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DYNAMICS, ORGANIZATION AND ECOLOGICAL STRUCTURE OF POPULATION*

Organization of population is defined as the frequency and charakter of life activities of individuals of a population generating complicated interdependences and integrating the population into an ecological unit. The effect of population organization on population numbers is illustrated by factual examples.

A discussion is given of the concepts of population organization and population structure, and the following general properties of the population organization have been postulated: a complexity of action of various phenomena of organization, mutual dependences of organization and population numbers, a certain relative inertness of organization. The organization influences on population numbers through a diversity of population elements and differentiates them and by this renders different chances to different individuals or groups of individuals.

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1. INTRODUCTION

The presented treatise is an attempt to sum up a great many papers of the Institute of Ecology, Polish Academy of Sciences, as well as the numerous discussions and views in our Institute. As a matter of fact, this is the Institute of Ecology, who is the author of the ideas presented below.

The aim of this treatise is to discuss and to exemplify the following thesis: changes in population numbers always depend, to a lesser or greater extent, on the ecological organization of the population or in other words: there are mechanisms in a population, of a feed-back character between the way of its ecological organization and its numerical dynamics, that is, in the population itself, there are mechanisms which decide or codecide upon its numbers.

Such a conception arises from the thesis well-accepted among ecologists, that a population is a real entity, the thesis which has already found its place in ecological text books (e.g. Park in Allee et al. 1949, Naumow 1963), and which was formulated distinctly by Odum (1959, p. 146) who wrote: "population and community are real entities, even though one cannot usually pick them up and put them in the collecting kit as one would collect an organism. They are real things, because these group units have characterestics additional to the characteristics of the individuals composing them". And further, describing the population properties (o.c., p. 149) he says that "it has a definite organization and structure which can be described".

The idea of the dependence of population numbers upon population organization and structure is the underlying concept of a great many papers and theoretical considerations published in our Institute (e.g. Petrusewicz 1957, Petrusewicz, Ryszkowski, Tarwid 1958, Andrzejewski, Wrocławek 1961a and 1961b, Wierzbowska, Petrusewicz 1964, Petrusewicz, Andrzejewski 1962, Petrusewicz 1963a, 1963b). Further, we will try to generalize these considerations and the results of the material papers as well as to define exactly what we consider under the concepts known in ecology as "organization" and "structure" of population, and also to point out the known or presumed mechanisms by which the ecological organization can affect the population numbers. We are conscious that many of the ideas presented here are highly controversial.

2. ECOLOGICAL ORGANIZATION OF POPULATION. ITS DEFINITION

In any group of individuals of a species inhabiting some environment, various interdependences and relationships appear between individuals. These relationships integrate this group into specific entity – the population.

These interrelations can be direct, such as any kind and intensity of mutual effects of the individuals arising from the direct contacts between them (e.g.

cannibalism, killing or fighting, repugnance from certain places, the stress phenomenon, association, cooperation, collective search for food or collective hunting, reproductive activities, etc.).

Interrelations between population components can also be indirect, occurring through favourable or harmful changes in the environment, as a result from the same interest in the common food or in other environmental requisites, common attitude towards the same predators, etc.

All of these interrelations which integrate individuals into a population, their character and – what is very essential – also their frequency (probability of occurrence) as well as the spatial distribution can be defined as the ecological organization of population.

These interrelationships among the population components can exist due to the normal, everyday activities of the organisms. These activities depend, of course, on the property of the species, such as its ecological requirements, ecological valence, the way in which the species utilizes the environment, the type of reproduction, the character and degree of activity, whether it lives in flock, colonies or in solitary, the way it gets its food, and so on. and the like. However, they can also depend on the actual ecological conditions found in the population at the very moment. All of this is quite obvious and, said like this, becomes a truism. What is essential is that the character and frequency of life activities in one species, or even in the same population, can be entirely different, and therefore different can be also the organization of population of the same species.

The character and frequency of life activities can differ, since each species, not even excepting the most stenotope one, has for any life activity a broader or narrower range of possibilities; only some of these possibilities, different at different times, can be performed.

Which life activities and their character and quality from ammong the vast range of species possibilities are performed by the animal, and at what frequency, depends entirely on the existing (previously generating) organization of population in the particular ecological conditions. Such a dependence is alvays found, since in any population, i.e. a group of species representatives living together in an environment – the definite numerical relationships become established (e.g. size of population, i.e. absolute number of individuals, density, i.e. numbers per surface unit, sex ratio, age ratio, etc.), and naturally, individuals are distributed somehow in space.

Numerical relationships and the type of distribution are usually defined as the ecological structure of population (Odum 1959). Therefore, the character and frequency of life activities for a given species and under given ecological conditions depend obviously on its structure (i.e. the numerical relationships and the type of distribution).

Life activities of organisms, leading to interdependences among individuals and causing the integration of population, can be termed as intrapopulation processes (or inter-individual processes).

Thus, the following definitions can be given of the concept of "organization of population": it is the concept that involves both the population structure and intrapopulation processes (functions); it is the defined kind of existence of population; or still in other words, the ecological organization of population is the frequency (probability of occurrence) and the spatial distribution of certain life activities of population's individuals performed from the vast range of species possibilities. Due to these activities, a complicated net of interdependences originates which intergrates the population into an unit, and decides or co-decides upon the chances of each cohabitand and, through this, upon the population dynamics.

Many ways are conceivable through which the population organization decides upon the chances of each individual.

One of them can be stress, the phenomenon well-known in the literature (Vogt 1954, Chitty 1960, Christian 1961).

We have mentioned the direct interdependences among the population components. It should be emphasized that, from the standpoint of influence of population on its individuals the range of life activities that can be performed not only among the individuals of one species but also within the same population can be very broad; in the same population, in different times or different pointe of space, opposite types of action (e.g. agressiveness or cooperation) can exist, and thefore the effect of activity of a given individual (or category, or group of individuals) on the chances of cohabitants can be entirely different.

The effect of organization of population "life" can proceed through modification of ecological factors that affect the individuals. It is conceivable that the climatic factors can exert quite different effects depending on spatial distribution of the organisms (occupation of more or less climatically favourable sites). Also the type of life activity, a phenomenon highly dependable on numbers and distribution of organisms, can affect differently the chances of organisms to find food, or their exposure to predator attacks, etc. Or, as the real observations have shown, migratory and settled forms in population have different chances to escape predators.

