CHAPTER 4

ECOLOGICAL PRINCIPLES AND CONCEPTS

4.1. ECOSYSTEM CHARACTERISTICS.

In Chapter 2 we mentioned how man can influence his environment or even the entire ecosphere by changing the global cycles of elements (see 2.5) or by discharging chemical compounds e.g. organic matter (see 2.6), nutrients (see 2.7) and pesticides (see 2.8) into the environment. The effect of such activity on the natural mass flows presents a threat to man's own survival on earth.

Man is facing three crises - an environmental crisis, a food crisis and an energy crisis, all of which are closely linked together. It is important to realize that he cannot solve these crises by violating the first and second laws of thermodynamics. His impact on the environment may modify the global energy balance and thereby the climate (see 3.5), which might have disastrous consequences, but it is also important to understand the behaviour of energy at the ecosystem level, if mankind is to attempt to find a solution for all three crises. To this end chapter three was devoted to the energy flow in the ecosphere and in different ecosystems, and to fostering an understanding of how the first and second laws of thermodynamics could be applied to these problems.

In an ecosystem two major processes are in operation: transformation of high-quality energy to low-quality energy, which results in chemical cycling of important elements accompanied by energy cycling. The former is a condition of the latter and relates mass flows to energy flows.

We often use the term "balance of nature", which must *not* be interpreted as the ecosystems do not change with time. Ecosystems are not static, but dynamic. The biotic communities that make up an ecosystem are continually changing in response to environmental changes caused either by the communities themselves or by external stresses, among which is the impact of man's activities.

An ecosystem is able to maintain its overall stability by three major mechanisms:

1. by controlling the rate of energy flow through the system,
2. by controlling the rate of element cycling within the system,
3. by maintaining a diversity of species and foodwebs - an ecological structure.

In Chapters 2 and 3 we discussed the first two mechanisms; this chapter is devoted to an explanation of the third.

P.4.1. The ecosystem is capable of self-maintenance and self-regulation.

But how does an ecosystem maintain its stability in spite of disruption? As we have illustrated all the components of an ecosystem are in constant interaction, and information from each component is continually feed back into the system. This interaction preserves the integrity of the system. Thus the science of control mechanisms, cybernetics, has an important role in ecology, especially since man tends to disrupt natural control.

P.4.2. Homoeostatis is the term generally applied to the tendency for biological systems to resist changes and to remain in a state of dynamic equilibrium,

and this chapter attempts to explain how this homoeostasis functions, in the context of the interplay of material cycles and energy flows already discussed in Chapters 2 and 3.

A good example of cybernetic control at the organism level is the method by which the temperature of the human body is kept within a few degrees of 37°C.

P.4.3. Any cybernetic system can, however, be overloaded. In spite of the feedback system there is a limited range of tolerance to variation, termed the homoeostatic plateau, which applies equally at all levels within an ecosystem.

Our knowledge about the cybernetic system at the ecosystem level is quite limited due to the complexity of ecosystems. However, some ecological feed back mechanisms are known and can be used to illustrate how ecosystems respond to stress. The following mechanisms will be discussed:

1. Adaptation
2. Self-regulated growth
3. Interaction between two or more species
4. Organization, development and evolution of the ecosystem
5. Diversity
6. Buffer capacity in the environment

4.2. ADAPTATION.

Living organisms occur in diverse habitats from tropical forests to the polar ice caps, and from small ponds to deep oceans.

P.4.4. Adaptation means both the genetic process, by which organisms become increasingly better able to exist under prevailing environmental conditions, and the specific genetic (phenotypic) trait that renders one organism more capable of existence than another.

A related but non-genetic process is acclimation, the modification of an organism's phenotypic trait by the environment, i.e. the environmental modification of gene expression.

An example of acclimation is given in Fig. 4.1. As seen there is an upper and a lower temperature which is lethal to fish. In between these extreme temperatures is a zone of tolerance where progressive rises in the acclimation temperature lead to a corresponding, but smaller rise in the upper temperature limit. The point (see Fig. 4.1, point A), where the acclimation temperature and the thermal death point are the same, is characteristic of each different species of fish (Erichson-Jones, 1964). The area of the polygon (in $^{\circ}C^2$) is a measure of the *thermal tolerance* of the organism (see Fig. 4.1). *The tolerance to elevated temperature* is related to the area between a 45° line intersecting the origin, the y-axis and the upper LC_{50} line.

TABLE 4.1
Tolerance to elevated temperature

Fish	Tolerance ($^{\circ}C)^2$
Mosquito Fish	676
Gold Fish	575
Brook Trout	306
Sockeye Salmon	282
Chum Salmon	260

Compiled from McErlean et al., 1969.

Previously we have referred to species as if they constituted ecological units. However, a species consistes of local populations that may differ conspicuously in their adaptive properties.

P.4.5. Genetic variation in a population is the raw material of adaptive change.

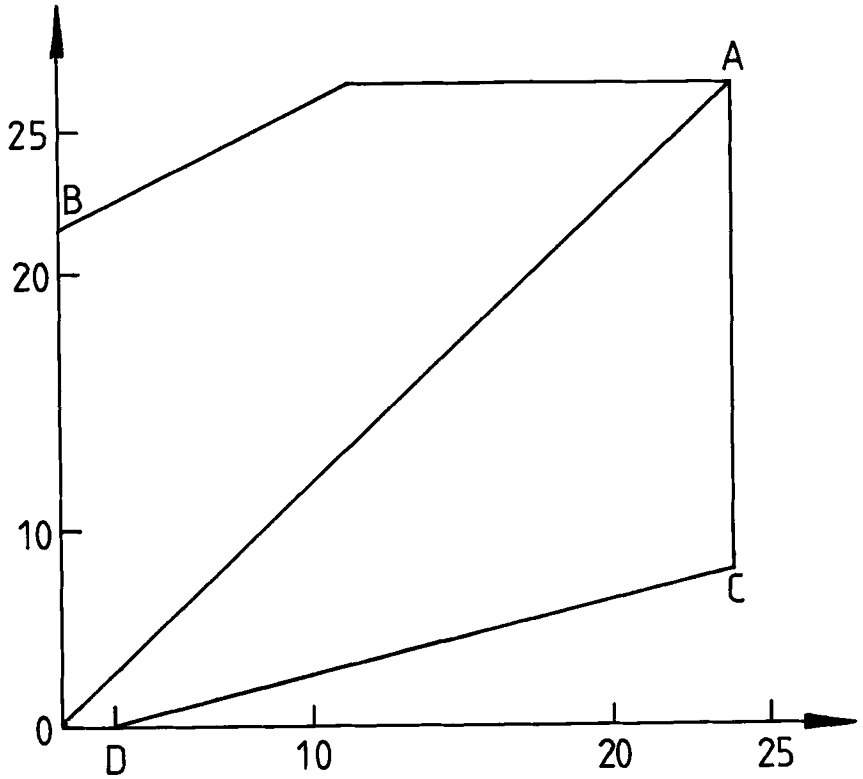

Fig. 4.1. Temperature of tolerance TT° versus acclimation temperature AT° for young sockeye Salmon (Brett, 1960). The area OBACDO is the thermal tolerance. OBA represents the tolerance to the elevated temperature.

Such variation may arise from **mutation**, a change in the basic composition of the genetic substance (DNA) - or from **recombination** - a change in the structural organization of the chromosomes.

At any instant in time a population will contain both old and new, or novel genes. Old genes are those which have been present in the population for a considerable period of time. During this period, the frequency of the occurrence of genes in the population depends on the mating patterns and natural selection occurring in the population. Novel genes may originate through mutation or by gene flow from other populations. The former is the most likely source for more or less isolated populations, while the latter is most likely to be responsible in a population in reproductive contact with several other populations.

We used to think of natural selection as a directional process, moving a population from one genetic constitution to another, but as pointed out by Mather (1953) this is only one of three possibilities (see Fig. 4.2).

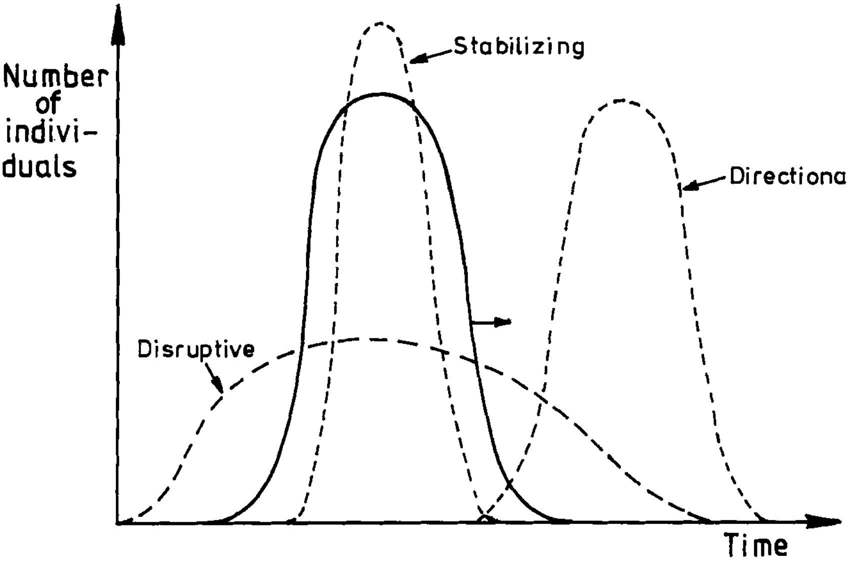

Fig. 4.2. Effect of different types of selection on the distribution of phenotypes in a population (Mather, 1953).

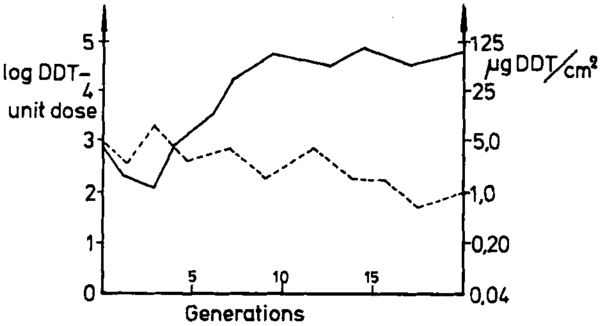

Fig. 4.3. Change in DDT resistance of fruit fly populations exposed to directional selection for high (——) and low resistance (- - - -). The left hand scale = log of dose tolerated. The right hand scale = the actual dose, which could kill half a population sample in standard exposure time.

An example studied by Bennett (1960) and of environmental interest is illustrated in Fig. 4.3. Two populations of fruit fly were studied, one of which was exposed to DDT-impregnated paper. The LD_{50}-value was found (after 18 hours exposure) for each generation of the two populations. Fig. 4.3 shows that after only five generations the two populations exhibited marked differences in DDT resistance. After 18 generations the LD_{50}-value was 125 times higher for the exposed population than for the non-exposed population.

It is also due to adaptation that the synthetic pesticides (aromatic chlorinated hydrocarbons) introduced shortly after the Second World War, were not as successful as they were expected to be after the preliminary results.

P.4.6. The application of this new generation of pesticides gave very promising results in the first couple of years, but then the insects became resistant to these chemicals.

When we also take into account the other properties of this group of compounds, such as low biodegradability (see 2.13) and an ability to be concentrated through the foodchain (see 2.8), it is easy to understand that the application of these pesticides has been questioned. In many countries today it is no longer legal to use DDT and some related compounds.

One of the best examples of natural selection under field conditions has been provided by Kettewell (1956). He has studied the British moth, Biston betularia. This species has a series of different ecotypic populations occupying different areas, and varying in colour from almost white to very dark grey. One of the consequences of man's increased consumption of fuel has been the heavy deposition of soot in industrial areas. The dark type moth is inconspicuous in polluted areas and conspicuous in unpolluted areas, whereas the converse is true for the light type. The frequency of the types in the two habitats is distinctly different with substantially more dark grey moths in the polluted habitats and many more light forms in unpolluted habitats. The results of an examination of the phenotypic patterns are given in Table 4.2.

Direct observations by Kettlewell indicate that there was substantially more predation by birds upon the maladapted forms, which goes some way to explain the distribution of the two forms. It has recently been found (Cook et al., 1970) that pollution abatement programs are being accompanied by an increase in the frequency of light coloured forms in previously polluted areas, indicating that selection is now being reversed. (The original moths were mostly pale coloured).

Many more examples could illustrate the concept of adaptation but both examples demonstrate that

P.4.7. the ecosystem responds to external stress by selecting the form that can meet the stress by the smallest change in the ecosystem.

TABLE 4.2
Phenotypic patterns in a moth occupying woodlands with dark coloured tree trunks resulting from the death of light-coloured lichens on tree trunks from air pollution and woodlands with unpolluted, lichen-covered, and light-coloured tree trunks

Moth phenotype	Polluted area	Unpolluted area
	Percent of phenotypes in native population	
White	10	95
Grey	85	0
	Percent of phenotypes recaptured	
White	13	13
Grey	28	6
	Observed predation, number taken	
White	43	26
Grey	15	164

4.3. GROWTH AND SELF-REGULATION.

A population is defined as a collective group of organisms of the same species. Each population has several characteristic properties, such as population density (population size relative to available space), natality (birth rate), mortality (death rate), age distribution, dispersion growth forms and others.

A population is a changing entity, and we are therefore interested in its size and growth. If N represents the number of organisms and t the time, then dN/dt = the rate of change in the number of organisms per unit time at a particular instant (t) and dN/(Ndt) = the rate of change in the number of organisms per unit time per individual at a particular instant (t). If the population is plotted against time a straight line tangential to the curve at any point represents the growth rate.

Natality is the number of new individuals appearing per unit of time and per unit of population.

We have to distinguish between absolute natality and relative natality, denoted B_a and B_s respectively:

$$B_a = \frac{\Delta N_n}{\Delta t} \tag{4.1}$$

$$B_s = \frac{\Delta N_n}{N \Delta t} \tag{4.2}$$

where ΔN_n = production of new individuals in the population.

Mortality refers to the death of individuals in the population. The absolute mortality rate, M_a, is defined as:

$$M_a = \frac{\Delta N_m}{\Delta t} \tag{4.3}$$

where ΔN_m = number of organisms in the population, that died during the time interval Δt, and the relative mortality, M_s, is defined as:

$$M_s = \frac{\Delta N_m}{\Delta t * N} \tag{4.4}$$

P.4.8. When the environment has unlimited space and food and no other organisms exert a limiting effect, the specific growth rate, i.e. the growth rate of the population per individual, becomes constant and reaches a maximum permitted by the climatic conditions.

Thus:

$$\frac{dN}{dt} = B_a - M_a = (B_s - M_s) * N = r * N \tag{4.5}$$

where

$$r = \text{growth rate coefficient} = B_s - M_s \tag{4.6}$$

or $$N_t = N_o * e^{r*t} \tag{4.7}$$

or $$\ln \frac{N_t}{N_o} = r * t \tag{4.8}$$

Fig. 4.4 shows a population growth curve based on equation (4.5). Here growth is **exponential, characterized by a fixed doubling time**. As seen in Fig. 4.5 this exponential growth curve is represented by a *straight* line in a *semologaritmic* plot.

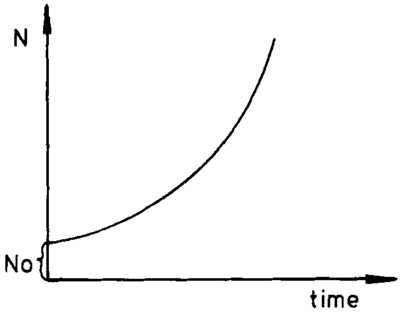

Fig. 4.4. Growth in accordance with $dN/dt = r * N$ $(r > 0)$ corresponding to exponential growth.

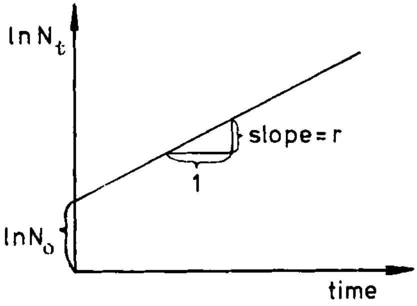

Fig. 4.5. $\ln N_t$ versus the time t. $\ln N_t = \ln N_0 + r * t$.

The growth coefficient, also denoted as *the intrinsic rate of natural increase, r,* should not be confused with *the net reproductive rate, R,* which is related to the *generation time, T*:

$$R = e^{r*T} \qquad T = \frac{\ln R}{r} \tag{4.9}$$

Some typical growth coefficients can be seen in Table 4.3.

