Einar Naumann: Some aspects of the ecology of the limno-plankton. With special reference to the phytoplankton.

Svensk Botanisk Tidskrift Bd. 13, h.2, 1919. pp. 129-163,

Transl. I.B. Talling.

The ecological aspects of marine as well as freshwater planktology have so far not been considered of much importance. In freshwater limnology it is mainly the study of polluted waters which has brought out the ecological aspects. Ecological studies within the limno-planktological sphere have without doubt especially favourable conditions. Water as an environment offers much more uniformity and it is surely easier there to survey factors affecting development than in other habitats. The distribution of plants and animals differs further from the usual pattern, and their dependence upon each other more pronounced. This is therefore real ecology which includes all living things and not only an arbitrary part.

I shall in this paper try to develop more generally some fundamental bases for the ecological study of freshwater plankton. A special attention will be given to the phytoplankton associations which can be separated out and made into groups according to their dependence upon changing environments. The extensive investigations which I have planned and partly executed in this field can only be presented after further detailed studies. Therefore I think it of value here to give a summarizing and introductory rewiew of these questions. It is also without doubt that the basic problems of planktology are of very great interest to plant ecology in general.

1. The plankton concept.

We no longer define plankton as any body which drifts in the water - as was Hensen's original definition. The definition should be restricted further to the community of living plants and animals which are primarily characterized by their adaptation to a mainly - drifting (planktonic) - life in the free water. Kolkwitz (1912), who further clarified these questions, defines therefore plankton as only the living part of all the floating and drifting bodies, or the whole seston. The plankton must further be separated from what I (1917) call the neuston: the community of plants and animals which have surmounted the difficulties of drifting by settling in the interface itself. They no longer drift as plankton in the free water but have settled at its outer interface. We must therefore from the beginning be sure to differentiate between seston, plankton and neuston. Their relationship can easily be seen from the following:

Seston: everything suspended in water and therefore drifting	A. Neustoseston: the living and dead bodies which belong to the interface	class of formation: Neuston
	B. Planktoseston: the living and dead bodies which belong to the free water	class of formation: Plankton

Plankton and Neuston thus represent totally different classes of formation.The following will only deal with plankton.

II. The relation of the ecological units to planktology.

The planktonic characteristic, to be able to exist free and drifting in the water, requires certain differences when compared to other communities and in comparing basic ecological issues. The environment (ståndort) is easily defined as a combination of all the ecological factors which interact here.

The plankton differs from other vegetation types in certain very important aspects. It occurs mainly in temporary aspects. There is thus no constant floristic background against which the annual change can be measured. It is obvious that such circumstances make difficult the introduction of a rational definition of a formation here. It is only the biochemical environment that is relatively constant, and from which the population increase happens either according to varying seasonal aspects or occasionally one single aspect within a very limited time span. The concepts of formation that I will propose here are therefore more abstract than is usual. But the empirical assumptions are more consistent, - this will be further discussed later - than has been customary in this field. But the characteristic change of aspect within the plankton causes certain difficulties in adapting the concept of succession in this field and this will be discussed in more detail below.

The plankton shows the most marked difference from other plant communities in the way in which the associations can and must be classified according to the nature of the environment. We must assume that the associations occur in nature and they can therefore be classified floristically. The present knowledge of the relationship of the different associations to the composition of the environment makes it possible to form higher units, formations.

The most important principles involved will be further discussed below. We would like to stress here in the introduction that our attempts are not based upon the acceptance of uncertainly deducted viewpoints, but on a natural progress of facts, obtained by empirical or inductive methods. The study of plankton should especially in this respect be of great importance for the study of plants in general.

III. The grouping of associations into higher units according to the composition of the environment.

Depending on which of the many factors in the environment is chosen as a starting point, different divisions of the plankton community are achieved. The great amount of information which we already have - mainly through the works by Kolkwitz and Marsson - concerning the close dependence of the phytoplankton production on the available nutrient in the water, should allow us to adopt an eco-chemical starting point in putting the associations into groups according to the composition of the environment.

We therefore accept fully the right to put the environmental chemical factors as the principal determining factors. There are indeed other factors which occur side by side with these but they act as secondary regulators. Especially temperature and light should be considered. These are also necessary for the development of plankton but by themselves they cannot accomplish anything. Thus they should only be considered as secondary regulators - the environmental-chemical conditions as the primary ones. The concept of formations within planktology must, according to our viewpoint, be based upon these. The other factors are thus only considered for division of the formation into lower units. It is evident that the light factor can only be of importance for the vertical zonation resp. the temporary distribution of the aspects within what we usually call the plankton - i.e. really within the upper interfacial plankton. But they can in general not determine its basic character.

The chemical factors are the prime determining factors, if their effects are not impeded by the temperature factor. The latter could obviously have a lasting effect upon the temporal distribution of the aspects, but it could also determine the character as a whole of the upper interfacial plankton if a certain temperature necessary for the development of the most important associations is not attained in the temporal development. In this way even temperature limited formations exist. But one can only expect this within the alpine or tropical areas. Our present knowledge of the ecology of plankton does not allow us a more detailed discussion here. We shall here further delimit our field to conditions within the north and middle European climate. The abovementioned conditions would not apply here and we can truly say that the chemical environmental conditions determine in the first hand the total character of the upper interface plankton.

Kolkwitz and Marsson (1908,1909) were the first scientists to study in a systematic way the dependence of the plankton on chemical-environmental conditions. The "ecological system" which summarizes their very great experience in this field, was indeed intended solely for the use in determining the purity of water which earlier had been polluted with organic pollutants. The different stages in the "mineralization scale" defined here, should also be present under unspoilt natural conditions and not only as a mineralising succession in polluted water. I think it is possible, by using a"system" like this as a starting point, to place into groups the algal communities which occur in natural waters and conditioned by the eco-chemical basis. It is first of all an attempt in a general direction like this which here is presented.

The Kolkwitz-Marsson system operates on 5 different stages according to amount of nutrient available in the water. The system relies upon a detailed chemical analysis of the water at these stages. Any questions about these, I shall refer to the original works. A large or small number of associations is attached to each stage, and the associations are either qualitatively different and therefore characteristic, or also - very similar to my own experience - quantitatively different within the different stages, so that one association represents the optimum with a peak production, another a nutritionally starved zone and so on. The different stages with their characteristics are as follows.

1. The polysaprobe type (p). Found mostly in waters rich in much rotting protein- Solely heterotrophic associations, represented by bacteria, fungi and other colourless organisms.