The operation of ecological factors, in turn, can bring about a change in the reaction standard of individuals, in the type and frequency of performance of their life activities (changing the population organization); it can also result in secondary changes of the direct or indirect interdependences, influencing by this further chances of cohabitants. These changes can be of the triggered processes character.

There are many ways through which the ecological organization of population can modify the effects of ecological factors, and thus it can affect the chances of some groups or categories of individuals. Certain groups can become more exposed to an action, the other groups – protected from it, and this is the way in which the ecological organization can decide or codecide upon numbers of individuals in a population.

The ecological organization of population can be highly diverse and of many aspects. In one time, some of these aspects are more clearly expressed and play an important role in the existence of population; and in another time – the others. Without claming to give a complete description of the known ecological phenomena which form this what we call the population organization, we will present a number of examples for better illustration of the idea which we put into this term. We will try to select, whenever we can, such examples of manifestation of population organization through which we will be able to show the dependence between changes in population numbers and in the character of organization. Exemplifying various manifestations of population organization and structure, we will rely on our own results obtained in the Institute of Ecology rather than giving broad discussion of the literature data.

3. MANIFESTATIONS OF POPULATION ORGANIZATION

3.1. Numerical relationships

3.1.1. Size (number of individuals) of population

The simplest feature characterizing the organization of population is its size. Size of population can be evaluated by measuring the population spatial range or by the total number of individuals. These two measurements form some elements of population structure, and therefore, they express, to some extent, the organization of population. It is rather obvious that number of elements can define a great deal of organizational phenomena, e.g. the probability of occurrence of a definite life activity. There are also numerous data pointing to the fact that the size of population can be a very essential factor in determining further chances of the population.

Wright (1949), analysing mathematically the population genetics data, has found that the rate and extent of genetic changes in population differed with population size. According to him, the most rapid changes occur in the smallest populations, and slowest changes in the average sized populations. The deepest changes are in the populations of the large size. These facts are in accordance with numerous evolutionary data. Simpson (1950) has accepted them also for the paleontological data.

In Institute of Ecology, investigations have been carried out on the dependence between the size of environment and numbers of self-ranging, confined populations of: *Paramecium caudatum* (Grębecki and Petrusewicz 1963), *Tribolium castaneum* and *T. confusum* (Petrusewicz, Prus, Rudzka 1963), and white house mouse (Petrusewicz and Trojan 1963). In all of these experiments, the varying ecological parameter was the size of environment, all other environmental conditions being constant for a given series of experiments. Results, as gathered and generalized by Petrusewicz (1963b), showed the same regularity for species belonging to protozoans, insects, and mammals: an increase in total numbers of individuals with the increasing size of environment (average numbers for the whole experimental period or for any given moment). However, the increase in the total population numbers is smaller than that of environment, therefore, the relative abundance (number of individuals per unit of environment) decreases with the increasing size of environment (and of total numbers of individuals in the population). One can assume that, since all other ecological factors were for a given species constant, the size of population, as measured by the total number of individuals, was the factor determining population numbers. It should be emphasized that this general regularity holds for representatives of such taxonomically and ecologically different groups.

3.1.2. Density (relative abundance)

In every moment of its existence, each population possesses certain density. Its density can be considered as the manifestation of numeraial relationships, but it can be also considered as the simplest expression of spatial organization, since it expresses the number of individuals per unit of space.

The role of density is very important, and sometimes decisive for further chances of population. In many investigations, the effect of density on manifold life manifestations of individuals has been ascertained, and also the way density may possibly influence the population changes. These problems are rather well-known in ecology, there are many generalizations concerning this topic, e.g. Allee (1931). From this work, based on the vast ecological material, it is evident that density can affect such diverse and significant life processes as quantity of food consumed by an individual, fertility,survival, resistance to various poisons, sex determination, respiratory rate, etc. Generalizing these data, Park (in Allee et al. 1949) pointed out that there are two types of dependences which are possible between these diverse individual processes and density (Fig. 1). He considered as more general the curve that showed maximum intensity of a process at a certain density, but not the lowest one, and called this relation Allee's principle.

Thus, one can see that effect of density on individuals is universal; affecting very important life processes, it can influence the numbers. This has found its manifestation in the theory of density-dependent factors. According to this idea factors, whose adverse effect increases with density, control population

