

ECOLOGO-EVOLUTIONAL BASIS FOR
CORRELATION ADAPTOMETRY

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Introduction

The purpose of this article is to make ecological-evolutional substantiation of a previously proposed [8, 21] method of comparative analysis of adapting populations - correlation adaptometry.

Adaptation of populations to altered habitat conditions is a process, continuously perfecting in the nature, both because of the natural reasons and due to anthropogenous effects. Human populations are subject to it, too.

Processing many years' observations, performed at the Institute of Medical problems of the North (USSR Academy of Medical Sciences, Siberian Branch), analyzing comparatively populations under different ecological conditions (Extreme North and middle latitudes of Siberia), we have come to a conclusion: correlations between physiological parameters bear most information about the extent of adaptation of a population to extreme or only altered conditions. With the adaptation load increasing, the correlation level elevates, while successful adaptation makes it decrease.

The effect of correlations between the physiological parameters, elevating due to increased adaptation load, is proved by literature data [1, 2, 13, 15, 17, 18, 24, 25].

Correlations between the physiological parameters in the course of adaptation are higher, than in adapted condition. This

effect was observed on vast and various material (indices of lipid metabolism, external respiration, enzyme activity, transport function of blood and so on) for different physiological parameters.

Under increasing adaptation load correlations can be elevated by particular mechanisms. For different groups of parameters such mechanisms are to be (and surely are) different. A question arises: what is the common cause of such effects? With questions of such generality arising, it is natural to turn to evolutionary explanations.

We suppose, that this effect can be explained by the following ecological-evolutional law: selection and succession lead from monofactoriality to polyfactoriality, from controlling a small number of factors to equality of many factors.

Polyfactoriality is closely connected with the limiting principle - the Liebig's principle. There is no contradiction between them, on the contrary, if under arbitrary (random) conditions limitation is done by a small number of factors (monofactoriality), selection and successive reconstructions make decrease relative significance of the limiting factors (polyfactoriality).

Adaptation causes analogous changes. At this corresponding to the many factors' effect (limitation) are high correlations and in the course of adaptation they decrease.

Single - and Polyfactor Limitation Theories

Single factor limiting theories are in wide use in ecological investigations. According to these theories survival and reproduction are, as a rule, limited by a single factor, or by a small number of them. This means, that among the factors, affecting a population, isolated is one or a small number of most essential ones (greatly lagging behind the optimum) and the rest do not have strong effect on the reproduction coefficient. Among these single factor theories are: parasitogenic [10, 34, 36], trophic [9, 20], genetic [30, 31], stress [29], synopsis, competition [32], epizootic [27] and a number of other. Most

reliable verification of single factor theories was made for agrocenoses - the yielding depends primarily on the factors most distant from the optimum and controlling other factors can't increase it appreciably.

On the other hand, many ecologists are inclined to accept the polyfactor theories - under natural conditions the reproduction coefficient is determined not by a single factor, but by many factors [4, 5, 6, 35, 37, 38] and other. Moreover, making appearance are proposals to consider the polyfactoriality as one of the basic laws of ecology [23]. It is stated at this, that as a result of the adaptation process playing their part in the dynamics of any population are all possible factors of numbers [23]. According to F. N. Semevsky and S. M. Semyonov, the Liebig's law is in good agreement with reality if the conditions of the environment block the adaptation reconstructions of the individuals. "There are grounds to suppose, that monolimiting may occur in nature on rather small times only" [23, p. 149]. But to solve the problems of global ecological monitoring applied can be the concept of polylimiting in the form "... variation of the press of any factor affecting a population is inevitably reflected in its population dynamics [23, p. 149].

The nature lacks constant monolimiting owing to the fact, that the organisms are adaptable systems. Of common knowledge are various mechanisms of organism adaptations at the behavioral, physiological and cell levels. So, dynamics of a biological population is determined not by the processes taking place in the environment only, but also by adaptations to the conditions of the environment, taking place by the virtue of the natural selection and preprogrammed adaptive responses at the level of an individual.

