish *Pisaster ochraceus* from an area on the rocks in the intertidal zone and subsequently examined the effect on species diversity [39]. This starfish, which is not very numerous, lives on the mussel, *Mytilus californianus*. In the absence of starfish, Paine observed that the species diversity went steeply down since the mussel gradually spread and eliminated the majority of other species. The experiment shows that *Pisaster* is a keystone predator, which exerts great influence on the number of species, although it is not abundant.

On the west coast of Alaska, the sea otter, *Enhydra lutris,* lives on the sea urchin, *Strongylocentrotus polyacanthus,* which again mainly feed on seaweed (macroalgae), dominated by the genera *Laminaria* and *Agarum*. In areas with many otters, urchins are rare and forests of seaweed are therefore well-developed. Conversely, in areas with few sea otters, there are many sea urchins and therefore seaweed is absent [43]. In the years between 1987 and 1997 it was observed that the orca *Orcinus orca* had begun to predate on sea otters, due to a reduction in the orca's usual prey. The result was that the population of sea otters went significantly down in large areas along the west coast of Alaska. This loss of a keystone predator allowed the sea urchin population to increase, resulting in a pronounced reduction and loss of seaweed forests [44].

Finally it can be mentioned that some organisms may exert a significant influence on a community, not through their trophic interactions, but by causing physical changes in the environment. Species that can dramatically alter the physical environment on a big scale are called "ecosystem engineers". A well-known representative is the beaver, which by wood cutting and building of dams, can transform large areas of forest to flooded marshland.

4.1.2.4 Invasive species

An invasive species is a plant or an animal that has been spread by human action over large geographical distances to a new area. This new species reproduce unrestrained and out of control due to not having any natural enemies, thereby out-competing the native species. In recent years, problems with invasive species have been increasing. This is primarily due to increasing global transportation, for example, man has also deliberately introduced many species to agriculture, forestry, horticulture and aquaculture. Some of these species, however, have later spread to the countryside and become invasive species.

But also shipping between different parts of the world contributes to spreading of invasive species. The comb jelly or sea walnut, ctenophore *Mnemiopsis leidyi*, lives naturally off the US East Coast, but from ballast water from ships, it has now found its way to Europe and Asia. The ctenophore lives mainly on zooplankton. During the late 1980s in the Black Sea, there was a mass occurrence of this invasive ctenophore resulting in a drastic reduction of zooplankton. Since zooplankton is also the food for anchovy and sprat, which in turn are food for larger fish higher up the food chain (mackerel, tuna), this resulted in a total collapse of the Black Sea fisheries [45]. In 2006, the ctenophore was observed for the first time along the Dutch coast where it had probably been transported with ballast water from large cargo ships. In the following years, the invasive ctenophore spread with the northbound currents and since 2007, it is has been observed in mass occurrence in Danish and other Scandinavian waters [51].

4.1.2.5 Symbiosis

Two species' populations can be linked together in a cohabitation called symbiosis. Symbiosis may be beneficial for one or both species. Therefore it is common practice to distinguish between two main types of symbiosis, namely commensalism and mutualism. Commensalism is a form of partnership where one species ("the guest") is given food, shelter, transportation etc., without demonstrable disadvantages or advantages to "the host". Mutualism is a form of cohabitation, which implies that both parties benefit from the partnership. There are countless examples of mutualism in nature. Here are just a few examples:

a) Lichens are "double creatures" consisting of a fungus and an algal species. The algae produce photosynthetic products that the fungi make use of. In return, the fungi provide water and inorganic minerals to the algae.
b) Ruminants are totally dependent on cellulose degrading bacteria in the rumen because they cannot produce enzymes that break down the cellulose in plant cell walls.
c) Most living plants are angiosperms, flowering plants, that require pollination by animals (insects, birds) flying from flower to flower, while the animals benefit from the plant nectar or pollen. Animals also play an important role by spreading plant seeds and fruits. Many small forest plant seeds are spread by ants, due to the seeds are equipped with a small organ (elaiosom) with nutritious ant food. Some birds spread seed kernels by passing the seed through their gut, resulting in a convenient dropping of fertilizer ready to sprout. This well-known example of partnership benefits both parties.

d) Root infections by nitrogen fixing bacteria and fungi are widespread in nature. Examples are nodule bacteria (*Rhizobium*) in sweet peas and similar bacteria included under actinomycetes in alder, buckthorn and other trees that provide nourishment for the bacteria, while they in turn benefit from the nitrogen compounds that the nitrogen fixing bacteria produce.

e) Many forms of mutualism are not very conspicuous. For example, many aquatic animals have unicellular algae in their cells. One of the best studied examples is the ciliate *Paramecium bursaria* which is filled with single-celled green algae when it is in light. In light, the ciliate can only utilize inorganic nutrients, but in the dark (without the algal cells' photosynthesis) the animal requires organic matter.

f) There are many indications that mitochondria and chloroplasts were originally symbiotic oxygen breathing bacteria and blue-green photosynthetic bacteria, respectively. They were amoeba-like cells, which during prehistoric times developed into animal and plant cells ("the endosymbiosis theory").

4.1.3 IMPORTANCE OF INTRASPECIFIC FACTORS FOR THE REGULATION OF POPULATIONS

Many biotic factors that help to regulate the densities of populations are intraspecific. These factors are never completely separated from interspecific- and abiotic factors, but together these intraspecific factors may ensure the stability of a population. Intraspecific factors can be passive (e.g. competition between a plant population's individuals) or active (e.g. social organization within a population).

Competition for limited resources between a species' individuals is a common feature of all populations. The clearest examples of intraspecific competition can be obtained from the plant kingdom due to plants not masking competition with social mechanisms. Two examples that demonstrate this are: 1) In a beech forest the big trees overshadow the small beech trees in the undergrowth. The growth here is therefore very slow. However, if an old tree falls over in a storm resulting in plenty of light coming down to the forest floor, the small beech trees begin to grow rapidly. But only the fastest growing tree will replace the fallen tree because the other more slowly growing trees will eventually be outmatched by shading.

The woody plants in the arid (dry) and semi-arid regions can compete so aggressively for the sparse amount of water that they form a dispersed but very regular distribution of plants. This distribution is is determined by the extensive root system of the individual plant. When a plant has first established a root system, it will outcompete all other plants within its root zone.

Many animals mark out a certain area (territory) for their activities (foraging, mating, nesting, etc.). This territory is defended aggressively or more peacefully with signals (odours, sounds, threatening postures etc.) against intruding individuals of the same species. This territoriality is an expression of intraspecific competition. At low population densities there are enough optimal territories for all, and territory defence has no effect on the reproductive success. At moderate population densities, there are not enough optimal territories for everyone and some individuals are forced out into "marginal territories". At even higher population densities, there is a need for even marginal territories and some individuals become "floaters" without any territory. These individuals' reproductive success is very small, but "floaters" act as the population's buffer, by taking over territories that become empty due to death of the territory owner. When a population's density is approaching the area's ability to feed the population, the number of "floaters" with poor reproductive success and scanty territory assertive behaviour decrease, and in this way the population regulates itself. For example, studies of the reproduction speed of great tits have shown that there is a clear decline in the number of nestlings per couple with increasing population density. The number of nestlings per couple can thus be reduced from 16 young birds per year when there is a population density of 1 pair per 10 ha to only 6 young birds per couple when there are 16 pairs per 10 ha.

Defending of territories can also help to regulate a population by forcing “floaters” to search for territories in new areas. Studies have shown that the number of deer in a forest is kept constant by territory defending behaviour that forces the excess deer without a territory to emigrate. In this way, intraspecific competition can also affect the spreading of a species [34].

4.2 POPULATION GROWTH AND MATHEMATICAL MODELS

If the number of births per individual and per unit time (birth rate = natality) is called x, and the number of deaths per individual and per unit time (mortality) is called y, the specific growth rate is defined as: $r = x - y$. If a population has N individuals, the population specific growth rate can be described by the equation:

$$r = (1/N)dN/dt \tag{I}$$

The unit of r is time^{-1}, and it is noted that the population growth rate, dN/dt, is proportional to the size of the population, N. If r is constant, the growth is said to be exponential. If r is positive then the population increases in size (positive growth); if r is negative, then the size of the population is decreasing (negative growth), and if $r = 0$, then N is constant (zero growth).

The differential equation can be solved by separation of the variables:

$$\int(1/N)dN = \int rdt$$

and

$$\ln N = rt + c$$

If $N = N_0$ for $t = 0$, then $c = \ln N_0$, and

$$\ln N = rt + \ln N_0$$
$$\ln(N/N_0) = rt$$
$$N/N_0 = e^{rt}$$

or

$$N = N_0e^{rt} \tag{II}$$

where N is the population size at a given time t, and N_0 is the population size at time $t = 0$. If you insert a theoretical value of the specific growth rate in this equation (e.g. $r = 1.15$) and plot the number of individuals (N) as a function of time (t) in an arithmetic plot, the result is a J-shaped curve pattern, see Fig. 34A. But if you choose to plot N as a function of time in a semi-natural logarithmic (semi-ln) plot, a linear line with slope r is obtained, because $\ln N = \ln N_0 + rt$, see Fig. 34B.

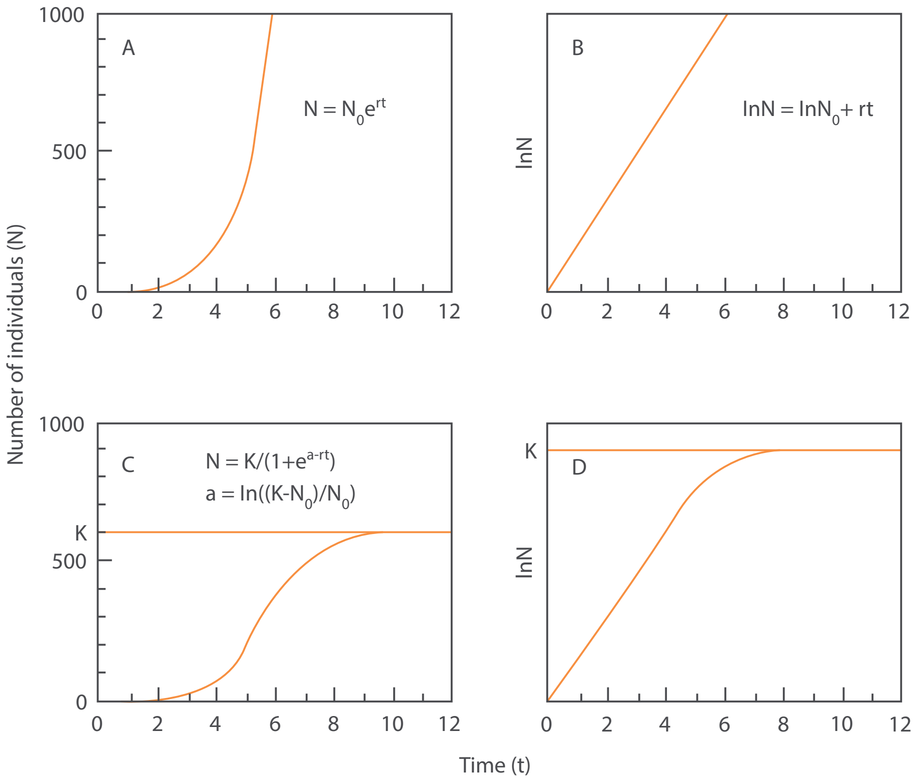


Fig. 34. Growth of two theoretical organisms where one grows exponentially (A) while the other displays "sigmoid" growth (C). The arithmetic plots to the left (A & C) are comparable to the semi-logarithmic plots to the right of (B & D). r = (unlimited) specific growth rate, K = carrying capacity. The examples are based on one individual at t = 0.

The doubling of time (t_2) for a population exhibiting exponential growth is obtained by inserting $N = 2N_0$ in the growth equation (II) which gives $2 = e^{rt}{}_2$ or:

$$t_2 = \ln2/r = 0.693/r \tag{III}$$

If the exponential growth is negative (by analogy with the decay of radioactive substances), the population is reduced by half at regular time intervals: $t_{0.5} = \ln0.5/r$.

Growth in one period of time is: $N_{t+1}/N_t = e^r$. For example, if the growth is expressed by periodical increments in percentage, then: $e^r = 1 + r_{per}$ or $r = \ln(r_{per} + 1)$, where r_{per} is called the periodic specific growth (= percentage growth/100). Since $r_{per} = e^r - 1$, it follows that:

$$N = N_0e^{rt} = N_0(1 + r_{per})^t \tag{IV}$$

For small values, the specific growth (r) and the period specific growth (r_{per}) are almost equal: $r = 0.02$ implies that $r_{per} = 1.01r$. For populations the concepts of generation time can be introduced: t_g = the average difference between the date of birth of the offspring and the parents, and net reproduction; R_0 = the number of offspring each individual on average produces (= number of new individuals per individual). Therefore, from equation (II) it will:

$$R_0 = e^{rtg} \tag{V}$$

In the previous section, it was shown how the growth of a population can be described mathematically, if the specific growth rate (r) is constant. But is the population specific growth rate ever constant? Fig. 35 shows the growth of a ciliate kept in the laboratory at different temperatures, and this experiment confirms that a population can in fact have a constant r value and thus increase exponentially. But it is clear that the exponential growth can not continue indefinitely; resources will eventually be exhausted and the growth will stop.

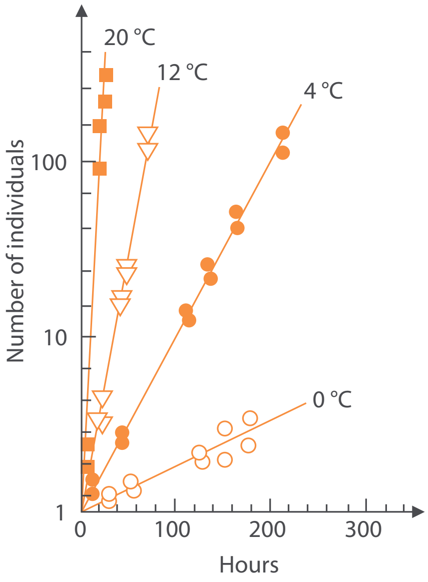


Fig. 35. Population growth in the ciliate *Uronema marina* at different temperatures. The population growth is exponential due to the number of individuals over time being described by a straight line in the semi-logarithmic plot. The slope of each line expresses the specific growth rate (r) at the specified temperature [64].

All populations will grow exponentially under constant conditions, but usually growth is inhibited before all resources are exhausted, so growth is only exponential in the beginning. However, there may be examples from nature where the growth is exponential until food becomes limiting. Populations which grow exponentially are characterized by being unstable and highly volatile (infestations and bacterial growth).

Many populations inhibit their own growth when their sizes approach the carrying capacity of the area. The inhibition takes place through a so-called negative feedback, , dN/dt, which reduces the growth rate of the population more and more as the number of individuals approach the carrying capacity, K. This can be expressed by modifying the equation for the unrestrained exponential growth with the function f(N). Small values of N ($N << K$) assumes values near 1 (almost exponential growth); but as N approaches K the function f(N) goes towards 0 (zero): $dN/dt = rNf(N)$ (r = maximum unlimited initial growth rate). The requested function f(N) can be expressed by the size $(K – N)/K$, which has values close to 1 for $N << K$ and approaching 0 for N going towards K. The differential equation thus becomes:

$$dN/dt = rN(K - N)/K \tag{VI}$$

The growth model is called “the logistic model” or “the Pearl-Verhulst model” after its two (independent) developers. It is immediately seen that (K – N)/K is an expression of the number of “seats” that, at any time, are left over in relation to the maximum possible number of “seats”, namely the carrying capacity (K). By integration (not to be shown here; see e.g. reference [59]) the logistic growth equation is obtained:

$$N = K/(1 + e^{[a-rt]}) \qquad \text{(VII)}$$

where $a = \ln [(K - N_0)/N_0]$.

The number of individuals (N) versus time in an arithmetic plot describes an S-shaped (“sigmoid”) curve, see Fig. 34C. It can be seen that the population growth is (almost) exponential for small values of N, and that N with time approaches asymptotically to K. The growth rate of the population is maximal when the population density is half of the carrying capacity (the sigmoid curve’s tangent line). The optimum yield $(dN/dt)_{opt}$ that can be obtained from the population is determined by inserting N = K/2 in the expression:

$$(dN/dt)_{opt} = rN(1- N/K) = r(K/2)(l -1/2) = rK/4 \qquad \text{(VIII).}$$

If for example a fish population follows the logistic model, then the fish population will be overfished (i.e. the population is driven towards extinction) if the yield is larger than rK/4. If less is being fished, the maximum yield is not obtained. The simple rule of “half the carrying capacity” is based strictly on the logistic growth model. Populations with more complex, non-linear relationships between specific growth rate and population density will have different points of optimum yields, for example (⅓)K, or (¾)K.

In Fig. 34 there has been made a comparison between sigmoid and exponential growth, partly in an arithmetic plot, partly in a semi-log plot. It is noted that the curves coincide at the beginning. In the semi-logarithmic plot, the sigmoid growth curve approaches asymptotically to K (Fig. 34D), whereas the exponential growth curve is linear with time (Fig. 34B). The logistic growth model shows the relationship between the elements, all of which can be ascribed a biological meaning. But the model has so many significant simplifications, that it can not be expected to give a realistic picture even in relatively simple situations. Thus, the model does not taken into account: 1) the age structure of the population, 2) the minimum size of the population for survival, 3) social animals have a minimal density, 4) changes in the environment are not immediately reflected in a changed population growth rate, 5) competition with other species’ populations, 6) it is unreasonable simply to assume that the specific growth rate decreases linearly with population density, see Fig. 36.