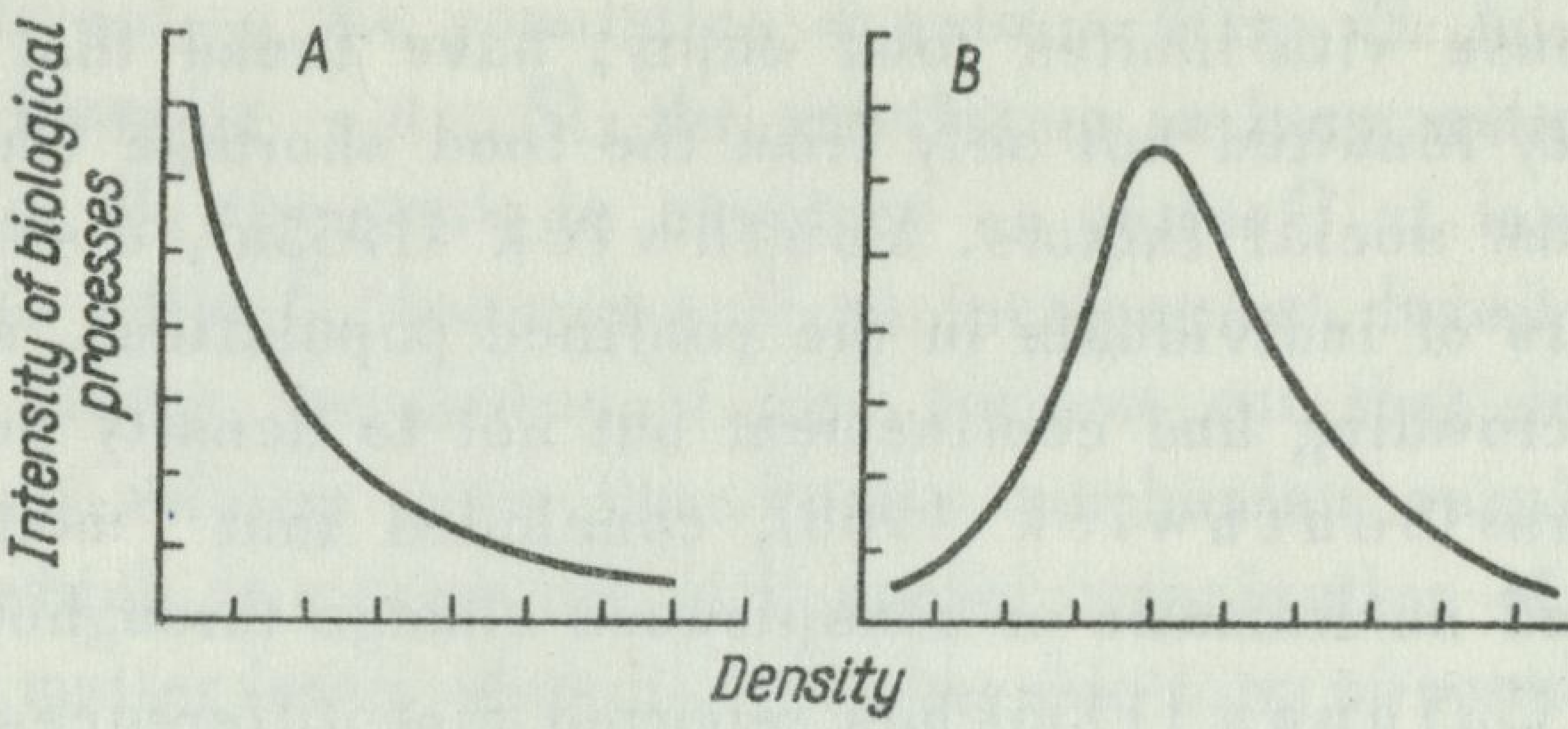

Fig. 1. The density effect on the course of biological processes (after Allee and others 1949)

numbers. This approach has a great many followers who believe that the processes which determine population numbers (determination of numbers) and maintain them at a given level for a long time (regulation), are mainly (or even exclusively) based on the density-dependent factors. This view became generalized, for example, by Park (1942), who presented a model of a population oscillating between two different levels of density; or in numerous works by Nicholson (1950, 1954, 1957), and also in paper by Varley (1947) and in collective works as that by Allee et al. (1949).

There are also many opponents to these views, let us but mention Andrewartha (1961), Andrewartha and Birch (1954), who fiercely criticized the whole theory. The discussion concerning this problem, so violent in ecological periodicals several years ago, ceased recently, but the dispute seems to be still unsolved.

We have decided to present here only verbal, most general view on this matter without going deeply into details or attempting to prove it: 1) on the basis of the literature data (we have no data of our own on this subject), one can assume that there are some cases when population numbers are determined and controlled by density-dependent factors, but certainly it is not the only way the population can be controlled in nature, or even not the most common one; 2) it seems to be unjustified to divide ecological factors into density-dependent and density-independent, since any ecological factor can become either density-dependent or density-independent, according to the ecological situation of the population.

There is no doubt that such an aspect of population organisation, as that of density, is extremely essential and some ecologists consider it as the exclusive or main mechanism of population control. Therefore, there is no need for further exemplification of this view. On the contrary, we shall show a number of works whose authors conclude that changes in numbers of investigated population were not dependent of density.

Strecker and Emlen (1953), for example, studying the confined populations of house mouse with limited food suply, have found that the observed decrease in natality resulted not only from the food shortage (thus, from density), but also from social factors. Southwick (1955a), discussing factors that limited numbers of individuals in the confined populations, says that they "were related to crowding and confinement but not to density per se". In one of his recent papers (Southwick 1958), concluded that "mortality rates of populations revealed no dramatic or conspicuous change throughout the density classes studied". Calhoun (1956) has reported that differences in social behaviour affected the population growth in various tribes of mice examined.

On the basis of three-year observations on four confined populations of *Microtus arvalis*, Wijngaarden (1960) concluded that there are some ecological processes, of a great importance for population existence, that do not depend directly on density. He write: "In general, I may say that mortality was not density-dependent in these confined populations, not even in juvenile age classes".

In his most interesting paper, Anderson (1961) presented a list of works that deal with factors determining numbers of house mouse populations. This presentation indicates that, according to these authors, at a high density numbers depend mostly on social hierarchy, at an average density – on tendency to togetherness, and on territorial relationships – at low densities.

In several works carried out in our Institute (e.g. Petrusewicz 1957, 1963a, Petrusewicz and Andrzejewski 1962) it was found that survival of litters, mortality and natality in the confined population of white mouse are not density dependent. Attention was drawn (Petrusewicz 1963b) to a considerably different value of the identical density in relation to the phase of population cycle. And so, with the identical density (the same numbers of