2. The mesosaprobe type (m) - Assymetrical and consisting of 2 special types, alpha (α),beta (β). The former group represents a rather illdefined transition between p and alpha; the latter are represented by waters rich in amino acids and other late or endproducts of protein synthesis. The associations in the latter group are mainly autotrophic: algae and chromoflagellates with a similar physiology to that of the(amino organisms).

3. The oligosaprobe type (o) - Found mostly in waters rich in nitrates. The associations purely autotrophic, nitrate organisms.

see page 22

Fig. 1. A graphic representation of the different groups of associations as distributed in a water body during self purification. In the top one the heterotrophic dominates, in the middle the eutrophic and in the last the oligotrophic associations, represented by the association groups of p and alpha resp. beta and o, resp. k.

4. The katarobe type (k) - represented by waters poor in nitrates According to my experience it could be described as one which in the first hand is limited by nitrogen. The associations are purely autotrophic, and according to my experience likely to be qualitatively very similar to the ones in o. The k is thus, at least to a great extent a quantitatively impoverished type of o.

These 5 types of the Kolkwitz-Marsson system should include all the associations which we are likely to deal with in this sphere.It is perhaps easiest to visualize it in a diagram of an "Ecological"spectrum", with the 5 above distinguished types grouped after each other as shown in Fig. 1. In here is then fitted the type which is found in nature, and we ashieve a good survey of the basic characters of the associations in question. We shall elaborate on this question below.

The system of Kolkwitz and Marsson can, we think, be further developed and adapted for a rational classification of the plankton communities in general. It had indeed developed from studies on freshwaters polluted with organic waste materials. The different "degrees of mineralization" thus obtained can also occur under strictly natural conditions in freshwaters and equivalent to permanent formations and not only to successions as is the case with "self-cleaning".The system also includes organisms with very different types of nutrient physiology, from pure heterotrophs to the most developed autotrophs. It is worth pointing out here that the general application of the system in pollution studies has so confused otherwise critical workers, such as when Warming-Græbner (1918) gave it as a form of "saproplankton" classification. And still it can include all the plankton - and not least the groups which since long have carried this name.

IV. The relationship between the different association groups. The successions.

The association groups, which according to the preceeding were erected after the Kolkwitz and Marsson system, could represent either relatively fixed types or only a link in a succession. In large natural lakes the former is generally the case.But a succession could also occur naturally in a pond. This is only known from culturally polluted waters, where the "self-purification" of the water gives the successions $p \rightarrow \alpha \rightarrow \beta \rightarrow o \rightarrow k$. The pollution operates of course as a succession in reverse, if the pollutant is not added too suddenly. We obtain thus the same sequences of the different mineralisation stages which occur naturally in lakes, ponds and rivers.

In natural bodies of waters one anticipates relatively fixed associations of the type p, α, β, o, and k., which depend on the prevailing nutrient conditions in nature.Only the nutrient poorest waters give the k type, the nutrient rich ones different stages of α and o. But the types p, α, and k represent under natural conditions an exception. The former can only be found e.g. in ponds especially rich in vegetation, and the purification capacity of the water is incapable of coping with the very large amounts of organic material, which to a great extent are produced by relatively autrophic forms and here heterotrophic types dominate the plankton development. This condition can become permanent - I know of one such pond where the sulphur bacteria is the main plankton- but it can also occur periodically when becoming auto saprobic with "self purification" following. We can then again consider these types as successions in a development, the climax of which will be the de-saprobised endproduct. The difference between the relatively fixed formations and those that are only a link in a eco-chemically conditioned succession, must be kept separated in ecology.

The types which show the extremes(p,m, and k) are always easy to keep separated.It is less easy to deliminate the others. We therefore do not think it appropriate to designate these types as proper formations, but to make out only 3 nutrient - physiologically definable formations to include all and as follows:

Mainly heterotrophic types	p α & m	The heterotrophic formations
Mainly autotrophic types	β- m o k	The eutrophic formations The oligotrophic formation.

In this way we obtain a natural grouping of the different definable floristic associations, and a similar example does hardly exist at the present within ecology.

According to the above presentation, we get 5 nutrient-physiological delimited groups, each one made up of an often considerable number of associations. We shall here further develop the question of how these could combine in a variety of ways to be made into the 3 formations we proposed, and how they develop in the groups of freshwater bodies that we have acknowledged for a long time namely, Lakes, rivers and ponds.

The plankton of lakes, ponds and rivers was sharply distinguished from each other by older phytologists. It is also evident, that different physical factors within these types of waters must selectively have been important for the origin of different associations, but its prime basis must be found in the eco-chemical conditions.Generally in the lakes and ponds many different associations develop, even though we are dealing with by definition the same formation. Sometimes the associations are absolutely identical. It is not possible to speak of specific association types for running waters.

For this reason it is obviously not possible to attach too great an importance to the old concepts of limno-, helo-, and potamo-plankton. To accept this delimitation to formations would mean ignoring the main regulating factor, the eco-chemical one.For practical reasons it is here more suitable to characterize separately the eco-chemical dependent associations in lakes, ponds and rivers.

V. The plankton formations in lakes.

From an ecological point of view, mainly the north and middle European lakes have been studied in some detail. If we exclude the exception, represented by very deep lakes, then - as I already in 1917 have explained in detail - the material can roughly be grouped under two headings: a nutrient rich, and a nutrient poor, each of these directly influenced by the surrounding nature.Here we have thus primarily two formations.

1.The eutrophic formation of the eulimnoplankton.

This formation is characteristic for lakes situated within electrolyte rich soil formations where also are available organic substances resulting from normal degradation. The plankton thus works towards high peaks of productivity and the colour of the vegetation dominates the waters own colour. From a nutritional-physiological point of view the associations which occur here must be located between α and o. The ecological spectrum will appear as shown in Fig. 2.

The characteristic of the eutrophic formation is obviously the high production of the relevant associations. Myxophyceta can generally be considered as the most characteristic, represented nearly all year round in different aspects.

(see page 22)

Fig. 2 Graphical illustration of the distribution of the association groups within the oligo resp. eutrophic type of lake.

Smaller and shallower lakes of this type should be considered as a facies by themselves sufficiently characterised for this association. But it is often richly interspersed by *Pediastra*, *Scenedesmus* and other forms.

Deeper lakes offer a special facies, mainly characterized by many and long peaks of high productivity through the associations with *Melosira* and *Peridineta* - limited to the cold resp. the warm water period of the water. Even here the *Myxophyceta* can become important.