In response to a negative affecting press of a factor the population's individuals adapt to it: altering are the phenotypes of the individuals. Formally these changes show in the shift of the points depicting them on the Matthew-Kermak set.

By the virtue of the principle of optimality, adaptation of individuals makes realize the phenotype optimum with respect to the condition of the environment. If the question is about "fast"

reconstructions in development and functioning of an organism, the optimum is achieved in conformity with the current condition of the environment. If the question is about slow reconstructions (changes in the genofund of the population), to realize them necessary is the process of selection, and optimality of the phenotype is achieved in the sense of time averaged adaptation only.

Adaptation results in making up for the effect of the "pressing" factor, and population dynamics is getting to be determined by other earlier "insignificant" factors. This is the cause of the polyfactoriality in the population dynamics, i. e. the essential part of all factors of the environment in forming the process of varying numbers. This statement in [23] is considered to be one of the laws of ecology (the law of many-factor effect on population dynamics). Mathematically it is described as follows.

Let R be the maximum possible resource of an individual; x_1, \dots, x_M is the press of independent mortality rate factors; r_1, \dots, r_M are the parts of the resource spent to protect from the respective mortality rate factors; and $r = r_1 + \dots + r_M$. Then, the fecundity of an individual Q with excessive food is the function of the resource remnant ($R - r$) and survival rate f_i on the i -th mortality rate factor is the function of the press x_i and expenditures for protection r_i . By the definition of [23] $Q(R)$ is the biological potential of an individual. In these assumptions the reproduction coefficient of an individual is set by formula

$$k = Q(R - r) f_1(r_1, x_1) \dots f_m(r_m, x_m).$$

By virtue of the principle of optimality, the distribution of the resource to reproduce and protect it is optimum, i. e. r_1, \dots, r_m provide maximum of k . When considering the slow reconstructions of an individual k, f_1, \dots, f_m are substituted by their time standard means k, f_1, \dots, f_m .

Liebig's Principle and Polyfactoriality

In our opinion, there are no essential contradictions between the Liebig's principle (monofactoriality) and the principle of polyfactoriality. What is more, the polyfactoriality may be

considered as a consequence of the Liebig's principle. The thing is in "adaptation process", eventually making monofactoriality change for polyfactoriality. This viewpoint will be supported by analysis of some classes of models generalizing constructions from [23].

Important class of models, making account of the adaptation process, is based on the concept of generalized adaptation resource of an individual. It is assumed that this resource can be redistributed to resist various adverse factors, but can't grow within the limits of the given population. The adaptation resource is redistributed either in the course of the life time of one individual (individual adaptation), or in the succession of generations (long-duration modification). Long-duration modifications can for some time be inherited under changing environment, too.

For the models, based on the adaptation resource concept, the Liebig's principle can be formulated as follows: at given distribution of the resource under randomly chosen conditions the reproduction coefficient is, as a rule, a function of primarily one factor (or of a small number of them). A simplest model of formalization is constructed as follow. Considered is a mean reproduction coefficient (with fixed distribution of the resource) in continuous time, i. e. the coefficient in the equation $N = kN$ (N is the numbers of the population). It is assumed, that k may be represented as the sum $k = k_0 + k_1$, where k_0 does not depend on the numbers N , and k_1 is the function of N , independent of the distribution of resources. The press of each factor is specified by number f_i , to resist the i -th factor mobilized is the resource $f_i \leq r_i$, normalization of f_i is chosen for f_i to conform to the optimum, resource distribution r_i satisfies the limitation $\sum_i r_i \leq r$. Real interaction of the the i -th factor is specified by the number $f_i - r_i$. According to the Liebig's principle the coefficient k_0 is determined by the factor, for which $f_i - r_i$ is maximum

$$k_0 = \varphi(\max_i (f_i - r_i)), \quad (1)$$

where φ is some monotonically decreasing function.