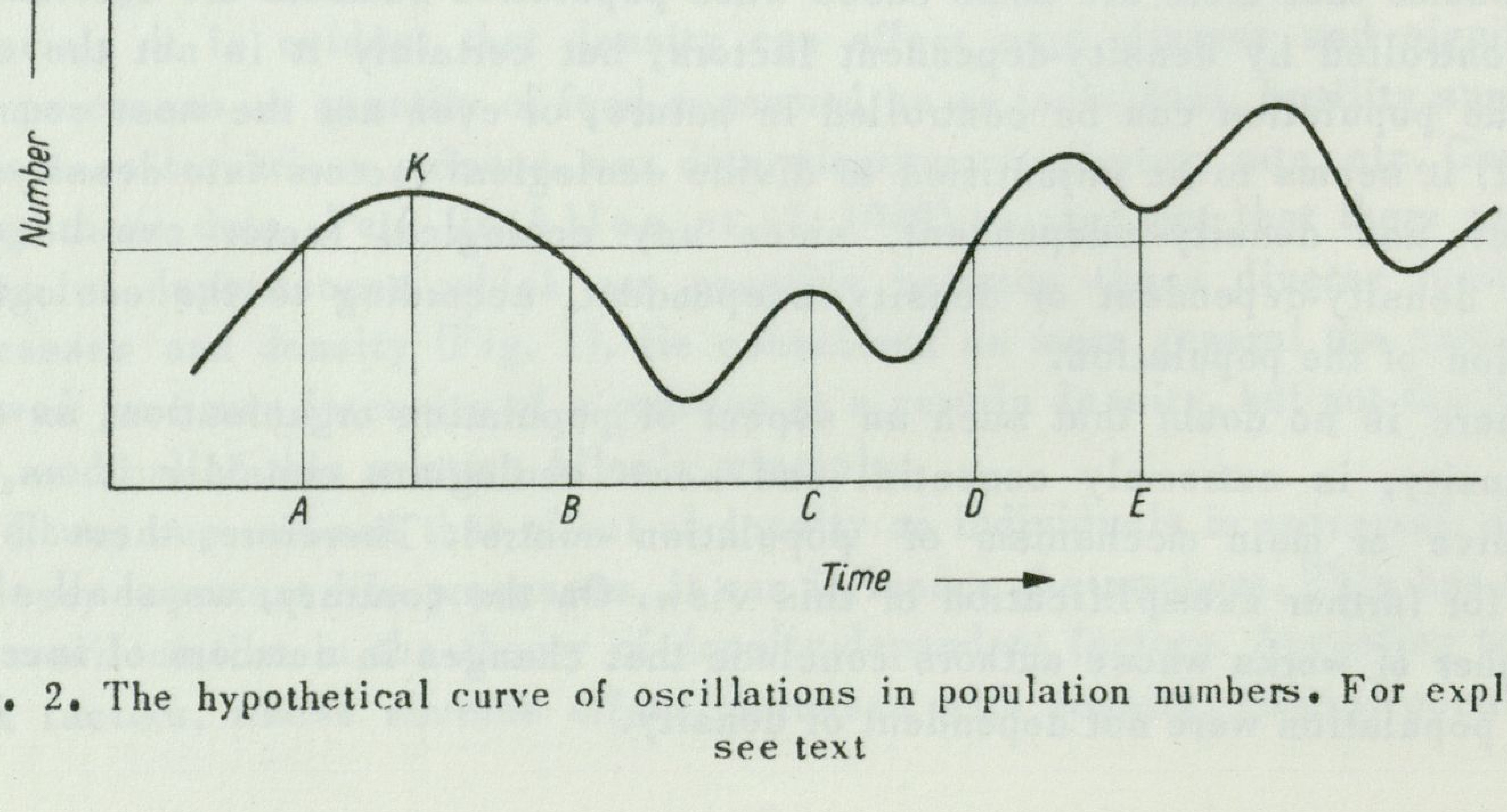

Fig. 2. The hypothetical curve of oscillations in population numbers. For explanation see text

individuals in constant environment P), the state of population can be something entirely different in the population dynamics (Fig. 2). At the same level of n individuals (density – $n : P$), the population is increasing in points A and D, decreasing in B, the peak is observed in point C at lower density, and the depression in point E (beginning of an increase) at density higher than $n : P$.

Studying these population it was pointed out that such populations can existe for an infinite time due to the mechanism regulating numbers, the mechanism which is connected with social organization of population (we will discuss this matter later, when considering this form of population organization). Here, one should also mention numerous papers dealing with stress effect (e.g. Chitty 1960, Christian 1961). In these papers, the presence of other individuals, and the indirect dependence of stress and density, are often mentioned.

All of these papers provide good evidence that there are some situations, when population numbers are not density dependent or, at least not only or indirectly density-dependent. Although density is an extremely important element in population life, other forms of population organization must also exist that affect population existence and population dynamics.

3.1.3 Age and sex ratio

The literature dealing with age and sex ratio in population is very abundant. Further chances of population can depend considrably on a given sex ratio of age structure of this population. And, contrarily, the age and sex structures of population can be modified and determined by the actual state of population. In confined mouse populations, for example, females prevailed over males much more when population was in its depression rather than in its maximum numbers (Petrusewicz 1960). In nutria, the 24-hour cycle of activity is different for young and matured animals (Ryszkowski 1962). Pinowski (1965) reported that mainly young tree sparrows of late broods underwent depression.

3.2. Spatial organization of population

Dependences and relationships among population components always occur in space, and that is why spatial organization is one of the better explored aspects of population organization.

As we have already said, the simplest characteristic of spatial organization of individuals in a population is number of individuals per surface unit, or density; the simplest and in some cases the most important, it is difficult to overestimate these matters, but certainly not the only one possible. Organization of individuals in space reveals a vast scale of ecological phenomena (states or processes) that create different levels of probability for individual contacts, and they also form the basis for stimulation and even determination of the character (tolerant, protective or antagonistic) of these contacts. We will only indicate some of these phenomena. Distribution can be even, random, or clumped. Home ranges can show an overlapping tendency (cruising range), or they can be defended areas (territories). The way in which an animal utilizes its life space can differ; an animal can penetrate the whole territory randomly, or only certain paths, or it can show preference to certain places, etc.

It is quite obvious that spatial distribution and the way in which certain individuals (or groups, or categories of individuals) utilize the space can essentially affect the survival of individuals; thus, it can influence or determine the population numbers.

In various ecological conditions, even for one species different manifestations of spatial organization can occur, which affect differently the chances of survival of certain individuals (their groups or categories) and population life phenomena (e.g. activity, number and character of individuals, degree of migration, probability of exposure to enemies, etc.). The spatial organization renders unlimited life possibilities, the possibilities of different probability to survive for individuals, groups of individuals or categories. Thus, it can affect the population numbers, but, on the other hand, it can be also affected by them. These problems have been known in ecology for a long time. In literature, there are many works generalizing and summing up these problems, let us but mention the views on interdependences among individuals in the population by Alle et al. (1949), these on spatial organization of species and on geographical population by Naumov (1956, 1963), or considerations on biological significance of territorial behaviour by Lack (1954).

In confined mouse populations which were bred in cages with dimensions up to 160 by 80 cm, no differences were observed in utilizing the life environment between individuals. Nevertheless, the population was somehow associated with the given cage. Shifting the population to other cage, no matter if larger, equal, or even smaller, brought about an increase in population numbers (Petrusewicz 1957).

A male in its own cage wins over another male from other cage (Petrusewicz 1959, Petrusewicz and Wilska 1959, Petrusewicz and Andrychowska 1960).

Populations bred in compartments with a surface of 6 m² and of rather complicated interior showed some elements of spatial organization: at daytime, animals stayed in certain nest boxes, generally they stayed more often in some parts of the compartment than in others (unpublished data), and some of the individuals were more often captured in certain, always the same, places (Andrzejewski, Petrusewicz and Walkowa 1959).