In summarizing the above, we obtain the following groups of the eutrophic formation.

Eutrophic formation	Hydrographically or chemically dependent types	*Myxophyceta*, *Peridineta*, *Melosira* etc.
	On previous history dependent	Unknown types

The associations mentioned here have been known from the very beginning of plankton study in the nutrient rich lakes of the Baltic lowland. Floristically they have also been classified as the characteristics of the "Baltic" type of lake. But are we really entitled to take these floristic viewpoints for granted, as we have done here, and further expand a viewpoint?

There should be no doubt about this. A considerable amount of chemical data exist on this lake type and they show a general agreement with conditions attained during the self-purification of the water at the stage β m and o. I here refer to the numerous publications by Kolkwitz. By drawing a simple analogical conclusion we can lump all the "Baltic" associations exactly in the nutrient-physiological groups of β m and o. Here again we have shown the justification of the principle which we follow here - grouping of associations into higher units according to the conditions of the environment.

2. The oligotrophic formation of the eulimnoplankton.

This formation is characteristic for lakes situated within soil formations definitely lacking in soluble electrolytes, and here might also occur great amounts of products from the peat formation of the organic substances. The plankton is here in a minimum production curve and a colouration from vegetation is really missing here.

I shall group this lake type as the first known example of a katarobe association on a larger scale. The ecological spectrum of this is already shown in Fig.2.

The characteristic of the oligotrophic formation is firstly the accentuated low level of productivity in which these associations occur. They also differ qualitatively from the eutrophic formations. Especially characteristic is the absence of great numbers of *Myxophyceta* which in the peak of high production characterises the eutrophic formation. There are indeed quite a number of species common to both the eutrophic and the oligotrophic formations and the difference between these formations must to a great degree rest upon quantitative aspects. As purely qualitative characteristics for the oligotrophic type the following associations can be mentioned:

Chlorophyceta, Chrysomonadineta, and Desmidieta etc. within the limits imposed earlier (1917).

These different katarobe associations typified by their production minima (low production) may occur combined but they often represent different types of the oligotrophic formation. It is possible that among these the occurrence of Desmidietum may be dependent upon historical factors. Teiling (1916) emphasized this by naming the association the "caledonian formation" - a term which could be accepted for the historically dependent types of the oligotrophic formation - but not more than that. The association in question is first of all a typical oligotrophic formation and emphasis should be put on this in the terminology. It is possible that it also represents a historically dependent type of the oligotrophic limnoplankton formation and should thus be the sole known example from North and Middle Europe of the importance of historical factors in the composition of the plankton communities in our fresh waters.

In nature the oligotrophic lake type occurs especially within the areas with primitive rock formations, partly as a clear primitive rock - lake, partly as a humus lake. A parallel between the hydrographical resp. chemical conditions and the development of the plankton has not yet been shown. It further appears as if the different associations of the oligotrophic formation may occur in either of these lake types. This is of great importance for Desmidietum - and I have earlier elaborated on this (l.c. 1917).

If we summarise the above, we clearly obtain the following groupings of the oligotrophic formation within the eulimnoplankton.

Oligotrophic formation	Hydrographically or chemically dependent types	Chlorophyceta, Chrysomonadineta, etc.
	Historically dependent types	Desmidieta

The abovementioned associations were first floristically separated out in the work of Huitfeldt-Kaas (1905) and referred to as a characteristic for the "north European" lake type. I have gone even further(1917) to say that the basis is purely eco-chemical - a procedure one is entitled to use from evidence from the field. If we further study our lakes in the primitive rock formations, as did Hoffman -Bang (1904), Aschen (1906) - and with the chemical analysis available from these, make a comparison with the "degrees of mineralisation" from Kolkwitz and Marsson, then it becomes obvious that we cannot any longer deal with the saprobe definitions. The only thing we can do is to include these associations in the katarobe type. Kolkwitz and Marsson were most likely not aware of this - for the simple reason that the lakes in the north German lowland do not represent such an eco-chemical poverty.

The oligotrophic formation thus becomes the characteristic formation of the really nutrient poor, katarobe waters. The eutrophic formation, on the other hand, shows under most conditions a leaning towards the saprobic because of the abundance of organic material, which is broken down here. This autosaprobing process only leads to the [illegible] stage and it is unrealistic to vizualise other formations in the upper interface of our lakes.

3. The heterotrophic formation in lakes.

There is obviously only a small number of heterotrophic formations mixed in with the formations which consist mainly of autotrophic organisms. It is selfevident that every form of organic life must depend upon a greater or lesser autosaprobising of what is available - and thus heterotrophic organisms must always exist there. From this condition to the formations dominated by the latter a very long bridge must be built. Theoretically as well as actually the upper interface(surface) water would hardly exhibit this.
The bottom water behaves quite differently. Because into this water sinks all the time the considerable number of dead bodies from the pelagic zone - and here is a continued contact with the bottom mud which within the eutrophic lake type is well known to contain considerable amounts of nutrient. The conditions for the autotrophic way of life are limited by the light conditions. Theoretically one can assume that the formations of the bottom water are rather heterotrophic - that a vertical zonation exists within the lake, a vertical connection of the ecological system, very similar to the type shown in Diagram 3.

It is obvious that this sort of phenomenon must occur within the eutrophic lake. But they have not been studied yet. This vertical zonation was first described by Ruttner (1914) at Lunz in Lower Austria and by me at about the same time from Kloten (Væstmanland) in oligotrophic lakes where a"summer2 prevented the vertical circulation and conditioned its occurrence.

see page 22

Fig. 3 Graphical illustration of the distribution of the association groups in a vertical direction within a nutrient-physiologically layered water.
On top the real surface(upper interfacial) plankton which belongs to the oligotrophic formation. In the middle an in-between-stage characteristic of the eutrophic formation. At the bottom the bottom water with its heterotrophic formation.

This heterotrophic deep water formation can (because of special circumstances it has not been possible to publish the raw material for this) be broken up into a great number of associations which according to their nutrient physiology prove very heterogeneous. Within the bacterial world it is clear that both H_2S oxidising as well as H_2S producing bacteria of different types are here of importance. To these can be added a series of less specialized saprobes as well as certain other iron bacteria. Whether the last mentioned associations are possible without an addition of the allochthonus iron is in doubt.

We already have investigations - indeed only for a few lakes - which make it possible to place them into groups. I do it in the following way, with the reservation that autotrophs with chemosynthesis have till now not been separated from the heterotrophs.