TABLE 4.3
Typical growth coefficients (r) at optimal conditions

Escherichia coli	60 day $^{-1}$
Protozoa	0.8 - 1.3 day $^{-1}$
Phytoplankton	1 - 3 day $^{-1}$
Fish	0.02 - 0.04 day $^{-1}$
Octupus	0.006 - 0.02 day $^{-1}$
Ptinus tectus (insect)	0.05 day $^{-1}$
Daphnia pulex	0.1 - 0.4 day $^{-1}$
Flour beetle	0.71 week $^{-1}$
Human louse	0.78 week $^{-1}$
Brown rat	0.104 week $^{-1}$
Dog	0.06 week $^{-1}$
Man (world average)	0.02 year $^{-1}$

The growth rate represented by equation (4.5) assumes, as previously mentioned, *unlimited space and food* , but this is of course an unrealistic assumption. In reality the growth rate will slow down gradually as the environmental resistance increases, until a more or less equilibrium level is reached and maintained. These observations can be described by use of the following equation:

$$\frac{dN}{dt} = rN \frac{(K - N)}{K} \qquad (4.10)$$

As seen, the upper limit beyond which no increase can occur is represented by the constant K, denoted as

P.4.9. the carrying capacity. If N = K, the growth rate is zero in accordance with this equation.

A growth curve which follows this expression is called a **logistic growth curve** and has a characteristic s=shape, (see Fig. 4.5). On solving equation (4.10) we find:

$$N = \frac{K}{1 + e^{a-r^*t}} \qquad (4.11)$$

where

$$a = \ln \frac{K - N}{N} \quad \text{when } t = 0; \text{ it means } a = \ln \frac{K - N_0}{N_0} \tag{4.12}$$

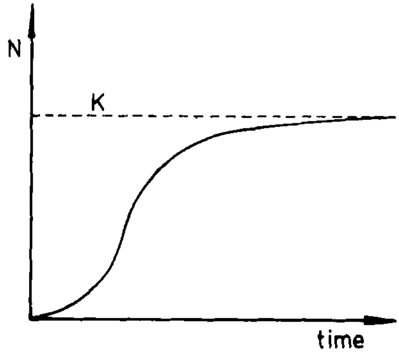

Fig. 4.6. Logistic growth.

This simple situation in which there is a linear increase in the environmental resistance with density seems to hold good only for organisms that have a very simple life history.

P.4.10. In populations of higher plants and animals, that have more complicated life histories, there is likely to be a delayed response.

Wangersky and Cunningham (1956 and 1957) have suggested a modification of the logistic equation to include two kinds of time lags: 1) the time needed for an organism to start increasing, when conditions are favourable, and 2) the time required for organisms to react to unfavourable crowding by altering birth- and death rates. If these time lags are $t - t_1$ and $t - t_2$ respectively we get:

$$\frac{dN(t)}{dt} = r\, N_{(t-t_1)} * \frac{K - N_{(t-t_2)}}{K} \tag{4.13}$$

Population density tends to fluctuate as a result of seasonal changes in environmental factors or due to factors within the populations themselves (so-called intrinsic factors). We shall not go into details here but just mention that

P.4.11. **the growth coefficient is often temperature dependent and since temperature shows seasonal fluctuations, it is possible to explain some of the seasonal population fluctuations in density in that way.**

Another modified logistic equation was introduced by Smith (1963):

$$\frac{dN}{dt} = r * N \frac{K - N}{K + \frac{r}{C} * N} \tag{4.14}$$

where
C = the rate of replacement of biomass in the population at saturation density.

P.4.12. **The r value in equation (4.10) is strongly influenced by any environmental factor. Such physical factors as temperature, light, humidity, etc., or such chemical factors as the nutrient concentration and trace element concentration are examples of environmental factors affecting the growth of plants or animals. Toxic pollutants affect the growth of the individuals as well as the mortality rate,**

as demonstrated in Appendix 5. The data here are only a minor selection of the data available in the literature, see Jørgensen et al. (1979a).

The energy available to an organism capable of reproduction may be directed either toward the survival and growth of that organism, toward the production of offspring or apportioned between the two.

All the equations (4.1) - (4.14) consider growth in terms of the numbers in a population, but to understand fully the concepts of self-regulation, it is necessary to discuss in detail two possible strategies, called K-strategy and r-strategy.

P.4.13. **The K-strategists have a stable habitat with a very small ratio between generation time and the length of time, habitat remains favourable.**

They evolve toward maintaining their population at its equilibrium level, which is the carrying capacity in the logistic growth equation.

They will often be selected for *large size*, and *high levels of fecundity are not essential if the reduction in birthrate can be matched by increased* *survival* . K-strategists make a significant investment in defence mechanisms. Parental care is facilitated by low fecundity, longevity and size. This reduction in mortality may be considered to lead to a more efficient use of energy resources (Cody, 1966).

If K-strategists suffer perturbations, their populations need to return quickly to equilibrium levels or competitors may seize the resources. Because there is little mortality, this will tend to be accomplished through the birth rate, which will be very sensitive to the population density and will rise rapidly if density falls.

K-strategists are recognized by **large size, longevity, low recruitment and mortality rates, high competitive ability and a large in- vestment in each offspring.**

K-strategists will tend to have a stable equilibrium point E, to which the system returns after moderate disturbances. They are unlikely to be well adapted to recover from population densities significantly below their equilibrium level, and depressed to such low levels they may become extinct.

P.4.14. They, rather than the r-strategists, therefore need the concern of the conservationist. They follow what is called Cope's rule: they will evolve toward increased size until extinction,

a pattern often found in the fossil record.

The K-strategists become more and more adapted to a specialized and hitherto stable habitat (Bretsky and Lorenz, 1970). Thus the extinction of the extreme K-strategists dinosaurs was probably due to their inability to respond to the changes in climate at the end of the Cretaceous (Axelrod and Bailey, 1968; Southwood et al., 1974).

Other examples of extreme K-strategists are the Andean condor, the albatros and large tropical butterflies.

P.4.15. The r-strategists are basically opportunistic "boom and burst" species. They are exposed to selection at all population densities and are continually colonizing habitats of a temporary nature. The r-strategist's population grows rapidly at low densities, has an equilibrium point about, which it is able to oscillate and crashes down from high densities.

The ratio between generation time and the length of the time the habitat remains favourable is not small. *Migration* will be a major component of their population process and may even occur every generation (Dingle, 1974;

Southwood, 1962; Kennedy, 1975; Southwood et al., 1974). Selection will favour a high r arrived at by a **large fecundity** and **short generation time**. High competitive ability is not required and individuals will typically be **small in size**. Very high values of r lead to instability (May, 1974 and 1975) and their **high mortality, wide mobility** and **continuous exposure to new situations by migration** are likely to make them *fertile sources of speciation* . Perhaps the best way to see the difference between the two strategies is to look at the relationship between the population size at time t + 1 and the population size at time t (see Fig. 4.6).

Temporal heterogeneity in the habitat will increase instability, but animals with K-strategy will average out over the variations, while animals with r-strategy will closely follow the variations in the environment. This difference is illustrated in Fig. 4.7, where tawny owls (K-strategists) and voles and mice (r-strategists) have different scales and amplitudes of fluctuation.

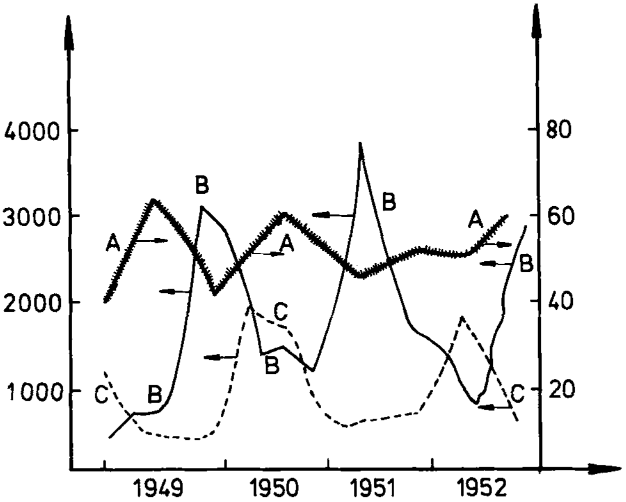

Fig. 4.7. Fluctuation in the number of animals in the same habitat: A) Tawny Owls (K-strategists), B) Bank Voles and C) Woodmice in Wythan Wood (both r-strategists). Data from Southern (1970). A) right hand scale, B) and C) left hand scale.

4.4. INTERACTION BETWEEN TWO OR MORE SPECIES.

There are 8 possible observable interactions between two species (see Table 4.4).

P.4.16. In terms of population growth these interactions involve adding positive, negative or zero terms to the basic equations presented in 4.3.

All these population interactions are likely to occur in the average community. For a given pair of species, the type of interaction may change under different environmental conditions.

Various terms have been suggested for a mathematical description of two-species interactions. The effects, beneficial or detrimental, of all the other species can be taken into account by adding $\pm C * N * N_1$ to the equation (4.10).

Some of the most widely discussed aspects of competition revolve around the so-called Lotka-Volterra equation, which consists of the following two expressions:

$$\frac{dN}{dt} = r * N \left(\frac{(K - N)}{K} - b * N_1 \right) \qquad (4.15)$$

$$\frac{dN_1}{dt} = r_1 * N_1 \left(\frac{K_1 - N_1}{K_1} - c * N \right) \qquad (4.16)$$

where

N = the first population

N_1 = the second population

r, r_1, K, K_1, b and c = constants

It is difficult to approach the subject of parasitism and predation (see Table 4.4) objectively, since we have a natural aversion to both types of interaction, although man is in fact the greatest predator the world has ever known. Predation and parasitism should be considered from point of view of the population and not from that of the individual.

P.4.17. Predators and parasites play a major role as regulators, e.g. by keeping herbivorous insects at a low density.

TABLE 4.4
Two-species population interactions

0 : No significant interaction
\+ : Positive term (effect) added to growth equation
\- : Negative term (effect) added to growth equation
Population 1 is larger than population 2

Effect population 1	Effect population 2	0	+	-
0		Neutralism	Commensalism	Amensalism
+			Protocooperation Mutalism	Predation
-		Amensalism	Parasitism	Competition

Deer populations are often cited as examples of populations that tend to erupt when predation pressure is reduced. The Kaibab deer herd, which was originally described by Leopold (1943) based on estimations by Rasmussen (1941), allegedly increased from 4000 (on less than 300,000 ha on the north side of the Grand Canyon in Arizona) in 1907 to 100,000 in 1924 coincident with an organized governmental predator removal campaign. Caughley (1970) has re-examined the case and concludes, that there is no doubt that the population did increase, overgraze and then decline drastically. There is, however, doubt about the extent of over-population and no real evidence has been presented to support the belief that it was due solely the removal of predators. Cattle and fire may have played a part, as well.

However, this example shows that human interaction can easily disturb the delicate balance of an ecosystem.

P.4.18. If an ecosystem is stressed by man it will, of course, find a new equilibrium after some time, but a disaster might occur before that new equilibrium is reached. Sudden changes in an ecosystem might cause such catastrophies.

An understanding of the influence, that all species in an ecosystem have on the overall balance is most important.

P.4.19. This is also the case when pesticides are used for pest control, but unfortunately many case studies illustrate that pesticides have been misused by ignoring ecological

principles. In such cases, far from controlling them, pesticides often cause pests to increase.

Table 4.5 shows results obtained from tests on the effects of DDT on red scale in a variety of citrus groves in southern California over a period of years. As can be seen the red scale population has risen considerably under the use of DDT (Debach, 1974).

TABLE 4.5
Adverse effects of DDT, southern California
Relative California red scale population densities in various biological control plots (untreated) and in plots in which natural enemy activity had been suppressed by prior application of a light DDT spray

		Final scale population density #		
Property and location	No. of DDT applications	Un-treated	DDT sprayed	Fold increase, DDT-sprayed/ untreated
Bothin, Santa Barbara	11 +	3	425	142
Sullivan, Santa Barbara	11 +	16	575	36
Beemer, Pauma Valley	9 *	1	580	580
Irvine Company, Irvine	29 +	6	1336	223
Rancho Sespe, Fillmore	54 +	1	1250	1250
Ehrler, Riverside	10 *	4	390	98
Sinaloa Ranch, Simi	55 +	3	1015	299
Stow Ranch, Goleta	37 +	8	850	112
Hugh Walker Grove, Orange County	47 +	1	463	463

\+ Monthly applications
* Quarterly applications
\# Initial scale population densities were similar in all plots

There was a period following the widespread adoption of chlorinated hydrocarbons and organophosphorus pesticides when the first documented reports of striking upsets in crops generally met with disbelief or disapproval from pesticide-oriented entomologists and industries. Today few, if any, knowledgeable professionals deny such effects to be rather commonplace. They are in fact extremely commonplace, as can readily be ascertained from the entomological literature.

Table 4.6, taken from Huffaker et al. (1962), provides another example. Light dosages of DDT were used on olive trees to fight olive scale. The procedure was repeated over a period of several years in many olive groves. Some typical results are summarized in Table 4.6, and as can be seen the relative population increase of olive scale in sprayed over unsprayed trees is truly amazing, ranging from 75 fold to nearly 1000 fold within a period of two years.

TABLE 4.6

Relative population density increase of the olive scale on unsprayed trees and on DDT-sprayed trees (Adapted from Huffaker, Kennett and Finney, 1962)

	1958		1959				1960				
	Fall *)		Spring		Fall		Spring		Fall		Relative fold
Location	DDT spr.	Un-spr.	DDT spr.	Un-spr.	DDT spr.	Un-spr.	DDT spr.	Un-spr.	DDT spr.	Un-spr.	increase DDT-spr. to un-spr.
Lindsay	0.0	0.0	0.3	0.3	5.5	1.2	25.5	1.9	67.6	0.9	75:1
Seville	2.0	1.6	4.2	9.0	2.7	0.0	12.6	0.0	29.8	0.03	993:1
Hills Valley	0.8	1.3	10.6	0.1	12.1	0.4	25.6	0.2	90.7	0.1	907:1
Clovis	1.2	3.0	12.4	0.2	43.9	0.5	55.6	1.9	287.8	2.5	140:1
Herndon	2.0	3.8	38.1	3.2	134.0	0.7	60.4	0.0	169.8	1.5	113:1
Madera	16.9	11.6	23.9	3.4	43.5	0.4	120.3	0.6	204.2	0.5	408:1

*) Pretreatment counts

Such results, of course, raise the question of how we can solve the pest problem. The answer is not an easy one, and will be dependent on the *ecosystem, the species, the climate and a number of other factors* . However, the general opinion among professionals today is that

P.4.20. pesticides alone can never solve the problem and that they should be used only to a very limited extent and always selectively. Furthermore, only biodegradable pesticides should be used.

New, far more selective, pesticides are under development - the so-called **third generation of pesticides**. These are based on hormones which affect the biochemical balance of the pest organism.

Another powerful method, that has developed rapidly during the last two decades, is the use of **biological control**. This can be defined as the regulation by natural enemies of another organism's occur. In other words the method uses the ecological possibility of interaction between two species. A comparison of biological and chemical control is given in Table 4.7, where the disadvantages of the two methods are listed.

Biological control has recently been successfully applied in control of the California red scale, although it had been regarded as a failure for nearly 60 years. Completely satisfactory control is established in some groves year after year and the pest is kept to reasonable levels in the entire district. Four species of parasites are responsible for the degree of biological control now achieved, all established between 1941 and 1957. Each of these can keep the red scale population at an extremely low level. These four parasites are the most recent enemies to become established and are by far the most effective of all the species of predators and parasites imported and liberated since 1890. This illustrates the value of continued research and indicates that it may be unwise ever to condemn a biological control project as a failure: The best weapon may as yet be undiscovered.

TABLE 4.7
A comparison of biological and chemical control

Category	Biololgical control	Chemical control
Environmental pollution; danger to man wildlife, other non-target organisms, soil etc.	None	Considerable
Upsets in natural balance and other ecological disruptions	None	Common
Permanency of control	Permanent	Temporary - must repeat one to many times annually
Development of resistance to the mortality factor	Extremely rare, if ever	Common
General applicability to broad-spectrum pest control	Theoretically unlimited but not expected to apply to all pests. Still underdeveloped. Initial control may take 1-2 years but then pest remains reduced	Applies empirically to nearly all insects but not satisfactory with some. Can rapidly reduce outbreaks but they rebound. Psychologically satisfying to the user at first

Other non-chemical approaches to pest management include three methods of proven practical use in the field as well as several still in the theoretical stage or in pilot tests. The three methods now in practical use are:

1. **the development of plant resistance to insects and plant diseases,**
2. **cultural techniques or habitat modification designed to control pests,**
3. **the genetic technique of sterile male release in the field** which mate with wild females and prevent progeny production.