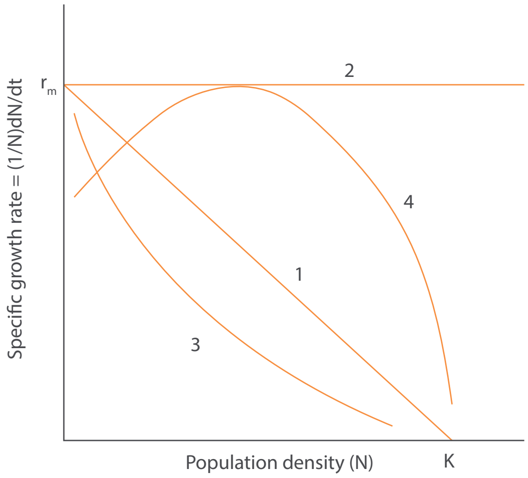


Fig. 36. Possible relationships between a population's specific growth rate and its density. Curve no. 1 shows the hypothetical line for a population which has a specific growth rate $(1/N)dN/dt = r_m(1 - N/K)$, where r_m = the maximum specific growth rate, which decreases linearly as a function of population density (N) (one of the prerequisites of the logistic growth equation). Curve no. 2 shows the specific growth rate in a population that has a density-independent growth, and hence is growing exponentially. Curve no. 3 shows a form which is often found in a density-dependent, self-regulating population. Curve no. 4 shows the specific growth rate in a population that has a maximum growth rate at a medium population density.

In spite of these objections, the logistic model has frequently been fitted to experimental data from both laboratory and field studies. The reason for this is that the model is simple, that the used terms can be attributed biological meaning, and that there is often a surprisingly good agreement with the experimental data. In Fig. 37, the logistic growth model is used to describe the sigmoid growth of a population of yeast cells. The concept of "negative feedback" covers different conditions increasingly inhibiting the growth of the population when its density increases. In the case of yeast cells (see Figs. 37 & 38), the inhibition is caused by the yeast cells' production of harmful substances (including alcohol).

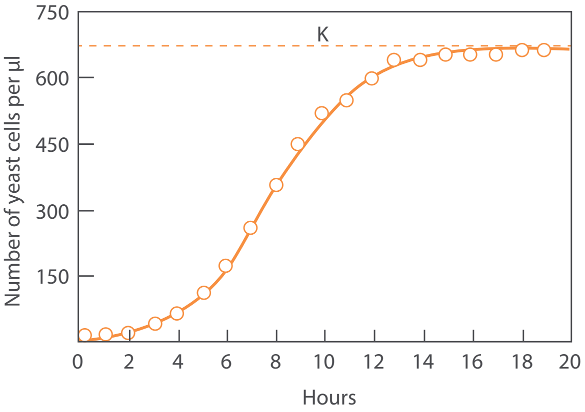


Fig. 37. The growth of yeast cells in a culture is self-limiting, since the "negative feedback" or "ambient resistance" is linearly proportional to the density of yeast cells. In the figure, the logistic growth model is used to describe the yeast population's "sigmoidal growth" in an arithmetic plot [1].

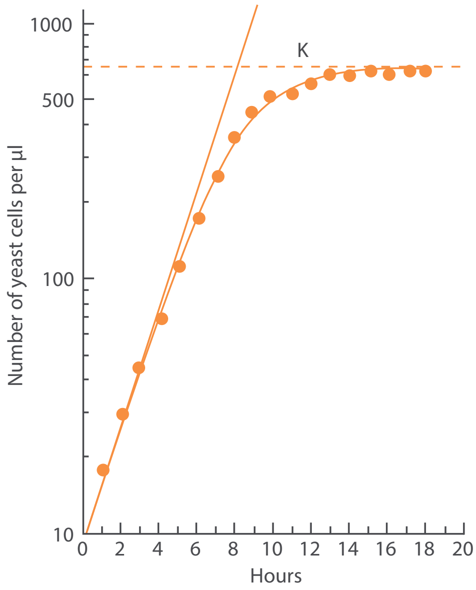


Fig. 38. The same data for the growth of yeast cells in culture, as shown in Fig. 37 but depicted in a semi-log plot. An exponential curve that describes the growth of the yeast culture during the first 4 hours has been plotted to illustrate how the growth would be if there was no "negative feedback". The area between the two curves, and the line for the carrying capacity (K), can be perceived as a quantitative expression of the "ambient resistance".

In larger animals, such as feral sheep (see Fig. 39), the negative feedback is caused by food scarcity due to an increasing degree of overgrazing as the population approaches the area's carrying capacity. In territory defending animals, negative feedback is often caused by reduced reproductive success of individuals without a territory. If the exponentially growing human population in many developing countries should be lowered, it is a widespread assumption that a negative feedback is needed in the form of social and material goods for families with few children.

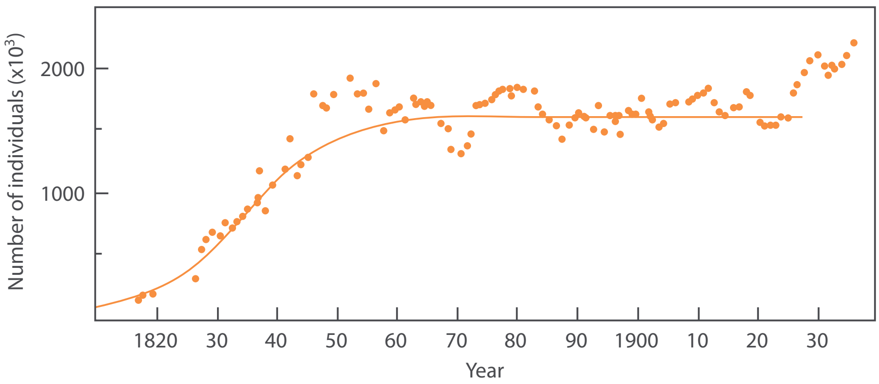


Fig. 39. Around year 1800, sheep were released into the wild on the island of Tasmania, south of Australia, and for a period of more than 100 years, there exist reasonably good countings of the sheep population [35]. In the new environment, with temporary unlimited food resources, the sheep population grew exponentially at the beginning, but because of the delay in the feed-back mechanism for the self-regulating population and consequent overgrazing, the stock began to decline, followed by a series of "damped oscillations" around the carrying capacity of about 1,700,000 sheep. The plotted curve is based on the logistic growth equation (VII) fitted to the dots showing data for the individual countings [7]. The increase in population size after 1925 can be attributed to better living conditions due to cultivation of land.

Independently of each other, the American mathematician, physical chemist and statistician Alfred J. Lotka and the Italian mathematician Pierre F. Volterra in the mid-1920s, generated a set of differential equations to describe the growth of two species' populations that compete for the same food resource, and similar equations for two species of which one species is the other species' prey [36, 37]. The equations have been known as "the Lotka-Volterra equations" and are briefly presented below.

First we discuss a growth model that takes into account the competition between two species competing for the same limited resource (i.e. "the competitive exclusion principle"). Each species' population will be limited not only by its own individuals but also by the growth of the other species. If the two species' populations are called N_1 and N_2, the following growth equations for the two species can be established:

$$dN_1/dt = r_1N_1(K_1 - N_1 - \alpha N_2)/K_1$$

and

$$dN_2/dt = r_2N_2(K_2 - N_2 - \beta N_1)/K_2$$

where r_1 and r_2 are the two species' (unlimited) specific growth rates, K_1 and K_2 are the two species' carrying capacity when each of the species live alone, and α (alpha) and β (beta) are conversion factors so that N_1's and N_2's inhibitory effects on each other can be made equivalent to a corresponding number of individuals of the same species that "inhibit itself". For example is αN_2 = inhibitory competitive effect of species 2 on species 1. It can thus be seen that α/K_1 is a measure of how much an individual of species 2 inhibits species 1. Further it can be inferred that:

$$\beta/K_1 = 1/K_2 \text{ or } \beta = K_1/K_2$$

and

$$\alpha/K_2 = 1/K_1 \text{ or } \alpha = K_2/K_1$$

In the experiments with the ciliates *Paramecium aurelia* and *Paramecium caudatum* (see Fig. 27), it is found that $\beta = 1.64$ and $\alpha = 0.61$. The higher β-value indicates that the individuals in population N_1 has a larger "competition efficiency" and therefore always will win.

The established growth equations for the two species can not be integrated; but the consequences of the equations can be realized. N_1 is in equilibrium when $K_1 - N_1 - \alpha N_2 = 0$ and N_2 is in equilibrium when $K_2 - N_2 - \beta N_1 = 0$. If the equations are graphically depicted in a coordinate system, where the abscissa is N_1 and the ordinate N_2, it can be seen from the points located either above or below the lines of equilibrium that N_1 and N_2 will either grow or decrease, i.e., dN_1/dt and dN_2/dt are either positive or negative. The growth of the populations can be depicted as vectors, as shown in Fig. 40. If $\alpha = 0.6$ and $\beta = 1.6$, the outcome of the competition can be graphically assessed and displayed, see Fig. 41. It appears that N_1, which has the highest competitive efficiency, will always win.

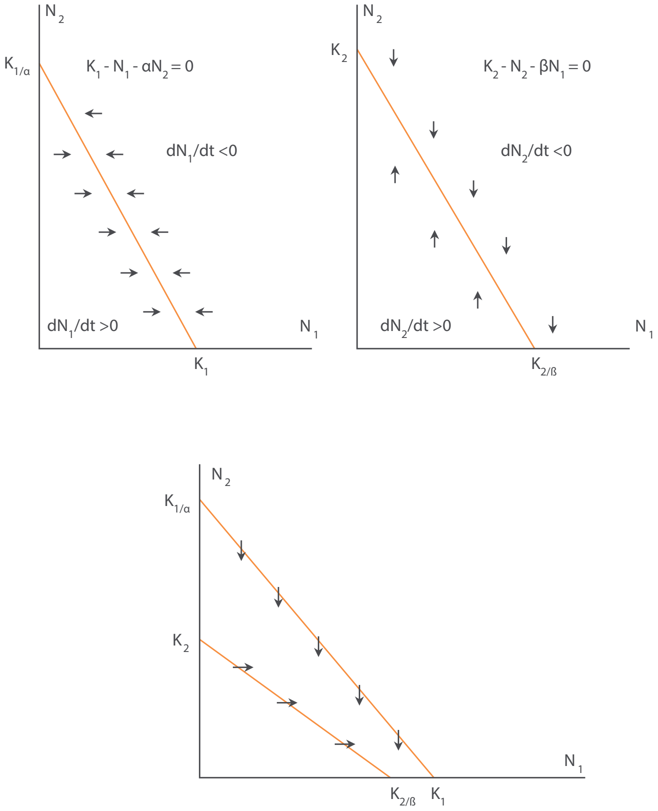


Fig. 40. Graphical solution of the Lotka-Volterra model for two species, N_1 and N_2, competing for the same food resource. The shown example is for $K_2 < K_1/\alpha$ and $K_1 > K_2/\beta$; the analogous possibility is $K_2 > K_1/\alpha$ and $K_1 < K_2/\beta$. Another two instances are when the isoclines for $dN/dt = 0$ cross each other. In one case this indicates stable coexistence, but lower population density for both species, the other case that one of the species is outcompeted, depending on the initial population sizes (cf. Fig. 28)

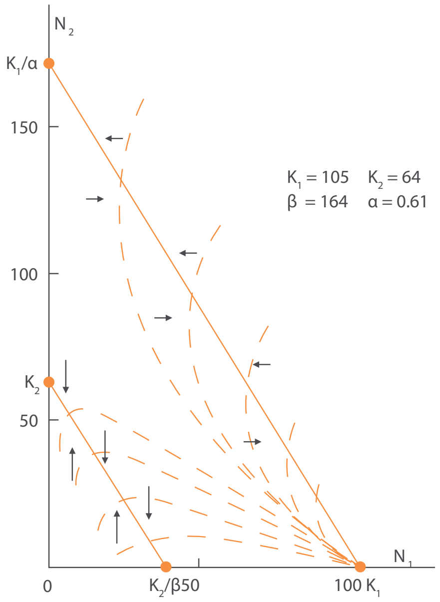


Fig. 41. Graphical presentation of the outcome of the Lotka-Volterra model for interspecific competition for the same food between the two species of ciliates (N_1 = *Paramecium aurelia*; N_2 = *P. caudatum*) shown in Fig. 27. It is seen that N_1 always wins, regardless of the initial population densities.

In the following we discuss the predator/prey model. In words the model can be described as follows:

> { *The change in the number of prey per unit of time* } = { *Unlimited growth of prey per unit of time* } – { *Extermination of prey per unit of time caused by the predator* }
>
> and
>
> { *The change in the number of predators per unit of time* } = { *The increase in the number of predators as a result of the change of prey per time unit* } – { *Deaths among predators per unit time* }

Mathematically, the predator/prey model can be formulated as:

$$dN_1/dt = r_1N_1 - k_1N_1N_2$$

and

$$dN_2/dt = k_2N_1N_2 - d_2N_2$$

where N_1 and N_2 are the population size of the prey and the predator, respectively, r_1 is the population growth rate of the prey in the absence of a predator, d_2 is the predators' mortality rate, and k_1 and k_2 are constants. The model assumes that the consumption of prey is directly proportional to the size of the two populations, assuming that this is equal to the probability that a predator and prey meet.

At the equilibrium point where $dN_1/dt = dN_2/dt = 0$, this implies that $N_1 = d_2/k_2$ and $N_2 = r_1/k_1$. It is seen that N_1 increases when N_2's death rate increases, and conversely that N_2 increases when N_1's growth rate r_1 increases. Use of insecticides has in some cases unexpectedly led to an increase in the number of pests because the insecticide resulted in an increased mortality of the predator of the pest organism. Anecdotally it can be mentioned that it was a similar phenomenon that made Volterra interested in population dynamics: during World War I, when the fishing effort as a whole went down, he observed an increase in the percentage of predatory fish at the fish market in Venice.

Although the Lotka-Volterra predator/prey model, in certain situations, is fairly robust, one must not forget that the model is based on at least three major simplifications: 1) the population growth rate of the predators is only limited by the population size of the prey, 2) none of the populations are limited by their own density, and 3) the population size of the predator has no effect on the number of prey caught (no intraspecific competition between predators).

Several attempts have been made to correct for some of the foregoing simplifications. Here only a single further development of the original Lotka-Volterra equations is mentioned , namely the following differential equations:

$$dN_1/dt = N_1(r_1 - k_1N_1 - k_2N_2)$$

and

$$dN_2/dt = N_2(r_2 - k_2N_2/N_1)$$

These equations take into account that the prey population restricts itself (made by introducing the term k_1N_1 and that the unlimited growth of the predator population is increasingly inhibited when the total number of predator to prey organisms (N_2/N_1) is growing.

In recent years, several books have been published on this subject and they give detailed outlines of the consequences of the differential equations [37, 38, 60, 61], which are not mentioned here.

In the following, some examples of the practical use of mathematical growth models are given.

Example 1

A culture of bacteria cells undergoing bifurcation (binary fission) has a constant generation time, t_g. The number of generations after time t is therefore t/t_g so that $N = N_0 2^{t/tg}$ is the number of cells at the time t, and N_0 is the initial number of cells. The concentration of bacteria was measured during the exponential growth phase. Initially it was measured to be 2×10^4 cells l^{-1}. After 10 hours, the concentration was measured to be 5.96×10^7 cells l^{-1}. What was the generation time of the bacteria culture?

Answer: $N = N_0 2^{t/rt}$

$5.96 \times 10^7 = 2 \times 10^4 \times 2^{10/tg}$

$t_g = 0.866$ hours

Example 2

A green algal species has a constant generation time, t_g, but do not divide in 2 but rather in 4 cells.

a) Derive an expression for the number of cells after g generations.
   Answer: 4^g
b) Derive an expression of the population specific growth rate.
   Answer: $N = N_0e^{rt}$
   $4 = e^{rt}$
   $r = (1/t_g) \ln 4$

Example 3

A population of algae is growing exponentially. It is observed that after 2 days there are 400 algal cells are present, while after 6 days there are 800 algal cells.

a. What is the size of the initial population?
b. If the specific growth rate is constant, what is then the population size after 10 days?

Answer: a) $t_2 = 6 - 2 = 4$ days

$r = \ln 2/t_2 = 0.693/4 = 0.173\ d^{-1}$

$N = N_0e^{rt} = 800 = N_0e^{0.173 \times 6}$

$N = 283$

b) $N = 283e^{0.173 \times 10} = 1596$

Example 4

The human population in a city grows with a constant rate of 4% per year. If the population in 2001 was 100,000, how big will it be in 2017?

Answer: $N = N_0(1 + r_{per})^t$

$N = 100{,}000\ (1 + 0.04)^{16} = 187{,}298$

Example 5

A population of yeast cells grows 48.2% per hour. At time t = 0 the population size is N_0 = 8.34 g biomass (DM = dry matter). During this growth period, the consumption of glucose is f = 0.345 g per g of biomass (DM) per hour (h). What is the consumption of glucose, $F_{t=4-5}$ from t = 4 to t = 5 h?

Answer: $r = \ln(1 + r_{per}) = \ln 1.482 = 0.393\ h^{-1}$

$N = N_0e^{rt} = 8.34e^{0.393t}$ g DM

At time t = 0 the instantaneous consumption is $F_0 = 0.345 \times 8.34 = 2.88$ g glucose h^{-1}.
$F_{t=4-5} = \int^5_4 F_0e^{rt}dt = \int^5_4 2.88e^{0.393t}dt = (2.88/0.393)\ [e^{0.393t}]^5_4 = 17$ g glucose.

5 SPECIES DIVERSITY

Species diversity is the multiplicity of species. If an area has high species diversity with regards to butterflies, it is a good locality for a butterfly collector. As a measure of diversity the number of species per individual can be used. If you collect 100 individuals in a community and find 50 species, one can say that species diversity is 0.5. If there are 10 species then the species diversity is only 0.1.

The distribution of species in a community can be very different. There may be approximately an equal number of individuals of each species, but there may also be a few species with many individuals and many species with few individuals. The experience shows that natural communities almost always have a very large number of species, of which only a few are very common.

When you describe the diversity of a community and want to compare the number of species with the number of individuals, various diversity indexes may be applied depending on what you are interested in information on [1, 36]. If you are interested in the dominant species, you can use a diversity index that weights the most common species in favor of the more rare. Such an index is, for example, the Simpson index = $\Sigma(n_i/N)^2$ where n_i is the number of specimens of the species i and N is the total number of individuals of all species. It is seen that rare species, which represents only a small percentage of the total number of individuals, contribute very little to this because of the squaring.

