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GENERAL REMARKS ON THE PRODUCTIVITY
OF CONFINED POPULATIONS*

It was found that in confined populations of *Paramecium, Tribolium castaneum, T. confusum* and mice productivity (from a unit of population area) decreases with an increase in the size of the population area. This is considered as a general rule, and the hypothesis that the ecological structure of the population is responsible for this phenomenon is put forward and discussed.

A series of experiments were carried out in the Institute of Ecology of the Polish Academy of Sciences on population growth, in which the variable parameter was the total size of the medium. These experiments were made using *Paramecium caudatum* (Grębecki and Petrusewicz 1963), *Tribolium castaneum* and *T. confusum* (Petrusewicz, Prus and Rudzka 1963) and white laboratory mice (Petrusewicz and Trojan 1963).

METHODS

As the methods used were described in detail in the above mentioned studies, I shall only give the most general data here.

In all the experiments the populations were confined, i.e. they had no opportunity of either emigration or immigration. All the populations reproduced freely; after the population was constituted no individuals were either added or removed.

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An abundance of full value food was maintained in all the cultures, with uniform — for the given series of experiments — temperature, lighting and humidity conditions, pollution of the habitat etc. The only variable was the size (area or volume) of the medium. The size of the media in which the experiments. were made are given in Tab. I.

Size of medium of all populations, and in mice populations: number of replications (N of replic.), and mean time of observation (months)

.Tab. I

Relative size	Paramecium ml	Tribolium g	Mus		
			m²	N of replic.	Mean time (months)
1x	100	4	0.06	12	13.0
2x	200	8	0.12	12	13.0
4x	400	16	0.23	12	13.0
8x	800	32	—	—	—
11x	—	—	0.64	61	25.1
16x	1600	64	—	—	—
22x	—	—	1.28	6	29.2
105x	—	—	6.00	4	43.6

Mice were kept in cages of different sizes, size being measured by the area of the bottom; the number of mice born and dead individuals were recorded daily.

Tribolium was cultured in dark incubator, with a temperature of 29°C and 70% humidity, in test-tubes of different sizes, of approximately the same shape. Every month (strictly speaking every 30 days) the whole population was counted and the flour changed.

Three types óf experiments were made using *Paramecium*:

1) in a non-buffered medium, with test-tubes of a constant shape, i.e. with a constant ratio of diameter of bottom to height (constant $\varphi : h$),

2) in test-tubes of uniform shape with buffered medium,

3) in a medium with a constant ratio of surface to volume (constant $s : v$); the constant ratio of free surface to volume was obtained by ensuring a constant height of the column of liquid — which gave uniform aeration in media of different size. The constant ratio of wall surface to volume was obtained by inserting small glass plates of calculated area, which gave a constant size (in relation to volume) of surface more favourable to the life of the *Protozoa*; as is well known, the great majority of *Protozoa* accumulate near the walls of the vessel (Grębecki, Petrusewicz 1963).

In further considerations we shall not give the data from the experiment

with a buffered medium, as its results did not differ from the results of the experiment with a non-buffered medium (variations in pH in a non-buffered medium were completely insignificant).

Ten replications (populations) were made in each series of experiments with *Paramecium*, and the cultures were continued for periods from 36 to 140 days; there were 15 replications in the experiments with *Tribolium*, and observations lasted for 12 months. The number of replications and average duration of cultures of mice are given in Tab. I. In all cases the duration of the observations exceeded the time in which the populations attained peak numbers, and sometimes even covered several population cycles. It may therefore be assumed that the mean numbers and density calculated from so long a period will be free from accidental fluctuations, and will correctly reflect the connection with the gradient of volume of the medium.

RESULTS

Calculation was made in all the experiments of:

1) mean numbers (N) — for the whole period of observations, for all the replications in a given series,

2) average density (D) — the number of individuals per unit of medium: density in the case of *Paramecium* means the number of individuals per 1 ml, for *Tribolium* the number of beetles per 1 g of flour, for mice the number of mice more than 3 weeks old (independent component of the population) per 1 m^2,

3) relative density (RD) — the percentage formed by density with a given size of medium in relation to density with a medium = 1x.