The question arising is about the choice of resource distribution r_i . It is solved by the Haldane principle of optimality [26], according to which the parameters of an individual, forming in the course of evolution (succession, adaptation) should bring the reproduction coefficient to its maximum. For dependence (1) this means, that the maximum value $f_i - r_i$ is to be minimal out of the possible ones, i.e. the distribution r_i must be the solution for problem

$$\begin{aligned} \max_i (f_i - r_i) \rightarrow \min & \quad (2) \\ r_i \leq f_i, \sum_i r_i \leq r & \end{aligned}$$

If $r \geq \sum_i f_i$, then $r_i = f_i$ is the solution of (2). Otherwise, ($r < \sum_i f_i$) its solution is given by the formula

$$f_i - r_i = \frac{\sum_i f_i - r}{n}, \quad r_i = f_i - \frac{\sum_i f_i - r}{n}, \quad (3)$$

where n is the number of factors.

According to (3), the difference $f_i - r_i$ is similar for all factors and deviation of any factor from the settled value f_i will affect the reproduction coefficient k_0 (1).

So, from the simplest formalization of the Liebig's principle (1) with the aid of the extreme principle of Haldane we arrive at the many-factor principle: evolution (succession, adaptation) results in such settlement of the resource, that makes all factors equivalent.

Two questions arise here: first, how much does the obtained corollary depend on the form of model (1) and, second, how rightful is to use one and the same principle of Haldane to describe basically different processes: evolutions, successions, adaptations.

Model (1) is the simplest formalization of the Liebig's principle. Its small variations do not change the essence of the whole. Thus, for example, if

$$k_0 = \varphi(\max_i (a_i f_i - b_i r_i); \quad (a_i b_i > 0)) \quad (4)$$

then, instead of problem (2) have

$$\begin{aligned} \max_i (a_i f_i - b_i r_i) \rightarrow \min, \\ b_i r_i \leq a_i f_i, \quad \sum_i r_i \leq r \end{aligned} \quad (5)$$

Its solution is given by the analogy of (3):

$$\text{if } r \geq \sum_i \frac{a_i f_i}{b_i}, \text{ then, } r_i = \frac{a_i f_i}{b_i}, \text{ otherwise } r_i = \frac{1}{b_i} (a_i f_i - \rho), \quad (6)$$

where

$$\rho = \frac{\sum_i \frac{a_i f_i}{b_i} - r}{\sum_i \frac{1}{b_i}}$$

and all $a_i f_i - b_i r_i = \rho$, the maximum in (4) is achieved simultaneously at all i , deviation of the press of each factor from f_i (excess) with the given distribution of resource affects the reproduction coefficient.

The following generalization of (1) preserving the Liebig's principle (the reproduction coefficients determined by the factor most distant from the optimum) is given by dependence

$$k_0 = \varphi_0(\max_i (\Phi_i(\varphi_i(b_i f_i)) - \psi_i(r_i))), \quad (7)$$

where φ_0 is monotonically decreasing; and $\Phi_i, \varphi_i, \psi_i$ ($i \geq 1$) are monotonically increasing functions. Here "the degree of deviation from the optimum" is estimated by the value of $\Phi_i(\varphi_i(f_i)) - \psi_i(r_i)$. Additional condition: $\Phi_i(0) = \varphi_i(0) = \psi_i(0) = 0$ (normalization). And for model (7) the maximum of the reproduction coefficient is achieved in the cases when all values $\Phi_i(\varphi_i(f_i)) - \psi_i(r_i)$ are equal to each other. To prove it, suffice is to note, that if for some $i = i_0$

$$\Phi_{i_0}(\varphi_{i_0}(f_{i_0})) - \psi_{i_0}(r_{i_0}) < \max_i (\Phi_i(\varphi_i(f_i)) - \psi_i(r_i)), \quad (8)$$

then, r_{i_0} can be diminished by some sufficiently small Δr , increasing at this those r_{i_0} , for which in (8) the maximum on

$\Delta r/m$ (m is the number of such r) is achieved so, that the maximum value, and consequently, of k_0 (7) diminish.