Heterotrophic formations

1. Associations with a general saprobic tendency.
   Example: Infusoria, colourless flagellates. Common in the deep waters in the tarns of Kloten.

2. Specialized associations.
   1. H_2S oxidising bacteria.
   Examples: some tarns by Kloten.
   2. Different types of H_2S producing bacteria.
   Example: Obersee near Lunz.

The above can easily be adapted for freshwaters other than lakes. It is of great importance that we finally make it clear that the conventional meaning of "plankton" only represents a comparatively narrow layer, wherein the autotrophic life can exist. It does not go very deep, but below it is another type of plankton, just as important, where the remains of the organic autotrophs are broken down and reincarnated in the heterotrophic deep water plankton.

Ruttner has dealt in detail with the eco-chemistry of the deep waters. With respect to chemistry the agreement with the polysaprobe respective α mesosaprobe water types is generally good amd puts still more weight towards the grouping based upon the nature of the place or environment, which I have been doing.

4. Lake formations as fixed entities or as a part of a succession.

We have already pointed out that the lake formations under natural conditions must in general be considered relatively fixed. From the present point of view successions as such could not be included here. But every organism-production conditions a autosaprobising of the environment. Within the oligotrophic lake type the production is generally so low that it is hardly possible that the k-stage can be crossed. This nutrient poor formation can doubtless be considered the most stable of the plankton formations.

But conditions are different within the eutrophic formation. Here everything is aimed at high production and it is in reality fantastic amounts of organic substances which are incarnated by the plankton. An elucidative example of this is the quantity(numbers) of our most common nannoplankton forms published~~xbyxKolkwitzx(1909)x~~ by me (1918)and for a larger alga by Kolkwitz (1909). It is evident that this must, at certain times, make necessary a considerable autosaprobising of the environment. As a general rule the eutrophic type must oscillate between o and the β m stages- similar to a model for a reversible reaction. When the available nutrient has been totally exploited, the production goes back towards o, but the β m stage is realised soon again through autosaprobising and thus the preconditions for a new production. Such a point of view deserves without hesitation a greater attention in the interpretation of conditions for periodicity in general.

Other successsions of some importance can hardly be expected within the present framework of life in the lakes. The oscillation between the association groups $\beta \rightleftarrows o$ mentioned above, invokes a doubt whether it is right to call them successions. It is not until historical-geological view-points are established that such phenomenon can be expected. It is thus evident that the re-growth in the lakes must as far as plankton is concerned be correlated with changes in associations and formations. One must, for example, assume that a maximal development of life in a eutrophic type of lake starts from a basic type which falls within the framework of oligotrophic mode of life and at a time when the water still could not draw upon the mobile organic substances which along with a plentiful supply of electro lytes condition the beginning of high production. On the other hand, other new successions must follow the eutrophic stage - either in the direction of increase in nutrients or sooner or later of decrease. For the oligotrophic lake type at its peak it seems very difficult to assume form the eco-chemical point of view a succession of different formations- at the very peak really a definite change of aspect through and association-shift. Each opportunity for a succession in the true meaning (change in formations) is blocked by nutrient-biological reasons; the nutrient reserves of the environment are small during the whole development and increase, and thus not - as is the case for the eutrophic lake type - oscillating from poverty to riches and vice versa. It is evident that such successions can be reconstructed paleontologically to a greater degree and more successfully here. To take even further such point of view should offer an interesting and fruitful work for the paleo-limnological aspect within the studyof the peat moss.

VI. Plankton formations in ponds.

If our view, that the formations are limited by the eco--chemical conditions of the environment, is accepted then we can hardly speak of a specific plankton for ponds. In general there is a difference here in respect to the associations which occur here and the lake plankton, both in a positive and a negative direction. Zacharias, who created the concept of heloplankton in 1898, emphasized that there was a positive deviation in the phytoplankton from that of the true limnoplankton through a considerably richer representation of the lower green algae, flagellates and other forms. On the other hand, certain associations which characterize lakes were missing here, f.ex. <u>Melosireta</u>.

These differences depend on eco-chemical conditions and they have been discussed earlier. If we, e.g., compare the ecological spectrum of the eutrophic lake type with that of a pond in the same area then we find that the latter spectrum often lies a bit further to the left. The associations will thus differ as well as the formations because of the varying eco--chemical conditions.This is the decisive factor in comparisons between lake and pond plankton. The formations are primarily determined by eco-chemical factors, and other factors can decide variations on these, of which some will be specially characteristic for lakes, others for ponds. It is evident that other factors along with the eco-chemical ones can be of importance in a secondary area so that the possible primary associationgroups for eco-chemical reasons are excluded. As example we can mention conditions for dispersal, thermal conditions, ice cover, condition of currents and so on. - all factors the specific influence of which is unknown. These are, of course, already important for the differences in formations within different lakes and should be much more important when one compares lakes and ponds. But there seems no reason what-so-ever to justify equating their importance with that of the eco-chemical factors on which we have defined our formations.

In the true sense of the word, we cannot speak of a special pond-plankton but only of certainn helofilic variants of the formations formed according to nutrient-physiological conditions. It is only for practical reasons that we here deal with these formations.

Our knowledge of pond plankton is very defective. Most of our modern studies have been made on parts that can dry out, and the conditions of plankton in the more natural pomds have only in a few cases been studied with the help of modern technical aids which are the only ones that give a true basis for ecological works.

We shall here use the same division for the pond plankton as the one used for the lake plankton.

1. The eutrophic formation.

This formation is characteristic for ponds situated within the same area as the eutrophic lake type. Ponds of this type have been studied by Diefenbach and Sachse (1912),Schædel (1910), Wagler (1912) and others. I have myself studied several which belong to this group and culturally conditioned in the lowlands of Skåne.

The plankton production is here towards peak production and the ecological spectrum agrees with that of the eutrophic lake type.

These studies have first of all shown that the eutrophic pond formations can to a great extent be formed by the same associations that are characteristic for the eutrophic lake formation.Alongside these associations are some specifically helophilic (helofilic), such as Euglena, certain of the lower green algae and so on, - all associations with a nutrient-biological spectrum far out in the ∅ region, that is, considerably more to the left of the typical distribution of an eutrophic formation; compare Fig. 2 and 4. The reason is obviously the greater availability of exploitable nutrients, which ponds - ceteris paribus - have to offer than lakes where in comparison with the volume of water there is a dominating mass of higher plants, and through the contact of the water with the nutrient rich bottom etc.. Similar associations can occur in lakes, but then mainly as the consequence of culturally caused pollution. This sort of enriched water in pondsvcould only occur as a part of the auto-saprobising of the water.

see page 22

Fig. 4. Graphical illustration of the distribution of the association groups within a eutrophic pond. The uppermost spectrum agrees very closely with the eutrophic lake type in a typical development of it. There is in general an increase towards the saprobe areas.