The results of all the experiments (Tab. II and Tab. III) show that:

Average numbers of investigated populations
(ϕ : h — constant shape of vials, s : v — constant surface/volume ratio)

Tab. II

Relative size of medium	*Paramecium* constant:		T. cas-taneum	T. con-fusum	Mus
	ϕ : h	s : v			
1x	113 500	85 700	84.5	139.4	12.1
2x	214 000	—	156.0	201.4	16.0
4x	297 200	273 600	245.5	327.2	—
8x	513 600	—	399.1	455.5	—
11x	—	—	—	—	30.5
16x	608 000	969 600	699.3	779.1	—
22x	—	—	—	—	34.1
105x	—	—	—	—	92.5

Relative density of investigated populations

Tab. III

Relative size of medium	Paramecium, constant:		T. cas-taneum	T. con-fusum	Mus
	$\emptyset : h$	$s : v$			
1x	1191 ind/ml=-100%	857 ind/ml=-100%	21 ind/g=-100%	35 ind/g=-100%	212 ind/m²=-100%
2x	83%	—	92%	72%	66%
4x	65%	80%	72%	59%	35%
8x	56%	—	59%	41%	—
11x	—	—	—	—	23%
16x	33%	71%	51%	35%	—
22x	—	—	—	—	· 12%
105x	—	—	—	—	7%

1) the total numbers of the population increase — as was to be anticipated — with an increase in the size of the medium, but

2) increase in numbers is not so rapid as the increase in the size of the medium and hence,

3) density decreases with an increase in the size of the medium.

The results obtained may also be expressed as follows: production of a confined, self-ranging animal population decreases with an increase in population area[1].

The agreement of results obtained from species greatly differing from each

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[1] The term "production" used in this study does not fully correspond to the fairly exactly defined term used in hydrobiology "net production" (Odum 1959, Windberg 1960). Of course the average density for a certain period (number from a unit of area) even if it were expressed in units of biomass or the energy corresponding to it — which would be relatively easy to do — would not be equal to the amount of organic matter produced. The biomass, or number from the unit of medium is always smaller than net production, since it does not take into consideration, for instance, the number of individuals (biomass, energy) which died or entered the population between two inspections: it does not contain the number of young individuals up to three weeks of age in the case of mice, nor the eggs, larvae and pupae of Tribolium which died before reaching the imago stage; it contains only the balance result for given moments (or the mean figure for them). In the case of species with a quick turnover, such as, for instance, Protozoa, the mean biomass calculated from mean density may differ considerably from net production. Nevertheless, if one and the same species is considered, then the mean numbers (or density) from long-lasting and frequently taken samples depend to some extent on production and may form its index. We are therefore justified in stating that the production of a population of a given species decreases with an increase in the size of the medium.

other, since they belong respectively to *Protozoa*, *Insecta* and *Mammalia*, and the actual essence of the results — the decrease in production with an increase in the size of medium — gives rise to many reflections of a more general nature, which I shall endeavour to present and discuss.

DISCUSSION

All the populations cultured reproduced freely, but their numbers did not increase without limit. After attaining a certain level, the curve of population numbers ceased to rise and usually after a certain period began to fall. Numbers were therefore regulated, the upper and lower limits of fluctuations in numbers were defined; it is true that these limits were sometimes contained in a fairly extensive amplitude of fluctuations, even for populations of the same species and in identical conditions, nevertheless such limits did exist.

Regulation could not be caused by the medium, since this was (1) experimentally rendered uniform for the populations of the given species, and in addition (2) even if it were subject to small fluctuations, these fluctuations influenced all the replications to a uniform degree. Thus the differences established above in the size of production cannot possibly be found due to environmental factors.

Neither can the biocenosis be considered responsible for these differences. The biocenosis in which the study populations lived was exceptionally poor and vestigial, there were no predators, food — so important a biocenotic factor — was always abundant, no epidemics were found during the course of the experiment, ectoparasites were few (fleas) on the mice, the experimenter fairly effectively protecting the mice from them. Thus from the aspect of the effect on the living conditions of the population, it may be said that the populations studied lived practically outside the biocenosis.

Regulation of numbers did, however, exist, and therefore its causes must be sought for within the population.

There is no doubt that density plays an important role in confined self-ranging populations. It is, however, easy to show that in the cultures investigated density-dependent population processes were not density (and therefore also numbers) governing factors. They were not, since the numbers themselves were maintained at regularly distributed different densities with marked trends.

The results obtained therefore lie to some extent on the way to the still existent and so far unsolved open problem in ecology of the existence itself of "density dependent factors" and "density independent factors", and their regulating values.