Finish this section by stating qualitative reasoning. If the Liebig's principle is correct, and under the randomly chosen conditions of survival and/or reproduction is limited by one factor or by a small number of them, then, the system of distribution of the adaptation resource, formed in the course of evolution is arranged to redistribute the resources to resist these limiting factors, to make up for the limiting and, thus, lead to polyfactoriality.

Haldane Principle Used to Describe Adaptation.

The extreme Haldane's principle was put forward to describe the process of evolution [23, 26]. To use it, we should fix the set on which the selection is made (Matthew-Kermak set [23]) and examine the points of extremum of average reproduction coefficient on this set. There are theorems on the efficiency of selection [7, 23] by which eventually in the course of selection there remains relatively small part of initial variety, corresponding to these points of extremum. It is the principle of maximum average reproduction coefficient that is called the Haldane's principle (Haldane-Semevsky principle).

Adaptation takes evolutionally insignificant time, raising a question: how rightful is it to use the Haldane's principle to describe the results of adaptation? It can be answered on the basis of the concepts about two levels of models.

The models of the first level allow to find out the optimum phenotypes. The Matthew-Kermak set X is taken as a set of possible phenotypes. Constructed for them is the reproduction coefficient k and the maximum points k , determined by the known rules [7, 23], give the positions of the optimum phenotypes.

The following disadvantages of these phenotypes are essential for us. First, selection on the phenotype set is considered so that they are reproducing by themselves and asexually. These is a merging of two expressions: the alleged asexuality of reproduction means that we are getting to the well-known alternative: the

equilibrium or classical hypothesis of selection and evolution [14] and, on the other hand, reproduction of phenotypes (and not the phenotypes, if only). Second, the phenotypes do not persist for the life time - they are subject to various changes, adaptation including. A point, representing an individual, moves in time over the space of phenotypes.

The second level of models is constructed over the first one. In it an individual is specified not by a point in the space of the phenotypes, but by a rule (equation) of movement over this space, including the external conditions. In the second level models, an individual is thus represented as "machine" for ontogenesis and adaptation. The simplest version of the second level models bring us, in its essence, back to the first. In this version of the models each point of the phenotype space $x \in \mathbb{X}$ is compared to "adaptation field" $\mathbb{V}_x \subset \mathbb{X}$, where the representing point can move in course of adaptation. The "adaptation rule" is to point out for each x the points $y(x) \in \mathbb{U}_x$, into which the phenotype moves because of the adaptation.

True is the following assertion: selection on the set of "adaptation rules" $y(x)$ is to result in the fact, that $y(x)$ for each $x \in \mathbb{X}$ will be the maximum point of the reproduction coefficient on \mathbb{V}_x . Thus, the simplest selection models for the "adaptation rules" result in the same Haldane's principle for phenotypes, but on reduced sets \mathbb{U}_x .

It is easy to construct the proof for this assertion in the cases, when it is supposed to divide the density-dependent and density-independent factors: $k = k_0 + k_1$, where k_0 does not depend on distribution of numbers, and k_1 - on all other factors.

It is the simplest models of this kind with the adaptation fields \mathbb{U}_x that are implied in the cases when the talk is about the adaptations' shifting the phenotypes in the same direction as selection and succession, but faster and less distant.

Much argument, connected with the inheritance of acquired features, was brought about by the so-called Baldwin's effect. The essence of it is that the phenotype changes, resulting from adapting to the altered conditions, in time get fixed in the population and genetically: modification is pushed out by its

genocopy. The term "genocopy" here is not quite accurate, for, if the modification were copied literally with all other things equal, there would be no pushing out. Replacement of modifications by the genocopies may, probably, be accounted for the fact, that to support the modification requires additional expenses of resources, while the genocopies realize the given phenotype without additional expenses, thus releasing adaptation resources.