In the unconfined mouse population at the attic of the Field Station building, mice showed a strong attachment to the definite feeding points. The degree of attachment depended on the total population numbers: it was higher in periods of high numbers and smaller in periods of depression (Petrusewicz and Andrzejewski 1962).

Populations of small forest rodents showed "pulsations" in the size of home range depending, to a certain extent, on numbers; and clearly uneven utilization of space, not always justified (at least for observers) by microphysiography of the terrain (Andrzejewski unpublished data). Migrating forms of these rodents less often visited these places which were frequently occupied by settled individuals (Opuszyński and Trojan 1963).

In many instances, the dependence was ascertained between the degree of clumping and density.

In the semi-free population of nutria, the overlapping territories were observed. At the same time, due to an atnagonistic reaction between individuals, the spatial distribution becomes more even with increasing numbers of the animals (Ryszkowski 1962).

The type of distribution and number of eggs in egg masses of the Colorado beetle alters the chance of eggs being destroyed or escaping predators (Kaczmarek 1955). The pattern of distribution of *Collembola* becomes more clumped with a lower total density (Kaczmarek 1960).

3.3. Migration

Migration is a form of existence of organisms in space, or a way of utilization of space, and thus the way in which a group of organisms (population, subspecies, species) organizes its life in space. It affects considerably and often directly the dynamics of population. We are far from discussing the obvious effect of emigration, imigration, or colonization of new environments on numbers. These matters are well known, have been often discussed, e.g. the excellent analysis of biological significance of migration given by Naumov (1963), or the species-forming role of migration and isolation discussed by Mayr (1947). We would rather deal with the phenomenon that we had termed earlier as the intra-population migration or micro-migration (Petrusewicz 1963c). This phenomenon depends on the fact that in any population, there are some individuals that are not settled, i.e. they have no permanent home range or cruising range, but wander around (actively or passively) within the population (sometimes they pass from one population to another which is adjacent). This form of population life organization in space can have a great, sometimes decisive, effect upon population numbers.

The significance and role as well as cause and effects of this type of migration were extensively discussed at the Symposium of the Ecological Committee. Pol. Ac. Sci. (Stańczykowska and Wasilewski 1963, Andrzejewski, Kajak, Pieczyńska 1963). Now, we will present here several examples. The relation between migration and density was observed in forest birds (Wasilewski 1961), in tree sparrow (Pinowski 1965), and in *Viviparus fasciatus* (Stańczykowska 1959). In *Calandra grenaria*, the migratory pattern follows the Allee's rule: the smallest migration is observed at the average densities (Sandner 1959). Rudzka (unpublished data) has found that in *Tribolium* migration brings the population to a certain level, and then it decreases. Pieczyńska (1964) has reported on the passive migration of peryphyton nematodes decreasing with the age of population.

In a number of studies on small rodents, it was found that adders prey mostly on the migrating individuals (Pielowski 1962). In traps, the mortality of migrating mice was higher, than that of settled individuals (Andrzejewski and Wrocławek 1961a). The fleas fauna found on migrating and settled mice differed (Janion 1960, 1961).

These examples demonstrate the dependence between migration and: density, sex or age structure, social organization, i.e. the phenomena that have some bearing on numbers. They indicate that the extent or state of migration in population, the ratio of migrating forms to settled ones, the migration rate, and random or selective migration of certain groups (age, sex or spatial groups) are the phenomena that decide, to a greater extent, upon the further chances of population as well as upon its elements (individuals, groups or categories of individuals). It should be emphasized that migration is a process which imposes the specific type of population organization, differentiating markedly the components of population into uneven elements.

3.4. Togetherness

Intrapopulation grouping of individuals can be another aspect of population organization, known in its ultimate form as flock or colonial life. In this case, the population element is not an individual but a flock or colony (e.g. bees or ants colony).

Tendency to associate among individuals can result secondarily from spatial distribution, however, it can be also independent from it and result directly from relationships among individuals. Division of a population into more or less long-lasting, and more or less distinctly outlined separated groups, can affect very different ecological processes such as the way of utilization of space, the probability of encounter between population elements, the character of these contacts; it can differentiate individuals into these belonging to a given group, and those which do not belong to it, etc.

In house mice, bred in cages of a surface of 6 m², a formation of such groups was observed; the groups consisted of individuals that more often stayed together, and, sometimes, distinctly separated from other groups or solitary individuals (Report presented at the AAAS meeting 1962, and the Institute data being elaborated by Petrusewicz and Walkowa). These groups were loosely connected with a certain place, they were rather based on contacts among individuals.

Some groups (perhaps territorial ones) in the free-living mouse population at the attic were inferred from the fact that males showed flea infestations persistently different from the rest of population, in spite of the fact that fleas were several times removed from these individuals (Janion 1960).

3.5. Social organization (hierarchy)

The phenomenon of social organization in animals, known as hierarchy of domination or social hierarchy, is a common way of arrangement of relationships and dependence existing between population elements; it is one of the better studied manifestations of ecological organization in population. The phenomena of hierarchy can be very diverse; sometimes, it can be an arrangement of domination into a kind of ladder, known as "peck order" (Allee 1931) – this type is most often found in flock animals. It can be also the domination of one or a few individuals over the others, termed by Allee (1931) as "peck right", described for mice by Uhrich (1938). Dominance relationships occur in space and this supplies a rich scale of complicated dependences. Domination can also occur as a partly defended home range, with its utmost form of thoroughly defended territory.

What is most essential is that social organization differentiates the populatin composition into uneven elements.

In white mouse populations bred in compartments with the surface of 6 m², it was found that the male which was the first dominant on the floor can be surrendered to the other male in other places of the compartment e.g. on shelves with nest boxes (unpublished data). Domination can differ in the feeding box or outside of it (unpublished data of the Institute of Ecology).

As it has been revealed in numerous investigations, at least in the confined populations of mammals or birds, hierarchy is one of the aspects strongly influencing chances of survival of individuals as well as of the whole population. Frequency of fights, degree of antagonistic attitudes among individuals and its further consequences such as cannibalism especially of the litters, quantity of food consumed, natality and the type of copulation, all this depends on the state of hierarchy (Southwick 1955b, Petrusewicz 1957, 1963a). In white mouse populations bred in compartments with the surface of 6 m², it was found that the main dominant can occupy a number of nests, whereas the individuals that are low in hierarchy stay for nights in bunches, over ten individuals each, in one nest, sleeping in piles one over the other, sometimes in three layers (unpublished data of I.E.). Trappability of males (in traps) is not a random phenomenon: males that take high position in hierarchy show higher trappability, and those low in hierarchy show lower than the random trappability (Andrzejewski, Petrusewicz and Walkowa 1959).