Two useful general references covering this subject are Kilgore and Doutt (1967) and the National Academy of Sciences (1969).

In order to be succesful, a biological control agent must possess certain attributes:

1. The species must be able to find whichever species it is supposed to contol. This is termed *searching ability.*
2. It must have a high *enough reproductive rate* to build up in numbers fast enough to prevent build-up in numbers of the pest.
3. It must *not interfere unduly with other members* of its own species.
4. It must *perform well in the climate* in which it is released.
5. It must be *intensitive to competition* from other enemies of the pest that might be released or already present in nature.
6. It must be certain that it will *confine its diet to the pest species* and avoid interference with other species of economic value.
7. It should have *no special requirements for resources* that the environement cannot supply in sufficient quantity to maintain the agent's density.

Several equations have been proposed to account for the numbers of the pest that are attacked over a given time interval.

A simple preliminary model, which is very useful but which has now been superseded by slightly better models, is:

$$N_A = P \cdot K(1 - e^{-a*N_0*p} (1 - b)) \qquad (4.17)$$

where N_A is the number of pests attacked by parasites, N_0 the numbers vulnerable to attack and P the parasite population density. a, b and K are constants, namely the searching rate, the parasite intraspecific competition pressure and the maximum egg-laying rate, respectively.

4.5. ORGANIZATION OF ECOSYSTEMS.

Out of thousands of species that might be present in an ecosystem relatively few exert on major controlling influence by virtue of their numbers, size, production or other activities. Intracommunity classification therefore goes beyond the taxonomic listing and attempts to evaluate the actual importance of organisms in the community. Three types of indices are used to describe the organization in an ecosystem:

1. **indices of dominance,**
2. **indices of similarity** and
3. **indices of diversity.**

Some of the most commonly used indices in these three groups are listed in Table 4.8.

P.4.21. Species diversity tends to be low in physically controlled ecosystems and high in biologically controlled ecosystems, but this rule is not always valid, and takes only the tendency into account.
There is a relationship between the stability of the ecosystem and its diversity, but the detailed relationship has still to be discovered.

The general relationship between species and numbers of individuals takes the form of a curve, see Fig. 4.8. Stress will tend to flatten the curve as illustrated in Fig. 4.8 by the dotted line.

Two broad approaches are used to analyze species diversity in different situations, namely:

1. a comparison based on **diversity indices** (see Table 4.8),
2. a comparison based on the **shapes, patterns and equations of species abundance curves.**

P.4.22. Two stability concepts are generally used. Stability is either understood as maintenance of constant biological structure or as resistance to changes in external factors.

However, to avoid misunderstandings this last stability concept will be defined as an **ecological buffer capacity**, see section 4.8, while "stability" will be reserved for the former definition. The relationship between this stability concept and diversity has been widely discussed in the literature, see e.g. Jacobs (1974). One of the crucial questions is whether *stable physicochemical conditions will cause high diversity or whether high diversity will produce a stable environment.* For those who want further information about this complex relationship, see Margalef (1969); Pielou (1966); Slobod- kin and Sanders (1969); Paine (1966); Sanders (1968); Boesch (1974); Goodmann (1974); May (1974); Orians (1974); Preston (1969).

It is essential to recognize that species diversity has a number of components which may respond differently to external and internal factors of importance to environmental conditions.

TABLE 4.8
Some useful indices of species structure in communities

A. Index of dominance (c) [+]

$c = \Sigma(ni/N)^2$ where ni = importance value for each species (number of individual, biomass, production, and so forth)
N = total of importance values

B. Index of similarity (S) between two samples[o]

$S = \frac{2C}{A + B}$ where A = number of species in sample A
B = number of species in sample B
C = number of species common to both samples

Note: Index of dissimilarity = 1 - S.

C. Indices of species diversity

(1) Three species richness or variety indices (d)[++]

$d_1 = \frac{S - 1}{\log N}$ $d_2 = \frac{S}{\sqrt{N}}$ $d_3 =$ S per 1000 ind.

where S = number of species
N = number of individuals, etc.

(2) Evenness index (e)[§]

$e = \frac{H}{\log S}$ where H = Shannon index (see below)
S = number of species

(3) Shannon index of general diversity (H)[*]

$H = -\Sigma \left(\frac{ni}{N}\right) \log \left(\frac{ni}{N}\right)$

or

$-\Sigma P_i \log P_i$ where ni = importance value for each species
N = total of importance values
P_i = importance probability for each species = ni/N

[+] See Simpson (1949)

[o] See Sørensen (1948), for a related index of "% difference" see E.P. Odum (1950)

[++] d_1 see Margalef (1958). d_2 see Menhinick (1964). d_3 see H.T. Odum, Cantlon and Kornicker (1960).

[§] See Pielou (1966); for another type of "equitability" index, see Lloyd and Ghelardi (1964).

[*] See Shannon and Weaver (1963); Margalef (1968).

Note: In d_1, e and H natural logarithms ($\log_e$) are usually employed, but $\log_2$ is often used to calculate H so as to obtain "bits per individual".

Areas with very predictable and stable climates *tend to support* fewer different plant life forms than regions with more erratic climates, as is demonstrated in Fig. 4.9.

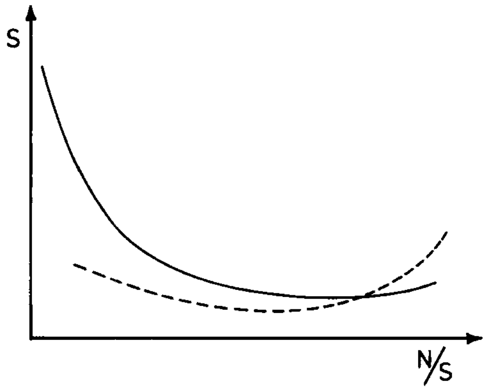

Fig. 4.8. Relationship between the number of species (S) and the number of individuals (N) per species. Environmental stress tends to flatten the curve as indicated with the dotted line.

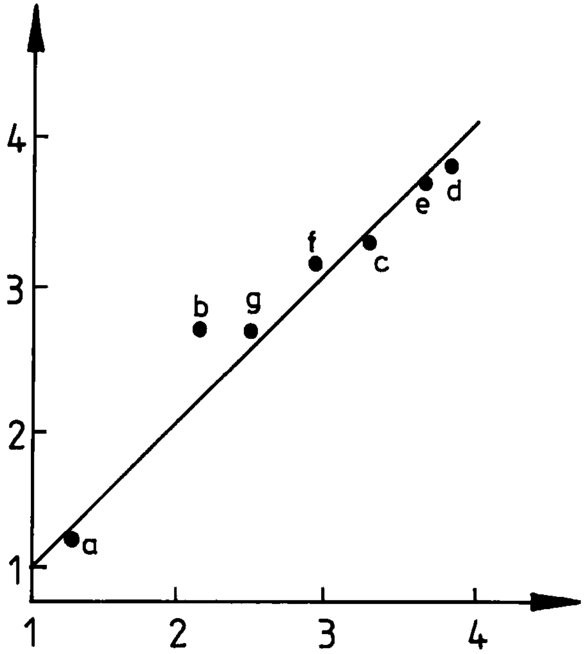

Fig. 4.9. Rainfall unpredictability or climate diversity is plotted versus plant life form diversity (from May (1975) and other sources). Both diversities are computed as Shannon indices. a: Tropical rain forest, b: Subtropical forest, c: Deciduous forest, d: Mediterranean scrub, e: Desert, f: Steppe, g: Arctic tundra.

The most widely used index of diversity is **the Shannon index**. It is *normally distributed* (Bowman et al., 1970; Hutcheson, 1970), so the *routine statistical methods* can be used to test for magnificance of differences between means. It is also reasonably independent of sample size as illustrated in Fig. 4.10.

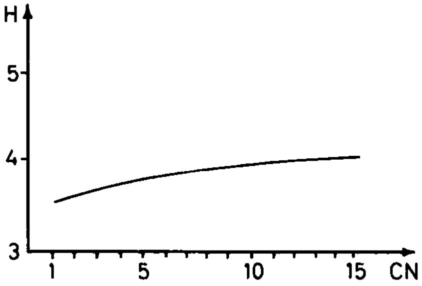

Fig. 4.10. The effect of increasing sample size on the Shannon index. H is plotted against cumulative number of samples (CN).

Higher diversity means longer foodchains, more cases of symbioses and greater possibilities for negative feedback control, which will reduce oscillations and hence increase stability. This expresses the general interest for the ecologist in the concept diversity, as he sees in any measure of diversity an expression of the possibilities for constructing feedback systems (Margalef, 1960).

P.4.23. Diversity indices can be used to evaluate man-made stresses on ecosystems,

as clearly demonstrated in Figs. 4.11 - 4.14.

The use of grafic methods in this context is illustrated in Fig. 4.15.

Before diversity indices are used to compare one situation with another, the effect of sample size should be determined (compare with Fig. 4.8).

The relationship between diversity and buffering capacity, and the development of diversity in an ecosystem will be discussed in the following sections.

Ecosystems are usually very difficult to manipulate experimentally. For this reason, ecologists have long been especially interested in islands, which constitute some of the finest natural ecological experiments. Through such studies it has been found that larger islands generally support more species of plants and animals than smaller ones. In many cases, a tenfold increase in area corresponds to an approximate doubling of the number of species.

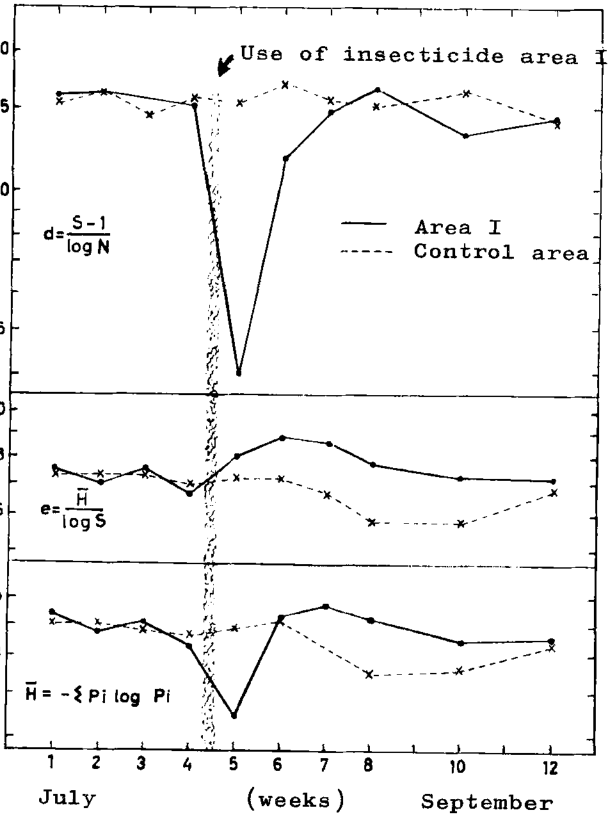

Fig. 4.11. Effect of insecticides on diversity.

P.4.24. The number of species, S is related to the area of the islands concerned as follows

$$S = C * A^z \quad (4.18)$$

where C is a constant that varies between taxa and from place to place, and z generally ranges from about 0.24 to about 0.34.
Estimated z-values are shown in Table 4.9.

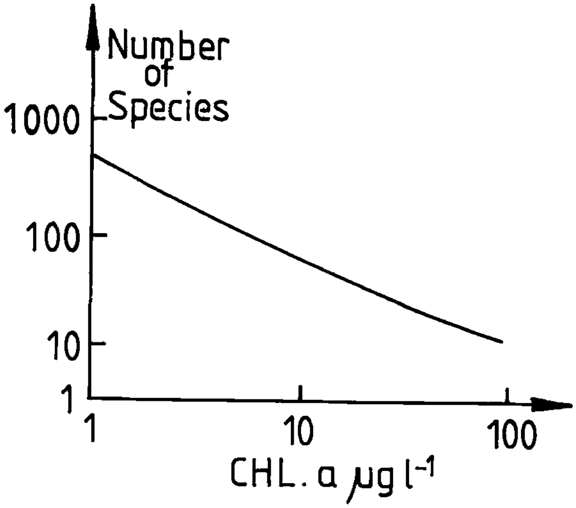

Fig. 4.12. Weiderholm (1980) obtained the shown relationship in a number of Swedish lakes between number og species and eutrophication, measured as chlorophyll a (µg l^{-1})

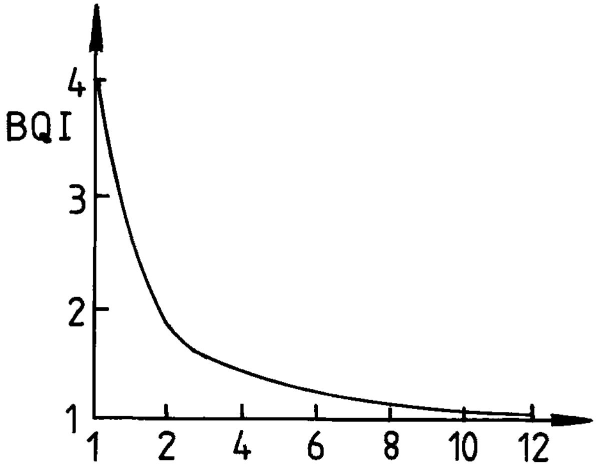

Fig. 4.13. Ahl & Weiderholm (1977) found the shown relationship between BQI and total phosphorus concentration divided by depth. BQI is a diversity index for the benthic fauna (benthic quality index). It is defined as

$$BQI = \sum_{i=0}^{i=5} \frac{k_i n_i}{N}$$

where k_i represents a value for each species, n_i the number of individuals in the various groups and N the total number of indicator species.

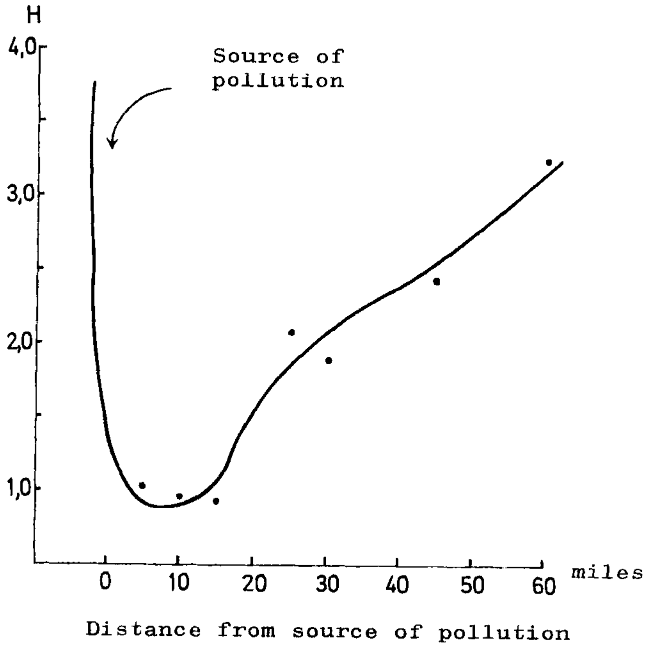

Fig. 4.14. Shannon index (H) plotted versus distance (0 = discharge of waste water).

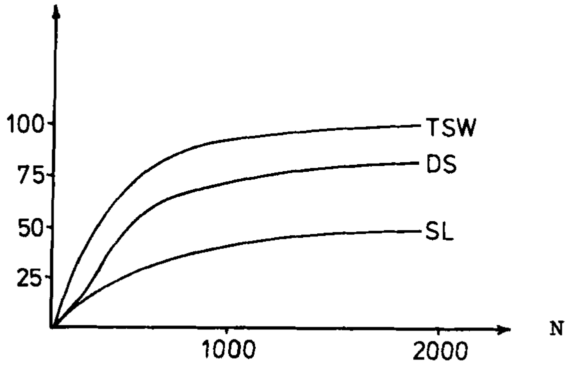

Fig. 4.15. Number of species plotted against number of individuals. Typical plots are shown for TSW (Tropical Shallow Water), DS (Deep Sea) and SL (Shallow Lake).