There is no doubt that the basic determining factors are only the eco-chemical conditions, and that lakes and ponds which belong to the eutrophic type with respect to plankton production composition must be considered in the same way.

2.The oligotrophic formation.

The formation is characteristic for ponds situated within the same area as oligotrophic lake types. Plankton production is here low and the ecological spectrum agrees with that of the oligotrophic lake.

Relatively unspoilt ponds of this type have planktologically not been studied in detail. The above characteristics are based upon my experience with relatively recent - not more than 10 years old - ponds that can dry out. The associations which occur here belong typically to group k but agree floristically not at all with the oligotrophic lake type. The reason for this is very likely the drying out of the pond, conditions for dispersal, and so on. It is obvious that the cultural impact must cause many modifications on the association picture. For a further discussion on the oligotrophic pond formation under natural conditions such material is of course not usable, and we shall not discuss it further here. The only possible starting point must be from studies on relatively natural ponds within that area.

3. Heterotrophic formations.

Ponds which are situated within a nutrient-rich drainage area, could under natural conditions finally belong to a biochemical environment where only purely heterotrophic forms can develop. The autosaprobising can start both from a disappearing high respective over-production with respect to the plankton, as well as - and especially - from the mass of phanerogamic plants.

Examples of this type are especially to be found in Kolkwitz (1911). As for other things concerning the grouping of the heterotrophic formation, I shall refer to my abovementioned summary on p. 143.

4. Successions within the pond plankton.

Firstly, it is self-evident that the relationship of the successions within the pond plankton must be the same as that for the lakes. I shall here limit myself by referring to the earlier discussion of this.

But there is one case, where the successions within the pond plankton is more distinct than within the lake plankton. namely, as shown earlier, the the autosaprobising within the surface water never exceeded the β m type and that a succession within the typical eutrophic lake type was limited by the oscillating between the stages β m ≶ o. Within the oligotrophic lake type all autosaprobising is unthinkable and thus also successions in this meaning.

The oligotrophic type of the pond plankton thus agrees completely with the lake plankton. The eutrophic pond can, because of the enormous quantities of organic material which accumulates here - because of the phanerogamic plants - in an environment inductive to rotting, get further. We must thus here assume a succession which cuts through all the stages - except for k, where, because of the nutrient poverty, such a thing could not exist. Furthermore, this succession runs parallel with time of year, so that during the autumn - when the phanerogamic vegetation dies down and begins to break down under largely heterotrophic forms - it is the time for beginning of the autosaprobising. The associations can hardly be considered as aspects in the true sense of the word. In extreme cases the successions make a complete circle with "aspects", which from nutrient-physiological point belong to different formations. This can obviously be represented by a simple equilibrium equation. But it should be presented as Fig. 5 shows. For the purpose of comparison I also give a typical, but shortened mode of succession (Fig. 6).

The different "aspects", occuring at different time of the year, represent in this case very different formations. I think that I am also entitled to consider these as real successions. But this is obviously very opposite to normal conditions, where the biochemical environment is nearly constant during the year, and at the most has some small deviations of the type β m ≳ o, where the aspects only represent different associations as an expression for the same nutrient physiological formation, with relative homogeneity.

The completely circular type of succession represents rather the exception, according to my experience. But it is anyway of great importance that the shift caused by the autosaprobising in general goes further in ponds than in lakes, and thus associations from very different formations can appear as dominant "aspects"also in the yearly variation of the surface plankton.

VII. Plankton formations in running water.

A special "potamoplankton" exists hardly in a plant biological sense. The plankton of the running water should really be considered a large potamo-allochthon- transport; or - if the current is very slight - a true production of such forms which the biochemical environmental factors allow. The physical factors can later have a selective influence, as is the case with ponds, that is indeed selfevident.Among these we must firstly consider current.

In accordance with the views that we have developed here, we are justified in grouping the plankton formations in the rivers, which truly show a autochthon production, in the same way as we did for lakes and ponds. Even here we maintain the abovementioned types.

Autumn

Winter

see page 22

Spring

Summer

Fig. 5 . A schematic survey over the circular successions type characteristic for very nutrient-rich ponds. Whole lines mean desaprobising, broken lines mean saprobising parts.

1. The eutrophic type.

The distribution and characteristics agree with what earlier has been mentioned for the eutrophic lake type. Such rivers have been studied by Kofoid (1908), Bethge (1911, 1915), and others.

Floristically the associations agree here nearly completely with that of the eutrophic lake type.

see page 22

O O O

K

K

Fig. 6. A schematic survey of the shortened types of succession.These should really be considered as an association shift within the same formation.

On the left hand side at the top is the idealised scheme for the eutrophic lake type, which in nature nearly always occurs in the right hand form. At the bottom the katarobe lake type without successions.

Whole lines mean desaprobising, broken lines autosaprobising.

2. The oligotrophic type.

The distribution and characteristics agree with what earlier has been mentioned for the oligotrophic lake type. - Rivers of this type have so far not been studied in detail.

Chemically the eutrophic type indicates abundance of electrolytes, whereas the oligotrophic indicates poverty of these. For Sweden reference can be made to the analysed material published by Hoffman Bang (1904).

Any further types of formations are hardly to be expected under normal conditions in this area. The problem of relationship of successions can be referred back to what has already been said about lakes. - Only very few studies are available on the biology of rivers under natural conditions, and among these especially Kofoid's (1908). But there is much more material available - especially German studies - on culturally caused changes in the normal combination of associations.

VIII. A summarizing survey of the limnological plankton formations.

We have here developed the concept that one can completely carry out the division into groups by using the three formations, eutrophic, oligotrophic and heterotrophic, on any sort of fresh water, - a lake, a pond or a river. The associations which come under these headings may be diffusely spread out within any one of these water types, - or else occur especially within any one of these water types. I therefore think it justified to consider these water types as a special facies of the three formations defined in the first place through nutrient physiology. The limnological terminology for the formations and their distribution is then as follows.