Basing on a vast material of observations carried out on about 150 populations (the total time of observation amounting to 3000 months), and on the results of experimental studies on the induced growth of population, it was possible to put forward a thesis that it is social organization which is responsible for both the determination and control of numbers in confined mouse populations (Petrusewicz 1957, 1960, 1963a). In these populations, social organization was what we call the density governing factor. It is in agreement with the Anderson's (1961) thesis, according to which social hierarchy in house mouse populations with high density defines their dynamics.

On the basis of the above discussed analysis, the probable regulatory mechanism was formulated; its abbreviated form cited after Petrusewicz (1963a), is as follows: Normal and healthy mice, usually the majority in a population, are always potentially capable to multiply and increase their numbers. Hence, after a preliminary period of organization, characterized by aggressive relations between males, a certain hierarchy becomes established, which is based on mutual discrimination of particular individuals. Next, numerical increase leads eventually to overcrowding. This cannot be gauged by any reference or standard density, but may become manifest at widely varying densities. Density as such is a purely statistical notion (number of individuals per unit area); it obviously can – but need not – have important biological consequences, such as shortage of food or space. Overcrowding, on the other hand, is a biological notion, meaning excessive density from the standpoint of an organism. Hence, the symptoms of overcrowding are invariably biological.

In confined populations of mice, overcrowding is manifest in a conspicuous increase in aggressive encounters (noncompetitive fights between males). During overcrowding (1) fecundity diminishes or ceases, and (2) survival of litters (to the age of 3 weeks, when they become self-dependent components of the population) diminishes, or (usually) become ail, which together with (3) an at best unchanged, but usually increased adult mortality either lead to a decline, or keep population size at some constant level, sometimes over many months.

The simplest is the mechanism that abolishes survival of litters. It is released by noncompetitive fights among males, which become eminently numerous during peaks, i.e. during overcrowding period (Brown 1953, Southwick 1955b, Petrusewicz 1960). The increased number of fights among males triggers, as it were, a number of processes: fights between females, lack of care of the young (which are often seen outside the nest), trampling (and crushing) of litters, and finally general cannibalism (Brown 1953, Southwick 1955b, Petrusewicz 1957, 1960, and present observations).

More complicated is the machanisms of fecundity failure or diminution. During overcrowding, per capits food intake diminishes as a rule, even though food is overabundant. In starved females the oestrous cycle is known not to run the complete course, and the females are not ready to be fertilized. To these another factor must be added: inadequate copulation. Hence, even in spite of excessive copulation there is often, perhaps even usually, no fertilization.

These processes adequately account for the decline or failure of both fecundity and survival of litters, which eventually arrest population growth.

Yet another phenomenon is worth noting: the fairly high permanence and a certain "inertia" of the population structure responsible for growth inhibition. Increased fighting among males lasts short, a few or several days. But infecundity and litter mortality often continue for months on end. All sign of overcrowding has vanished, and the populations still fails to grow.

We cannot say why growth is resumed (i.e., why the growth-inhibiting processes cease to operate or become ineffectual). The following is the usual, though not invariable pattern. Fecundity rises, but cannibalism still inhibits growth. It even happens that relatively brief increased fecundity subsides again without having caused growth, or alternatively, continues even some months but is offset by the devouring of all litters. Eventually, mortality of litters diminishes or becomes nil, and than the population resumes growth.

The usual pattern is the following. At a peak growth ceases (failure or decline of fertility, cannibalism), and adult mortality rises: the population diminishes. Next, adult mortality returns to normal and growth remains absent: the population continues on a constant low level. All we can say is that such disinhibiting processes exist, since in far the most cases the decline that follows a peak does not wipe out the population; it become arrested, and growth is resumed.

Resumed growth means that inhibition has been abolished. And the inhibition – as we have sought to demonstrate – was conditioned by some specific relations between the members of a populations, i.e. by the population's structure. Hence, removal of the inhibition may be supposed to have connexion with a change in population structure. This surmise may be made oven though we do not know the exact mechanisms responsible for disinhibition.

Some light is shed on the process by the experiments[1] already described (Petrusewicz 1963a), and by the studies on growth induced by a changing cages (Petrusewicz 1957). In either the population was subjected to an experimental shock (change of cage, and removal or addition for a time of a few

[1] The experiment consisted of removal several females (or males) from the populatior for a period of about one week, or on introduction of virgin females, also for one week. After that time elapsed, the removed individuals were reintroduced to the population, or the additional females removed from it (Petrusewicz 1963).

individuals). In consequence of the shock, the growth-inhibiting relations that have become established between population members vanish; the natural upward trend is resumed and the population growth.

To sum up: underlying the mechanism of growth regulation in confined populations of mice is a permanent capacity for multiplication and its periodical inhibition (at population peaks) by partial or complete failure of fecundity and increased mortality of sucklings. The inhibitory factors, such as undernourishment (failure of oestrus), probably resorption, defective copulation, and devouring of sucklings, are released by more frequent noncompetitive fights among males. These inhibitory factors may be operative over an appreciable period of time. Usually fecundity is restored first, and only then subside cannibalism and mortality of suckings. The mechanisms responsible for fecundity restoration and suppression of mortality of sucklings remain obscure.

4. GENERAL REMARKS ON POPULATION ORGANIZATION

It is obvious that the above given examples do not make a complete list of diversity found in ecological organization of population. Other aspects can be still mentioned, one can further illustrate the complexity of the discussed phenomena. It seems, however, that the general outline has been already drawn, and there is no need to supply further examples. Instead of this, we will discuss some general regularities characteristic for all or most of the phenomena defined here as the aspects of ecological organization of population.