TABLE 4.9
Estimated z-values for various terrestrial plants and animals on different island groups. (MacArthur and Wilson, 1967)

Flora or fauna	Island group	z
Carabid beetles	West Indies	0.34
Amphibians and reptiles	West Indies	0.30
Birds	West Indies	0.24
Birds	East Indies	0.28
Birds	Islands of Gulf of Guinea	0.49
Birds	East Central Pacific	0.30
Land plants	Galapagos Islands	0.33
Land Vertebrates	Islands of Lake Michigan	0.24
Ants	Melanesia	0.30

Variety of species and their relative abundance are by no means the only factors involved in community diversity. Arrangement patterns also contribute to community function and stability. Many different kinds of arrangements in the standing crop of organisms contribute to pattern diversity in the community, following for example: 1. *horizontal zonation pattern,* 2. *stratification pattern,* 3. *reproductive pattern* (parent/offspring), 4. *social pattern* (flocks, herds etc), 5. *periodicity pattern,* 6. *stochastic pattern* (results of random forces).

There seems no doubt about the existence of some relationship between diversity in space and species and the ecosystem stability in its broadest sense, but a quantitative ecosystem theory which includes these relationships is still not available. However, an examination of the diversity is very useful for providing information about ecological conditions, although such information is qualitative and cannot be used to give quantitative assessments of environmental impact.

To understand diversity fully we must consider the related concepts of **the ecotone** and **the ecological niche.**

An ecotone is a transition zone between two or more diverse communities, for example between forest and grassland, between a fjord and the open sea, etc. The ecotonal community commonly contains many of the organisms of both overlapping communities, as well as organisms, characteristic of and often restricted to the ecotone. Often, the number of species and the population density of some of the species are greater in the ecotone than in the communities flanking it. The tendency for increased variety and density at community junctions is known as the "*edge effect* ".

The ecological niche is primarily the physical space occupied by an organism (the so-called spatial niche), but the term also encompasses its functional role in the community and its position in environmental gradients of temperature, humidity, pH, soil composition, etc. In this context such expressions as *trophic niche* or *multidimensional niche* are used.

A complete description of the ecological niche for species would require an infinite set of biological characteristics and physiocochemical parameters. The concept is most often used in terms of differences between species. Organisms that occupy the same or a similar ecological niche in different geographical regions are called ecological equivalents. Species that are ecologically equivalent tend to be closely related taxonomically in regions, which are contiguous, but are not necessary closely related in regions widely separated or isolated from each other. There are several exceptions for this rule, however.

The role of diversity is very well illustrated by presentation of the advantages of mixed forests: these can be listed as follows:

1. A greater density of crop is attainable in mixed forests. A complete utilization of the soil can only be attained when each portion is stocked with the species best suited for growth there. Furthermore, they maintain a closed canopy for the longest period of time, thereby fully utilizing the light resource as well as the soil. The different growth rhythms can be utilized with suitable thinning methods in order to enable the maximum volume and dry-matter production to be achieved.

2. Different light requirements of the species participating in a mixture may produce an increased assimilation efficiency of mixed stands compared with pure stands. The intermediate and lower stories of shade- and semishade-tolerant species are capable of utilizing the light which has been transmitted through the crowns of light-demanding species in the upper canopy, thus producing an additive increment.

3. If the mixed species occupy different root horizons, the sites can be utilized more fully. The species with strong roots are able to open soil layers in which rooting is otherwise difficult, enabling the whole to benefit from this and from an improved nutrient supply by way of the litter from such mixed species.

4. The character of the litter from mixed species, especially litter which is rich in nitrogen and easily decomposed, improves productive capacity by stimulating the soil fauna. A recent result of planting nitrogen-fixing species as an admixture to more classical tree crops appears most encouraging.

5. Plants have favourable as well as unfavourable effects on each other. It has been demonstrated that some chemical substances might have a strong effect on germination.

6. Natural reproduction of mixed woods is easier than for pure stands. Mixed stands have characteristics which are more favourable for the evolution of abundant fruit production than those usually encountered in pure stands.

7. Mixed forests are less exposed than pure forests to external disruptions. Shallow-rooting species, for instance, are much less exposed to damage from storms when mixed with deeper-rooting kinds of trees than when grown alone.

4.6 DEVELOPMENT AND EVOLUTION OF THE ECOSYSTEM.

Ecosystem development or succession, as it is often called, is a process, which can be defined by the following three steps:

1. The changes in the **physicochemical environment** initiate the process. These changes can be either natural or a result of human interference.
2. The rate of change in the community is **community controlled** and it is an orderly process involving changes in species structure and community processes with time.
3. The process is a development toward **a stabilized ecosystem** (here defined as an ecosystem which has the highest possible ability to maintain its ecological structure independent of external changes).

The whole sequence of communities that replace each other in a given area is called the sere; the relatively transitory communities are called seral stages, while the final stabilized system is known as *the climax* . Species replacement in the sere occurs because populations tend to modify the physical environment making conditions favourable for other populations until an equilibrium between biotic and abiotic factors is achieved.

The ecological succession process includes a series of changes, of which changes in adaptation, diversity and other mechanisms play a part. Ecological investigations, and more recently functional considerations, have led to the results presented in Table 4.10, which is based on works by Odum and Pinkerton (1955), Lotka (1925), Margalef (1963 and 1968) and Jørgensen et al. (1977 and 1979). The concept of ecological buffering capacity is included in the table, but will be discussed in the next paragraphs. All the other concepts presented in this table have been defined already. Trends are emphasized by contrasting the situation in early and late developmental stages of the ecosystem. Early and late are understood here to represent the time after a substantial change in the ecological condition has occured. The time required for the transition form one stage to another may vary with climatic, physiographic and ecosystem factors. However, the changes will usually occur more rapidly when the ecosystem is far from stabilization.

P.4.24. One of the characteristic trends to be expected in the development of an ecosystem is that the P/R ratio (P = gross production, R = respiration) approaches 1 and that P/B (B = biomass) decreases.

This is illustrated in Fig. 4.16 based on data of Cooke (1967) and Fig. 4.17 based on results presented by Kira and Shidei (1967).

TABLE 4.10
Ecological succession

Properties	Early stages	Late or mature stage
A <u>Energetics</u>		
P/R	>>1 <<1	Close to 1
P/B	High	Low
Yield	High	Low
Entropy	High	Low
Exergy	Low	High
Information	Low	High
B <u>Structure</u>		
Total biomass	Small	Large
Inorganic nutrients	Extrabiotic	Intrabiotic
Diversity, ecological	Low	High
Diversity, biological	Low	High
Patterns	Poorly organized	Well organized
Niche specialization	Broad	Narrow
Size of organisms	Small	Large
Life cycles	Simple	Complex
Mineral cycles	Open	Closed
Nutrient exchange rate	Rapid	Slow
C <u>Selection and homoeostatis</u>		
Internal symbiosis	Undeveloped	Developed
Stability (resistance to external perturbations)	Poor	Good
Ecological buffer capacity	Low	High
Feedback control	Poor	Good
Growth form	Rapid growth	Feedback controlled growth

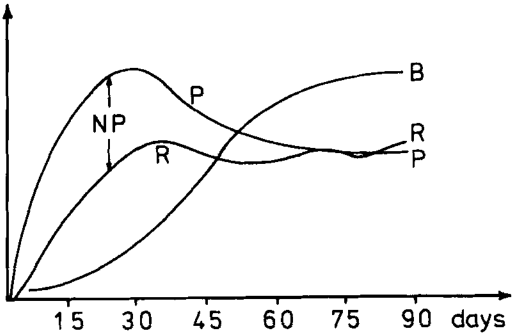

Fig. 4.16. Microcosm succession. P = gross production, NP = net production, R = respiration and B = biomass plotted against time.

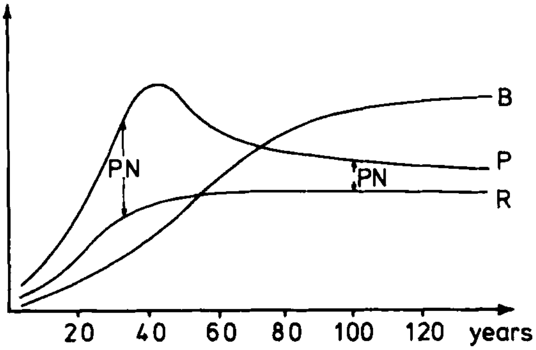

Fig. 4.17. Forest succession. P = gross production, PN = net production, R = respiration and B = biomass are plotted against time.

Communities can be *classified in accordance with the P/R ratio,* see Fig. 4.18. The diagram consists of three areas. Ecosystems with a high P/R ratio are represented in upper left of the diagram, while those with a low P/R ratio are situated in the lower right of the diagram. The direction of succession is indicated by the arrows pointing toward what is called the balanced ecosystem.

Balanced ecosystems represent the mature stage, and although there is a pronounced difference in production and respiration in the ecosystems in this part of the diagram all have a P/R ratio close to 1. The production in a coral reef is almost 1000 times greater than that in a desert. The diagram is based on the classification of Odum (1956).

Figs. 4.19 - 4.24 show some characteristic observations of succession patterns in ecosystems. As seen, the figures demonstrate the expected trends, compare with Table 4.10.

The changes referred to in these diagrams and in Table 4.11 are all brought about by biological processes within the ecosystem. Geological and human forces acting on the system can reverse the trends, in which case the ecosystem has to start again from the very beginning.

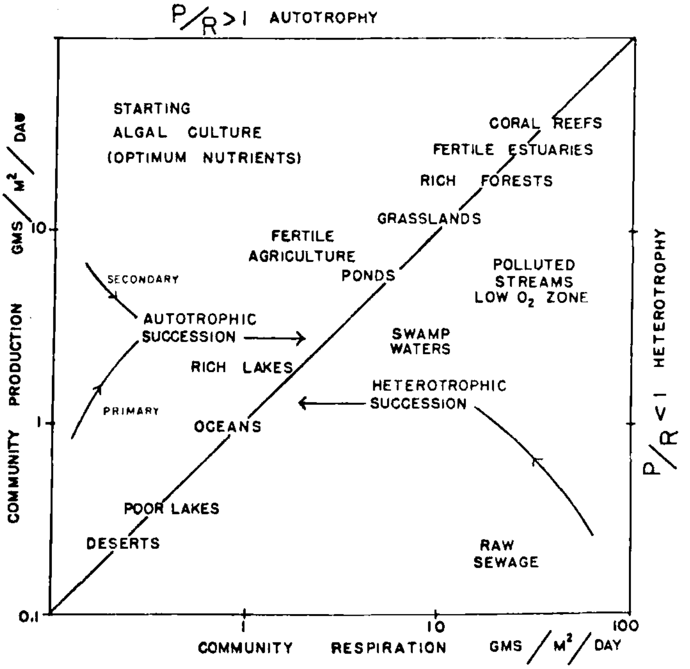

Fig. 4.18. Position of various community types in a classification based on community metabolism. Gross production (P) exceeds community respiration (R) on the left side of the diagonal line (P/R) greater than 1 (= autotrophy), while the reverse situation holds on the right (P/R) less than 1 (= heterotrophy). The latter communities import organic matter or live on previous storage or accumulation. The direction of autotrophic and heterotrophic succession is shown by the arrows. Over a year's average, communities along the diagonal line tend to consume about what they make and can be considered to be metabolic climaxes. (Redrawn from H.T. Odum, 1956).

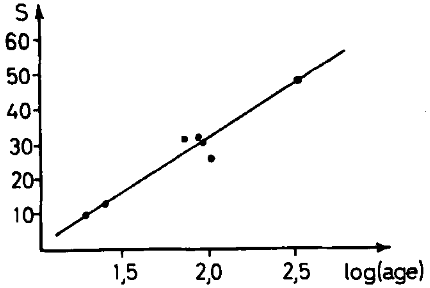

Fig. 4.19. Number of plant species, S, against log(age) in years in a pond. (Godwin, 1923).

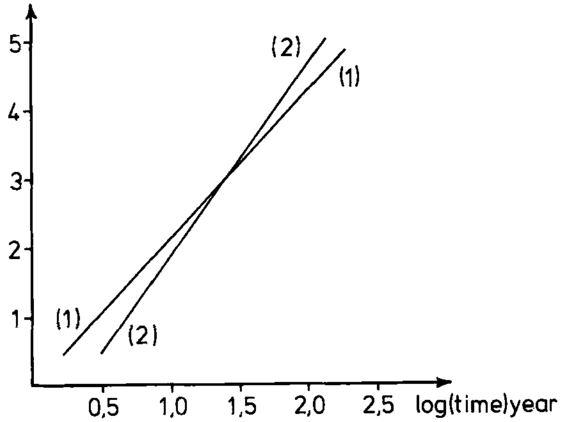

Fig. 4.20. Succession of bird community. (1) Number of pairs per ha or (2) number of species per 10 ha follow the same pattern, as shown on the figure. (Johnston and Odum, 1956).

Eutrophication of lakes is a good example, where th high nutrient concentration pushes the system back to a simpler system with high P/R ratio and little diversity. Such a system is better able to cope with the high nutrient concentration by high production, because more dissolved nutrient is removed from the water, (see also next paragraph, where the concept ecological buffering capacity is discussed - the high production in a eutropic lake acutally gives a better buffering capacity for changes in nutrient concentrations).

P.4.25. The structure of the ecosystem is changed in accordance

with changing environmental factors. (In ecological modelling often named forcing functions).

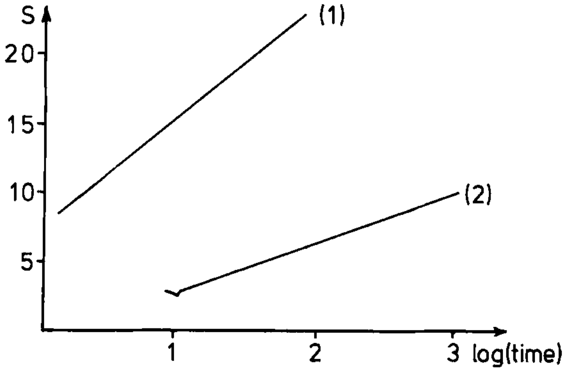

Fig. 4.21. Number of species (S) plotted against log(time) in years for (1) a plant community in Illinois, (2) in Idaho. In the midler climate (1) species are added more rapidly. (Bazzas, 1968 and Chadwick and Dalke, 1965, respectively).

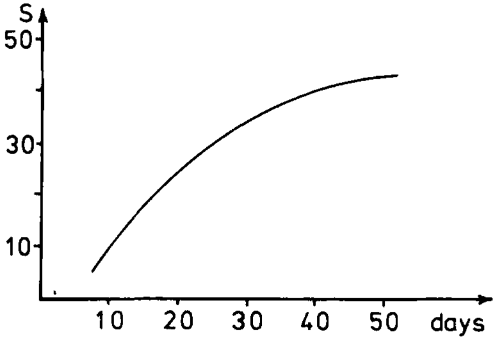

Fig 4.22. Number of protozoan species on spongy blocks suspended in a lake plotted against time (days).

In the eutrophic lake the nutrient concentration is high and consequently the ecosystem will change in structure to become one, which in the long term, can reduce the nutrient concentration. Recent studies on land sediment as well as theoretical considerations have indicated that lakes can and do progress to more oligotrophic conditions when the nutrient input ceases, see

Mackers (1065); Cowgill and Hutchinson (1964); Harrison (1962); Jørgensen (1976); Jørgensen and Mejer (1977), see also section 4.8.

Coevolution is a type of community evolution which occurs in ecosystem development.

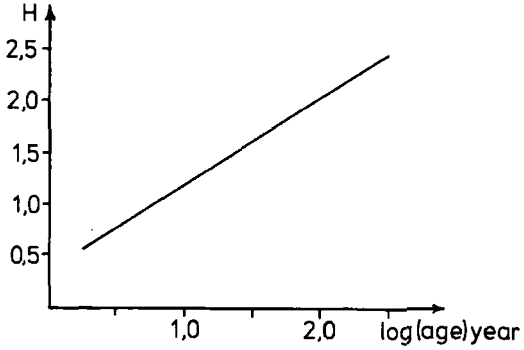

Fig. 4.23. H of bird community plotted against time. (Johnston and Odum, 1956).