I. The eutrophic formation.
- A. Horizontal distribution: only in nutrient rich bodies of water.
  - a) Eulimnic facies.
  - b) Helophilic facies.
  - c) Potamic facies.
- B. Vertical distribution: strictly in the surface water only

II. The oligotrophic formation.
- Same grouping as in I.

III. The heterotrophic formation.
- A. Horizontal distribution: strictly in saprobe waters only.
  - a) A limnic facies does not occur under natural conditions.
  - b) Helophilic facies.
  - c) The potamic facies does not occur.
- B. Vertical distribution: Photic conditions do not limit it to surface water only. But it can form a special very deep facies of the eulimnic life.

With the abovementioned forms which exist under natural conditions as a base, it may be suitable to discuss here their relationship to cultural influences.

IX. Natural and cultural formations.

It is not our purpose here to give a complete survey over all the culturally caused interference in limnological life. But we shall limit ourselves to the phenomenon directly related to the questions which we have been dealing with in the previous chapters. It is thus an elucidation of the formations limited by nutrient-physiological factors, and how they are dependent upon cultural factors, which first of all demand our attention.

In the previous chapters we have found that three large formations are to be found in natural waters - the eutrophic, the oligotrophic and the heterotrophic - which in their distribution are directly dependent upon the nature of the environment.

Culture can cause a pollution of water - that is a shift of the nutrient biological spectrum towards p. Kolkwitz and Marsson were the first scientific workers to give a systematic explanation to these questions, summarized in the ecological system of 1908 and 1909. As we have shown earlier in this paper, this can also be used for water-bodies under completely natural conditions and has been used as a foundation for a rational classification of formations in general. The study of water pollution must therefore, according to our concept of the natural formations, be considered of basic importance - which really means full-scale experimental elucidation of the impact of the environment upon the formation type. In the following we shall limit ourselves to a few elucidating examples of this.

1. Lakes.

According to our previously developed concept, the eutrophic lake represents the limnological expression for a good soil in the neighbourhood. The biology of the water must all the time be considered against the surroundings in general when following our concept, - a point which obviously can be very profitable.

For the formation of the eutrophic lake type within the fertile fields of the lowland, we do not, according to our concept, have to assume cultural influence. It very simply arises by itself as a result of the auto-saprobising going on there for some time.

It is most remarkable that the above points have been left unnoticed till now. We consider them very simply of fundamental importance for the rational development of the plant ecological concept.

It is indeed obvious, that our idea of the origin of the natural eutrophic lake type can hardly be proven by plankton studies in that area. On top of this comes the dominating role of culture in these areas. Teiling (1916) said " The natural factors themselves around the lake do not play a decisive role ----, but it is indirectly the surroundings, that is, the degree to which it favours settlement and crops". We can of course not accept this statement, which is opposed to our own fundamental concept, that in the direct character of the environment can be seen the first condition for the further shaping of the formation. As a proof that our interpretation is right we can refer to a paper dealing with the effect of autosaprobisation (Kolkwitz 1911). An experimental proof for this can be found in my own work where nutrient poor waters were enriched, where the combination of electrolytes and organic material - thus the same material as that for the eutrophic lake type, regardless of the cultural effect - gave the greatest peak production. The literature dealing with this was summarized by me in 1917, 1918. Studies of relatively natural association groups - see Naumann (1911 - 1919), Plümecke (1914), and others - further point in the same direction. All this is really valid for heloplankton;

but these findings ought to be acknowledged to be of as great importance for the eulimno-plankton. It should be pointed out here that a direct explanation of these could be obtained from a critical interpretation of the eutrophic mud deposits in relation to planktology. A paleolimnological study with special reference to the biological parts which are now unknown, but could offer something of great interest.

Within an area which is oligotrophically determined by the quality of the surrounding fields, a naturally occurring eutrophic lake type would be unthinkable. But if such a one does occur there, then it must be culturally conditioned. As an excellent example to illustrate this for Sweden is the lake system by Växiö , the chemistry of which has been studied in detail. Here we find - see Sondén (1914) for further information- four lakes "connected" one after the other and in the direction away from the source of pollution showing a complete transition from the eutrophic to the oligotrophic type. The first one in the chain can hardly be distinguished,planktologically, from a natural eutrophic lake type, and the last one agrees completely with the oligotrophic type which is a characteristic natural type for this landscape. This is one of many experiments, which clearly shows the dominating influence of the eco-chemical conditions and from our point of view very clearly shows the true motivation for the grouping of the associations, which we here have done.

It is self-evident that this concept that I have developed on the eu- and oligotrophic lake types can also in actual practise - the pollution studies - be of decisive importance. It is namely not the plankton production by itself that is of prime importance but it in relation to the condition of the environment. What is very natural and obvious in the flat Baltic countryside - the eutrophic lake with high plankton productivity- is as unnatural and out of place in for example the geologically old (primary rocks) parts of Småland. Here the oligotrophic type is the natural one, and the eutrophic on the culturally conditioned one.

2. Ponds.

To ashieve a really empirical collection of material for the study of the problem of the dependence of the plankton formation upon the biochemical environment, the pond culture especially is of great interest with its dependence on culture formations.

It is evident that the pond culture in many ways is an excellent experiment on a larger scale for the purpose of elusidating different ecological realities. The periodical drying out of the pond and local differences caused by this, possibility of dissemination from pond to pond, but this is all of less importance than the biochemical which is in practice realised through liming, fertilisation,mechanical bottom cultivation and so forth. But it was I who first brought this out to any extent at the first Swedish Fisheries Laboratory in Aneboda. A few examples of this might be of interest.

In the area I have studied the natural formation is typically oligotrophic. The result of enriching the water with appropriate fertilizer, performed by the fodder-producing technique prevailing and during the years of 1912, 1913, and 1914, was a very characteristic eutrophic formation with associations of the typical ρm. The natural formation disappeared completely and we were faced with a eutrophic richness, which must seem very peculiar to anyone not familiar with the proper conditions. By 1915 the abovementioned fodder-producing technique was stopped and the productivity decreased immediately with a return to the former natural formation with its both qualitatively and quantitatively poor associations. For further details I refer to my publication on this (1914). It is hard to think of a more beautiful and on a bigger scale experimental elucidation of the problem on the dependence of the plankton formations upon the conditions of the biochemical environment. The above--mentioned situation might also show to which degree the pond culture could be used for studies of plankton ecology.

It must be obvious that the pond culture in general offers a very rewarding field of study for ecology. It further must be unquestionable that future studies will utilize these possibilities more and more where the adoption of a rational scheme of fertilization would give the importance of the large scale but with detailed precision. As for the questions concerning the practical importance and the experimental details of the studies of the original production of the water in its relation to the composition of the environment, I shall refer to my summary about this (l.c. 1918).