4.1. Population organization as a whole

We have discussed various aspects or manifestations of population organization and their effects on population numbers. Such a partition into several aspects was, of course, a kind of simplification. Organization operates as a whole, as a complex of phenomena; the perticular manifestations of organization are intermixed and connected each other. Let us but mention that all the phenomena of life processes (therefore, also these that affect other individuals) occur in space and always involve the define number of individuals. The probability of occurrence of each phenomenon will always depend on number of individuals involved and their distribution in space. Usually, this dependence concerns not only the frequency of phenomenon, but also its character; the character and frequency of life phenomena affect, in turn, the distribution and numbers of individuals in population. All this causes that organization of population is a kind of resultant and as a whole[2] it affects or decides upon further chances of individuals, their groups or categories, and finally upon

[2] This is analogous to environmental factors: analysing them, one can speak about humidity, temperature, etc., but they affect an organism as a whole.

the entire population. One can discuss separate manifestations of population organization such as, for example, social or spatial organization, only for the practical and exploratory purposes. This, of course, does not deny that at one time some manifestations are of a greater importance for the future of population, and at another time – the others.

4.2. Diversity and differentiation of population elements

Attention should be drawn to the fact that the phenomena discussed above as the aspects or manifestations of population organization are based on uneven values of population elements. In any situation, when we were able to point out the effect of population organization on population numbers its mechanism was always differentiating the members of population, putting them into different conditions and giving different chances to various elements of population (to individuals or some categories of individuals). It seems that this is a common and general regularity of the way of living of each population. Further, it seems that the main mechanism through which population organization can affect population numbers, does not usually depend on an increase or change in mortality, natality and survival of all individuals, but on creation of different chances in population for certain groups and categories of individuals. These categories or groups differ from the organizational aspect (e.g. migratory and settled forms, dominant and subdominant, individual of different age or belonging to a given group and that which does not belong to it, individual within a group and outside of it, etc.). Naturally, one can conceive such manifestations of population organization that will concern equally all the individuals for example, the daytime and night activity, but we suppose that the regulatory processes, resulting in permanent existence of population, are mainly based on phenomena which differentiate individuals in population.

4.3. Relative stability of population

The ecological organization of population can reveal certain interness, the ability to exist for some time. Any population growth curve proves it clearly. In the discussed populations of white mice at overcrowding conditions (e.g. point K, Fig. 2), a certain organization of population originated which favoured mortality and restricted natality and survival of litters. Population numbers were decreasing, in point B the curve dropped down below the level at which in point A the numbers were increasing, and it was decreasing further. It is often so that in the period of decreasing numbers the overcrowding phenomena are not traceable already, nevertheless, mortality prevails over natality and population numbers decrease further for some period. The situation, when slow decrease or maintainance of numbers at a certain level may last for several months, almost a year, was often observed in the examined populations of white mice. At the same time, the individuals were apt to reproduce, since often, after such a long period of a decrease or equilibrium, the population restored its numbers. Here, again, we can observe a situation, when population, promoting an increase in numbers (relations between individuals are favourable for natality and survival of litters) continues, in spite of the fact that the numbers of the individuals had surpassed the level at which a decrease usually begins.

The property of population organization depending on ability to last for certain period in the unchanged form is extremely important. Organization of population arises in the definite ecological conditions. There is no doubt that population organization is a kind of expression of adaptation to these particular ecological conditions. If, however, a population had responded immediately and directly to an external change, it would have been hardly possible to conceive the mechanism that could modify the influence of external environment. Organization of population arises in certain, ecological conditions (environmental and biocenotic), and the action of these conditions can be modified by the already existing organization, which had been generated by a previous ecological situation. This is the relative interness of population organization that allows organization to act not only as an adaptational mechanism, but also to modify the external effects, and through this to affect these processes which are important for changes in population numbers.

4.4. Reciprocal dependence of population organization and population dynamics

Finally, the last general property of population organization has been often mentioned in the above considerations, therefore here we will summarize it only. There is a reciprocal dependence between population structure and population dynamics. The population organization of a species, arising under given ecological conditions (environmental and biocenotic), is highly dependable on population dynamics, but it can affect, in turn, this dynamics (becoming the density governing factor), it can modify the effect of external environment (weaken their intensity, or even change the direction of environmental or biocenotic influences on some individuals or groups of individuals).

5. ORGANIZATION VERSUS POPULATION STRUCTURE

A broad meaning was put into the concept of population organization. It involves the states of population (e.g. sex or age ratio, clumped or random distribution, the size and configuration of home range, etc.) thus, the phenomena that can be defined as ecological structure of population, as well as processes (e.g. antagonistic or tolerant relationships, micromigration, defending the territory, activity, etc.). Thus outlined the concept involves both structure and processes, the categories of phenomena that are subjects of different disciplines of "aut-biology", namely, morphology and physiology. Such a broad scope was consciously chosen for this concept. There are premises from which one would infer that at the collective unit level such as population. The organization of population is a suitable subject of exploration and consideration — the phenomena comprising both the structure and the intrapopulation processes.

P r e m i s e 1. One of the general and ultimate aims of ecology is to learn about regularities and laws governing numbers. Hence, an ecologist is interested both in structure and in intrapopulation processes, in their influence and importance for population dynamics. From this point of view, the concept of population organization is more universal. Population dynamics is ultimately defined by natality and mortality. One can conceive two types of organization effects (of structure and of processes) on numbers: population organization can modify (1) the influence of external factors or (2) the action of individuals in population affects the chances of other individuals (their natality and mortality).

In the first type (modification of external factors), both the structure (state) and processes play an important role, for example, the distribution in space (structure), can alter the survival and reproduction of different individuals according to the place they take in the habitat. Also activity and micromigration (processes) can affect the chances of individuals, e.g. more active individuals can have better chance to find or prey, or migrating forms have different probability to become a prey than the settled forms. In this way, modifying the action of ecological (biotic and environmental) factors, the structure as well as the processes can codecide upon changes in population numbers. We have termed this combined effect as population organization.

A different situation is observed in the second type of effect, that is in that of the individuals themselves. This type of influence on survival or natality can follow through life processes of individuals. The population structure (state) itself can form only a background that affects the character and frequency of life actions.

This what we said above can be formulated in another way: the ecological phenomena that can be defined as the ecological structure of population can differentiate the effect of external factors, and those termed as functions (processes) can also modify the effect of external factors as well as affect directly the population (direct and indirect interdependences among individuals). Therefore, population organization, involving both the structure and intra-population processes, is a more convenient conceptional device.