If you are interested in the more rare species, which empirically are the first to disappear if an area becomes polluted, you can use an index that favors the rare species. Such an index is for example the Shannon index = $-\Sigma\ (n_i/N)\ \log(n_i/N)$. It is seen that the smaller the percentage of the total number of individuals a species constitutes, the relatively more importance is attached to it (for example: $\log 0.5 = -0.30$ and $\log 0.05 = -1.30$).

When a plant or animal community is exposed to pollution (eutrophication, toxic substances), it is characteristic that the diversity falls simultaneously with an increase in the breadth of the niche of the surviving or newly established species, i.e. the populations of these species increase (Fig. 42). demonstrates the number of species (S) as a function of the number of individuals per species (N/S), both in a natural community and in a community exposed to pollution. It is seen that the total number of species decreases while a few species of the survivors will have many individuals.

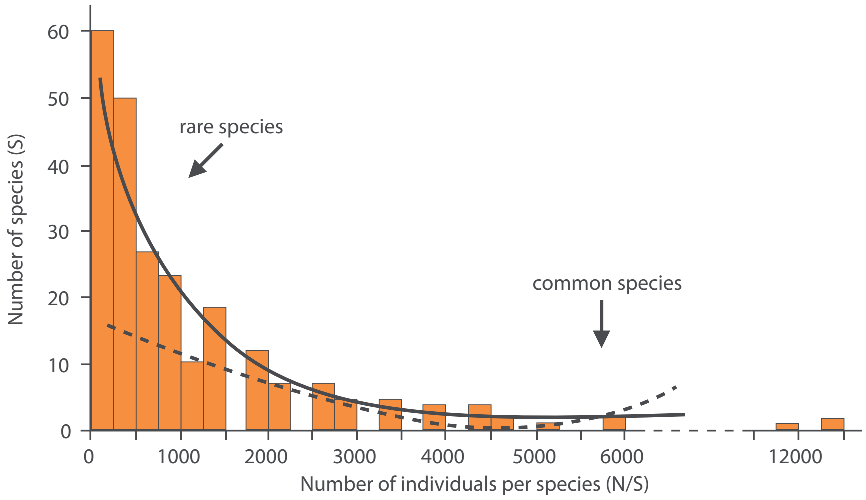


Fig. 42. The relationship between the number of species (S) and the number of individuals per species (N/S). In most natural communities, there is almost always a large number of species of which only a few are very common. When a community is exposed to pollution, it is characteristic that the rare species disappear while a few pollution-tolerant ("pollution indicators") survive and possibly get a large number of individuals – see dotted curve in the figure.

A number of biological and physical conditions that affect a community's species diversity can be pointed out:

The physical variation of the environment. Physically diverse (heterogeneous) habitats contain more niches than physically homogeneous habitats. Therefore, relatively few species are found in the homogeneous water masses of the oceans compared to the number of species in the coastal areas where there are varied habitats (stones, rocks, coral reefs etc.).

In total about 1 million plant and animal species are described, but only one-sixth are living in the sea. The remaining numbers of species live on land. The far greater number of terrestrial species can be associated with a considerably higher physical heterogeneity on land. A possible explanation for this phenomenon is that the smaller an animal is, the more physically heterogeneous the environment appears to be (Fig. 43).

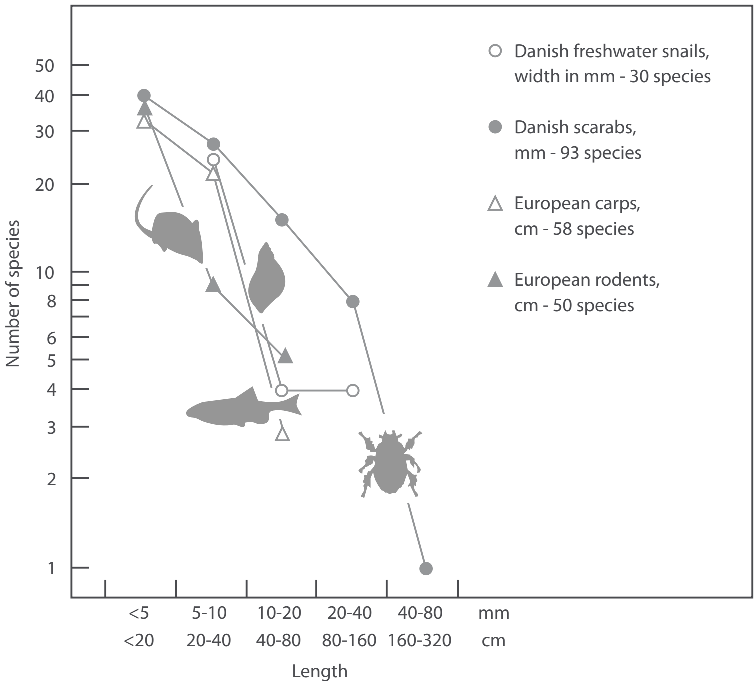


Fig. 43. When different groups of animal species are divided into size classes, the result is that the small species dominate, and that there are only a few large species within each group of animals [67]. The size distribution of species belonging to very different animal groups shows that there usually are many small but only a few large species in each group of animals, see Fig. 42. This statement applies when looking at a local community or within a narrow group of organisms (taxon). But globally, the picture does not fit because there are for example far more species of insects than of single-celled organisms (protozoans). The reason for this is that small organisms have a far greater distribution and no local (endemic) species. A given microorganism will occur when the environment fits it, and for microorganisms historical (in geological sense) events are not important. Thus, small organisms tend to have wider or even cosmopolitan distribution, a higher efficiency of dispersal, a lower rate of geographic speciation (i.e. allopatric speciation), and lower rates of local and global extinction than do larger organisms which may have endemic species on oceanic islands, mountain peaks, etc. [79].

High/low productivity. In a given ecosystem, there is only a limited amount of energy available; and the less productive an ecosystem is, the fewer number species can maintain a minimum population. High productivity is a precondition for high species diversity.

The age of the biotic community. Age, seen from a geological time scale, affects species diversity. Young ecosystems have lower species diversity than old stable ecosystems. Thus, there are fewer species in the "young" Baltic Sea than in the "old" Caspian Sea.

Stable/unstable environmental factors. In areas with strong fluctuations in the environment (salinity, temperature, water level, etc.), there are few species compared to areas with high stability. For example, only a few species have adapted to the instability in estuaries and other brackish waters. It is a characteristic of many brackish water species that they have broad niches. Thus, the bivalve *Macoma balthica* lives in brackish water at all depths and in all types of substrates (sand, mud, clay), but if the sea water has a high and constant salinity, it lives only on sand bottom in very shallow water. Due to interspecific competition caused by closely related bivalve species, *Macoma balthica* can only realize a fraction of its fundamental niche in seawater with constantly high salinity.

Age and stability alone do not explain high species diversity in a community. According to the so-called "intermediate disturbance hypothesis", high species diversity is also determined by a certain frequency of disturbances [58, 63]. In any community, organisms are killed or damaged by disturbances that occur with varying frequency. In the tropical rain forest, trees are damaged when they are pushed over in stormy weather or struck by lightning, insect infestations, landslides etc. Corals are destroyed by storms, freshwater flooding, sedimentation of mud or large flocks of predators. Small plant and animal communities on larger and smaller stones in shallow water near the shore are disturbed by storms that relocate the stones. The smaller the stones are, the more frequent and severe are the degree of disturbance caused by stormy weather. According to the hypothesis, high species diversity is only maintained if there is an appropriate frequency of disturbances of intermediate strength, see Fig. 44.

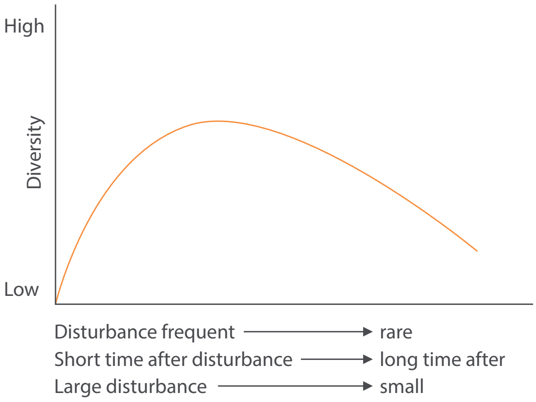


Fig. 44. High species diversity is, according to the "intermediate disturbance hypothesis", when high species diversity is determined by frequency, extent, and time after a disturbance of a community.

Disturbances interrupt and switch back the competitive elimination process that takes place during an ecological succession. When species that competitively exclude other species are removed, the weaker competitors invade the area. Although large geographical areas are stable in the sense that new species come and old species disappear with imperceptible speed, disturbances keep local communities in a state of imbalance, which promotes high species diversity. Gradual climatic changes will also act as disturbance, which helps to maintain high species diversity. If the frequency of disturbance is reduced, the species diversity decreases. In the struggle for the limited resources, the most effective species are allowed to outcompete the weaker species, and the species that are most resilient to disturbances, will occupy all vacant places and exclude potential immigrants, although these (in the longer run) are more effective.

Flowering plants		**Land snails**	
Labrador	390	Labrador	25
Massachusetts	1650	Massachusetts	100
Florida	2500	Florida	250
Marine mussels		**Ants**	
Newfoundland	30	Alaska	7
Cape Hatteras	150	Iowa	73
Florida	200	Trinidad	134
Beetles		**Coastal fish**	
Labrador	169	Labrador	25
Massachusetts	2000	Massachusetts	225
Florida	4000	Florida	650
Snakes		**Breeding birds**	
Canada	22	Greenland	56
U.S.A.	126	New York	195
Mexico	293	Colombia	1395

Table 4. Number of species in various systematic groups in areas with different climates (arctic cold temperate, temperate, tropical). Note that the number of species increases from north to south.

The four types of factors discussed above as being important for species diversity, have collectively led to the existence of a global variation in species diversity. In general, the diversity of biotic communities increase from the north towards the equator, see Table 4 and Fig. 45. The reasons for this change in diversity towards the equator are:

a) Higher degree of environmental stability from the poles towards the equator, allowing plants and animals to have a smaller niche width (they are more specialized).
b) A constant production throughout the year at the equator allows a smaller niche width and greater splitting of resources.
c) The tropical regions have been climatically stable for a long time (since the Cretaceous period), while the temperate and polar regions have been exposed to climate fluctuations, particularly during ice ages.

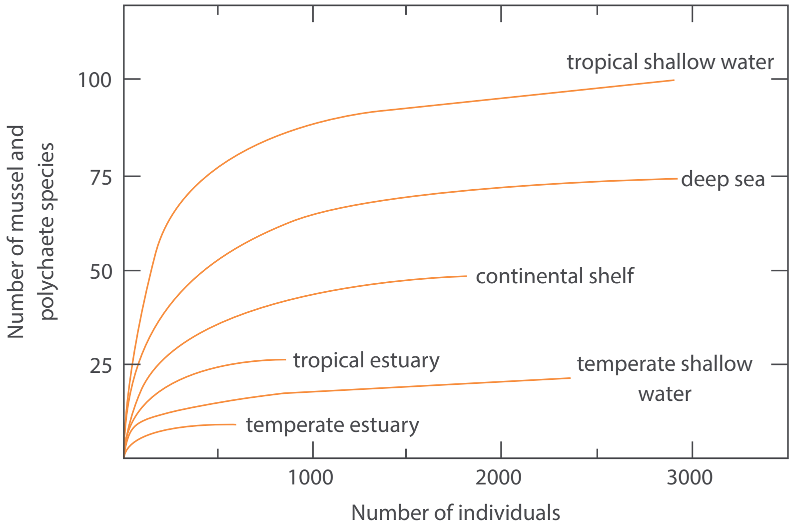


Fig. 45. The number of bivalve and polychaete species in bottom samples of increasing size and thus with an increasing number of individuals divided between an increasing number of species [40]. It is seen that the number of species is highest in the productive tropical shallow water where a constant high production throughout the year allows narrow widths of niches, and thus a large number of species in relation to the less productive and more environmentally unstable temperate shallow water. The species diversity is low in both the tropical and temperate estuary due to strong fluctuations in salinity, temperature, water level, etc. The great richness of species in the unproductive deep sea is remarkable. The explanation for this is that the deep sea has been very environmentally stable for many millions of years, so that in spite of the very meager food resources, many species have been able to evolve.

5.1 TRANSITION ZONES AND EDGE EFFECTS

It is often difficult or impossible to determine where plant and animal communities end and new ones start. The reason is that they are usually interconnected with an environmental gradient (temperature, rainfall, water depth, etc.) that causes smooth transitions. If the environmental gradient between two communities is steep, it is called a "transition zone". The communities on either side of a transition zone may be very different, and individuals of all species from the neighboring communities can invade the transition zone. Although fluctuations in the environmental conditions allow the species to survive, the transition zone is constantly being invaded by new individuals as well. In addition to species from neighboring ecosystems, the transition zone may also contain species that are specially adapted to this zone. The result is that the transition zone has higher species diversity than is found in each of the adjacent ecosystems. The ability of a transition zone to be a habitat for a species that cannot only live in one of the adjacent ecosystems is called the "edge effect". An example is the owl, which requires trees for nesting and hiding place, but with regard to food, it depends entirely on small rodents in the open land.

5.2 ISLAND BIOGEOGRAPHY

In 1917, the bird fauna was registered on nine islands off southern California. In 1968, the study was repeated. A comparison of the two studies demonstrated several notable features, see Table 5. Most notable was that the total number of species on the islands were almost unchanged over the past 51 years, but from 18% (on the largest island, Santa Cruz) to 63% (on the smallest island, Santa Barbara) of the species were replaced. On basis of these and similar types of observations made by the American biologists MacArthur and Wilson, the so-called “island-biogeography theory”or the “island-biogeographical equilibrium hypothesis” were established. According to this theory, the number of species on an island is due to a dynamic balance between immigrations of new species and the extinction of previously established species [41]. It has been found that small islands (even with the same biotopes as found on the mainland) have a poorer fauna than can be observed on similar biotopes on the mainland. The reason should be sought in the fact that all populations have a certain probability of extinction and that this probability is rapidly increasing with decreasing population size. On small isolated islands the total number of individuals of a species is modest and local extinction of the species will occur intermittently, thus leaving “empty niches”. This phenomenon explains the lower species diversity on small islands (and other isolated habitats). In line with the lower interspecific competition pressure on small islands, species living here have extended ecological niches compared to their fellow species on the mainland, see Fig. 46.

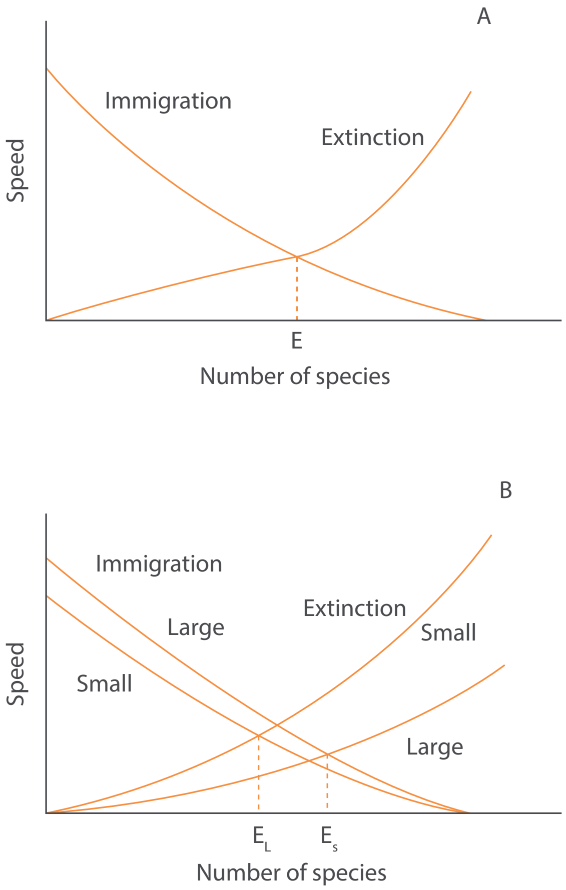


Fig. 46. (A): The number of immigrations of new species decreases and the number of endangered species increases as the total number of species on an island increases. The two processes balance when the island has E species, i.e. there is a dynamic equilibrium of the species. The steep increase in the number of extinct species takes place when all the island's habitats are occupied by reasonably well-adapted species. (B): The dynamic equilibrium of species is greater on a large island (E_s) than on a small island (E_l) when the distance from the mainland is the same.

The above principle has proven not only to apply to real islands, but also for "inverted islands" in the form of inland lakes and small ponds that are isolated in a "sea" of land. A study of lakes has shown that the number of species of freshwater snails is directly proportional to the area of the lakes, that the number of species decrease faster with decreasing size in nutrient-poor than in eutrophic lakes, and that the remaining snails in the small lakes utilise a larger part of their fundamental niche compared with their fellow species in larger lakes. Some snails that are strictly related to rooted aquatic plants in the shore zone of large lakes can thus be found everywhere in small lakes [42].

Familiarity with the island biogeographic principles has great practical importance for nature conservation. Nature sanctuaries that are surrounded by houses, farms, roads, etc. can be thought of as a kind of island. A consequence of this is that even if the public authorities preserve an area in order to sustain a certain fauna, some of the species will sooner or later, depending on the size of the area, become extinct. Thus, although some Danish moorland bogs may still be suitable habitats for the black grouse, these bogs are too few and small, and also too widely dispersed to allow the black grouse in the long term to maintain a sufficiently large population. As a result it was declared extinct in Denmark in 2001.

Another example is the bell frog, which in 1850 was fairly widespread on the Danish islands. Today there are only 8–10 small entirely separate populations left, mostly on small islands. By means of conservation planning, landscaping and new structures, efforts are being made to ensure the remaining populations from extinction.