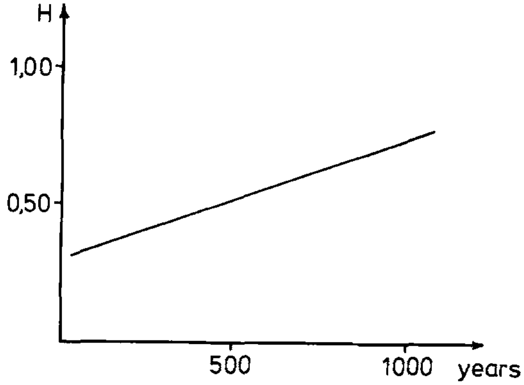

Fig. 4.24. Density based H of cladoceran community in Lago di Monterosi, Italy, against age in years. (Goulden, 1969).

P.4.26. Coevolution involves reciprocal selective interaction between two major groups or organisms with a close ecological relationship, such as plants and herbivores, or parasites and their hosts.

Ehrlich and Raven (1965) have outlined the theory of coevolution, which can be described by an example: Suppose a plant produces, through mutation or recombination, a chemical compound not directly related to those involved in its basic metabolism, by chance one or these compounds serves to reduce the palattability of the plants to herbivores. Such a plant is now better protected and will in a sense enter a new adaptive zone. Selection will now carry the line of the herbivores into a new adaptive zone, allowing them to diversify in the absence of competition with other herbivores. Thus, the diversity of plants may not only tend to augment the diversity of herbivores, but the converse may also be true. In other words the plant and the herbivores evolve together in the sense that the evolution of one is dependent on the evolution of the other. This is named coevolution.

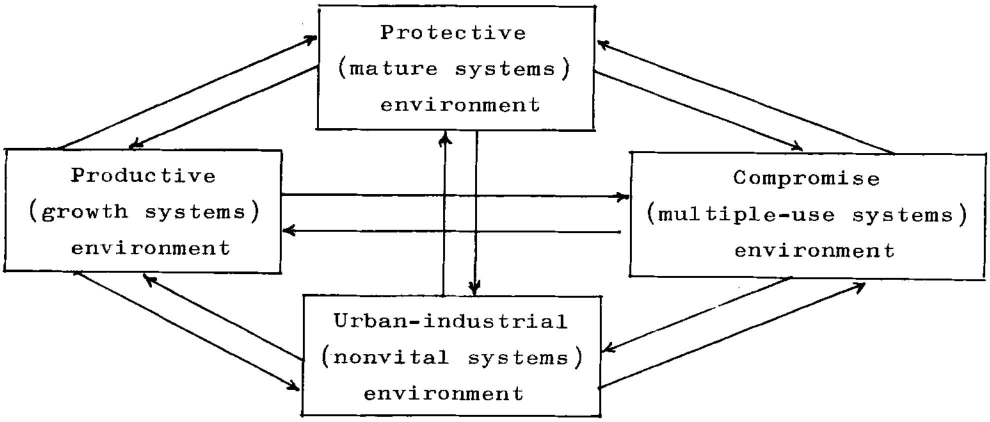

Fig. 4.25. Compartment model of the basic kinds of environment required by man, partitioned according to ecosystem development and life-cycle resource criteria. (After E.P. Odum, 1969)

There is apparently a *conflict between the strategies of man and nature*. The goal of agriculture and forestry is highest possible production, while nature attempts to achieve maximum support of a complex ecosystem structure, which implies thet P/R must be close to one and that net production is around zero. However, the problem is not that simple, since man is dependent not only on food, fibers and wood, but also on the oxygen concentration in the atmosphere, the climate buffer, and clean air and clean water for many uses. Until recently man has taken it for granted that nutrient cycling, water purification and other protective functions of self-maintaining ecosystems will work independently of environmental manipulaitons such as discharge of pollutants, or changes to ecological structures (forest to agriculture land). The most pleasant landscape to live in from an aesthetic point of view and the safest ecologically is one containing a variety of crops, forest, lakes etc. i.e. a **large pattern diversity.**

In other words it seems essential for man to plan the landscape with a large pattern of diversity, and which allows for exchange between different types of ecosystem. Odum (1969) has conceptualized these considerations in the construction of a compartment model of the basic kinds of environment required by man, see Fig. 4.25. Thus *the preservation of natural areas is not a luxury for society* but a capital investment of crucial importance for our civilization and our life on earth.

4.7. pH-BUFFERING CAPACITY IN ECOSYSTEMS.

The concept of buffering capacity is generally used in chemistry to express the ability of a solution to maintain its pH value.

Buffering capacity in this context is defined as:

$$\beta = \frac{dC}{dpH} \tag{4.19}$$

β = buffering capacity
C = added acid or base in moles H^+ resp. OH^- per l

As pH is one of the important factors determining life conditions directly or indirectly, it is *crucial for ecosystems to have a high pH-buffering capacity,* see Figs. 4.26 and 4.27, and Tables 4.11 - 4.12.

TABLE 4.11
Fish status for 1679 lakes in Southern Norway grouped according to pH

pH	No. of lakes in pH range	% of lakes with no fish	% of lakes with sparce populations	% of lakes with good populations
<4.5	111	73	25	2
4.5-4.7	245	53	41	6
4.7-5.0	375	38	41	21
5.0-5.5	353	25	40	35
5.5-6.0	164	8	36	56
>6.0	431	1	13	86

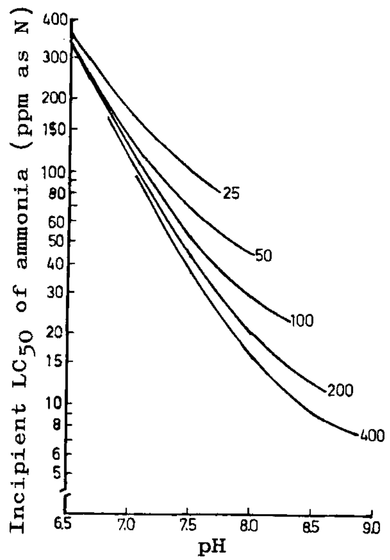

Fig. 4.26. LC$_{50}$ of ammonia for trouts versus pH at different HCO_3^- alkalinities.

P.4.27. **A low pH implies that hydrogen carbonate is coverted into free CO_2, which is toxic to fish and other animals as respiration is controlled by the difference between CO_2-concentration in the blood and the environment.**

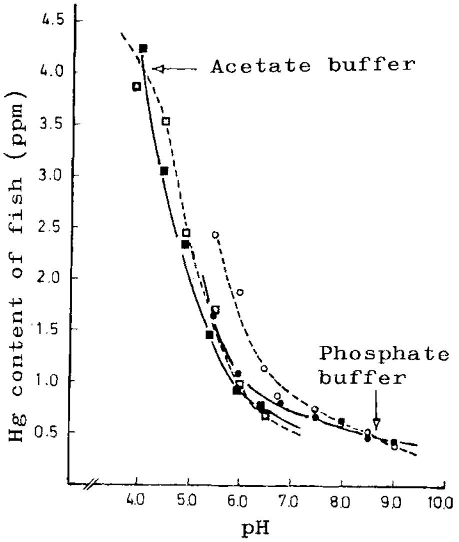

Fig. 4.27. Effect of pH on the mercury content of fish.
Emerald shinner □; Fathead minnows □; Emerald shinner o;
Fathead minnows o. Exposure to 1.5 ppm Hg from $HgCl_2$ solutions.

TABLE 4.12
Effects of pH values on fish (Alabaster and Lloyd, 1980)

pH-range	Effect
3.0 - 3.5	Unlikely that any fish can survive more than a few hours
3.5 - 4.0	Lethal to salmonoids. Some other fish species might survive in this range, presumably after a period of acclimation to slightly higher pH
4.0 - 4.5	Harmful to salmonoids, bream, goldfish and carp, although the resistance to this pH increases with the size and age
4.5 - 5.0	Likely to be harmful to eggs and fry of salmonoids. Harmful also to adult salmonoids and carp at low calcium, sodium and/or chloride concentration
5.0 - 6.0	Unlikely to be harmful, unless concentration of free CO_2 is greater than 20 mg l^{-1} or the water contains freshly precipitated $Fe(OH)_3$
6.0 - 6.5	Harmless unless concentration of free CO_2 > 100 mg l^{-1}

The processes involved can be described by the following chemical equations:

$$CO_3^{2-} \xrightarrow{+H^+} HCO_3^- \xrightarrow{+H^+} H_2O + CO_2 \qquad (4.20)$$

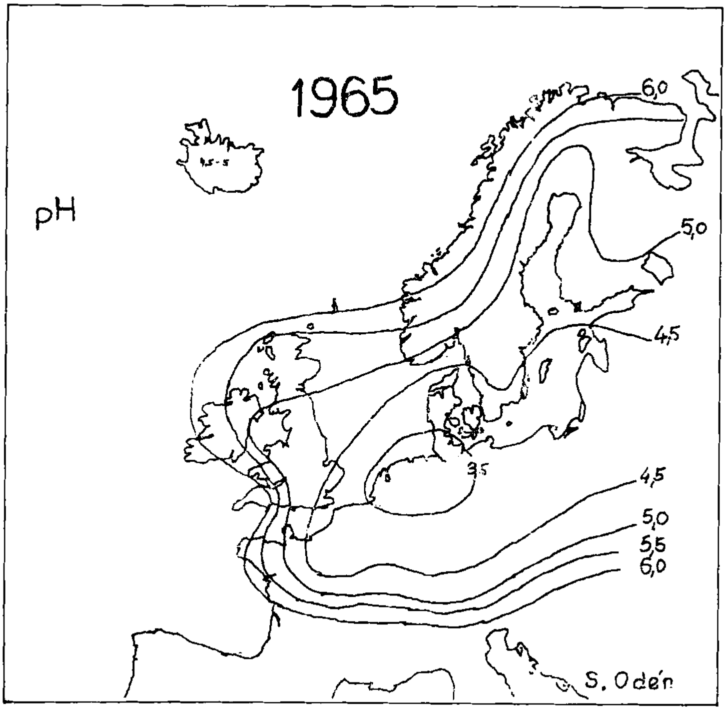

Fig. 4.28. pH is lowest close to industrial areas.

A lowered pH will affect the entire ecosystem and the ecological balance. Three serious environmental problems will be mentioned below to illustrate the importance of pH as an environmental factor, and consequently of a high pH-buffering capacity in ecosystems:

1. The acidification of lakes caused by SO_2-pollution.
2. The effect of decreased pH on soil and plants.
3. The possibility of maintaining the pH in the oceans in spite of the increased uptake of CO_2.

1. Continuous acidification has been observed in many lakes in parts of North America and Scandinavia. The geographical position (see Fig. 4.28) and the inflow conditions of these lakes suggest that the increase in acidity is the result of deposition of an air-borne substance that lead to the formation of acid, such as SO_2. This deposition is, of course, not restricted to lakes, but also affects soil, forests, etc. (see point **2** below).

Affected areas are characterized by a low pH-buffering capacity. Surface water in these areas is soft and has a low conductivity. The buffering capacity of surface water is mainly related to hydrogen carbonate ions, which are present in small concentrations in lakes. These ions are able to take up hydrogen ions in accordance with the following process:

$$HCO_3^- + H^+ \text{ — } H_2O + CO_2 \,| \qquad (4.21)$$

During the combustion of sulphurous fuels, sulphur is primarily converted to SO_2 (97-98%), but 2-3% is oxidized to SO_3, which reacts with water to form sulphuric acid:

$$SO_3 + H_2O \text{ — } H_2SO_4 \qquad (4.22)$$

The SO_2 on the other hand when released into the atmosphere comes into contact with very small particles covered by an aqueous film or with water droplets, and forms H_2SO_3, a medium strong acid:

$$H_2SO_3 \text{ — } H^+ + HSO_3^- \qquad (4.23)$$

Under the influence of iron compounds acting as catalysts, HSO_3^- and SO_3^{2-} are rapidly oxidized to sulphuric acid (Brosset, 1973).

The geographical distribution of acids in precipitation over Europe as a consequence of these processes is shown in Fig. 4.28. Values are expressed as annual mean pH. Together with the increased combustion of fossil fuels, the observed pH values in precipitation have decreased with the time, see Fig. 4.29. Fig 4.30 shows the total SO_2-emission in Europe plotted against the time.

Similar trends have been observed in many North American and Scandinavian lakes and even some of the great lakes of Europe have been affected by this acidification process, as shown in Table 4.13. In smaller lakes, where precipitation forms a greater portion of lake volume, pH values as low as 4.0 have been observed. The effect of low pH on the fish population can be seen in Table 4.14, which is based on an examination carried out by Jensen and Snekvik (1972).

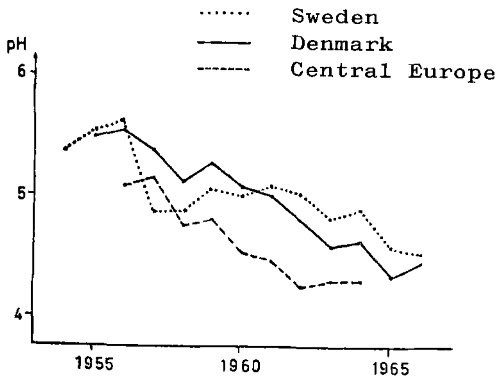

Fig. 4.29. pH in rainwater against year.

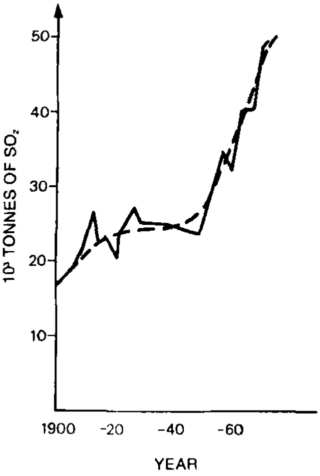

Fig. 4.30. Emissions of sulphur dioxide from the combustion of fossil fuels in Europe.

Two other observed effects are illustrated in Table 4.15 and in Fig. 4.31, where it is shown that

P.4.28. the number of fish and zooplankton species is decreasing in acidified lakes.

TABLE 4.13

Acidification of soft-water lakes in Scandinavia and North America

Region	No. of lakes	pH Early measurements	pH Recent measurements	Average change ΔpH/year
Scandinavia				
Central Norway	10	7.3 ± 0.8 (1941)	5.8 ± 0.7 (1975)	-0.05
Westcoast of Sweden	6	6.6 ± 0.2 (1933-35)	5.4 ± 0.8 (1971)	-0.03
	8	6.8 ± 0.2 (1942-49)	5.6 ± 0.9 (1971)	-0.04
West central Sweden	5	6.3 ± 0.3 (1937-48)	4.7 ± 0.2 (1973)	-0.06
South central Sweden	5	6.2 ± 0.2 (1933-48)	5.5 ± 0.7 (1973)	-0.03
Southernmost Sweden	51	6.76 ± 0.14 (1935)	6.23 ± 0.44 (1971)	-0.015
North America				
La Cloche Mtns.	7	6.3 ± 0.7 (1961)	4.9 ± 0.5 (1972-73)	-0.06
Ontario	8	5.0 ± 0.7 (1969)	4.8 ± 0.5 (1972-73)	-0.05
North of La Cloche	7	6.6 ± 0.8 (1961)	5.9 ± 0.7 (1971)	-0.07
Mtns. Ontario	19	6.7 ± 0.8 (1968)	6.4 ± 0.8 (1971)	-0.10
Adirondack Mtns.				
New York	8	6.5 ± 0.6 (1930-38)	4.8 ± 0.2 (1969-75)	-0.05

TABLE 4.14

Trout population and pH in 260 lakes

		pH							
No. of		4.00-4.50		4.51-5.00		5.01-5.50		≥5.51	
lakes	Population	No.	%	No.	%	No.	%	No.	%
33	Empty	3	9.1	17	51.5	7	21.2	6	18.2
87	Sparse population	2	2.3	15	17.2	21.2	24.1	49	56.3
82	Good population	-	-	9	11.0	14	17.1	59	72.0
58	Over-populated	-	-	3	5.2	13	22.4	42	72.3
260	total	5	1.9	44	16.9	55	21.2	156	60.0

The decreasing pH has a striking effect on the fish population. At extremely low pH values all yong fish disappear completely (Almer, 1972). Nevertheless, spawning and fertilized eggs have been observed even at low pH values, so **it seems that the development of eggs may be disturbed by high activity of hydrogen ions in aquatic environments.**

This is illustrated in Fig. 4.32, where percentage of hatched eggs is plotted against pH value. The period from fertilization to hatching also tends to be prolonged at low pH values, as shown in Fig 4.33.