P r e m i s e 2. In exploratory practice, it is often difficult, if at all possible, to discriminate between structure and function of the collective entities. Let us take migration as an example. The process of migration itself has the controlling and differentiating effect. It can be described by proportion of migrating and settled forms (migration structure of population), but it is difficult to express in structural categories the rate of migration – the phenomenon of a great importance. The same holds for such phenomena as protection of progeny, fights between mouse males, the aggressive, protective or tolerant relationships among individuals in population. It is extremely difficult to separate these phenomena into concepts of structure and those of functions. But these are the phenomena as we have seen, that can not only modify the environmental effect but they can also decide upon population dynamics.

Seperation of structure from function in population would lead to partition of almost any ecological phenomenon into "state" and "process", which would be extremely difficult, if at all possible.

Premise 3. It seems that the difficulty found in precise and logical discrimination between structure and function is a common phenomenon in biology. It is difficult to discriminate structure and function in biology, since biological subjects are alive, and always in certain function. This might explain why difficulties in distingushing structure and function are found even in "aut-biological" concepts. Origination of such terms as morpho-physiology can be some evidence of this: the need for a conceptional device involving both structure and function. Is the blood circulation a function or a structure? In an organism, blood circulates incessantly, when it stops circulating the organism ceases to be an organism any longer, although the structure still exists. It is an inner property of an organism that its heart beats, blood circulates, the constant exchange of matter with the external environment occurs, and that as long as the organism is an organism, inner processes follow. If such questions concerning an organism can be posed, one will imagine that the difficulties will greatly increase when considering a population, that is, not an organism but the collective entity.

Many ecologists emphasize the fact that the ecological units are mostly of functional nature. Odum (1959), for example, wrote:

"The community is primarily a functional unit; it has definite structure, to be sure, but the structural pattern is often more variable than the community metabolism pattern because the species components of the community are to some extent interchangeable in time and space".

The thesis that the collective units are mainly functional seems to be right. One can, perhaps, risk a statement that there is a great difference in the gravity of the concept of structure when related to an organism and when to ecological units (population, ecosystem). However, the exploration of the pure static structure has other (more meaningful) sense when applied to an organism, and quite other – when it concerns a collective living unit.

Firstly, the structure of an organism is an archive of its history, learning about it is one of the tools which serve to investigate evolution. On the other hand, the ecological structure of collective units reflect only the recent past, and do it ambiguously, hence, it cannot be the proper device to explore the past of these units.

Secondly, an organism is the incomparably more integrated unit, hence, the degree of freedom in performace of a given process by certain structure is much more limited than in population (a collective unit).

Thus, in ecology, even from the theoretical point of view, more suitable and helpful is the concept that would involve functioning of population and would define the frequency (probability) and character of life processes occurring in space and depending on numerical relationships. Organization of population is such a concept.

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DYNAMIKA, ORGANIZACJA I EKOLOGICZNA STRUKTURA POPULACJI

Streszczenie

Rozprawa stanowi próbę podsumowania i częściowego uogólnienia szeregu prac wykonanych w Instytucie Ekologii PAN.

Każda populacja, czyli współżyjące w danym środowisku zasiedlenie jednego gatunku jest zorganizowana w określony sposób. W pojęciu „organizacji" zawiera się zarówno ekologiczna struktura populacji jak i procesy wewnątrzpopulacyjne (funkcja).

Ekologiczną strukturę populacji charakteryzują określone stosunki liczbowe (wielkość populacji czyli bezwzględna liczba osobników, zagęszczenie czyli liczba osobników przypadająca na jednostkę powierzchni, skład wiekowy, struktura płciowa, liczebność różnych kategorii osobników, np. migrantów, dominantów itd.) oraz określone przestrzenne rozmieszczenie osobników (przypadkowe, skupiskowe lub równomierne, życie w grupach, w stadach, migracyjność itp.).

Tym co integruje osobniki w specyficzną całość zwaną populacją są normalne, codzienne czynności życiowe organizmów prowadzące do wytwarzania się między nimi wszelkiego rodzaju wzajemnych stosunków i zależności. Te współzależności mogą być bezpośrednie – jedne osobniki populacji oddziałują bezpośrednio na inne w różny sposób i z różnym nasileniem (np. kanibalizm, walki, przepędzanie z danego miejsca, zjawiska stressu, grupowanie się, współdziałanie, wspóne poszukiwanie pokarmu, aktywność rozrodcza itp.). Mogą też być pośrednie – jak np. korzystne lub szkodliwe zmiany środowiska, konkurencja o pokarm, wspólni drapieżcy itd.

Dla danego gatunku, w danych warunkach ekologicznych charakter i częstość tych normalnych, codziennych czynności życiowych, prawdopodobieństwo ich wystąpienia, zależy od istniejącej, wcześniej wytworzonej organizacji (czyli stosunków liczbowych i przestrzennych) oraz od typu procesów życiowych wchodzących w zakres możliwości właściwy dla danego gatunku.

W pracy podano szereg przykładów ilustrujących przejawy organizacji populacji i jej wpływ na dynamikę liczebności. Nasuwają się następujące uwagi o ogólniejszych prawidłowościach organizacji populacji.

1. Organizacja populacji stanowi integralną jedność. W zależności od stawianych sobie celów praktycznych lub poznawczych można rozpatrywać takie lub inne jej przejawy. Zawsze jednak jest ona z jednej strony wypadkową wszelkich możliwych przejawów, a z drugiej – wywiera decydujący wpływ na zachowanie się i losy organizmów żyjących w populacji.

2. Organizacja populacji opiera się na zróżnicowaniu jej elementów składowych, ale i odwrotnie – oddziałuje ona jak mechanizm różnicujący, który stwarza różne sytuacje i warunki, a więc daje różne szanse przeżycia różnym osobnikom, różnym ich grupom lub kategoriom.

3. Organizację populacji cechuje pewna trwałość, bezwład. Wytwarza się ona w pewnych określonych warunkach i utrzymuje się przez czas jakiś jeszcze wtedy, gdy warunki uległy zmianie. Można więc przypuszczać, że organizacja jest nie tylko mechanizmem przystosowawczym ale również czynnikiem modyfikującym środowisko zewnętrzne.

4. Istnieje stała, wzajemna zależność – sprzężenie zwrotne – między dynamiką i organizacją populacji.

Przeprowadzono próbę określenia treści pojęć „struktury", „funkcji" i „organizacji" oraz ich zastosowania do różnych poziomów zjawisk biologicznych.

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