Limitation of the numbers of a confined population is, however, a fact. Although being unable to give a definite explanation of the mechanisms of this

determination of numbers, it is possible to put forward the following hypothesis, as an assumption: limitation of numbers is the result of the connections and relations between the individuals in a population, the result of the way in which they are organised, that is, the organisation of what was defined in previous studies as population structure (Petrusewicz 1957, 1960, 1963).

The character of these processes determining numbers, and resulting from the relations and interdependences between individuals in confined populations of mice, were given in detail in the studies mentioned above. The regulation mechanism in these populations may be summed up as follows: a tendency to reproduction constantly exists in mice populations; when the population attains a certain — even a different one in the same population — level, symptoms of overcrowding occur, including intensification of the non-competitive fights between males; these latter, as "triggered reactions" cause: fights between the females, less care of the young, cannibalism (in relation to the newborn mice), reduced consumption per head (with an overabundance of food) and in consequence absence of the oestrus in females, faulty copulation etc. As a result reproduction is reduced or ceases, and mortality among the adults increases (usually) — the population ceases to increase or begins to decrease.

We cannot point to the mechanisms limiting the growth in numbers of populations of *Tribolium* and *Paramecium*. In the case of *Tribolium*, cannibalism of the eggs certainly plays an important part, but we cannot say whether it is the determining factor or only one of several. It may be imagined — we emphasise only imagined — that the movements and presence of a large number of *Paramecium* may make it difficult for these animals to obtain food.

If regulating processes arise from the character of the relations and connections between elements of the population, then such interdependence between individuals which limit numbers are not a simple consequence of density. An intensification of these processes inhibiting population growth, which would equal or exceed the tendency to numerical growth of the population, are attained at different densities.

It may be imagined that the organisation of the life of these populations differs in media of different size; in media of smaller dimensions either the probability of contacts, from which the processes inhibiting population growth arise, taking place is smaller, or the character of these contacts changes. It may, for instance, be imagined that there is less activity in a smaller medium. If activity decreases, the probability of contacts would decrease also — the population could attain greater density.

It may also be imagined that a habitat so restricted for the given species that each individual can traverse it in a matter of a few seconds, that the number of contacts depends not only, or not so much on density (number of individuals per unit of medium) as on the absolute number of individuals.

The considerations so far discussed may be summed up as follows:

1) there is no doubt that there are factors determining the numbers of confined, self-ranging populations,

2) the numbers of the populations investigated are not determined by either environment or biocenotic factors, neither have they the character of density dependent factors,

3) the mechanisms regulating numbers should probably be sought for among the interdependences between individuals.

The results obtained from the above experiments lead to consideration of the ecological and individual processes. Even without knowing the mechanisms limiting numbers in populations of *Tribolium* and *Paramecium*, we may be certain that in all three species different individual processes form the factor limiting population numbers. For instance the fact that, contrary to the situation in the case of *Tribolium* and mice, by *Paramecium* there is no cannibalism; that in the case of mice organisation of the population is based on individual differentiation on between individuals. which of course is absent in the case of *Paramecium* and *Tribolium*. Nevertheless these different processes give a uniform effect from the ecological aspect: reduction of production with the increase in living space.

An interesting problem (not solved in the experiments made) is that of the scope of the above regularity i.e. if the population area were further increased, would a moment occur when productivity ceased to decrease with an increase in the size of the medium? It would seem that with considerable increase in the size of the habitat a moment must occur when production would cease to vary. The numbers of mice in an area of 2 ha would probably be twice as great as in 1 ha. Certain indications that this is the case are given by comparison of relative densities. The decrease in relative density is slower in the largest areas examined.

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OGÓLNE UWAGI O PRODUKTYWNOŚCI ZAMKNIĘTYCH POPULACJI

Streszczenie

Wykonano szereg eksperymentów dotyczących wzrostu populacji, w których jedynym parametrem zmiennym była ogólna wielkość siedliska (Tab. I). Eksperymenty te wykonano z *Paramecium caudatum*, *Tribolium castaneum* i *T. confusum* oraz z białymi myszami. We wszystkich eksperymentach populacje były zamknięte t.zn. nie miały możności ani emigracji, ani imigracji. Wszystkie populacje rozmnażały się swobodnie, po założeniu nic nie dodawano ani ujmowano.

Wyniki eksperymentów wskazują że:

1) ze wzrostem środowiska wzrasta — co było do przewidzenia — ogólna liczebność populacji (Tab. II), jednak

2) wzrost liczebności nie nadąża za wzrostem liczebności, i stąd

3) zagęszczenie spada ze wzrostem wielkości środowiska (Tab. III).

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