Adaptation for Synergistic Groups of Factors

Earlier basing on the basis of the Liebig's principle and the extreme Haldane's principle we showed, that adaptation leads to many factors' effect, to the equivalence of many (ultimately - all) factors. However, the reproduction coefficient isn't always determined by the factors lagging most behind the optimum. The cases of synergistic effect of the factors, of their mutual amplification are not rare [23, 26]. Within the group of mutually reinforcing factors, the Liebig's principle does not hold, as the effects of mutual reinforcement result in the general case in the significance of all factors. Call the groups of mutually reinforcing factors synergistic.

For the cases, when the effects of mutual enhancement of adverse factors are strong enough, we can put forward the following hypothesis. Adaptation to the synergistic group of factors makes the resources distribute so, that part of the factors is neutralized completely, while spending none to resist most of the remaining resources, it is these remaining factors that will primarily determine the success of survival and reproduction. Qualitatively this hypothesis can be motivated as follows: with complete neutralization of a part of adverse factors eliminated is not their direct effect on the organism only, but the corresponding effects of amplification of the other factors, to neutralize which the resources are not sufficient.

Show the validity of this hypothesis within the limits of the model with the common adaptation resource concept.

Assume, again, the reproduction coefficient to be represented

in the form of the sum $k=k_0+k_1$, where k_1 depends on the numbers, but does not depend on the resource distribution r_i , and k_0 does not depend on the numbers and is determined by the values of factors f_i and resource distribution r_i . Division of dependencies of this kind can be based for many factors (climatic, chemical and so on) and regularly used in the research based on the Haldane's principle [19, 22, 26]. Assume further, that

$$k_0 = \Phi(f_1 - r_1, f_2 - r_2, \dots, f_n - r_n), \quad 0 \leq r_i \leq f_i, \quad \sum_i r_i \leq r. \quad (9)$$

Of interest is only the case when $r < \sum_i f_i$, i. e. the resource isn't excessive. Otherwise, naturally, appears trivial distribution: $r_i = f_i$. If, as it is assumed below $r < \sum_i f_i$, then we can assume $\sum_i r_i = r$ - that all this given resource is distributed to resist the adverse factors.

Synergism means, that the function $\Phi(x_1, \dots, x_n)$ determined in the orthant $\mathbb{R}_+(x \geq 0)$ has the following property - its mixed derivatives are non-positive

$$\frac{\partial^2 \Phi}{\partial x_i \partial x_j} \leq 0 \quad (i \neq j) \quad (10)$$

In addition, Φ is a monotonically decreasing function of each of its arguments, hence its first derivatives are non-positive:

$$\frac{\partial \Phi}{\partial x_i} \leq 0. \quad (11)$$

It is required to find maximum of Φ in polygonal $0 \leq r_i \leq f_i$, $\sum_i r_i = r$ at fixed f_i , i. e. to solve problem

$$\Phi(f_1 - r_1, f_2 - r_2, \dots, f_n - r_n) \rightarrow \max; \quad 0 \leq r_i \leq f_i, \quad \sum_i r_i = r. \quad (12)$$

If Φ is a convex function of values r_i on the hyperplane assigned by the equation $\sum_i r_i = r$, then, the maximum is achieved in one of the vertices of the polygonal. The condition of convexity can be considered as the requirement of sufficiently strong synergism - sufficiently great value of the mixed derivatives (1.10).

Illustrate this by a model with two factors. Let $k_0 = (f_1 - r_1, f_2 - r_2)$. Then, convexity of Φ in the limitation over the straight line $r_1 + r_2 = r$ means, that

$$\left. \frac{d^2 \Phi(f_1 + x, f_2 - x)}{dx^2} \right|_{x=0} \geq 0 \quad (13)$$

for any $f_1, f_2 > 0$. Hence

$$\frac{\partial^2 \Phi(f_1, f_2)}{\partial f_1^2} - 2 \frac{\partial^2 \Phi(f_1, f_2)}{\partial f_1 \partial f_2} + \frac{\partial^2 \Phi(f_1, f_2)}{\partial f_2^2} \geq 0$$

or

$$-2 \frac{\partial^2 \Phi(f_1, f_2)}{\partial f_1 \partial f_2} \geq -\Delta \Phi \quad (14)$$