Island	Area (km²)	Distance from land (km)	1917 number of species	1968 number of species	Extinct species 1917-1968	New species 1917-1968	Pct. species replaced 1917-1968
			C	D	E	F	(E+F)/(C+D)
Los Coronados	3	13	11	11	4	4	36
San Nicolas	56	98	11	11	6	6	55
San Clemente	143	78	28	24	9	5	27
Santa Catalina	192	32	30	34	6	10	25
Santa Barbara	3	61	10	6	7	3	63
San Miguel	36	42	11	15	4	8	46
Santa Rosa	215	43	14	25	1	12	33
Santa Cruz	246	30	36	37	6	7	18
Anacapa	3	21	15	14	5	4	31

Table 5. Land and freshwater birds on 9 islands off southern California in 1917 and 1968 [41].

6 ECOLOGICAL SUCCESSION

An ecological succession is a characteristic temporal order in which plant and animal species replace each other in an ecosystem. A succession can for example be initiated by burning a forest area or by adding nutrients to a biotope. One can distinguish between two different models that describe ecological successions:

1) *The facilitation model* describes ecological successions, where the first pioneer plants pave the way for the later succession stages that would not have been able to survive under the pioneer conditions. Examples of facilitation-successions can be obtained from ecosystems that start on sand, rocks or the like, and where the first succession stages generate topsoil and other vital conditions (e.g. a favourable microclimate) for the species that come later during the succession, see Fig. 47.
2) *The tolerance model* describes ecological successions where the way has previously been opened for a quick growth of pioneer plants whose existence has been "tolerated" in the earlier ecosystem in which they had a slow growth in the background. By shading, the pioneer plants inhibit themselves from reproducing, and other plants that tolerate shade turn up. If a forest is burned or a cultivated field is abandoned, fast growing annual and perennial plants will be the first to arrive. After 10–25 years, shrubs and low trees have suppressed the pioneer plants. After 25–100 years, the shrubs have been replaced by tall conifers, and the succession will then slowly reach its "climax" by possibly establishing a mixed forest of conifers and deciduous trees.

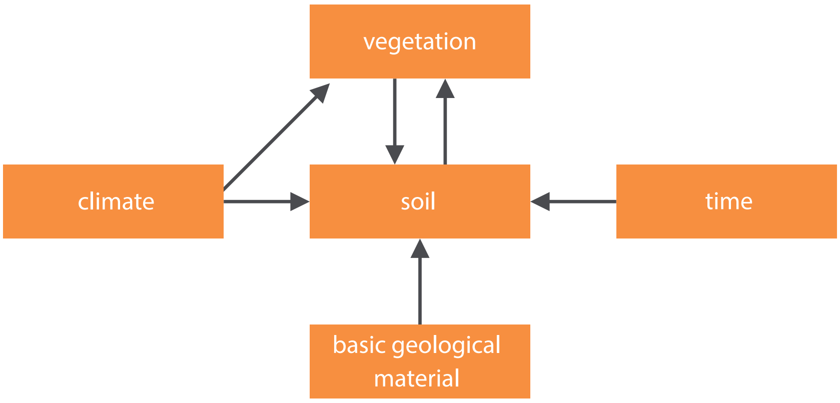


Fig. 47. Soil characteristics are determined by the geological starting material (granite, sandstone, limestone, etc.), climate (wet/dry, cold/hot), the vegetation and the time spent on soil formation.

6.1 AUTOGENOUS SUCCESSION

All ecosystems have a tendency to develop along certain predictable trajectories when under stable external conditions. An ecological succession is called *autogenous* if it is allowed to proceed to climax without any external physical disturbances. A succession where the primary production is dominating in the beginning is called *autotrophic*, while a succession where the respiration is dominating in the beginning is called *heterotrophic.*

The following is given an example of an *autogenous, autotrophic succession*: If inorganic nutrients (e.g. in the form of biologically treated wastewater) is added to an illuminated aquarium with sea water (with a natural content of living organisms), the following sequence of events can be observed: There is a rapid proliferation of one or a few species of single-celled plankton algae that have relatively large outer surfaces which effectively take up the nutrients. The plankton algae are followed by an increase of "grazers" (copepods, daphnia, large ciliates), which in turn forms the basis for an increase of predators (rotifers, predatory daphnia). The increase in primary production gives rise to a production of detritus (dead algae, dead animals, faeces), which sinks to the bottom where it is decomposed by bacteria and fungi. The succession in the ecosystem of the illuminated aquarium with seawater is characterized by:

1) The concentration of nutrients decreases (i.e. nutrient cycles tend to be "closed") with time.
2) Increasing species diversity and increasing complexity (simple food chains in the beginning followed by a more complex food web).
3) Larger organisms play an increasing role (the biomass increases).
4) The gross primary production (P) decreases in proportion to the biomass (B), i.e., P/B-ratio is decreasing because larger organisms play an increasing role.
5) The gross primary production (P) is far greater than the total ecosystem respiration (R) in the beginning, but it decreases with time so that P = R when the succession is completed.

If organic matter (e.g. in the form of untreated sewage water) instead of inorganic nutrients had been added to the above illuminated aquarium with seawater, the succession would have been dominated by respiration in the beginning. The succession would then have been an example of a so-called *autogenous, heterotrophic succession*. The succession process would go as follows, see Fig. 48.

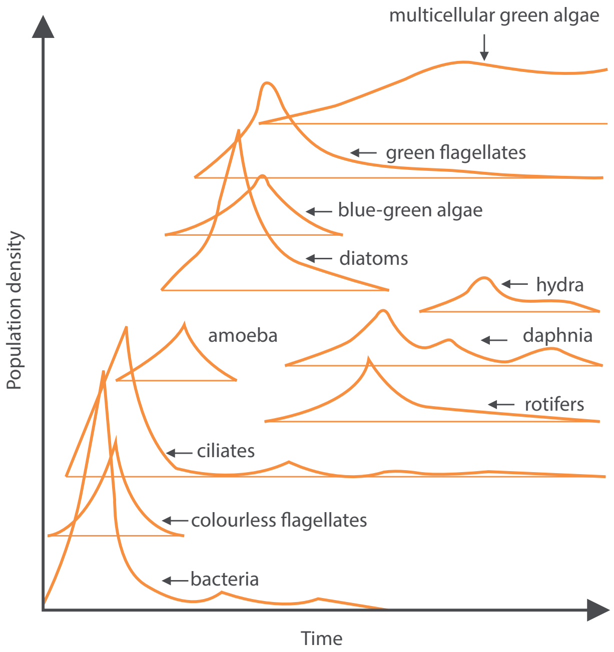


Fig. 48. Heterotrophic succession of freshwater organisms in an aquarium with sea water enriched with organic matter [68].

There is a strong increase of bacteria that have a high reproductive potential (high r-value) and are able to utilize the initially high substrate concentrations (bacteria are known as opportunists). The bacteria form the basis for an increase of bacteria-eating microorganisms (colourless flagellates and small ciliates). The bacteria-eating flagellates and ciliates form again basis for an increase of predators (amoebas, rotifers, large ciliates). Because of a progressive mineralization of the organic matter, this creates the basis for growth of photoautotrophic organisms (diatoms, blue-green algae, green flagellates). These photoautotrophic planktonic algae are "grazed" by daphnia, large ciliates and other herbivores. This grazing of plankton algae leads to growth of multicellular green algae, because these "big" filamentous algae cannot be eaten by the small herbivores. Finally, the herbivores serve as food for larger predators (hydra, a sessile freshwater polyp).

Based on the above two examples of autogenous successions, a number of characteristics can be pointed out of how an ecosystem evolves from a young (juvenile) to a mature climax ecosystem:

1) Increasing species diversity.
2) Increasing dominance of larger organisms and thus:
   - greater total biomass (B).
   - smaller production (P) per unit biomass (P/B decreasing).
   - essential nutrients are to a higher extend, being bound into living tissue and thus "closed material cycles".
3) Increasing degree of stability, as shown by reduced rate of changes in the ecosystem's species composition.
4) Development towards such a balance between photoautotrophic and heterotrophic processes that the gross primary production in the climax stage becomes equal to the total respiration in the ecosystem, see also Figs. 49 & 50.
5) The rate at which living matter in an ecosystem is theoretically renewed is called the "turnover rate", and is calculated as the ratio of the gross primary production and the ecosystem's total biomass. It is characteristic that the turnover rate (P/B) in an ecosystem decreases during a succession. The inverse ratio (B/P) is called the "turnover time".

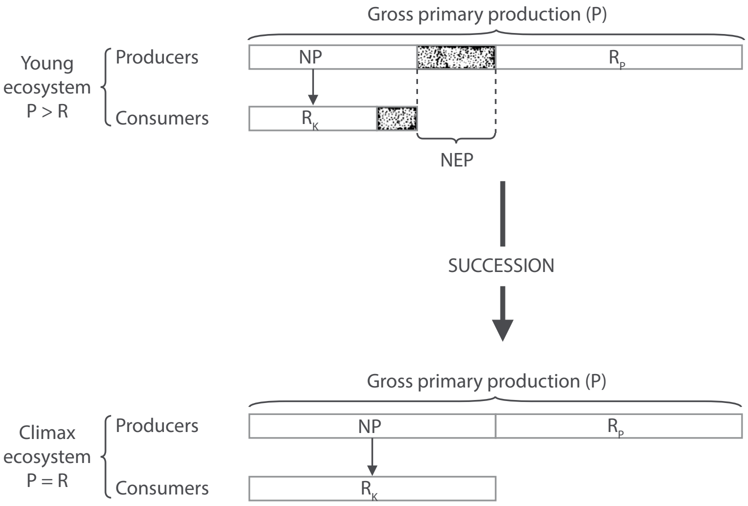


Fig. 49. The gross primary production (P) in a young autotrophic ecosystem is greater than the total ecosystem respiration = producers respiration (R_p) + the respiration of the consumers (R_c). In the young ecosystem, all the net primary production is not used for respiration, which implies that the system has a net production (NEP = net ecosystem production) which accumulates as organic matter. The accumulation of organic matter (detritus and living organisms) increases the physical heterogeneity of the ecosystem, and as long as there is a surplus of organic matter, there are "empty niches". Therefore, new species come and carry on the autogenous, autotrophic succession until all the niches are "filled in" and the whole the gross primary production of the ecosystem is spent on respiration (P = R) [46].

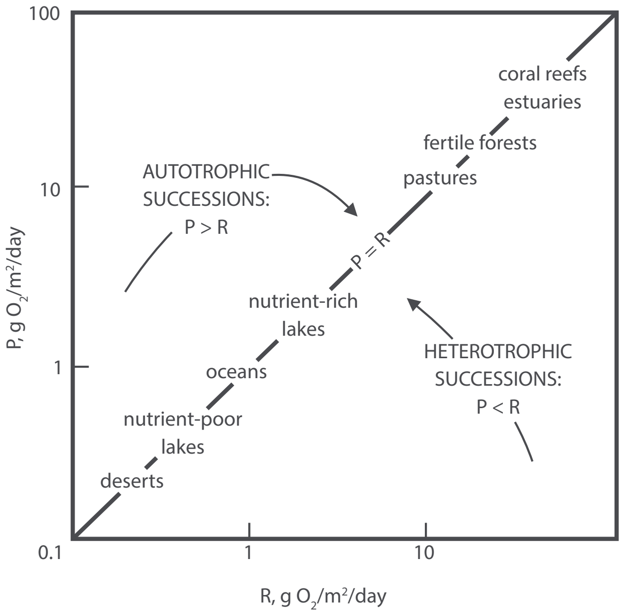


Fig. 50. In a mature climax ecosystem (on an annual basis) is the gross primary production of the system (P) = the respiration of the system (R). Both autotrophic and heterotrophic ecological successions will develop towards this condition. Ecosystems with high flow through of energy are placed high on the line P = R, while the opposite is true for ecosystems with low flow through of energy [47].

The above characteristics of an ecosystem that evolves from a juvenile to a mature system has by experience been shown to apply to any succession, whether it takes place over a few days, weeks, months or years. In Fig. 51 is shown the changes in a number of ecological parameters describing a succession following a forest fire, which proceed over a period of more than 100 years.

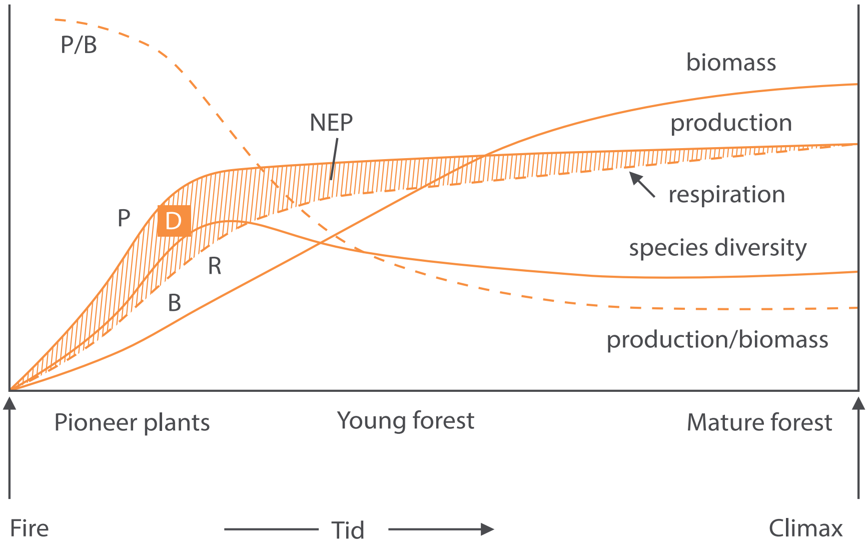


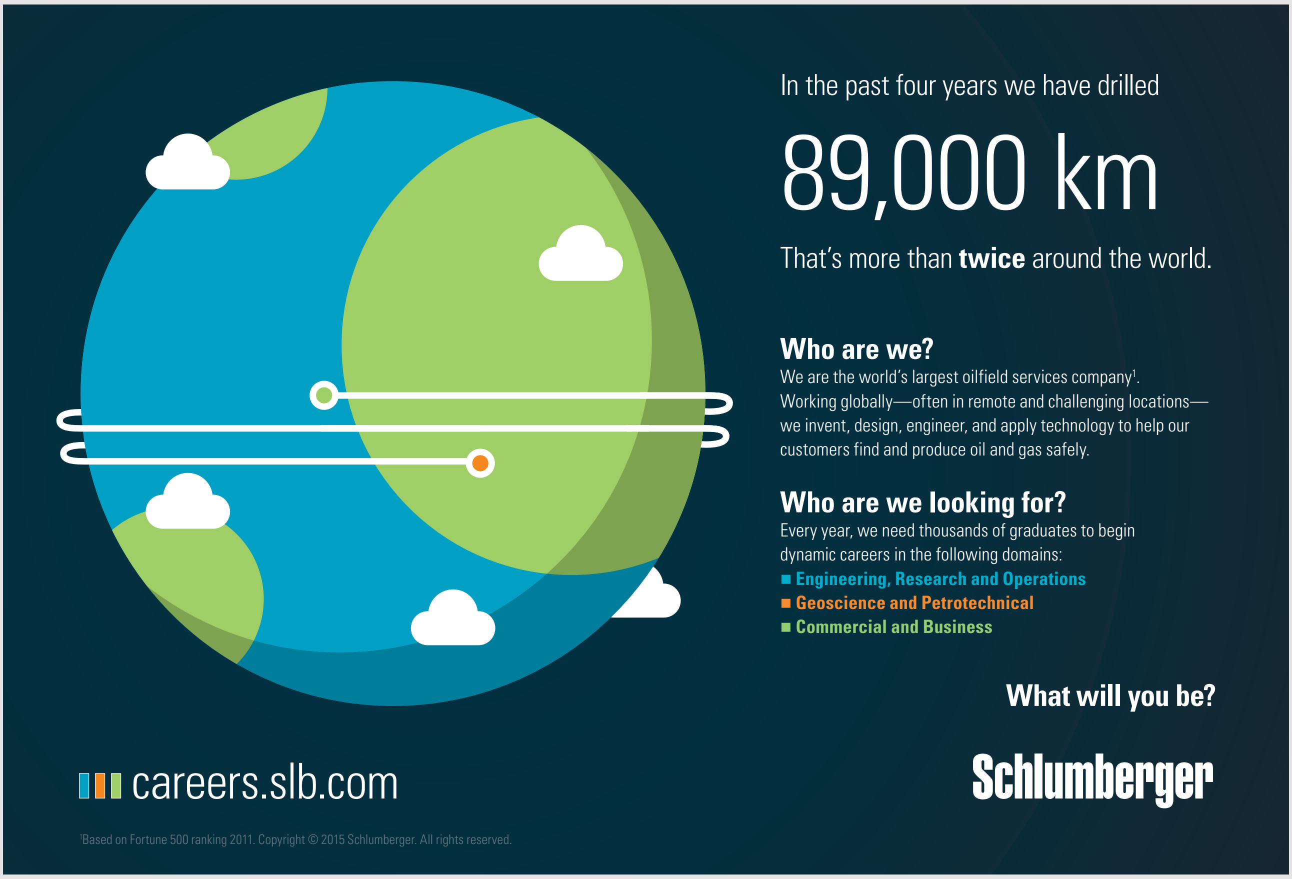
Fig. 51. Changes in different ecological parameters during a succession following a forest fire [1, 3]. The shaded area between the curve of the gross primary production of the ecosystem (P) and the total respiration of the ecosystem (R) is equal to the net ecosystem production (NEP), see also Fig. 49. It is noted that the species diversity (D) reaches a maximum at the time of invasion of the young forest trees, whereupon the diversity slightly decreases as pioneer species are eliminated. The biomass (B) rises slightly in the beginning where the plant community is dominated by herbs and scrub, but it increases as the larger trees grow up.

6.2 K AND R-STRATEGISTS

In the earliest stages of an ecological succession opportunistic, small organisms with a high reproduction potential (high r-value) are favoured, because these organisms are capable of utilizing the initially high substrate/nutrient concentrations. These organisms are called r-strategists. Gradually, as a succession in a community is approaching the climax ecosystem's equilibrium community, increasingly larger organisms are favoured because these have specialized niches, longer and more complex life cycles, good competitiveness, and a population growth that is characterized by an increasingly inhibited "negative feedback", as the area's carrying capacity (K) is approached. These organisms are called K-strategists.