To make a long story short, the ecological research can thus utilize to a great extent the purely practical work experiences. We should also not overlook the fact that ecology in the form of applied science can help practical life.

3. Rivers.

The cultural formations of lakes and ponds generally stay at the eutrophic level. This is done on purpose in fish ponds. A stronger saprobising could destroy the production possibilities which one can increase by the right amount of pollution. Oligotrophic environments are poor in production and this we must overcome. Fertilisation leads to saprobising of the water and , if properly kept within certain bounds, as explained earlier by me (1918), may lead to a general increase in production. The optimum would be represented by the highest β m type.

The saprobising of the lakes and thereby the appearance of culturally conditioned formations is an incidental side effect of increase in the spread of population and industrialisation. Also here the condition is that the β m stage is not surpassed in the water body.

But it is quite different with running water, along which industry also congregates. Here we find the deplorable phenomenon of culture formations of the p, α and β - thus in severe cases horizontal unrolling of the whole characteristic zonation. The German literature especially has to offer a large number of ecologically very instructive examples of this - summaries by Kolkwitz 1908, 1909, 1911.

A decrease in the water current generally offers the complete eulimnic respective helic conditions for the potamic facies. A correct interpretation of the associations which typically belong here must include the study of river pollution with its rich zonations.

X. Other ecological problems.

This presentation of some aspects of the ecology of the limnoplankton has on purpose been specialised. We have nearly exclusively dealt with the problem of the chemical factors of the environment and their importance in the classification of the formations.

We think this one of the most fundamental problems in the field. It is really the only one that can be dealt with in some degree of reliability within the present framework of these studies. The lucidity which can arise from a causal grouping of different association groups, does really represent a unique case within plant biology and should therefore be considered of not small fundamental importance.

But other ecological questions have hardly been touched so that preliminary conclusions can not be considered at this stage. This would include the problem of dissemination, immigration and so on.

Some of these questions I have already included for more detailed treatment in my planktological studies. I therefore hope at some stage to be able to present a short orientation about these problems and in that way lay the first base lines for a general ecology of the limnoplankton.

LITTERATURFÖRTECKNING.

ASCHAN, O., Humusämnena i de nordiska inlandsvattnen. — Hälsingfors 1906.

BANG, O. H., Studien über schwedische Fluss- und Quellwässer. — Diss., Uppsala 1904.

BETHGE, H., Das Havelplankton im Sommer 1911. — Ber. der Deutschen Botan. Ges., 1911.

—»—, Das Plankton der Havel bei Potsdam. — Plöner Berichte 1915.

DIEFFENBACH, H. och SACHSE, R., Biologische Untersuchungen an Rädertieren in Teichgewässern. — Int. Revue der Hydrobiologie, Biol. Suppl., Bd. III, 1912.

HUITFELDT-KAAS, H., Planktonundersøgelser i norske vande. — Kristiania 1906.

KOFOID, CH., The Plankton of the Illinois River 1894—99. — Urbana 1908.

KOLKWITZ, R., Über die Planktonproduktion der Gewässer, erläutert an Oscillatoria Agardhii Gom. — Landw. Jahrb., Berlin 1909.

—»—, Die Beziehungen des Kleinplanktons zum Chemismus der Gewässer. — Mitt. aus der Königl. Prüf.-Anstalt f. Wasserversorgung usw., Berlin 1911.

—»—, Über Plankton und Seston. — Berichte der Deutschen Botan. Ges., Berlin 1912.

—»—, och MARSSON, M., Ökologie der pflanzlichen Saprobien. — Berichte der Deutschen Botan. Ges., Berlin 1908.

—»—, —»—, Ökologie der tierischen Saprobien. — Int. Revue der Hydrobiologie, Leipzig 1909.

NAUMANN, E., Bidrag till kännedomen om vegetationsfärgningar i sötvatten. I—XII. — Botan. Notiser 1911—1919.

—»—, Beiträge zur Kenntnis des Teichnannoplanktons I, II. — Biol. Centralbl., Leipzig 1914, 1917.

—»—, Undersökningar över fytoplankton och under den pelagiska regionen försiggående gyttje- och dybildningar inom vissa syd- och mellansvenska urbergsvatten. — K. S. Vet.-Akad:s Handl. Bd. 56: 6, 1917.

—»—, Försök angående vissa avfallsprodukters och gödselämnens inverkan på vattnets biologi. — Skrifter utg. av S. Sveriges Fiskeriförening, Lund 1917.

—»—, Några synpunkter angående vegetationsfärgningens produktionsbiologi. — Skrifter utg. av S. Sveriges Fiskeriförening, Lund 1918.

—»—, Sötvattnets produktionsbiologi. — Lund 1918.

PLÜMECKE, Beiträge zur Ernährungsphysiologie der Volvocaceen. Gonium pectorale als Wasserblüte. — Ber. der Deutschen Botan. Ges., 1914.

RUTTNER, F., Die Verteilung des Planktons in Süsswasserseen. — Fortschritte der naturw. Forschung, Berlin und Wien 1914.

SCHÆDEL, A., Produzenten und Konsumenten im Teichplankton. — f. Hydrobiologie und Planktonkunde, Bd. XI, 1916.

SONDÉN, K., Anteckningar rörande svenska vattendrag. — Stockholr

STEUER, A., Planktonkunde. — Leipzig 1910.

TEILING, E., En kaledonisk fytoplanktonformation. — Sv. Bot. Tidsk

WAGLER, E., Faunistische und biologische Studien an freischwimn Cladoceren Sachsens. — Diss., Stuttgart 1912.

WARMING, E., och GRÆBNER P., Eug. Warmings Lehrbuch der gischen Pflanzengeographie. — 3. Aufl. Berlin 1918.

ZACHARIAS, O., Untersuchungen über das Plankton der Teichgewäs Plöner Berichte, Bd. 6, 1898.