Inequality (14) can be interpreted as follows. The negativeness of the second derivatives $\partial^2 \Phi / \partial f_i^2$ ($i=1, 2$) means, that the effect of the i -th factor grows non-linearly - it amplifies by itself (for example, double increase of concentration of a harmful substance more than doubles its contribution into the death rate). In this case (14) means, that mutual amplification of interaction is more than nonlinear self-amplification. Then, the function Φ is convex, and the maximum in problem (12) is achieved either when for one of the factors $r_i = f_i$ (the factor is neutralized), or when for one of them $r_i = 0$ (all resource is oriented to resist other factors).

In the general case (12) at each vertex of the polygonal of limitations, set by the equation $\sum_i r_i = r$ by inequalities $0 \leq r_i \leq f_i$ for some m factors $r_i = 0$, for $n-m-1$ factors $r_i = f_i$ and for one $0 \leq r_i \leq f_i$. If Φ is convex on the hyperplane $\sum_i r_i = r$, then, the maximum is achieved at the vertex, and we have a situation in agreement with the hypothesis put forward - the number of influencing factors decreases to $m+1$.

The number m has common for all vertices estimate from above. Arrange all f_i in decreasing order: $f_{i1} \geq f_{i2} \geq \dots$. Take

$$\rho_0 = 0, \quad \rho_1 = f_{i1}, \quad \rho_2 = f_{i1} + f_{i2}, \quad \dots, \quad \rho_k = \sum_{j=1}^k f_{ij}; \quad (15)$$

As it is assumed, that $r < \sum_i f_i$, then, for some $k = k_0 < n$ holds inequality $\rho_k < r < \rho_{k+1}$. Hence follows, that at any distribution $r_i (0 \leq r_i \leq f_i, \sum_i r_i = 1)$ the number of non-zero r_i is not less, than $k_0 + 1$. Thus,

$$m \geq k_0. \quad (16)$$

This very simple coarse error gives the idea of the minimal possible number of factors from the strongly synergistic group, whose effect on the organism owing to adaptation, is made up for completely. Adaptation results in decreasing number of the operating factors and there is shift towards monolimitation. Mind, that for the condition of strong synergism we took the convexity $\Phi(f_1 - r_1, \dots, f_n - r_n)$ on the hyperplane assigned by the equation $\sum_i r_i = r$.

So, we have distinguished two extreme situations: the Liebig's systems of factors, for which in the random combination phenotype-environment (before adaptation) holds the Liebig's principle, and the synergistic groups of factors, for which in random combination of factors leads to many factors' effect, adaptation to the synergistic groups decreases the number of operating factors, thus shifting the system towards single factor effect. These conclusions are supported by the analysis of the simplest base models, based on the concept of division of density-dependent effects and all other operating factors. The main instrument of analysis is the Haldane's extreme principle. The other simplifications made in the models and not connected with the given division aren't as principally; from this viewpoint there is considerable scope for simple generalizations. To abandon the main simplifying assumption is a more complicated problem, and the next section deals with its partial solution.

Selection Dynamics in Systems with Factors of Different Types

Make an attempt to simulate result of adaptation by selection models. The idea of this approach was already discussed in the

previous section: we introduced a set of "adaptive opportunities" \mathbb{U}_X and considered optimum (by Haldane) phenotypes from this set. In the given section this idea is somewhat modified: under consideration is the set of adaptive opportunities and selection on this set. As the results of selection can be described by the extreme principle, generalizing the Haldane's principle [7, 23] the modification proposed can be considered as the nearest generalization of the original idea.

So, the results of adaptation are modified as results of natural selection on assigned set of possibilities. Selection, however, is represented not in the form of individual "operating factor", but as results of population dynamics. Therefore, the first step to make is to describe the phase space and construction of equations of this dynamics.