6.3 ALLOGENEIC SUCCESSION

Successions in ecosystems that are caused by changes that come from outside are called allogeneic. Allogeneic successions take place in ecosystems where the plant and animal communities are not able to modify the physical environment to any particular degree – for example in the sea's free water masses. Here, the growth of phytoplankton and the species composition are to a large extent controlled by light, temperature and other seasonally controlled physical conditions, and therefore the "built-in" tendency of an autogenous succession is disturbed so that a climax stage is never reached. External physical forces can destabilize an ecosystem, but if the disturbances occur with regularity over a long time, plants and animals adapt to the conditions, so that an ecosystem is stabilised to a succession stage between the juvenile and the mature stage. Examples of such "pulse stabilised sub-climax" ecosystems are tidal estuaries and rice fields.



6.4 CLIMAX ECOSYSTEMS

If for example Denmark was uninhabited and uncultivated, this temperate country would (probably) be covered by deciduous forest, which is the climax ecosystem that would develop under the temperature conditions prevailing today. But looking back in time (using pollen analysis) on the historical development of the woody vegetation in Denmark, since the Ice Age, one will see that there have been various climactic stages at different times, depending on the temperature and thus periods dominated by different decidious tree-species such as birch, hazel, fir, lime and beech.

6.5 SUCCESSION IN "SPACE"

The natural autogenous succession that an ecosystem will go through in time, if the external physical conditions were stable, can often be studied in "space". The natural succession a sand dune close to the sea would undergo, if it was not constantly under strong influence of physical forces (coastal erosion, sand drifting), can be studied in space when walking from the sandy beach into the hinterland through the "white dune" which is without vegetation and to the "grey dune" with some plant growth, therefore less affected by sand drifting and erosion. This implies that the external conditions are relatively stable.

Another example that succession can be studied in "space" is illustrated in Fig. 52, which shows what happens if a stream is continuously fed wastewater with a high content of organic matter. By following the flow direction away from wastewater discharges, one can observe an autogenous, heterotrophic succession in space. If water discharge ceased, one would in time be able to observe a similar succession in the area near the discharge point.

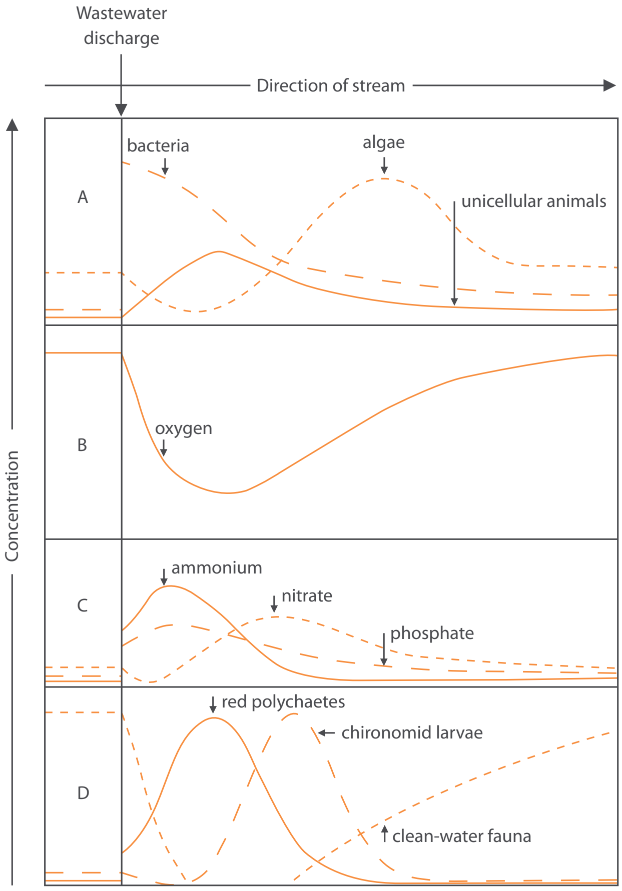


Fig. 52. Zonation (= succession in "space") in a stream supplied with untreated wastewater with a high content of organic matter [48]. Close to the discharge point, the organic matter causes a strong growth of bacteria. The bacterial decomposition causes a large consumption of oxygen. This may result in oxygen concentrations in the water being so low that only red worms (*Tubifex*) and red chironomid larvae (*Chironomus*) can live in the waste water community. The large amounts of bacteria give rise to a subsequent growth of bacteria-eating unicellular animals (protozoans). As the organic material decomposes, ammonium, phosphate and other nutrients are released and subsequently utilized by the photosynthetic algae. Further down the stream, where the water has become more oxygenated, ammonium is converted to nitrate, while the fauna increasingly resembles that which existed before the discharge.

6.6 THE BIOSPHERE AS AN ECOSYSTEM

The development (evolution) of the biosphere, which is the layer of the planet Earth where life exists, is an interesting example of how there can be an interaction between allogeneic succession processes caused by climatic/geological changes and autogenous succession processes which run on due to the activity of the living organisms [1, 49, 50]. The first living organisms developed on Earth more than 3 billion years ago were probably aquatic anaerobic bacteria and other heterotrophic unicellular organisms. They lived off of amino acids that were spontaneously formed due to strong ultraviolet solar radiation in an atmosphere consisting of nitrogen, hydrogen sulphide, carbon dioxide, methane and water – but not oxygen. However, this hypothesis of a "primordial soup" presented by John Haldane in 1929 [65], and which was very similar to Aleksander Oparin's ideas published in 1914, has more recently been questioned [66]. About 2 billion years ago the first photosynthetic autotrophic organisms emerged. They produced organic matter from carbon dioxide, water and light energy with concurrent formation of oxygen. Due to this oxygen production, an ozone layer was gradually formed in the stratosphere, which greatly reduced the lethal ultraviolet solar radiation so that life could exist also on land. Oxygen-breathing "grazing" organisms were gradually developed, but for a long period in the latter half of the Paleozoic Era, the biosphere's gross primary production far exceeded the total respiration in the biosphere ecosystem. This gave rise to a net production of organic matter that accumulated as coal and oil. Since there were many "empty niches", many new species could be developed. They became more and more specialized due to increasing interspecific competition. As the biosphere's ecological succession progressed, the atmospheric oxygen and carbon dioxide content changed resulting in changes in the climate. The climate changes gave rise to allogeneic succession processes that interacted with autogenous succession processes, which determined the onward evolution of the biosphere. In the last several millions of years, the biosphere's production has approximately been equal to its respiration and the number of species on Earth (the species diversity) has been roughly constant. The succession of the biosphere has thus been about to reach its climax until the industrialized world in recent times started to release large quantities of carbon dioxide into the atmosphere by burning of coal and oil. These resources were produced in an earlier geological period when the conditions of life on Earth were completely different from today.

6.7 ECOSYSTEM COMPLEXITY AND STABILITY

The food resources in nature are often found in a "continuum of qualities" (e.g. as a size-gradient of food particles) [60]. Various animals' use of a resource-continuum is depicted in Fig. 53.

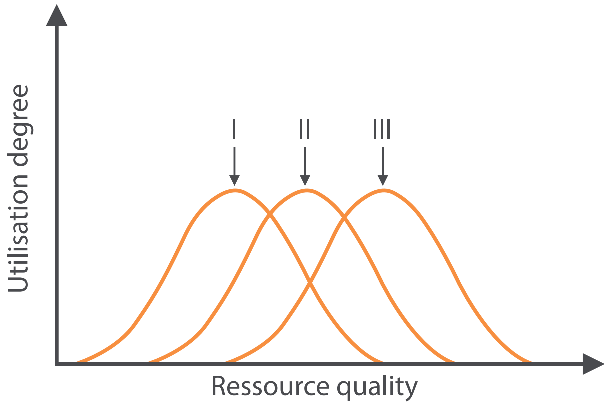


Fig. 53. Three species' (I, II, III) exploitation of a resource with a gradient of qualities (= resource-continuum), such as a size-gradient of food particles [60].

The bell-shaped curves show three species use of resources. It can be seen that each species has a preferred grade on which it has specialized in exploiting most efficiently. The number of species that may specialize in utilizing a certain part of such a resource-continuum is limited by the fact that the specialization determines the width of the niche (narrow niche = high specialization), the narrower the niche, the less food available to maintain a population. The specialization implies therefore that the population becomes smaller, which in turn means that the probability that the species die out becomes larger. The more productive and climatically stable an area is, the more highly specialized species with small populations will be able to develop. The tendency of ecosystems to evolve towards greater complexity and higher species diversity is therefore limited by increased sensitivity to climate change and other impacts from outside, which implies that the most specialized species die out.

The “stability” of an ecosystem is its ability to withstand external changes (climatic changes, pollution, etc.) without the ecosystem being significantly affected through loss of species and immigration of new species. It is still a common misconception – even among biologists – that complex ecosystems are more “stable” than simple ecosystems. The misunderstanding seems to depend on the assumption that the more ways food energy can be channeled through an ecosystem, the more robust is the system against impacts from the outside. However, the fact is that tropical ecosystems, which have a high degree of complexity and a large variety of species, because of the very constant environmental conditions in the tropics, have only a low degree of stability to changes in environmental factors. Conversely, arctic ecosystems have a high degree of stability against extreme climatic fluctuations due to simpler food chains with fewer specialist species that can utilize several different food resources depending on the current situation. Experience also shows that tropical ecosystems are more sensitive to disturbances than temperate ecosystems, and clearing of tropical rainforests can lead to irreversible damages.

6.8 ECOSYSTEM MODELS AND LIMITS TO GROWTH

In principle – and sometimes in practice – the energy flow through the various components of an ecosystem can be quantified by means of mathematical models (using computers). These models can analytically examine the characteristics of the system based on different assumptions. One can assess the consequences of intervention in nature, for example increased fishing or pollution, in order to make rational planning that aims not to destroy the natural balance of the ecosystem.

The book “Limits to Growth”, prepared by an American research group was published in 1972. The book contains the results of a number of model calculations of possible global developments until 2100. Using mathematical models for the growth of the world population, food production, consumption of natural resources, industrial production and pollution, the researchers set up models for global development. The book aroused a fierce debate and has been the most powerful contribution to the “ecology debate”. It points to a number of technological measures and growth regulatory interventions. These interventions must be made if humanity should not run into a disaster caused by an exponentially growing global population that will lead to lack of resources, which sooner or later will set a definite limit to further growth. The technical measures that the American researchers identified were “recycling of resources”, “pollution control”, “increased lifetime of industrial products” and other concepts that today form part of most people’s consciousness. Further, many other serious human-induced environmental problems have emerged in recent time and become part of the political agenda, e.g.: climate changes, loss of tropical rain forests, extinction of mammals, spreading of invasive species, acidification of the sea.

7 MARINE ECOSYSTEMS

Oceans cover about 70% of the Earth's surface, and this is where you find the biggest and the "thickest" ecosystems in the world. Fig. 54 shows a diagrammatic cross-sectional view of an ocean adjacent to a continent. It is seen that the continent continues beneath the ocean as a continental shelf which at a depth of 125–200 m continues in the continental slope. At a depth of 4–5,000 m the continental slope flattens off and becomes replaced by the abyssos plain (gr.: abyssos = "bottomless"). The flat abyssos plain is at several places disturbed by high mountain ridges or deep-sea grooves down to 10,000 m depth.

At all depths in the ocean there are animals living on the bottom, and therefore the sea floor has been divided into lifestyle zones (habitats) for bottom-dwelling (benthic) organisms: the littoral zone is the area between high and low water mark (intertidal zone), the sublittoral zone is the area between the low-water mark and out to the bathyal zone of the continental slope that continues into the abyssal zone of the deep sea. Likewise, the open waters can also be divided into several zones: the photic zone is the sun-light exposed surface water, and the lower boundary of this zone is indicated by the compensation depth, which is the depth where light intensity is so small that the entire primary production is used for the phytoplankton's own respiration. The open sea is called the pelagic zone, while the neritic zone represents the coastal areas.

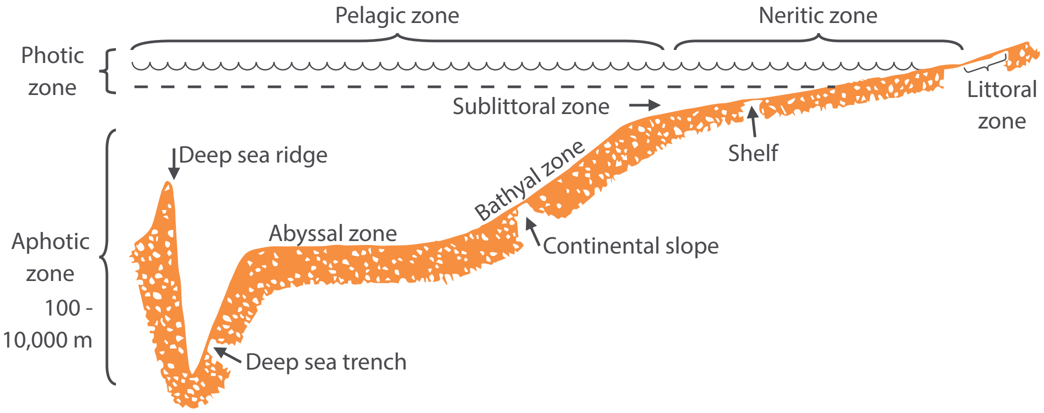


Fig. 54. Diagram of the most important life-zones in an ocean. The boundary between the photic zone and the aphotic zone is marked by the light-compensation depth – note that it decreases towards the coast due to a higher content of suspended particles in the water. The oceans are vast sea areas with depths down to 4–5000 m but with quite isolated, smaller areas with depths of up to 10,000 m. The boundary between the continents and the oceans is formed by the so-called shelf which has a varying width and depth. From the shelf, continues the quite steep continental slope down to the ocean bottom.

7.1 OPEN SEAS

The food chains in the open sea begins with the microscopic plankton algae, collectively called phytoplankton. It is phytoplankton's primary production that forms the basis of all higher and lower marine life. It is the smallest known autotrophic organisms (diatoms, dinoflagellates, coccolithophores and others) which fix all the energy used in the entire marine ecosystem, see Fig. 55. The herbivore grazers in the open marine waters are copepods, krill and other filtering zooplankton organisms. In the open sea areas, the main representatives of these filter-feeders are the copepods that for example as prey, provide food for herring and mackerel. Copepods assimilate about 60–70% of the organic matter in the consumed plankton algae, while the rest sink to the bottom as "faecal pellets". This faecal material, together with descending but not consumed phytoplankton, is the main food supply for the benthic animals.

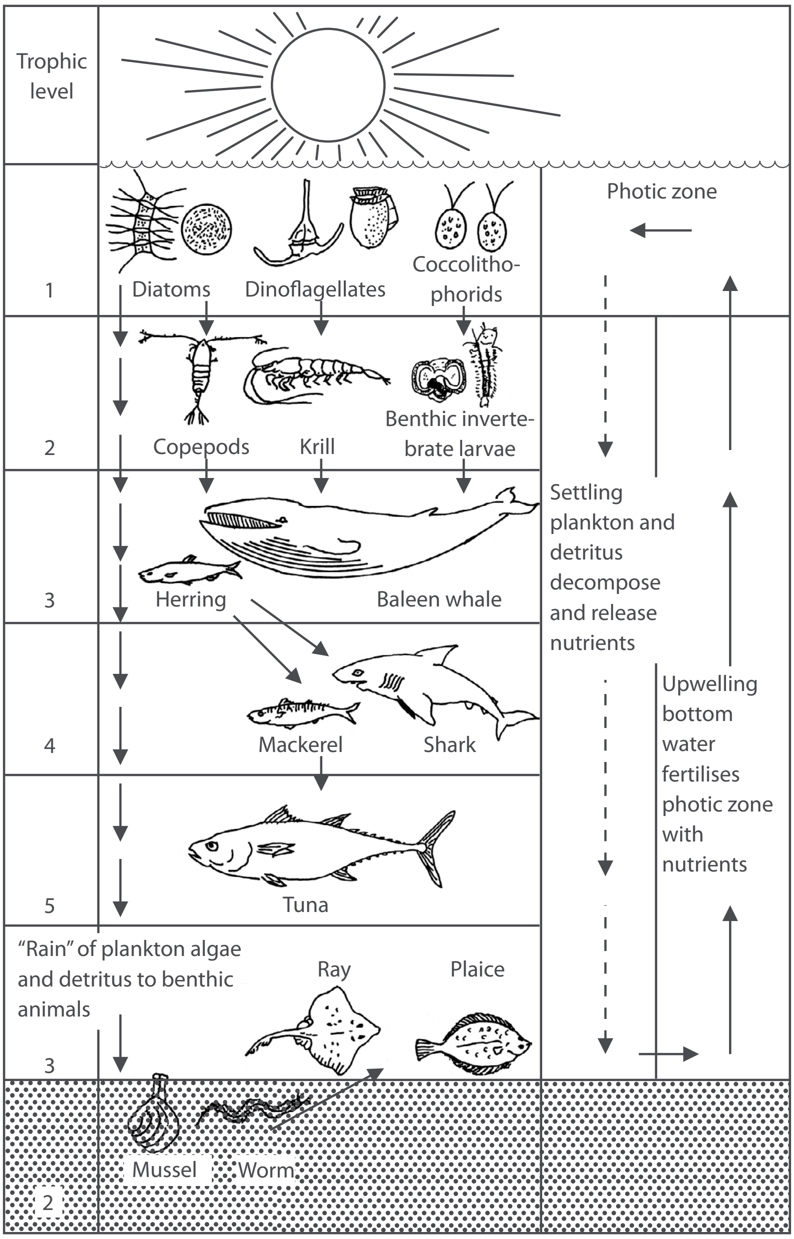


Fig. 55. Food chains and nutrient cycles in the open sea. The schematic presentation of the classical marine grazing food chains does not, however, take the "microbial loop" into account, see Fig. 56.