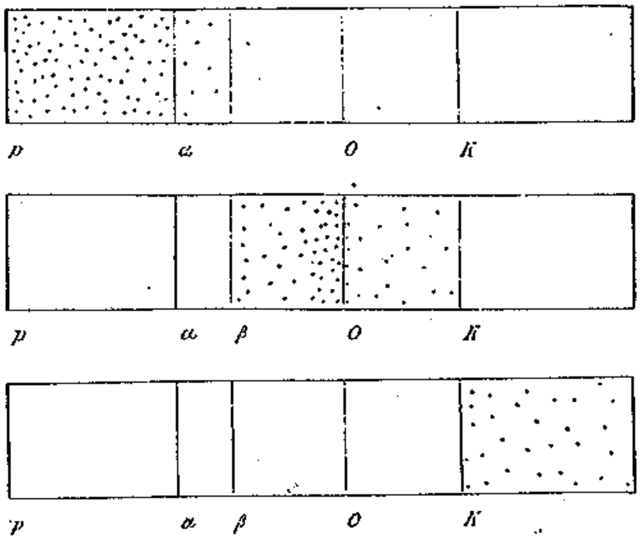

Fig. 1 (see p. 4)

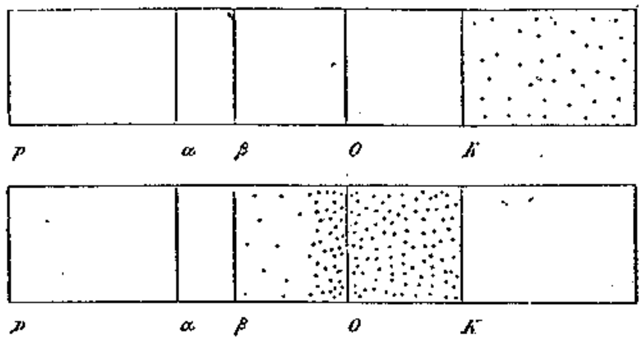

Fig. 2 (see p. 6)

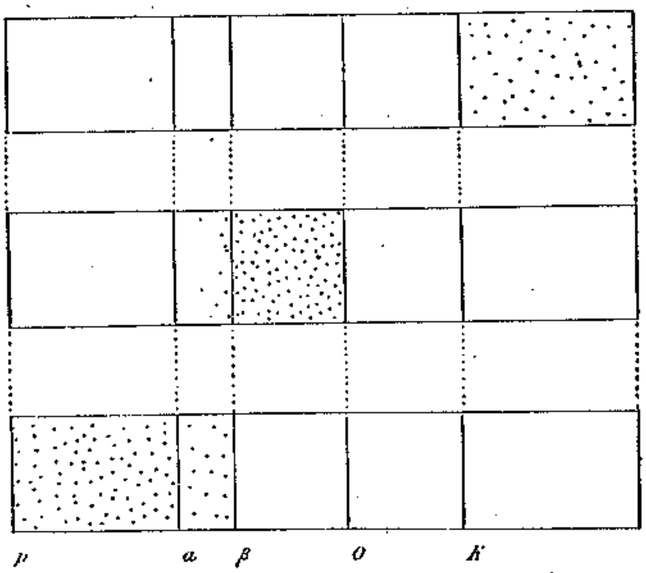

Fig. 3 (see p. 9)

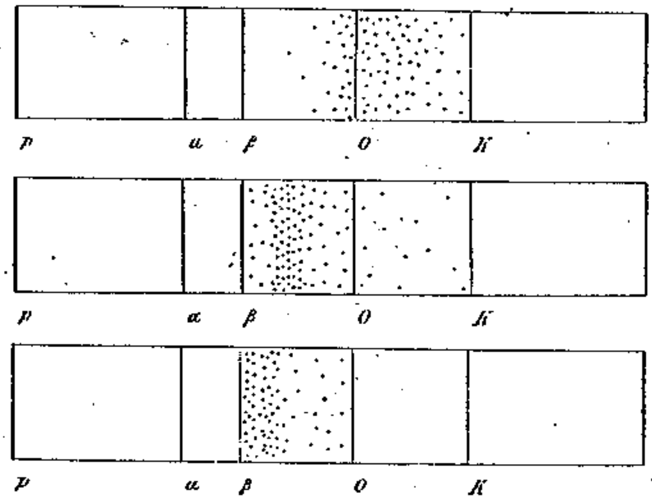

Fig. 4 (see p. 13)

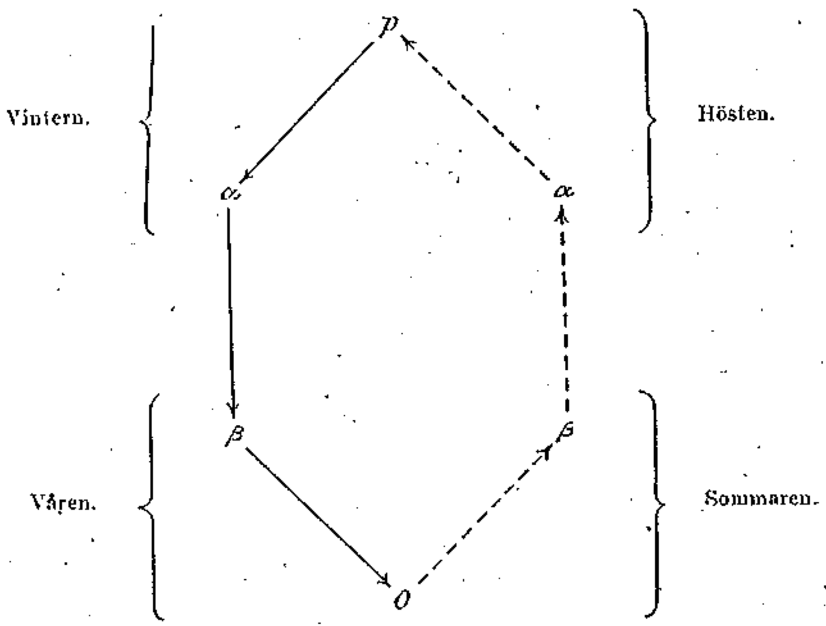

Fig. 5 (see p. 15)

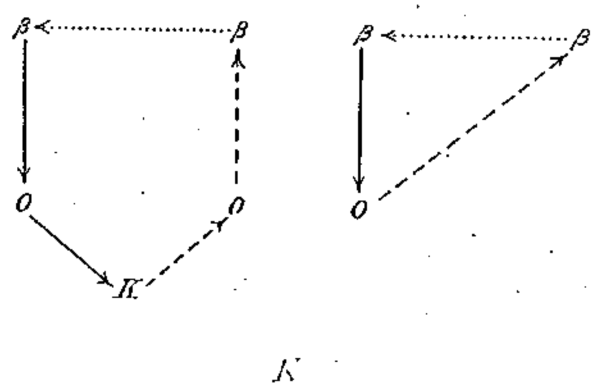

Fig. 6 (see p. 15)

Notice