TABLE 4.15
Occurrence of fish species before acidification and species found during the 1973

Lake	Species earlier forming permanent stocks	Species found 1973	Species reproducing 1973
Bredvatten	Pe Pi E	(E)	
Lysevatten	Pe Pi R E	Pe (E)	Pe
Gårdsjön	Pe Pi R T C E	Pe Pi E	Pe
Örvattnet	Pe St M	Pe	Pe
Stensjön	Pe Pi R St M	Pe Pi R	Pe Pi
Skitjärn	Pe Pi R L	Pe Pi R L	Pe Pi

Pe=perch (Perca fluviatilis, Pi=pike (Esox lucius), E=eel (Anguilla vulgaris), R=roach (Leuciscus rutilus), T=tench (Tinca tinca), C=Crucian carp (Carassius carassius), St=Brown trout (Salmo trutta), L=Lake whitefish (Coregonus albula), M=Minnow (Phoxinus phoxinus).

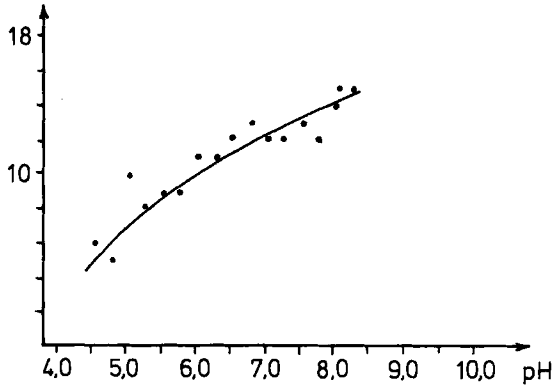

Fig. 4.31. Number of zooplankton species in Swedish Lakes according to pH. From a comprehensive examination of 84 lakes in Sweden.

Further to the primary biological effects of a continuous supply of acid substances on individuals and populations in a lake, more profound long-term changes, that force the lake into an increasingly more oligotrophic state, also take place, as suggested by Grahn et al. (1974). pH generally increases with eutrophication due to uptake (removal) of hydrogen carbonate ions and carbon dioxide by photosynthesis. This is demonstrated in Fig. 2.11, which demonstrates the seasonal pH-variations in an hypereutrophic lake.

P.4.29. **In an acidified lake the phytoplankton concentration will decrease, and so will the uptake of CO_2 and HCO_3^-, and the transparency of the water will increase.** (see Fig. 4.34)

P.4.30. **The biological pH-buffering capacity is reduced by this process and by means of this feedback mechanism the process of acidification is further accelerated.**

Finally, it should be mentioned that

P.4.31. **the concentration of free metal ions will increase with decreasing pH due to release of methal ions from sediment and their higher solubility and lower tendency to form complexes at lower pH.**

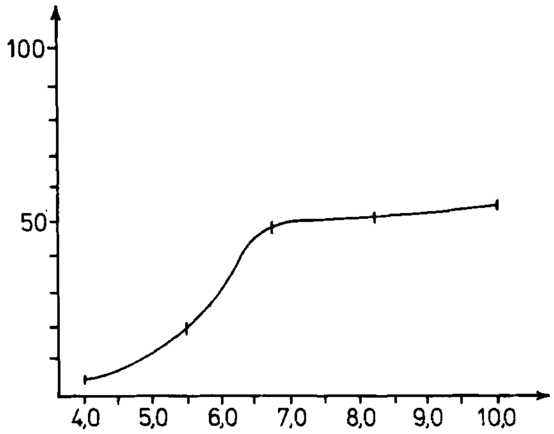

Fig. 4.32. % eggs hatched according to pH. Total number of eggs reared 253-274 by Brachydanio rerio Ham.-Buch.

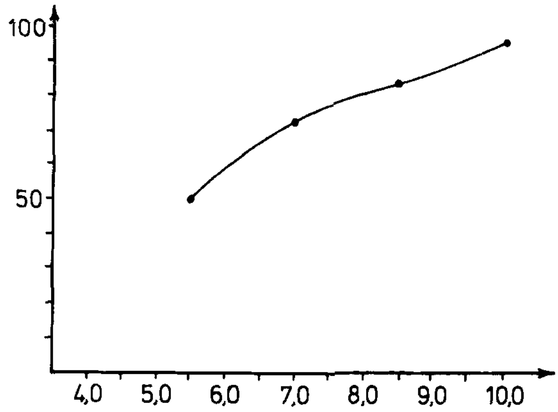

Fig. 4.33. Eggs hatched during the first 96 h after fertilization as % of total number of hatched eggs according to pH. Conditions, see Fig. 4.28.

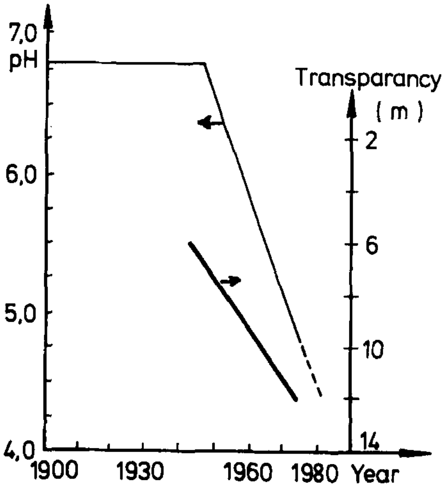

Fig. 4.34. pH and transparency of Lake Stora Skarsjön plotted against time.

In Sweden the addition of calcium hydroxide is widely used to rivers and lakes to reduce the damage of low pH. Hundred of millions of Swedish Krona are spent every year on increasing the pH of natural waters. This amount should be compared with the billions of dollars it would cost to reduce the sulphur content of fossil fuel to an acceptable level in Nortwest Europe.

TABLE 4.16.
[HA] and [A⁻] at various pH-values

pH	log [HA]	log [A⁻]
<< pK_a	log C	pH - pK_a + log C
>> pK_a	-pH + pK_a + log C	log C
= pK_a	log C/2 = log C-0.3	log C/2 = log C-0.3

2. Decreased pH values in the lithosphere also cause an overall deterioration in the environment.

P.4.32. The leaching of nutrients from soil is increased at lower pH.

as demonstrated for calcium ions in Fig. 4.35.

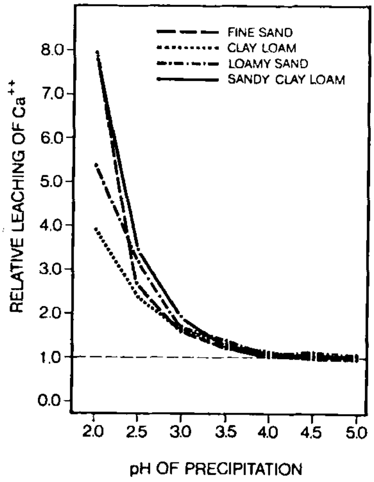

Fig. 4.35. Leaching of calcium in forest soil exposed to precipitation adjusted to pH values from 2.0 to 5.0 during a period of 40 days. The Ca leaching in the control (distilled water) is set at 1.0. Precipitation: 500 mm/month.

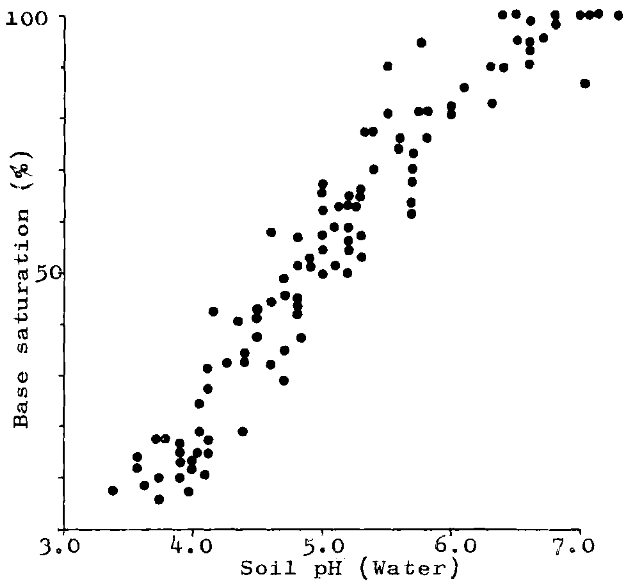

Fig. 4.36. The relationship between pH and base saturation illustrated in samples from the organic surface layer of Swedish soils. Base saturation determined through extraction with 1-N acetic acid and 1-N ammonium acetate (Brown's method), pH in water extracts (1:1). In both cases dried samples have been used.

P.4.33. The ability of the soil to bind ions is decreased at lower pH.

as illustrated in Fig. 4.36. Here the so-called CEC (Cation Exchange Capacity) is plotted against the pH value.

The leaching of ions from soil produces a change in the chemical composition of surface waters, which is illustrated in Fig. 4.37.

Further to these observations:

P.4.34. SO_2 has a direct effect on the degradation of plant pigments, and detritus is decomposed at reduced rate at lower pH,

as seen from Fig. 4.38, where the enzymatic decomposition of celulose is plotted as a function of pH. Plant growth is furthermore dependent on pH, as illustrated in Fig. 4.39. What effect the ever-decreasing pH in the soil of Scandinavia will have on the forestry, on which so many people are dependent is a worrying problem.

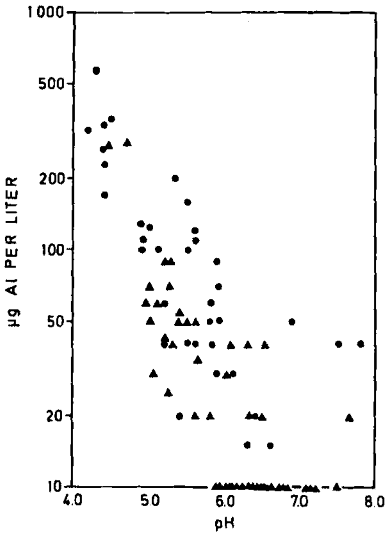

Fig. 4.37. Aluminium concentration in clear water lakes in Sweden (circles) and in Norway (triangles, unpublished data). Values plotted as 10 µg/l are below the analytical detection limit.

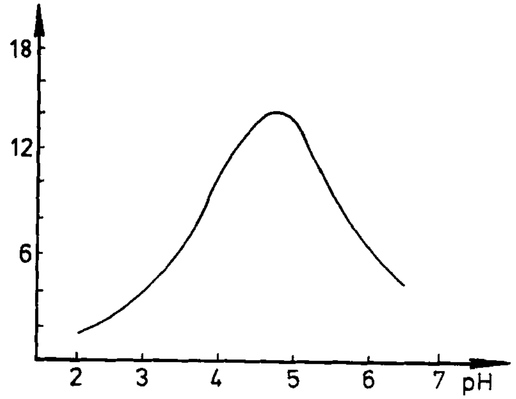

Fig. 4.38. Relative decomposition rate of cellulose plotted against pH.

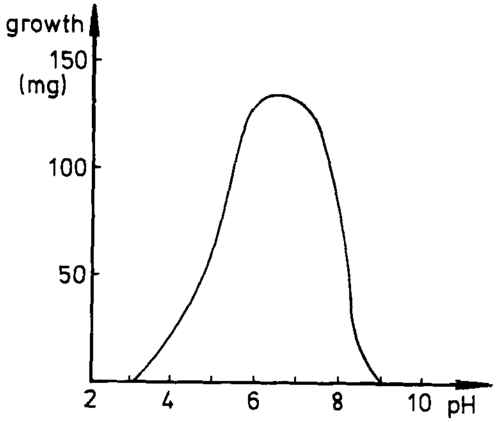

Fig. 4.39. Growth of a fungus Merasmius graminum as a function of pH.

3. Seawater contains several proteolytic species, including hydrogen carbonate (about 2.4 mM), borate (about 0.43 mM), phosphate (about 0.0023 mM), silicate and fluoride in various stage of protonation (=uptake of hydrogen ions).

The concentrations of proteolytic species are characterized by the total alkalinity A, and pH. The total alkalinity is determined by adding an excess of a standard acid (e.g. 0.1 M), boiling off the carbon dioxide formed and titrating back to a pH of 6. During this process all the carbonate and hydrogen carbonate are converted to carbon dioxide and expelled and all the borate is converted to boric acid. The amount of acid used (i.e. the acid added minus the base used for back titration) then corresponds to the alkalinity, Al, and the following equation is valid:

$$Al = C_{H_2BO_3^-} + 2C_{CO_3^{2-}} + C_{BO_3^-} + (C_{OH^-}\ C_{H^+}) \qquad (4.24)$$

where C = the concentration in moles per litre for the indicated species.

In other words the alkalinity is the concentration of hydrogen ions that can be taken up by proteolytic species present in the sample examined.

Obviously, the higher the alkalinity, the better the solution is able to maintain a given pH value if acid is added. The buffering capacity and the alkalinity are proportional (see e.g. Stumm and Morgan, 1970).

Each of the proteolytic species in an aquatic system has an equilibrium constant. If we conseder the acid HA and the dissociation process:

$$HA \rightarrow H^+ + A^- \qquad (4.25)$$

we have

$$K_a = \frac{[H^+]\,[A^-]}{[HA]} \qquad (4.26)$$

where K_a = the equilibrium constant.

It is possible, when the composition of the aquatic system is known, to calculate both the alkalinity and the buffering capacity, using the expression for the quilibrium constants. However, these expressions are more conveniently used in logarithmic form. If we consider the expression for K_a for a weak acid, the general expression (4.24), may be used in a logarithmic form:

$$pH = pK_a + \log\frac{[A^-]}{[HA]} = pK_a + \log[A^-] - \log[HA] \qquad (4.27)$$

multiplying both sides of the equation with -1 and using the symbol p for -log and pH for -log H^+.

It is often convenient to plot concentrations of HA and A^- versus pH in a logarithmic diagram. If C denotes the total concentrations $C=[HA]+[A^-]$, we have at low pH:

$$[HA] \approx C \qquad (4.28)$$

$$\log[A^-] = pH - pK_a + \log C \qquad (4.29)$$

This means that $\log[A^-]$ increases linearly with increasing pH, the slope being +1. The line goes through ($\log C$, pK_a) as $pH=pK_a$ gives $\log[A^-] = \log C$, see equation (4.29).
Correspondingly, at high pH, $[A^-] = C$ and

$$\log[HA] = pK_a - pH + \log C \qquad (4.30)$$

which implies that $\log[HA]$ decreases with increasing pH, the slope being -1. This line also goes through ($\log C$, pK_a).

At $pH = pK_a$, $[A^-] = [HA] = C/2$ or $\log[A^-] = \log[HA] = \log C - 0.3$

Table 4.16 and Fig. 4.40 show the result of these considerations for a single acid-base system.

Note that for H_2A the slope will be -2 at $pH>pK_2$, corresponding to the dissociation of $2H^+$:

H_2A — $2H^+ + A^{2-}$ and for A^{2-} the slope will be +2 at pH<pK. This is demonstrated in Fig. 4.41.

ß, the buffer capacity, is defined (4.19).
It can now be shown that

$$\log\left(\frac{\beta}{2.3}\right) = \log\left([H_3O^+] + [OH^-] + \Sigma\frac{[A^-]\,[HA]}{C}\right) \qquad (4.31)$$

At log pH [HA] = C, and only $[H_3O^+]$ plays a role.

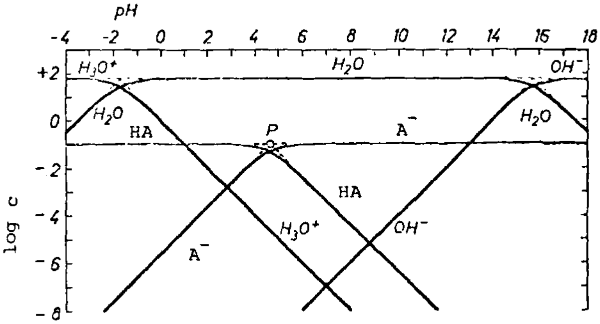

Fig. 4.40. H_3O^+, OH^- and water + HA/A^-. $pK_a = 4.64$ and C = 0.1 M.

At higher pH, also $\frac{[A^-]\,[HA]}{C} = [A^-]$ contributes to $\frac{\beta}{2.3}$

where $[H_3O] = [A^-]$, $\log\left(\frac{\beta}{2.3}\right) = \log\left(2\,[H_3O^+]\right) = -pH + 0.3 = \log\left(2\,[A^-]\right)$.

At still higher pH, but with values of $pH<pK_a$, log $[A^-]$ dominates.