A number of benthic animals are also adapted to a filtering life. Typical representatives of these filter-feeders, or suspension-feeders, are certain mussel species, which have developed large gills that pump large amounts of water while at the same time, are able to effectively retain suspended plankton algae. Other mussel species pick up food on the seabed ("selective deposit-feeders"). Some of the deposited organic material that these animals do not consume ends in the sediment where it is decomposed by bacteria. The remaining organic material can also be consumed by bivalves and polychaete worms ("non-selective deposit-feeders") that eat the sediment containing bacteria. All of these benthic invertebrates are important food sources for benthic fish, such as cod, plaice and eel.

In the 1950s it was realized that the open ocean areas, which were previously believed to be the population of the world's upcoming inexhaustible larders were "wet deserts". Measurement of the primary production using the so-called carbon-14 method, which measures the uptake of radiolabelled HCO_3^- in plankton algae in water samples taken at different depths, have shown that the gross primary production is often less than 500 kcal/m^2/year. This corresponds to the primary production in desert areas on land. Enrichment experiments where nutrients (ammonia, phosphate, iron or other trace elements) are added to water samples, have shown that the production in most open sea areas is limited by nutrients, primarily phosphorus and nitrogen. Only in sea areas where nutrients come to the surface with ascending bottom water ("upwelling"), are favourable for a high primary production, as well as a high secondary production of fish.

The perception of the classical grazing food chain, or rather the pelagic food web, has changed dramatically since the mid-1970s. Until then, bacteria had only been considered as decomposers of faeces and other organic material deposited on the sea floor. But with the introduction of new measuring techniques, it became clear that the biomass and activity of microorganisms in the water column (the pelagial) are significantly larger than previously thought. Heterotrophic bacteria can utilize up to about 50% of the primary production that is lost as dissolved organic matter (DOM), and the impact of protozoans is also far greater than previously thought. Moreover, it has been found that 0.5–2 µm photo-autotrophic bacteria (cyanobacteria) are important primary producers in many regions of the oceans. This new knowledge has led to the realisation of a "microbial loop" in which dissolved organic matter from phytoplankton is utilized by heterotrophic bacteria that are eaten by zooplankton, whereby a portion of the energy of the "lost" dissolved organic matter from phytoplankton is channelled back to the classic grazing food chain, see Fig. 56 [60, 62].

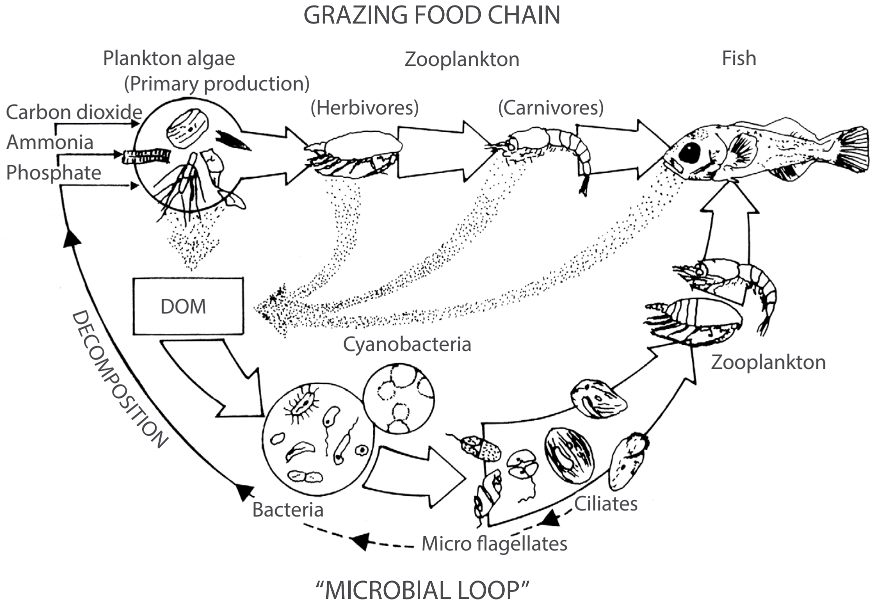


Fig. 56. The "microbial loop". A significant proportion (30–50%) of the primary production is lost from the classical grazing food chain, as dissolved organic matter (DOM). DOM is utilized almost exclusively by free-living heterotrophic bacteria and therefore gives rise to a significant bacterial secondary production. The free-living bacteria are eaten by protozoa (flagellates, ciliates), which in turn are eaten by zooplankton (copepods), whereby the "microbial loop" is coupled to the grazing food chain. Photosynthetic bacteria (cyanobacteria) also come into the "microbial loop" when they are eaten by protozoa. Since there is a high turnover in the microbial loop, a large fraction of the organic matter is mineralized to carbon dioxide, ammonia and phosphate.

The sea can be divided into an autotrophic layer (photic zone) and an underlying heterotrophic layer (aphotic zone). Because of this vertical division, the inorganic nutrients, which are incorporated into organic compounds in the photic zone, tend to be transported into the heterotrophic zone, partly through the food chains and partly by settling of plankton algae and faeces. The descending algae, dead animals and excrements are decomposed bacterially whereby essential nutrients (ammonium, phosphate, trace metals, etc.) for phytoplankton are released. Due to lack of vertical mixing of the water masses, the released nutrients cannot immediately come back and nourish the phytoplankton in the photic zone.

Returning of nutrients to the oceans' sunlight exposed water masses takes place by means of ocean currents that collide with a continent whereby the nutrient-rich bottom water is forced up to the surface. Here, the surface currents carry the nutrient-rich water to the open oceans photic zones. Sea areas with ascending, old, nutrient-rich bottom water ("upwelling zones") are very productive, and it is at such places that the world's best fishing areas are found. An example of such an area is the sea off Peru where the Humboldt Current forces nutrient-rich bottom water up to the surface. The productive fishing areas in the north-west Atlantic is not caused by "upwelling" but eddies where the Gulf Stream hits the North Atlantic "threshold", which "only" has a depth of 500 m.

7.1.1 PRIMARY PRODUCTION AND HYDROGRAPHY

The photic zone reaches down to approximately 100 m in the open ocean areas, but closer to land it does not penetrate that far down, due to suspended particles. The photic zone is typically 30–40 m in the more coastal waters. Nevertheless, the primary production is significantly higher in coastal areas than in the open ocean. This is caused by the nutrients which are much more limiting for the growth of phytoplankton in open ocean areas. These have been described as "wet deserts", see Figs. 55, 57 & 58.

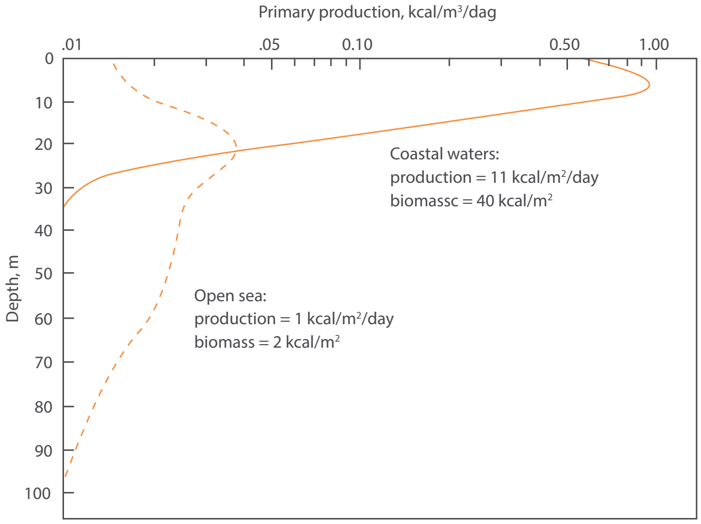


Fig. 57. Vertical distribution of the gross primary production in a coastal area and in an open sea area in the Northeast Atlantic [1].

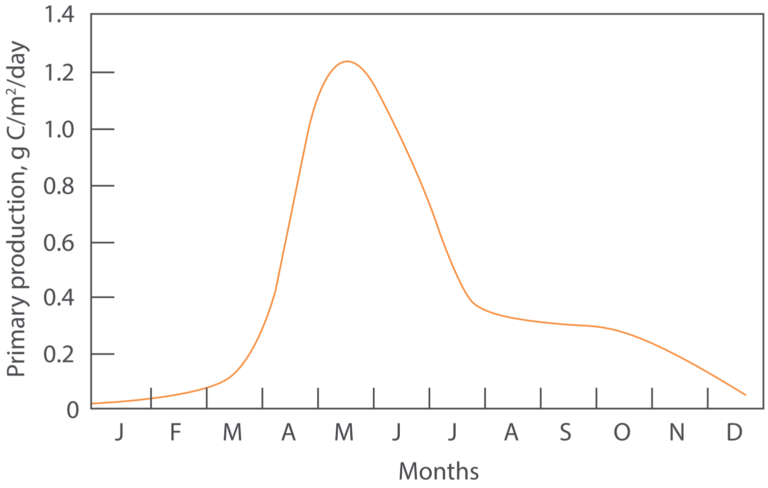


Fig. 58. Yearly cycle of the gross primary production in the Northeast Atlantic [52].

The vertical distribution of the gross primary production in a coastal and an open area in the Northeast Atlantic Ocean is shown in Fig. 57. It is noted that the maximum production takes place in a depth of 10–20 m. This is due to the planktonic algae circulating between the surface and the thermocline. This makes the algae more or less adapted to darkness so that they become light inhibited near the surface. The light-compensation depth in coastal waters is at about 35 m depth but can extend down to 100 m in the open sea. By integrating the primary production per m^3 from the sea surface to the compensation depth, the total production in the water column can be estimated. In the actual example, the production in the coastal area estimated to be 11 kcal/m^2/day, which is 11 times higher than in the open sea area (note that production scale is logarithmic). Also the biomass is higher – 20 times – in the coastal area. This difference between coastal and open sea is due to a significantly larger amount of nutrients in the coastal areas, which are constantly supplied with nutrients from the seabed and from land. Fig. 57 indicates the biomass of the phytoplankton expressed in energy equivalents: 1 kcal = ca. 0.5 g of algal biomass, and this makes it possible to calculate: 1) the turnover time = biomass/gross primary production, and 2) the turnover rate = gross primary production/biomass. In the coastal area, the turnover time is around 4 days, and in the open sea area, it is about 2 days.

The annual cycle of the gross primary production in the Northeast Atlantic Ocean is shown in Fig. 57. The formation of a thermocline in April-May gives rise to a "spring maximum" in the primary production. Later on, nutrients become limiting for the algal production. When the seasonal thermocline degrades in the autumn, nutrients return to the photic zone. This can give rise to a weak "autumn maximum" in the primary production. In late September through to April, light is the limiting factor for the primary production.

Figure 58 shows the vertical distribution of temperature and pH in the Northeast Atlantic Ocean. During summer, the upper wind-mixed water masses are warmed by the sun and this creates a thermocline at a depth of 100–200 m. Below this "seasonal thermocline" is a "permanent thermocline" which reaches down to a depth of approximately 1000 m. This temperature stratification prevents that the water masses are vertically mixed from surface to bottom. The seasonal thermocline causes, however, that the plankton algae are kept mixed within the photic zone, which results in the formation of a spring maximum in the primary production, see Fig. 58. The photosynthesis activity in the photic zone causes an increase in pH (since algae consume CO_2), while the bacterial decomposition of organic matter (dead algae, copepod faeces etc.) that falls from the photic zone, causes a decrease in pH (due to formation of CO_2). The from the pH- curve in Fig. 59 it is seen that the microbial degradation of organic material that falls down from the photic zone is brought to an end before the material has sunk halfway to the bottom.

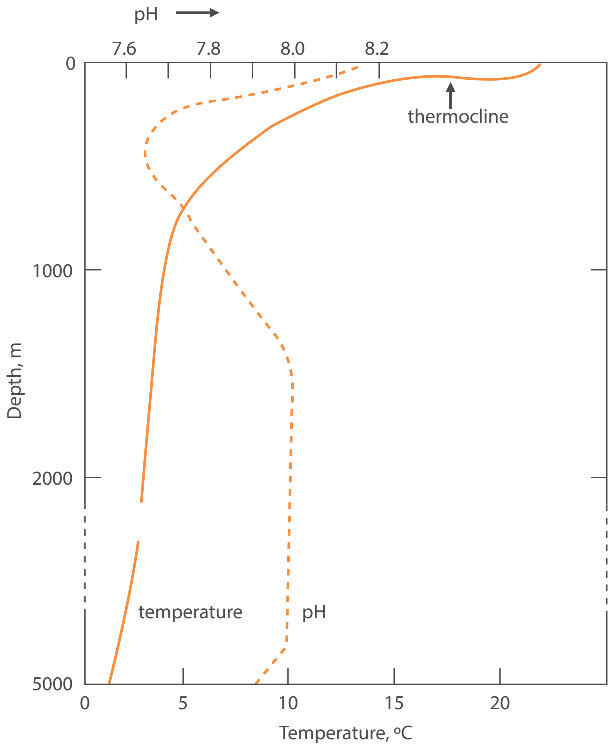


Fig. 59. The vertical distribution of temperature and pH in the Northeast Atlantic [52].

The upper water masses in the northern hemisphere are heated by the sun in spring (April-May) and a thermocline is formed between a warmer surface layer and a cooler (and heavier) bottom layer, see Fig. 59. This stratification of the water column prevents mixing that could provide a supply of nutrients from the underlying more nutrient rich water masses. The depth of the thermocline is largely determined by wind mixing which stabilizes the water masses. This implies that the phytoplankton remains in the photic zone where a "spring maximum" in the primary production is seen soon after the formation of the thermocline. The primary production becomes reduced when the nutrients are used up; therefore in the summer there is a minimum in the primary production.

In the autumn, when the water masses near the sea surface are cooled, the thermocline disappears and the wind mixes the water. The supply of nutrient-rich underlying water to the surface often causes a more or less pronounced "autumn maximum" in the primary production, which soon after begins to decrease because the light intensity and day length decreases. The light becomes the limiting factor for the primary production, see Fig. 58.

7.2 MARINE SHALLOW WATER AREAS

The main primary producers in protected marine shallow water areas are macroalgae, higher plants (eelgrass, seagrass) and microscopic diatoms (living on the surface of the sea floor). In the summer months, these areas are very productive. Macroalgae and eelgrass are negligibly being eaten, but they enter indirectly into the area's food chains. During winter, the macroalgae and eelgrass are being decomposed and mixed into the sediment. This input of organic matter gives rise to a rich production of bacteria and small organisms-eating bacteria (e.g. ciliates) in the sediment. In food chains, the so-called "browsers" appear that clean the sediment surfaces for diatoms, and the "non-selective deposit-feeders" that via bacteria and smaller bacteria-eating organisms, take up the organic matter from the sediment. Important representatives of browsers and deposit-feeders are found among crustaceans, snails, worms and clams. All these animals are food for fish, and the productive shallow water areas are in this way important nursery places for flatfish and other edible fish.

8 LAKE ECOSYSTEMS

Figure 60 shows a diagrammatic cross section of a lake with its various life zones.

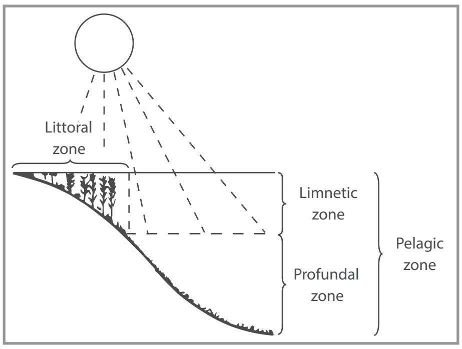


Fig. 60. The three main zones in a lake ecosystem. The boundary between the limnetic zone and the profundal zone is marked by the light-compensation depth. The littoral zone extends from the lake shore and out to where the vegetation of larger-rooted plants terminates due to lack of light.

Closest to the lakeshore is the littoral zone with larger roothold plants. The pelagic zone is the open water outside the littoral zone where light is the limiting factor for the roothold plants. The pelagic zone is subdivided into an upper limnetic zone and an underlying profundal zone. The border between the two zones is marked by the light-compensation depth. The photosynthetic unicellular planktonic algae in the autotrophic limnetic zone create (depending on the lake's size and depth) most of the primary production, which is the basis of all other life in the lake. However, many lakes receive large amounts of organic matter from the surroundings, such as dead leaves in the autumn. The plankton algae (green algae, blue-green algae, dinoflagellates and others) are "grazed" by many species of zooplankton (daphnia, copepods, rotifers, protozoa and others), which in turn are eaten by fish, etc., see Fig. 61. The life in the heterotrophic profundal zone is based on descending algae and detritus from the limnetic zone. The number of animal species that live on or in the lake bottom (benthos animals) is not overwhelmingly high, because the lake bottom is fairly homogeneous (i.e. there are few "niches"). Besides, the animals need to survive during prolonged periods without or with very little oxygen in the water. There are two main types of benthos animals: 1) "Suspension feeders" which live by filtering suspended food particles from the ambient water, and 2) "deposit feeders" (e.g. tube-dwelling worms, certain species of red chironomid larvae, snails) that live by eating the upper layer of bottom mud that receives organic matter in the form of sinking plankton algae and detritus from the limnetic zone. The benthic fauna is important prey for fish, where most larger fish live in the profundal zone.