Considered is unified space of possibilities \mathbb{X} . It is supposed to be compact. The points in \mathbb{X} are specified by a certain set of parameters. When studying the adaptation we are most interested in the distribution of the adaptation resource over the factors $(r_i; i=1, \dots, n)$, so, distinguish this group of parameters. Denote the vector with coordinates r_i by \vec{r} (mind, that $r = \sum_i r_i$). As above, consider one-resource model. Denote the set of other parameters by y . Distribution of individuals over the space \mathbb{X} is some non-negative measure μ . It is assumed, that μ is in agreement with topology, i.e. is the Radon's measure - the continuous linear functional on Banach's space of continuous functions.

On $C(X)$ we fix the topology of uniform convergence, on the measure space $C^*(X)$ - weak* (broad) topology. The result of effect of the functional μ on the function f (integration) is denoted as $\int f d\mu$. The product $\mu \mu$ of the measure μ by the continuous function φ assigns according to the definition, the functional $\int f \varphi d\mu$.

The equation, determining the change of μ in time is written as follows:

$$\frac{d\mu(t)}{dt} = K(X, \mu)\mu, \quad (17)$$

where $K(X, \mu)$ is a function continuous in the totality of arguments (reproduction coefficient).

It is assumed, that there is such limit numbers N for all μ

having meaningful sense, $\int I d\mu \leq N$. Persistence of this inequality by virtue of (17) in the time is maintained by this condition at $\int I d\mu = N$ the reproduction coefficient is negative $-K(x, \mu) < 0$ (after achieving the limit total number the quantity of any organisms begins diminishing).

The principal issue in the selection dynamics is to specify all ω -limit distributions. Distribution μ^* is called ω -limit to solve (17) $\mu(t)$ if there is such a sequence $t_i \rightarrow \infty$, that

$\mu(t_i) \rightarrow \mu^*$. The main tool to study ω -limit distributions is the following theorem [7]. Let $\mu(t)$ be solution of (7) with the initial condition $\mu(0) = \mu_0$, μ^* be some ω -limit distribution for solution $t_i \rightarrow \infty$, $\mu(t_i) \rightarrow \mu^*$. Consider the sequence of average reproduction coefficients on the segments $[0, t_i]$:

$$k_i(x) = \frac{1}{t_i} \int_0^{t_i} K(x, \mu(t)) dt. \quad (18)$$

From it we can distinguish converging subsequence, as the measure space

$$M_N = \left\{ \mu \mid \mu \in \mathbb{C}^\infty(x), \mu \geq 0, \int I d\mu \leq N \right\} \quad (19)$$

is weakly compact [3]. Let $K(x)$ be the limit of any such subsequence. Then, $K(x) = 0$ at $x \in \text{supp } \mu^*$, i.e. μ^* consists of the points of zero maximum $k(x)$ on the initial distribution support.

The average reproduction coefficients k_i and their limits k belong to a closed convex hull of the set $K(\cdot, M_N)$ in $\mathbb{C}(\mathbb{X})$. Denote this hull by \mathbb{Q} . The set of function \mathbb{Q} is compact. Examining the properties of the maximum points in \mathbb{X} of the function $k \in \mathbb{Q}$, we get the information on the possible supports of limit distributions for solution of (7). In this way were found the theorems of efficiency of selection [7, 23], estimates of the number of points in the limit distribution supports [7]. Here we used this device to extend the assertions obtained for the simplest cases in the previous sections, into the properties of the ω -limit (steady state including) distributions, forming the course of selection. Important is the following simple reasoning. Let all functions $K(\cdot, \mu)$ ($\mu \in M_N$) lie some closed convex subset $\mathbb{C}(\mathbb{X})$. Then, \mathbb{Q} lies in the this subset, too.