At pH = pK_a $\log \frac{\beta}{2.3} = \log \frac{\frac{C}{2}\,\frac{C}{2}}{C} = \log \frac{C}{4} = \log C - 0.6$

At pH>pK_a, $[A^-] = C$ and $\log [HA]$ contributes the most to $\frac{\beta}{2.3}$

At very high pH, $\log [OH^-]$ will dominate. These considerations are used in the construction of Fig. 4.43.

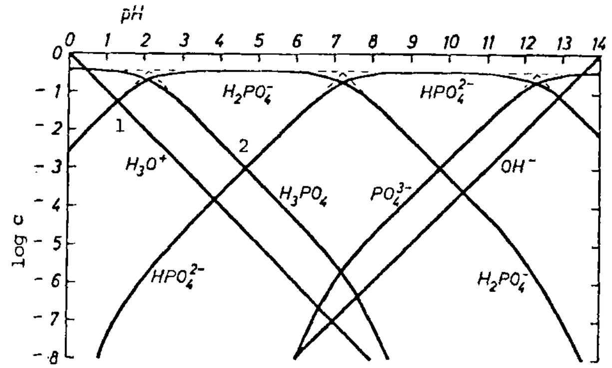

Fig. 4.41. pH-log c diagram for phosphoric acid.

Fig. 4.42 is a double logarithmic diagram for seawater. The proteolytic species mentioned above are represented in their appropriate concentrations. The important species are hydrogen and hydroxide ions, boric acid (HB) and carbonate ions (C^{2-}). The arrow in the diagram indicates the pH value of seawater - about 8.1.

Based on such a diagram it is possible to set up another diagram, representing the buffering capacity as a function of pH, see Fig. 4.43. For those who are interested in the relationship between the two diagrams, see Hägg (1979).

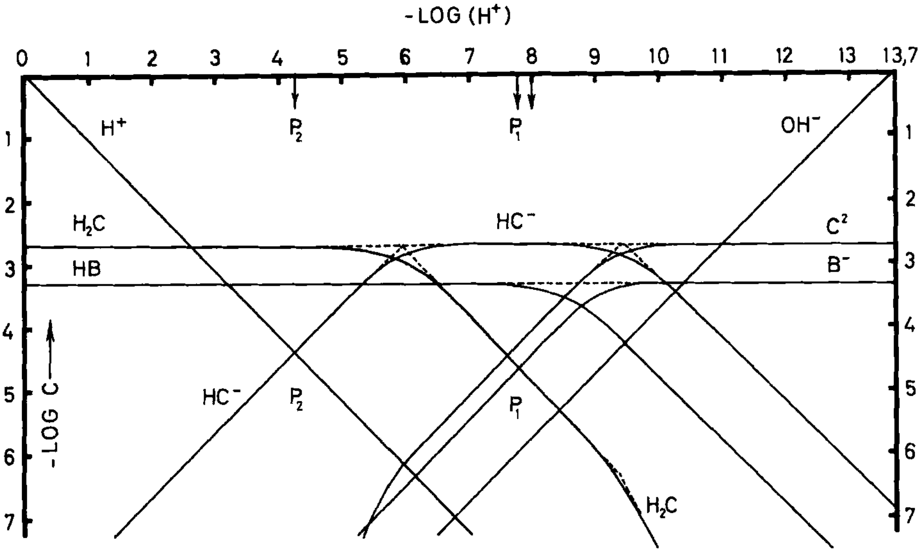

Fig. 4.42. pH-diagram. $H_2C = H_2CO_3$, $HC^- = HCO_3^-$, $C^2 = CO_3^{2-}$, $B^- = \text{borate}$. pH of the sea is indicated by an arrow.

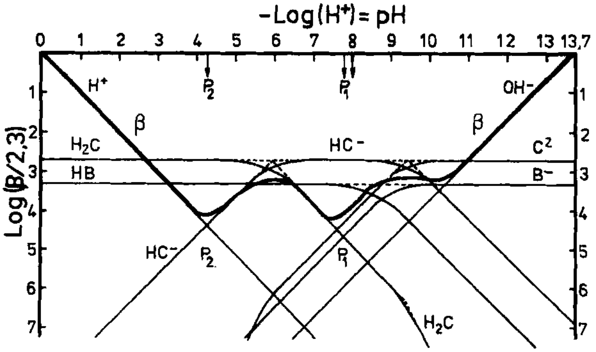

Fig. 4.43. Buffering capacity of the sea as a function of pH (ß).

From Fig. 4.43 we can conclude *that the buffering capacity of seawater is very limited. About 3 mM of strong acid will change the pH from 8 to 3.*

However, the pH of the entire ocean is remarkably resistant to change in pH caused by the addition of naturally occurring acids and bases, while the limited buffering capacity of an isolated litre of seawater accords with diagram 4.37. Sillen (1961) has suggested an explanation for the observed buffering capacity of the sea. A pH-dependent ion exchange equilibrium between solution and aluminosilicates (clay minerals), suspended in the sea is the main buffering system in oceans.

This buffering system may be represented by the following simplified equation:

$$3Al_2Si_2O_5(OH)_2 + 4SiO_2 + 2K^+ + 2Ca^{2+} + 12H_2O \text{ — } 2KCaAl_3Si_5O_{16}(H_2O)_6 + 6H^+ \qquad (4.32)$$

The pH-dependence is indicated by the corresponding equilibrium expression in logarithmic form:

$$\log K = 6 \log(H^+) - 2 \log K^+ - 2 \log Ca^{2+} \qquad (4.33)$$

Sillen (1961) **estimated the buffering capacity of these silicates to be about 1 mole per litre or approximately 2000 times the buffering capacity of carbonates.** However, as pointed out by Pytkowitcz (1967), the buffering capacity of aluminosilicates has a much larger time scale than the buffering capacity based on the carbonate system.

P.4.36. In conclusion it seems that radical changes in the pH value of the oceans should not be expected as a result of increased combustion of fossil fuel, although the effect is cumulative.

However, the regional effects of combustion of fossil fuel on pH, due to deposition of sulphuric acid, is a very severe environmental problem. Its solution lies in either drastic reduction in the combustion of fossil fuel or a corresponding reduction in the sulphurous content of the fossil fuel.

At present the pH values of lakes situated in districts where water has little buffering capacity are steadily decreasing and the only available remedy is the addition of calcium hydroxide to surface water. This will, however, change the chemical composition of the aquatic ecosystem in the entire region, which again will involve ecological changes. So, **the only real remedy is to reduce the emission of sulphurous compounds to an environmentally acceptable level.**

4.8. OTHER BUFFERING EFFECTS IN ECOSYSTEMS.

The ecologist working with environmental probelms is concerned with the response of the system to changed external factors. Fig. 4.44 shows the response of Lake Fure to increased phosphorus loading. During the period 1945-1973 increased loading was almost proportional to time, but as can be seen the concentration of phosphorus in the water remained almost unchanged for the first two decades, mainly because the added phosphorus was stored in the sediment by the following chain of processes:

Soluble P in water — uptake by algae — settling — P in sediment

Although some of the phosphorus in sediment was released to the water, a substantial part was stored in the sediment.

P.4.37. An ecosystem is able to minimize changes caused by external sources.
However, this buffering capacity is finite and once the capacity is used, the changes become more pronounced.

The course of the response then parallels the change in pH, caused by the addition of acids or alkalies (see 4.7).

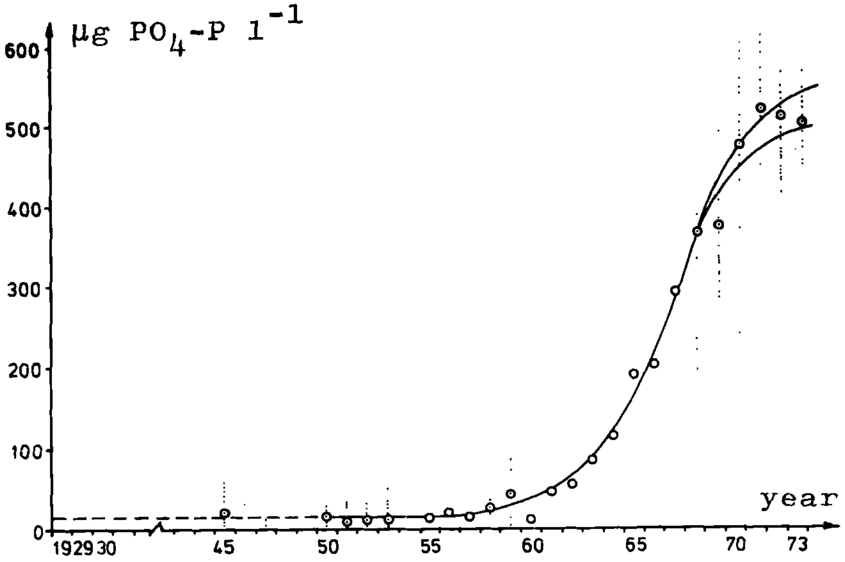

Fig. 4.44. The phosphorus concentration in Lake Fure plotted against time (years). During the period considered the phosphorus loading is increased.

It is of course extremely important to recognize the response of ecosystems to changes in external factors, such as increased discharge of pollution. As seen, throughout this book

P.4.38. the response is very rarely proportional to the external factor.

If such an assumption is used the prediction of ecosystem responses would be completely wrong in most cases and too high an environmental impact might be tolerated. If, for example, the observed response to increased phosphorus loading was used for Lake Fure in the period 1950-1956 (see Fig. 4.44) removal of phosphorus from the waste water would not have been required, as it is today, Of course the entire problem of lake management is much more complicated than that expressed in Fig. 4.44 (see Jørgensen, 1980), as many different processes are involved. But these observations demonstrate the non-linear response of ecosystems, which can be explained by the concept of buffering capacity.

Generally, the concept of **ecological buffering capacity** can be defined as:

$$\beta = \frac{d(\text{external variable})}{d(\text{internal variable})} \qquad (4.34)$$

where

external variable $\sim$ external factors $\sim$ forcing functions

internal variable $\sim$ state variable

The ecological buffering capacity is the reciprocal sensitivity of the considered state variable (see, e.g. Halfon, 1976):

$$\text{sensitivity of state variable} = \frac{d(\text{state variable})}{d(\text{external factor})} \qquad (4.35)$$

As it is not possible to measure differential coefficients, the ecological buffering capacity is found as (Jørgensen et al., 1977):

$$\beta = \frac{\Delta\text{external variable}}{\Delta\text{internal variable}} \qquad (4.36)$$

An ecosystem has almost an infinite number of buffering capacities. The buffering capacity related to the changes in soluble phosphorus caused by increased discharge of phosphorus can be defined as:

$$\beta_P = \frac{\Delta P\text{-loading}}{\Delta P\text{-soluble}} = \frac{\Delta P\text{-total}}{\Delta P\text{-soluble}} \qquad (4.37)$$

The change in the total phosphorus concentration is measured by the increased discharge of phosphorus, since the law of mass conservation states that phosphorus (mainly soluble phosphorus) put into the lake must be present in one form or another. But due to the buffering capacity, or rather the many processes in which phosphorus takes part, the soluble phosphorus in the lake will increase less than would be expected from its input, because the system will minimize the direct effect of an increased input of soluble phosphorus.

A similarly definition can be applied to the buffering capacity in response to chaged temperature. As it is difficult to compare changes in temperature with changes in concentrations of phytoplankton and zooplankton (or with other words the ecological buffer capacity should have no unit) it seems more reasonable in this case to use a related expression:

$$\beta_{T\text{-rel}} = \frac{\Delta\text{Temp} * \text{Phyt}}{\text{Temp} * \Delta\text{Phyt}} \qquad (4.38)$$

where
Temp = temperature
Phyt = phytoplankton concentration

The concept of ecological buffering capacity has been examined by Jørgensen et al. (1979) using ecological models. They set up the following hypothesis:

The ecosystem will respond to changes in external factors, such as nutrient input, climatic changes of temperature and irradiance, etc, by developing a structure with the best possible ability to meet perturbations. It can be shown that an ecosystem with little diversity (only a lake has been considered) has a better buffering capacity at a high nutrient input that a more complex ecosystem, which explains why many eutrophic lakes have low diversity. They also found that complex ecosystems have a very high buffering capacity for temperature changes and that species with a temperature dependence better suited to a new temperature pattern contributed more to the buffering capacity than species "ill" suited to the temperature pattern.

It seems, from these consideration, that ecosystems not only have a buffering capacity, which minimizes changes in the system caused by external factors, but also have the ability to change their structure in such a way that the highest possible buffering capacity is available for actual changes in external factors.

However, like buffering capacity, the ecosystem's ability to adapt its structure to a new situation is also finite. Drastic changes in an ecosystem cannot be tolerated under any circumstances, as we consider a simplification of an ecosystem (in terms of reduced diversity) to be an ecological deterioration. The buffering capacity may be increased for nutrient input or input of other pollutants by decreasing the complexity of the ecosystem, but the buffering capacity for temperature or other climatic variations is decreased simultaneously, which makes the ecosystem more susceptible to natural variations in external factors.

In Table 4.17 is listed some ecosystem reactions to changes in external factors, which can be interpreted by use of the ecological buffer capacity.

TABLE 4.17
Ecosystem reactions and ecological buffer capacities

Change in external variable	Ecosystem reactions	Increased buffer capacity
P-loading increased	Lower diversity. Species with lower specific surface, and thereby slower nutrient uptake	β_P
Temperature	Species with other temperature. Optimum take over	$\beta_{T\text{-rel}}$
Increased conc. of toxic substances	Some species become extinguished. Less suspectible species become more dominant	$\beta_{TOX} = \frac{\Delta\text{toxic subst.}}{\Delta\text{biomass}}$
Increased BOD_5	Some species become extinguished. Species less suspectible to low oxygen conc. become more dominant	$\beta_{BOD} = \frac{\Delta\text{BOD}}{\Delta\text{biomass}}$

4.9. THE ECOSPHERE.

The ecosystems, which constitute the ecosphere, can be classified according to their physical-chemical-biological characteristics.

Each type of ecosystem has its own characteristic habitat, which to a certain extent defines the environmental problems it experiences.

TABLE 4.18
Ecosystems

A. Aquatic Ecosystems		
FRESHWATER		
	Lotic	Rivers and streams: flow characteristic, (BOD$_5$/O$_2$-balance of importance) Rapids: ≥ 0.5 msec^{-1}, bottom particles ≥ 5 mm ≤ 0.5 msec^{-1}, bottom particles ≤ 5 mm Pools: very slow streams
	Lentic	Lakes and ponds: slow water renewal, (eutrophication ond acidification) Deep lakes Shallow lakes Ponds: shallow enough for sunlight to reach the bottom everywhere
MARINE		
	Littoral	Shoreline: reduced circulation (all types of aquatic pollution) Rocky Sand
	Neritic	Continental shelt: oil-pollution
	Upwellings	(Eutrophication)
	Coral reef	
	Pelagic	Open sea (oil pollution) Epipelagic Mesopelagic Bathypelagic Abyssal
B. Terrestrial Ecosystems		
	Desert	Annual rainfall ≤ 25 cm. Water shortage. Hot Cold
	Tundra	Long, cold harsh winter and short, cool summer. Treeless from forest limit to the ice caps or glaciers. Low diversity. Arctic Alpine
	Prairie	Grassland, now widely cultivated. Rainfall 40-100 cm year^{-1} Moist Dry
	Savannah	Trees scattered within a grassland matrix. Rainfall 50-150 cm year^{-1}. 5-20°N or S. High diversity. (Maintenance of ecological balance and a high natural diversity)
	Forest	Coniferous: Dominated by needle-leaved trees. Man's source of wood. (Deforestration) Deciduous: Warm summers, cold to cool winters. Broadleaves species. 60-150 cm yr^{-1} precipitation

	Tropical: 20°S-20°N. High rainfall. Very high diversity. Mean annual temperature ~ 25°C
<u>Bogs</u>	Have cushionlike growths of small plants, accumulation of peats. North America, Northern Europe. Include raised bogs or high moors
<u>Marshes</u>	Dominated by grasses, sedges, bulrushes, catstails etc. Warmer climate
<u>Swamps</u>	Are wooded. Higher diversity than marshes

TABLE 4.19

A. Primary productivity, net production and plant biomass of large biomes (expressed in tonnes of dry organic matter) (from Lieth & Whittaker, 1975)