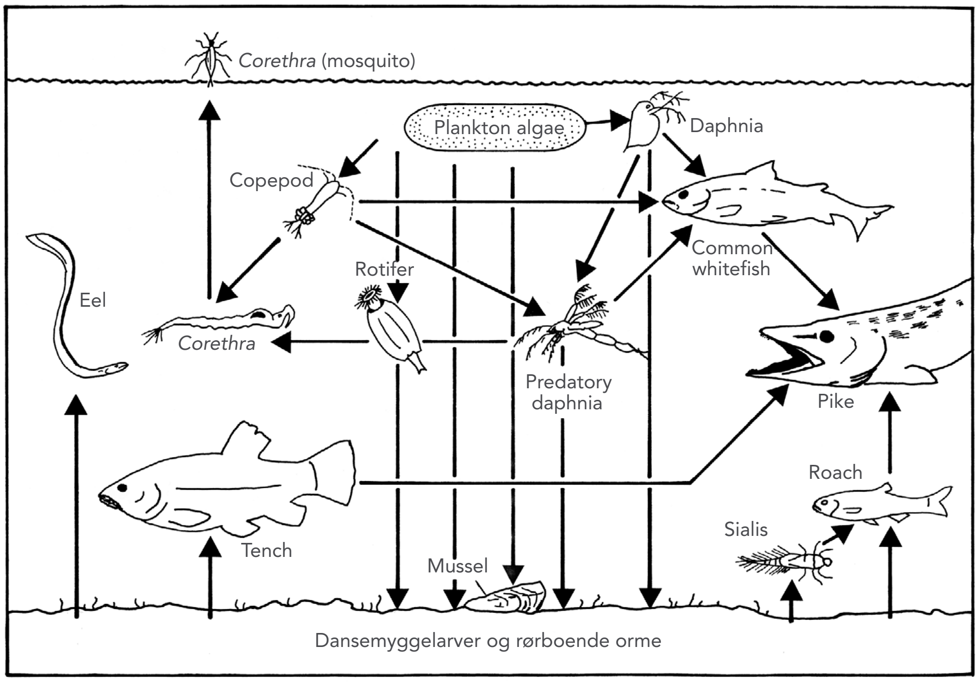


Fig. 61. Schematic representation of the food chains in a lake [53]. According to the "classical" view, the grazing food chains start with plankton algae, which are eaten by filter-feeding zooplankton (daphnia, copepods, rotifers, etc.). However, it has now been realised that about 30–50% of the organic matter that the plankton algae (in fresh water as well as in the sea) produce by photosynthesis is lost to the surrounding water as "dissolved organic matter". This substance is taken up by bacteria which converts the dissolved organic substance to bacterial substance which is available as feed for flagellates, ciliates and other organisms that feed by filtering microscopic food particles from the water. The "classical" description of the aquatic grazing food chains first link must therefore be revised.

8.1 TEMPERATURE STRATIFICATION IN LAKES

There are few examples of a physical factor that exerts a more direct control over an ecosystem than the temperature of a lake. In the following sections, this shall be explained in more detail. The density of freshwater is greatest at 4 °C, see Fig. 62.

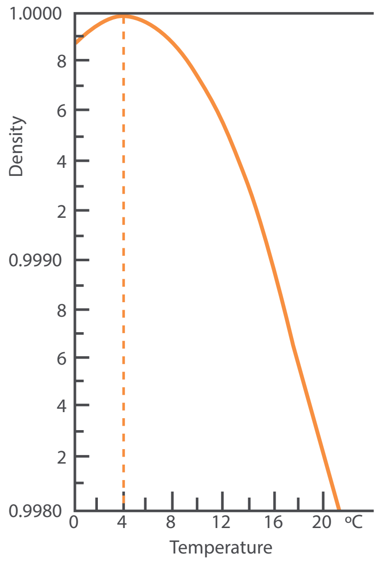


Fig. 62. The water density is highest at 4 °C [52]. A consequence in deep lakes, there is a stratification of the water column during the summer.

This means that freshwater with a higher or lower temperature is lighter than at 4 °C water and will therefore tend to float above this. By observing a deep lake with 4 °C water from surface to bottom (a normal situation in lakes in the temperate zone in the spring), you will see that the sun heats the upper water masses as the days become longer and the sun rises higher in the sky. If the water in the lake is not stirred, the temperature will drop gradually from the surface down to 4 °C. However, the surface water in a lake is not stagnant because the wind mixes the surface water down to a depth of 8–20 m. The result is the formation of a warm surface layer heated by the sun and stirred by the wind. Below this warm surface layer (epilimnion) is a thermocline (or metalimnion) that separates the warm surface layer from the deeper water layer (hypolimnion), see Fig. 63.

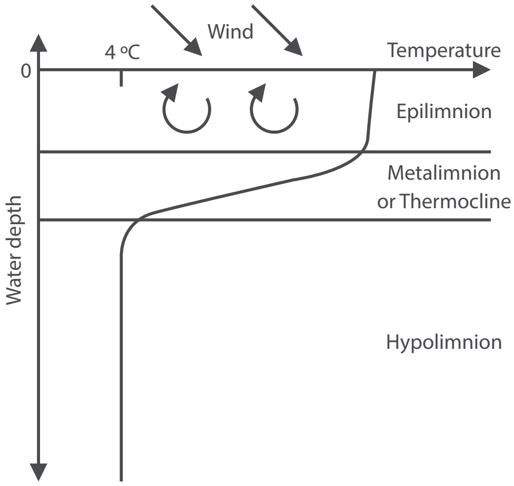


Fig. 63. Typical distribution of temperature in a deep lake during summer.

Once a thermocline has been established, the warmer surface water and the deeper colder water are in fact separated from each other since there is practically no exchange between the two bodies of water (“summer stratification”). The thermocline thus prevents a direct exchange of nutrients between the epilimnion and the hypolimnion, although the wind may cause a secondary weak circulation in the hypolimnion, see Fig. 64.

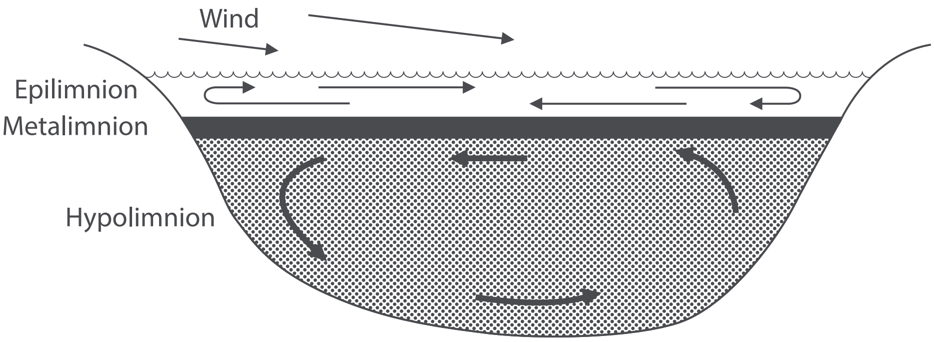


Fig. 64. Diagrammatic illustration of wind-induced circulation in the epilimnion and hypolimnion in a temperature-stratified lake.

In the autumn when the temperature drops in the epilimnion and eventually becomes the same temperature as the hypolimnion, the thermocline vanishes and the wind can now mix all the water in the lake, from surface to bottom ("autumn total circulation"). When the temperature in late autumn drops below 4 °C, a "cold" epilimnion and a "warm" hypolimnion is established so that the lake again becomes stratified ("winter stratification"). Ice on the lake surface often causes the winter stratification to become weak due to the wind not being able to stir the water in the epilimnion. In spring, when the ice melts and the temperature at the surface rises to 4 °C, the wind can again completely mix the water masses ("spring total circulation"), see Fig. 65.

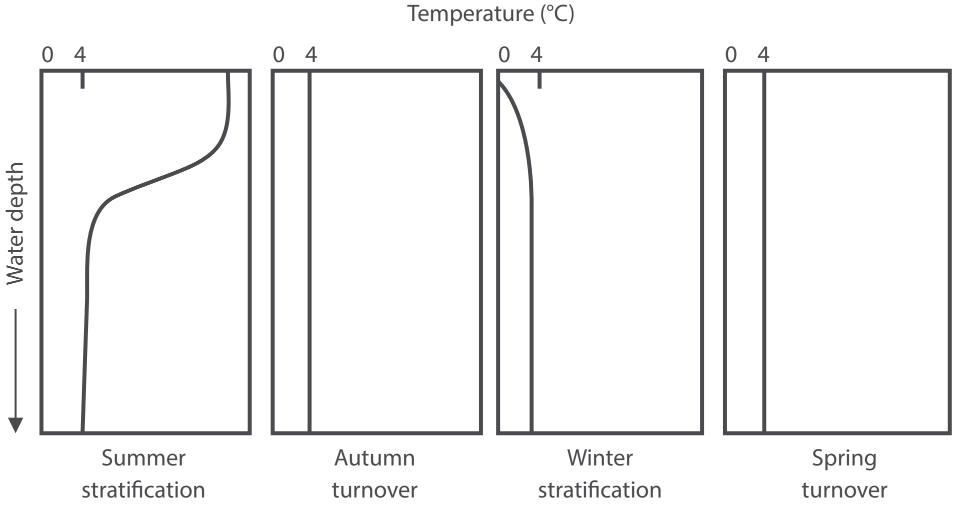


Fig. 65. The seasonal temperature distribution in a typical deep lake in the temperate zone. The thermal-stratification causes that the water masses are only totally mixed in fall and spring.

8.2 SEASONAL VARIATIONS IN LAKES

The seasonal thermal stratification and total circulation of the water masses in spring and autumn are critical to the energy and nutrient cycling in deeper lakes. This fact can be illustrated with an example from one of the world's most studied lakes, namely Lake Esrum in Denmark, see Fig. 66.

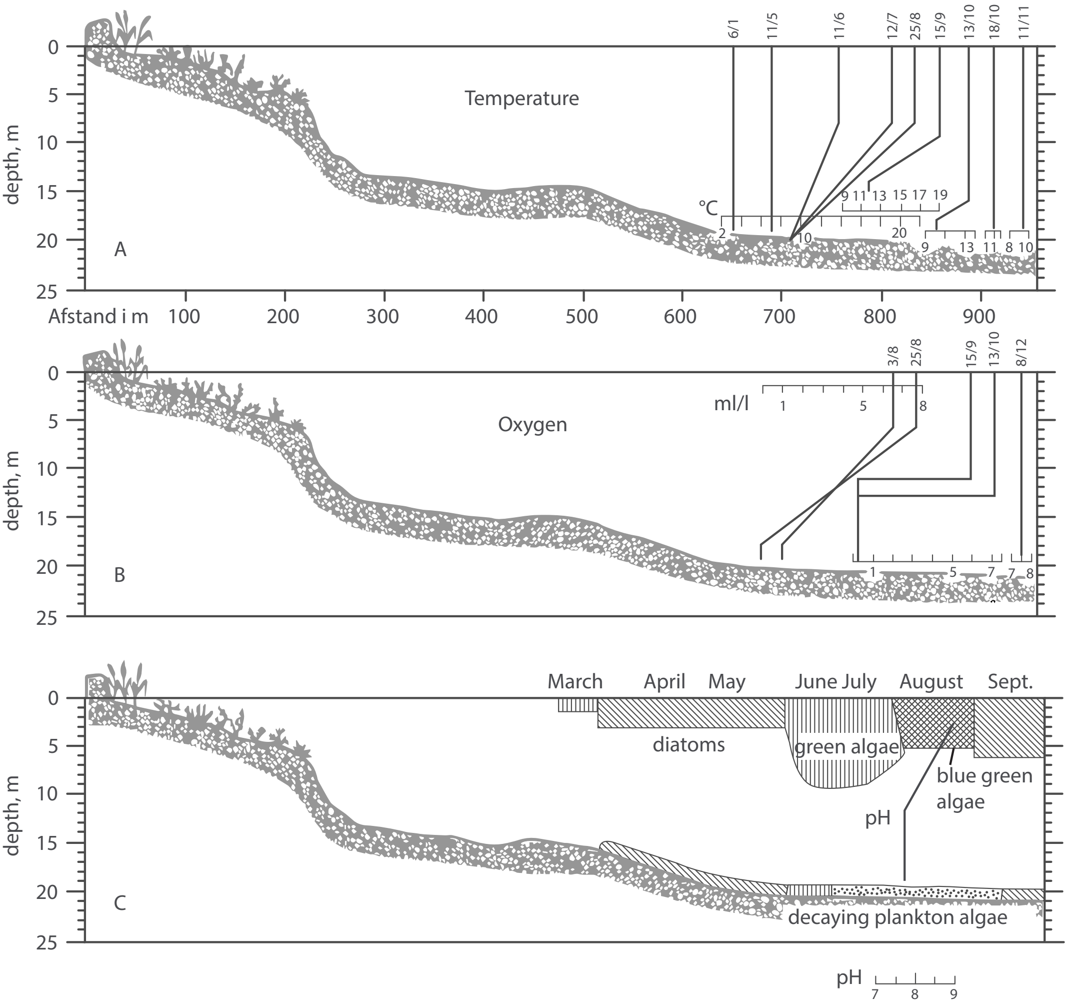


Fig. 66. Cross section of Lake Esrum, Denmark [54]. On the top section (A) is a series of temperature curves for year 1955 plotted. It is seen that the temperature is uniform from the surface to the bottom on 11 May. During the summer, a thermocline is established, which however, "eats" its way further and further down during the summer due to wind stirring the epilimnion. On 11 November, there is about 9 °C throughout the water column and this allows the wind to mix the water in the whole lake ("autumn total circulation"). Section B shows the concentration of oxygen in the same period. It is seen that the thermocline's stabilization of the water masses causes an extremely low oxygen concentration in the bottom-near water. Lower section C shows the phytoplankton succession during summer. The phytoplankton growth and species composition is controlled by the nutrient cycling and loss to the hypolimnion. Green algae start to grow under the ice in March and are replaced by diatoms in April, but due to the temperature stratification of the lake, the diatoms gradually use up all the silicon in the epilimnion and in June, it is green algae that dominate. In July, nitrogen probably becomes the limiting factor for the growth of green algae and these are replaced by nitrogen fixating blue-green algae. As the thermocline "eats" down into the more nutrient-rich bottom water, epilimnion is supplied with nutrients and this may the reason why diatoms become dominant again in September.

The growth and species composition of the phytoplankton is controlled by the cycling and loss of nutrients to the hypolimnion. But it is not only the allogeneic succession of phytoplankton in the summer season that is controlled by the temperature and its stratification of the water masses. Also the benthic fauna is affected, partly by the low oxygen concentrations in the near-bottom water, and partly by the food value of the organic material that sinks to the bottom. In the summer when the lake is stratified, the algae are dead and decaying when they settle to the bottom. This is of great importance for the growth of the red chironomid larva (midge larva) *Chironomus anthracinus* that is found in a number of about 20,000 individuals per m^2 on the lake bottom, where it lives on settled algal cells. When the temperature stratification causes low oxygen content and the food becomes more or less rotten, the chironomid larvae stop feeding. Between the spring and autumn total circulation, the larvae are hardly growing. On the other hand, they can make a tenfold increase of their weight in the course of the few weeks during the spring- and autumn total circulation last. In the summer stagnation period without oxygen at the bottom, the fish stay away, and during this time there is no fish consumption of chironomid larvae. The thermal stratification of the lake is critical not only for the population dynamics of the chironomid larvae, but also for the fish production, and therefore the whole lake's nutrient and energy turnover.

Seasonal variation in a lake is largely determined by the individuality of the lake, i.e. it's depth, it's exposure to wind, the amount of dissolved nutrients, the age of the lake, etc., which makes it impossible to generalize from conditions in Lake Esrum. Another example, also from Denmark, can illustrate this. Hjarbæk Fjord is one of Limfjorden's many branches and was, until the establishment of a causeway in 1966, a shallow brackish water area. With the dam construction Hjarbæk Fjord, it became a freshwater lake with poor water exchange. This, together with the input of significant amounts of nutrients (nitrate leaching from agricultural areas, phosphate from domestic sewage), has caused arise of a number of environmental problems, both within and around this former fjord. Hjarbæk Fjord can serve as a characteristic example of a lake ecosystem that has been brought out of ecological balance due to eutrophication.

In the early 1980s, the residents around Hjarbæk Fjord were plagued by billions of flying midges during the summer months. The plague has been described, in an ecological context, in a comprehensive environmental report [55]. Briefly, the plague by midges is explained as follows: Approximately 90% of Hjarbæk Fjord is so shallow that the wind can easily stir the water masses so that oxygen never becomes a limitation factor for the growth of the midges' larvae (chironomid larvae) living on the bottom. A large production of plankton algae ensures that more than 30,000 chironomid larvae per m^2 can live on the bottom. In the summer months, there is very little predation by fish on the larvae because the water quality from May to August is so poor (high pH, high concentrations of ammonia) that the fish perish or swim away, see Fig. 67. Therefore, billions of midges can hatch and spread their wings. It has been calculated that if ⅒ of the chironomid production were used for the production of eel biomass, then the annual eel production in Hjarbæk Fjord could be around 250 tons of eels.

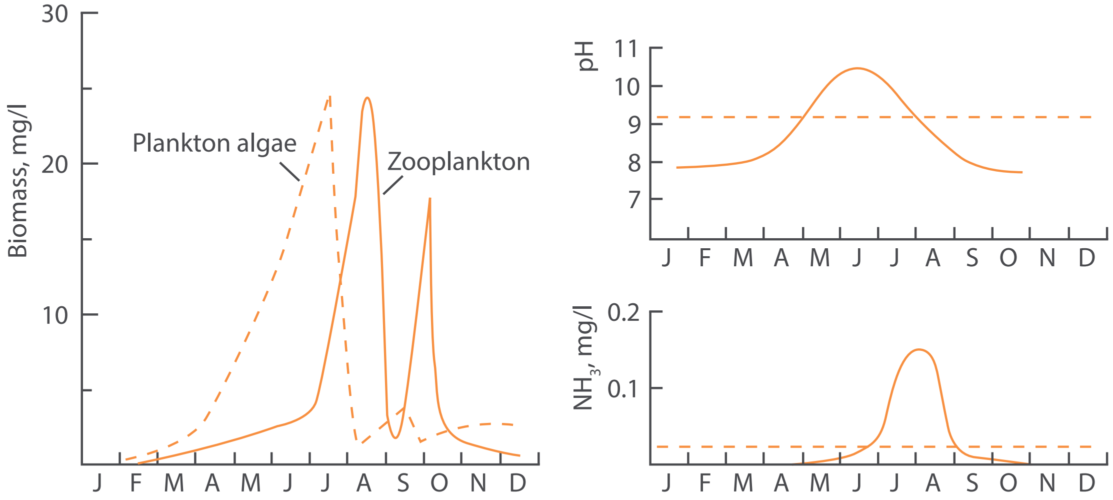


Figure 67. Seasonal variation of phytoplankton, zooplankton, pH and NH_3 (ammonia) in Hjarbæk Fjord, Denmark, in 1981 [55]. Due to the large amounts of plant nutrients (domestic waste water, trout farms, agricultural areas), there was an intense algae production, which in the period from May to July, resulted in a high pH that was so high that it was lethal for most fish (dashed line in figure), which therefore died or fled to adjacent watercourses. The reduced fish predation impact on the zooplankton resulted in a drastic increase in the population of especially daphnia, which gradually "grazed" down the plankton algae while releasing large amounts of ammonia in the urine. From late June to late August, the ammonia concentration in the water was mortally high for fish (dashed line in figure) and the total loss of fish as regulating factor for the zooplankton, resulted in a complete grazing down of the plankton algae, so that the zooplankton population was subsequently exposed for a drastic fall due to starvation. Consequently, the algal production increased again, forming the basis for a renewed large zooplankton population. The violent variations in the algal and zooplankton biomass show that the ecosystem is out of balance.

9 FOREST ECOSYSTEMS

A deciduous forest can be divided into several layers, with the highest peaks of trees forming a canopy, and below, where there is an undergrowth of smaller trees, can be found low shrubs and shrubbery. Finally on the forest floor, there may be found a layer of herbaceous plants. This stratification is caused by the light which is increasingly becoming a limiting factor for plant growth. The tendency for stratification becomes more and more pronounced when going from northern to southern geographical regions. In some tropical jungles, it is so dark that the bats are out in the daytime.

The part of a forest that receives sunlight, i.e. the treetops in a dense forest, constitute the autotrophic zone of the forest ecosystem, which is dominated by the photosynthetic tree crowns' primary production, while the underlying layer represents the forest ecosystem's heterotrophic zone, which is dominated by decomposition processes and thus respiration, see Fig. 68.

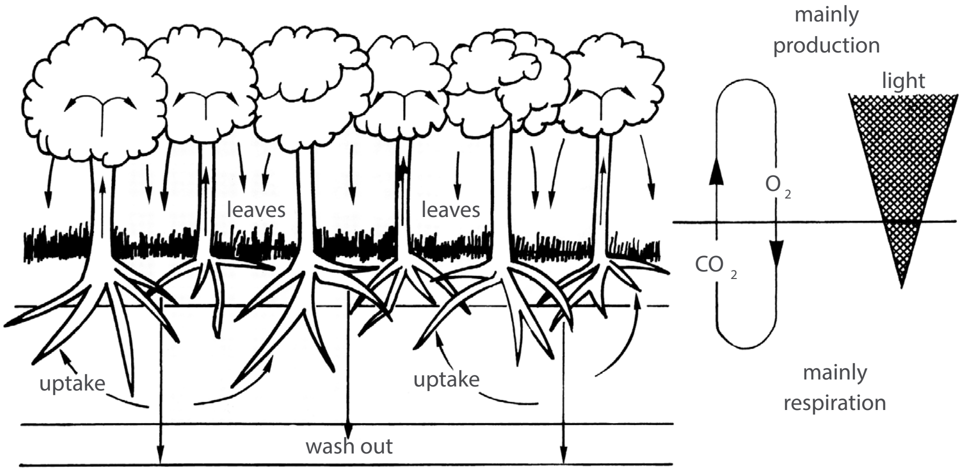


Fig. 68. A forest ecosystem can be divided into an autotroph zone, where primary production is dominant, and in a heterotrophic zone, where respiration is dominant. With fallen leaves, nutrients are lost from the autotrophic zone to the heterotrophic zone where decomposition takes place, whereby nutrients are released to the "abiotic pool". From here, the nutrients are absorbed by plant roots or they leach out. In a mature forest ecosystem, the leaching of nutrients is small compared to the exchange between the "abiotic pool" and "biotic pool" (living organisms, detritus), i.e. the nutrient cycles are "tight".

From the ecosystem's autotrophic zone, there is constantly loss of nutrients via fallen leaves, twigs and branches to the heterotrophic zone. Here, the decomposers in the detritus-food chain utilize the energy of dead organic material, which is mineralized with release of inorganic nutrients that can be taken up by tree roots, and once again brought up into the autotrophic zone. This cyclical transport of the chemical components between a biotic and an abiotic pool is in mature ecosystems characterized by a very small loss, since usually only a tiny fraction of the biologically available substances in the abiotic pool are leaching out and carried away. Intensive studies of a number of nutrient cycles and leaching in a temperate deciduous forest in New Hampshire (Hubbard Brook Experimental Forest) has shown, for example, that a small wooded area had an abiotic calcium pool of 690 kg/ha. About 12 kg/ha/year were leaching out while there was an input of 3 kg/ha/year from precipitation, and thus the annual net loss of calcium was 9 kg/ha or 1.3% of the abiotic pool. This loss is compensated for, however, through the weathering of minerals, see Fig. 69.

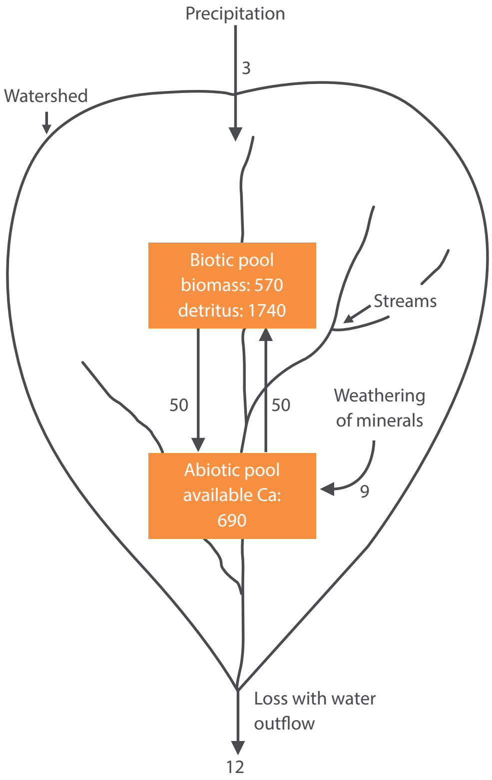


Fig. 69. Calcium's cycle in a forest ecosystem (Hubbard Brook Experimental Forest, New Hampshire, U.S.A.). The figure shows the amount of calcium (kg/ha) in the biotic- and abiotic pool, the rate (kg/ha / year) by which calcium moves from one pool to the other and input and loss of this chemical element. It is seen that there is a small net loss of 9 kg/ha/year (12-3 = 9), but this is compensated for by the weathering of minerals. It is noteworthy that the input and loss of calcium is very small in relation to the internal circulation in the ecosystem, which is bounded by a watershed. Studies of other nutrient cycles in the same forest ecosystems have shown similar closed cycles [56].

The distribution of nutrients in a biotic- and an abiotic pool in a temperate forest differ substantially from the nutrient distributions in a tropical rainforest. While about half of the organic carbon in a temperate forest is stored in the soil, only about one sixth of the total organic carbon is stored in the soil in a tropical rainforest. Almost 60% of the total amount of nitrogen in the rainforest is found in the biotic pool (leaves, wood), while it is only about 6% of the total amount of nitrogen that is found in the biotic pool in a temperate coniferous forest. In the tropical rainforest the abiotic pool of nutrients is thus very small, relative to the amount bound in the living tissue. Dead plants and animals decompose quickly in the humid and warm rain forest, and the released nutrients are immediately taken up again in living plant tissue. In other words, the mineralization speed is fast and the nutrient cycling "tight" in the tropical rainforest. When a temperate forest is cleared, the soil preserves it's structure and retains relatively effective nutrients. In this way, the land can be cultivated for centuries, as long as the soil is plowed and with appropriately intervals, fed manure equivalent to the amount of nutrients removed by crops. In addition, the cold winter that counteracts the tendency of pests and diseases in the annual monoculture crops, which are typical of temperate European agriculture. The situation is different in the tropics. Here soon after the clearing or burning of forests, results in an impoverishment of the soil due to the nutrients being quickly washed away or used up, after a few years of cultivation of "cashcrops" (cacao, coffee, etc.). Since the topsoil in tropical soils is very thin, the tremendous clearing of tropical forests (rainforests as well as forests with scattered growth of trees) in recent times, has led to extensive environmental devastations due to the topsoil being washed away by rain or blown away by the wind. Many tropical forest areas have by overexploited and foolishly have been transformed into shrub steppes or desert. The importance of the devastations can be seen in Ethiopia where forests have been cleared for fuel and timber and the bare fields have been overgrazed. About 100 years ago, half of Ethiopia was covered by forests but today forests cover only about 3%. Around 1 billion tons of soil is flushed down from the previous fertile highlands every year, causing the northern parts of this area to be lost for farming forever. Something similar can happen in Tanzania, where there will not be a tree left in a few years time, if the current trend continues.

Drought and hunger disasters in Africa are not only a question of declining rainfall, but largely a result of overexploitation and wrong use of natural resources. The presence of trees is crucial to evapouration in the tropics, and a large green cover can retain large amounts of water and prevent that water is lost through run-off to rivers and lakes. Treetops pick up a large part of the precipitation while the tree roots absorb and utilize the water that reaches the ground level. Large areas with trees act as a living sponge that stabilizes the water balance, the air humidity and the temperature. The conservation of forests and trees, to prevent loss of water and nutrients, and to protect against erosion, has become an essential part of the fight against drought and hunger in many developing countries. In recognition of the ecological impact of the extensive deforestation, future international assistance to African developing countries should support the introduction of new farming methods that combine forestry and agriculture (agroforestry).

9.1 FOOD CHAINS IN FORESTS

Only a few larger animals directly eat the vegetation in a forest, but some insects graze on, suck the fluids or eat their way inside the leaves (tunnelling). Fig. 70 shows an example of a grazing food chain in a forest. It is only a small part of a forest ecosystem's primary production that passes through the "grazing food chains" due to (in the order of) 90% of the energy flow, in a deciduous forest, goes through the "detritus food chain".

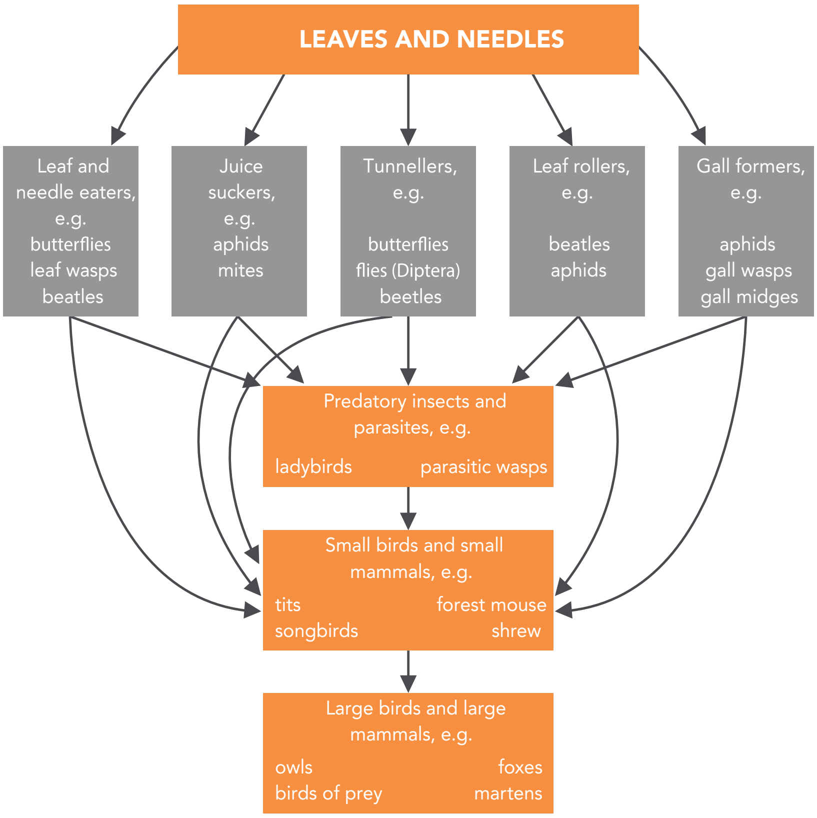


Fig. 70. Only few larger animals eat the vegetation in a forest, but some insects graze on, suck the fluids or eat their way inside the leaves and needles (tunnelling) [57]. The figure shows a number of examples of herbivorous insects and the predators that pursue them. It is noted that the secondary carnivores in the shown "grazing food chain" in a temperate forest, may also act as primary carnivores. However, only a small part of the primary production passes through the grazing food chains in forest ecosystems. The main part (approximately 90%) goes through detritus food chains.

Among the organisms in a detritus food chain, for example in an oak forest floor, one can (excluding of fungi and bacteria) find the following detritus eaters: woodlouse, snails, slugs, mites, springtails, nematodes and enchytrae (small whitish annelids), and the following predators: scolopendres, beetles, shrews. Most detritus-eating animals actually live off of the microorganisms sitting on dead organic matter. However, the rate at which the microorganisms grow is dependent on the activity of the detritus-eaters, since these mechanically degrade the dead organic matter. This produces small particles, which together have a very large surface area, upon which the microorganisms can act. In addition, the detritus-eating animals create a bioturbation ("stirring"), so that the microorganisms' environment does not become anaerobic.

Fig. 71 shows an example of how the energy can flow through a temperate forest ecosystem. It is seen that only 2.5% of the ecosystem's primary production goes through the herbivore organisms (30/1200 = 0.025), while 52% of the net primary production goes through the detritus food chain's decomposers ((250 + 370)/1,200 = 0.52). Further, note that the forest ecosystem's gross primary production (2650) is greater than the ecosystem's total respiration (2100), which gives rise to a net ecosystem production (NEP = 2650 - 2100 = 550). This accumulates in the form of an increase in plant biomass. The accumulation of organic matter occurs during an autotroph succession, and that this forest ecosystem is an approximately 80% mature ecosystem (2,100/2,650 = 0.79). In the present example, the biomass of the primary producers is 10,000 g organic matter/m^2, whereas their gross primary production (P_b) is 2.650 g organic matter/m^2/year, that is, the turnover time of the primary producers (B/P_b) is about 4 years (10,000/2,650 = 3.8).

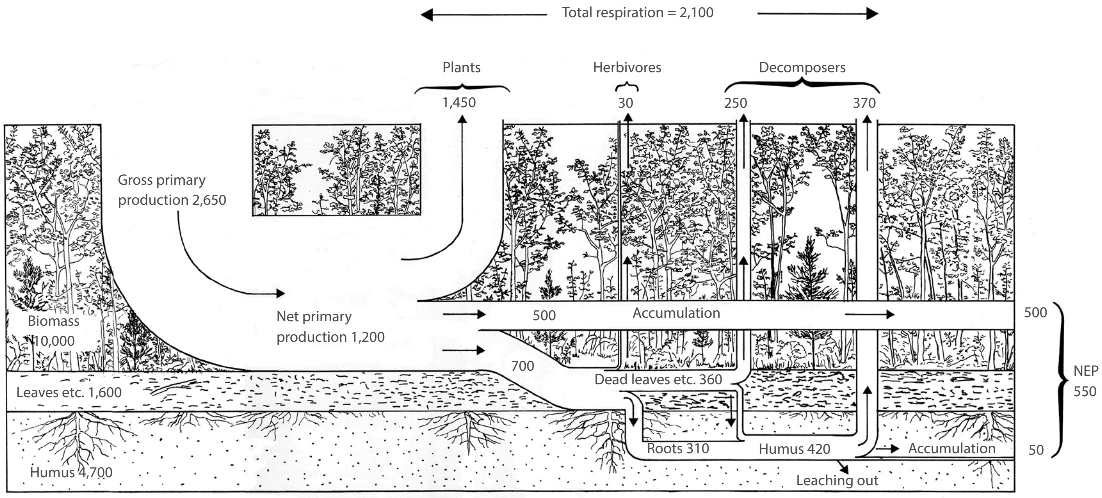


Fig. 71. The flow of energy in an oak-pine forest on Long Island, U.S.A. It is seen that about half of the gross primary production is used for the plants' own metabolism (respiration), which is normal for forests in the temperate zone. In the tropics, a greater part of the primary production is used for the plants' own respiration, whereas in the arctic regions, a smaller part of the total primary production is used for the plants' own respiration. The net primary production goes to: 1) herbivores, 2) decomposers, 3) accumulation (storage). The most important herbivores are insects and a scarce population of small mammals. But it is only a few percent of the net primary production that is consumed directly by the herbivores, and virtually everything that these animals consume is used for their own respiration. Thus, they do not contribute to the net ecosystem production (NEP = 550). But the growing biomass of trees contributes substantially to NEP, as more than 40% of the net primary production is used for this purpose. The remaining part of the net ecosystem production is made up of easily degradable humus, which is accumulated in the soil. All numbers for speed of energy flows are given in g organic matter/m^2/year [46].

9.2 HUMUS AND NUTRIENT BALANCE

In young forest ecosystems, it is characteristic that the organisms in the detritus food chain are not able to totally break down the dead organic material that is added to the soil in the form of leaves, twigs, branches, herbs, animal waste etc. The end products of the organic matter decomposition are typically a variety of organic molecules which are collectively called humus. These molecules are characterized by being negatively charged (as clay particles). A typical humus particle's ability to absorb positively charged ions is up to 50 times greater than that of a clay particle. The formation of humus in a forest ecosystem is therefore crucial for the ability of the soil to retain essential nutrients, such as Ca^{++}, K^{+}, Mg^{++}, NH_4^{+}, which would otherwise be quickly washed out of the soil. The trees can release the absorbed nutrients when their roots release H^{+} or the roots emit CO_2 that forms carbonic acid, which split off H^{+}. By ion exchange, this releases the positively charged nutrients, which can then be taken up by the tree roots. In this way, a delicate balance is established between the trees' nutrient needs and the abiotic pool of these substances. It is important to note that this balance can be disturbed by acid rain caused by air pollution with sulphur and nitrogen oxides that react with water to form sulphuric acid and nitric acid (see sections 3.3 and 3.4). Acid rain can indirectly damage the trees by causing leaching of nutrients, resulting in nutrient deficiency (the trees' leaves become yellow). In addition, acid rain releases poisonous heavy metals absorbed to humus and clay particles, which damage the tree roots resulting in the trees suffering from lack of water and nutrients. Finally, soil acidification inhibits the microbial processes causing the speed of the mineralization of detritus to be reduced, resulting in nutrient deficiency for the trees.

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