		Net primary productivity ($g\ m^{-2}\ yr^{-1}$)		Net production worldwide ($10^9 t\ yr^{-1}$)	Biomass per unit area ($t\ ha^{-1}$)		Total biomass worldwide ($10^9 t$)
Ecosystem type	Area ($10^6\ km^2$)	Normal range	Mean		Normal range	Mean	
Tropical rain forest	17.0	1000-3500	2200	37.4	60-800	450	765
Tropical seasonal forest	7.5	1000-2500	1600	12.0	60-600	350	260
Temperate evergreen forest	5.0	600-2500	1300	6.5	60-2000	350	175
Temperate deciduous forest	7.0	600-2500	1200	8.4	60-600	300	210
Boreal forest (taiga)	12.0	400-2000	800	9.6	60-400	200	240
Woodland and shrubland	8.5	250-1200	700	6.0	20-200	60	50
Savanna	15.0	200-2000	900	13.5	2-150	40	60
Temperate grassland	9.0	200-1500	600	5.4	2-50	16	14
Tundra	8.0	10-400	140	1.1	1-30	6	5
Desert and semi-desert scrub	18.0	10-250	90	1.6	1-40	7	13
Extreme desert (sand), polar regions	24.0	0-10	3	0.07	0-2	0.2	0.5
Cultivated land	14.0	100-3500	650	9.1	4-120	10	14
Swamp and marsh	2.0	800-3500	2000	4.1	30-500	150	30
Lake and stream	2.0	100-1500	250	0.5	0-1	0.2	0.05
Total continental	*149.0*		*773*	*115.0*		*123*	*1837*
Open ocean	332.0	2-400	125	41.5	0.01-0.05	0.03	1.0
Upwelling zones	0.4	400-1000	500	0.2	0.5-10	2.0	0.008
Continental shelf	26.6	200-600	360	9.6	0.1-4.0	1.0	0.27
Algal bed and corel reef	0.6	500-4000	2500	1.6	0.4-40	20	1.2
Estuaries	1.4	200-3500	1500	2.1	0.1-60	10	1.4
Total marine	*361.0*		*152*	*55.0*		*0.1*	*3.9*
Full total	*510.0*		*333*	*170.0*		*36*	*1841*

TABLE 4.19

B. Secondary production and productivity in the biosphere (from Lieth & Whittaker, 1975)

Ecosystem type	Leaf-surface area (10^6 km^2)	Biomass of litter (10^9t)	Animal consumption (10^9t/yr)	Secondary production (10^9t/yr)	Secondary productivity of animal matter (kg/ha/yr)	Animal biomass (10^9t)
Tropical rain forest	136	3.4	2600	260	152.9	330
Tropical seasonal forest	38	3.8	720	72	96.0	90
Temperate evergreen forest	60	15.0	260	26	52	50
Temperate deciduous forest	35	14.0	420	42	60	110
Boreal forest (taiga)	144	48.0	380	38	31.7	57
Woodland and shrubland	34	5.1	300	30	35.3	40
Savanna	60	3.0	2000	300	200	220
Temperate grassland	32	3.6	540	80	88.9	60
Tundra	16	8.0	33	3	3.8	3.5
Desert and semi-desert scrub	18	0.36	48	7	3.9	8
Extreme desert (sand), polar regions	1.2	0.03	0.2	0.02	0.008	0.02
Cultivated land	56	1.4	90	9	6.4	6
Swamp and marsh	14	5.0	320	32	160	20
Lake and stream			100	10	50	10
Total continental	*644*	*111*	*7811*	*909*	*61*	*1005*
Open ocean			16600	2500	75.3	800
Upwelling zones			70	11	275.0	4
Continental shelf			3000	430	161.7	160
Algal bed and corel reef			240	36	600	12
Estuaries			320	48	342.9	21
Total marine			*20230*	*3025*	*83.8*	*997*
Full total			*28041*	*3934*		*2002*

Ecosystems can be divided into two main groups: aquatic and terrestrial. The classification of ecosystems is presented in Table 4.18. Source of the major environmental problems is indicated in brackets for some ecosystems.

Table 4.19 gives area, primary productivity, net production, plant biomass, secondary production, secondary productivity and animal biomass of various types of ecosystems or large biomes (see also Table 2.16). From this table it is noticeable that no proportional relationship exists between total biomass and production.

4.10. APPLICATION OF ECOLOGICAL ENGINEERING.

Ecological engineering is the discipline that deals with methods of assisting and modifying ecosystems to overcome the impact of pollution. These methods are alternatives to the use of environmental technology, which is covered in part B of this book. However, combinations of the two types of methods might give an optimum solution in many cases.

It has been pointed out throughout this book that a close to optimum solution of an environmental problem can only by found by a quantification of the problem combined with a right selection among the wide spectrum of applicable methods. This principle is even more important to use when the solution requires interference with the ecosystem. Without a quantification of the problem, we are unable to measure and compare the effects of the various alternatives.

Ecological engineering is obviously more applicable when the pollutants are threshold, rather than non-threshold agents, although it has also been applied on non-threshold pollutants.

In this section an overview of ecological engineering methods will be given. Those who seek a more comprehensive introduction into the application of these methods are referred to Jørgensen and Mitsch (1988). The most important methods are listed below and a brief description of the application, advantages and disadvantages is given.

Ecological Engineering Methods.

1. *Diversion* of waste water has been extensively used, often to replace waste-water treatment. Discharge of effluents into an ecosystem which is less susceptible than the one used at present is, as such, a sound principle, which under all circumstances should be considered, but a quantification of all the consequences has often been omitted. Diversion might reduce the number of steps in the treatment, but **cannot replace** waste-water treatment totally, as discharge of effluents, even to the sea, always should require at least mechanical treatment to eliminate suspended matter. Diversion has often been used with a positive effect when eutrophication of a lake has been the dominant problem. Canalization, either to the sea or to the lake outlet, has been used as solution in many cases of eutrophication. However, effluents must be considered as a fresh-water resource. If it is discharged into the sea, effluent cannot be recovered; if it is stored in a lake, after sufficient treatment of course, it is still a potential water resource, and it is far cheaper to purify eutrophic lake-water to an acceptable drinking-water standard than to desalinate seawater. Diversion is often the only possibility when a *massive* discharge of effluents goes into a suscep-

tible aquatic ecosystem (a lake, a river, a fjord or a bay). The general trend has been towards the construction of larger and larger waste-water plants, but this is quite often an ecologically unsound solution. Even though the waste-water has received multistep treatment, it will still have a high amount of pollutants relative to the ecosystem, and the more massive the discharge is at one point, the greater the environmental impact will be. It it is considered that the canalization is often a significant part of the overall cost of handling waste-water, it might often turn out to be a both better and cheaper solution to have smaller treatment units with individual discharge points.

2. *Removal of superficial sediment* can be used to support the recovery process of very eutrophic lakes and of areas contaminated by toxic substances (for instance, harbours). This method can only be applied with great care in small ecosystems. Sediments have a high concentration of nutrients and many toxic substances, including trace metals. If a waste-water treatment scheme is initiated, the storage of nutrients and toxic substances in the sediment might prevent recovery of the ecosystem due to exchange processes between sediment and water. Anaerobic conditions might even accelerate these exchange processes; this is often observed for phosphorus, as iron(III) phosphate reacts with sulphide and forms iron(II)sulphide by release of phosphate. The amount of pollutants stored in the sediment is often very significant, as it reflects the discharge of untreated waste-water for the period prior to the introduction of a treatment scheme. Thus, even though the retention time of the water is moderate, it might still take a very long time for the ecosystem to recover.

   The method is, however, costly to implement, and has therefore been limited in use to smaller systems. Maybe the best known case of removal of superficial sediment is Lake Trummen in Sweden. The transparency of the lake was improved considerably, but decreased again due to the phosphorus in overflows from rainwater basins. Probably, a treatment of the overflow after the removal of superficial sediment would have given a better result.

3. *Uprooting and removal of macrophytes* has been widely used in streams and also to a certain extent in reservoirs, where macrophytes have caused problems in the turbines. The method can, in principle, be used whereever macrophytes are a significant result of eutrophication. A mass balance should always be set up to evaluate the significance of the method compared with the total nutrient input. A simultaneous removal of nutrients from the effluent should also be considered.

4. *Coverage of sediment by an inert material* is an alternative to removal of superficial sediment. The idea is to prevent the exchange of nutrients (or maybe toxic substances) between sediment and water. The general applicability of the method is limited due to the high costs, even though it might be more moderate in cost than removal of superficial sediment. It has only been used in a few cases and a more general evaluation of the method is still lacking.

5. *Siphoning of hypolimnic water* is more moderate in cost than methods 2 and 4. It can be used over a longer period and thereby gives a pronounced overall effect. However, the effect is dependent on a significant difference between the nutrient concentrations in the epilimnion and the hypolimnion, which, however, often is the case if the lake or the reservoir has a pronounced formation of a thermocline. This implies, on the other hand, that the method will only have an effect during the period of the year when a thermocline is present (in many temperate lakes from May to October/November), but as the hypolimnic water might have a concentration 5-fold or higher than the epilimnic water, it might have a significant influence on the nutrients budtget to apply the method anyhow.

   As the hypolimnic water is colder and poorer in oxygen, the thermocline will move downwards and the possibilities of anaerobic zones will be reduced. This might have an indirect effect on the release of nutrient from the sediment.

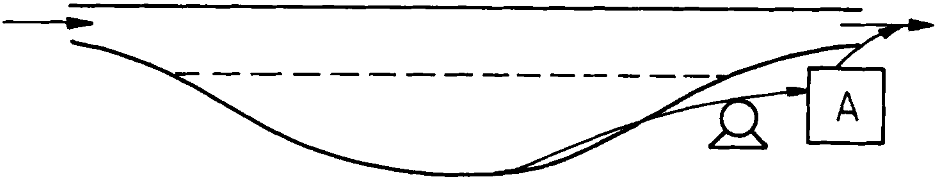

Fig. 4.45. Application of siphoning and ion exchange of hypolimnic water. The dotted line indicates the thermocline. 1 indicates the ion exchanger.

If there are lakes or reservoirs downstream, the method cannot be used, as it only removes, but does not solve the problem. A possibility in such cases would be to remove phosphorus from the hypolimnic water before it is discharged downstream. The low concentration of phosphorus in hypolimnic water (maybe 0.5 - 1.0 mg l^{-1}) compared with waste-water makes it impossible to apply chemical precipitation, see example 6.6 in section 6.3. However, it will be feasible to use ion exchange, because the capacity of an ion exchanger is more dependent on the total amount of phosphorus removed and the flow than on the total volume of water treated (see section 6.3). Figure 4.45 illustrates the use of siphoning and ion exchange of hypolimnic water.

6. *Flocculation* of phosphorus in a lake or reservoir is another alternative. Either alumsulphate or iron(III)-chloride can be used. Calcium hydroxide cannot be used, even though it is an excellent precipitant for waste-water, as its effect is pH-dependent and a pH of 9.5 or higher is required.

   The method is not generally recommendable as 1) it is not certain that all flocs will settle and thereby incorporate the phosphorus in the sediment, 2) the phosphorus might be released from the sediment again at a later stage.

7. *Circulation* of water can be used to break down the thermocline. This might prevent the formation of anaerobic zones, and thereby the release of phosphorus from sediment.

8. *Aeration* of lakes and reservoirs is a more direct method to prevent anaerobic conditions from occuring. Aeration of highly polluted rivers and streams has also been used to avoid anaerobic conditions.

9. *Regulation of hydrology* has been extensively used to prevent floods. Lately, it has also been considered as a workable method to change the ecology of lakes, reservoirs and wetlands. If the retention time in a lake or a reservoir is reduced with the same annual input of nutrients, eutrophication will decrease due to decreased nutrient concentrations. The role of the depth, which can be regulated by use of a dam, is somehow more complex. Increased depth has a positive effect on the reduction of eutrophication, but if the retention time is increased simultaneously, the overall effect cannot generally be quantified without the use of a model. The productivity of wetlands is highly dependent on the water level, which makes it highly feasible to control a wetland ecosystem by this method.

10. *Fertilizer control* can be used in agriculture and forestry to reduce the nutrient loss to the environment. Utilization of nutrients by plants is dependent on a number of factors (temperature, humidity of soil, soil composition, growth rate of plant (which again is dependent on a number of factors), chemical speciation of nutrients,. etc.). Models of all these

processes are available today on computers, and in the nearest future it must be foreseen that the fertilization scheme will be worked out by a computer on the basis of all the above-mentioned information. This will make it feasible to come closer to the optimum fertilization from an economic-ecological point of view.

11. *Insecticide control* by use of computer models has now been in use for several years. The idea is to use the pesticides when they have an effect on the harmful organisms - not when they might harm their predators. Observations on the appearance of the relevant species are used as input to a computer model, which gives the scheme for the use of insecticides.

12. *Application of wetlands or impoundments as nutrient traps* could be considered as an applicable method, whereever the non-point sources are significant. The use of wetlands has also been applied as a direct waste-water treatment method, for instance in Florida, but it will probably be most effective in dealing with nutrient losses from agricultural areas. Inputs of nutrients into a wetland will be denitrified, adsorbed on the sediment or used for growth of algae and macrophytes (phragmites, etc.), if it is not found in the outflows. Management of a wetland or an impoundment as a nutrient trap obviously requires that a major part of the nutrient input is removed by denitrification (nitrogen only) and stored in sediment and plants. The storage capacity is often large, but of course limited. This implies that nutrients must be removed by harvest of macrophytes, which is quite feasibel mechanically. However, if the retention time of a lake or reservoir in the temperate zone is short, it might be favorable to let the inflowing water pass through a wetland or an impoundment. In the wintertime, when almost no growth takes place in the wetland, the nutrients are washed out, but due to the short retention time, the water with high nutrient concentration will have passed the lake or reservoir before the spring bloom starts. The nutrients of the water which passes the wetland during the spring and summer will, on the other hand, be used to a large extent in the wetland or the impoundment for growth of algae and macrophytes. The water flowing to the lake or reservoir will therefore have a significantly lower nutrient concentration at the time of the year when eutrophication may appear.

    The role of wetlands in maintaining an ecological balance is still not fully understood, although our knowledge of the topic is far better today than 10 or 20 years ago. Lately, many large land-reclamation projects have been questioned due to increased experience in the field. Indications show that wetlands are important not only as nutrient traps but also for maintenance of species diversity and for an ecologically sound hydrology in the region.

13. *Calcium hydroxide* is widely used to neutralize low pH-values in streams and lakes in those areas where acidic rain has a significant impact.

14. *Biomanipulation* covers a wide range of possibilities. The role of diversity in a forest has been touched on in 4.5; it can be considered as biomanipulation when additional tree species are actually planted in a forest. Introduction of herbivorous fish (carp, etc.) into streams and lakes which suffer from eutrophication or uncontrolled growth of macrophytes is another example of biomanipulation.

    It has also been considered to reduce eutrophication by the introduction of top carnivorous fish species into lakes and reservoirs. They will reduce the populations of zooplankton-eating fish species and cause an increase in zooplankton populations, which again will imply reduced phytoplankton concentrations. The observed effects are clear, but it is indeed questionable whether the effect is permanent, if nutrient inputs continue. Some observations indicate that the ecosystem in this case will go back to its old equilibrium with reduced populations of top carnivorous fish species (observations by M. Straskraba and others).

QUESTIONS AND PROBLEMS

1. A fish has a growth coefficient of 0.02 day^{-1}. The carrying capacity in a lake is 120,000. At a given time 100 fish are introduced.
   When will the carrying capacity -2% relative be achieved? A logistic growth is assumed.
   What would the result be if the time lags t_1 and t_2 in (4.13) are 75 days? Only approximate result is required in this case.

2. Indicate how the development of man made ecosystem consisting of a concrete basin full of municipal waste-water will occur.

3. Indicate the expected difference in diversity between a shallow and deep lake and between a eutrophic and an oligotrophic lake.

4. What is the difference between fresh and salt water in relation to a)

solubility of oxygen, b) LC_{50} value for total ammonia (NH_3 + NH_4^+)?

5. Explain using the concept of ecological buffering capacity and energy, why anaerobic conditions give lower diversity than aerobic conditions.

6. In an island with an area of 100 km^2 120 bird species were found. How many would one expect to find on an island in the same region, but with an area of 20 km^2?

7. Find the buffer-capacity of a lake with 100 mg Ca^{2+} l^{-1} and a lake with 10 mg Ca^{2+} l^{-1} at pH = 8.0 and pH = 5.0. It is presumed that the buffer capacity is entirely related to HCO_3^- and this ion is equivalent with the calcium concentration. How much would pH change in the 4 cases, if the lakes are 10 m deep and they receive sulphuric acid by precipitation corresponding to 0.5 g S m^{-2}?