The reproduction coefficient K depends, of course, on the external factors f_1, \dots, f_n . Call the dependence $K(\bar{r}, y, \mu)$ the

Liebig's one, if

$$K = \Phi(\max_i (f_i - r_i), y, \mu) \quad (20)$$

and at any y , $\mu \in M_N$ the function $K(\cdot, y, \mu)$ - is monotonically decreasing. We'll also have to somewhat amplify this condition. Call the reproduction coefficient k uniformly Liebig's, if there is such a monotonically decreasing function $\varphi(c)$ of the real variable c , that the function (20) decreases faster, than the function φ : for any $y, \mu, c_1 < c_2$ from the respective fields the definitions

$$\varphi(c_1) - \varphi(c_2) \leq \Phi(c_1, y, \mu) - \Phi(c_2, y, \mu) \quad (21)$$

This condition is, in its essence, a technical one. It does not impose additional essential meaningful limits and only means, that the dependence of the reproduction coefficient on the totality of the external factors, if they are not compensated by the adaptation, can't become however weak. The set of functions monotonically decreasing faster than φ

$$\Phi = \Phi(\max_i (f_i - r_i)) \quad (22)$$

is closed and convex, therefore all functions $q(\vec{r}, y)$ from \mathbb{Q} have form

$$q = q(\max_i (f_i - r_i), y) \quad (23)$$

and at each y are the monotonically decreasing functions of the first argument. If $r < \sum_i f_i$, and it is this case that is of interest, then, at the points of maximum q on \mathbb{X} all values of $f_i - r_i$ are equal to each other, which can be interpreted as equivalence of all factors, polylimiting.

This reasoning proves the following theorem.

THEOREM 1. If the reproduction coefficient in system (17) $\mu(t)$ with the initial condition $\mu(0) = \mu_0$, $\text{supp} \mu_0 = \mathbb{X}$ in each ω -limit distribution the values of $f_i - r_i$ are equal to each other at all i (i.e. the resource is distributed so, that the factors become equivalent).

The condition $\text{supp} \mu_0 = \mathbb{X}$ means, that in the struggle for existence taking part are all elements of the possible variety.

Now, get down to analysis of synergistic groups of factors. Consider such dependencies

$$K=K(f_1-r_1, f_2-r_2, \dots, f_n-r_n, y, \mu), \quad (24)$$

that at any fixed f, y, μ limitation of function (24) on the hyperplane $\sum_I r_i = r$ - is a convex function. This is the condition of strong synergism that occurred earlier. For our purposes it should be added some condition of uniformity - so, that in transition to the limits of functions (24) constant functions would not arise. Similar to the Liebig's systems of factors this additional condition does not introduce anything new that is meaningful.

Let two convex φ_1, φ_2 functions be set on the closed convex set \mathbb{U} in \mathbb{R}^n . Say, that φ_2 is more convex, that φ_1 if for any $x_1, x_2 \in \mathbb{U}$ and $\alpha \in [0, 1]$

$$\begin{aligned} & (1-\alpha)\varphi_1(x_1) + \alpha\varphi_1(x_2) - \varphi_1((1-\alpha)x_1 + \alpha x_2) \leq \\ & \leq (1-\alpha)\varphi_2(x_1) + \alpha\varphi_2(x_2) - \varphi_2((1-\alpha)x_1 + \alpha x_2). \end{aligned} \quad (25)$$

The set of all functions, which are more convex, than some φ_1 , is closed and convex in $\mathbb{C}(\mathbb{U})$.

Say, that the strong synergism condition hold uniformly if there is such a strictly convex function $\varphi(r)$, assigned on the set $\sum_I r_i = r, 0 \leq r_i$, that for any fixed f, y, μ the function of r (24) is more convex, than φ_1 on the set $\sum_I r_i = r, 0 \leq r_i \leq f_i$ (of course, is assumed, that $\sum_I f_i > r$).

THEOREM 2. Let the condition of strong synergism hold uniformly. Then, for any ω -limit distribution of each solution of (7) $\mu(t)$ which has $\text{supp} \mu(0) = \mathcal{A}$, the distribution of resources is one of the vertices of the polygonal, set by the equation $\sum_I r_i = r$ and inequalities $0 \leq r_i \leq f_i$ (in the assumption of $\sum_I f_i > r$).

The proof is direct consequence of the extreme principle for the ω -limit distributions and of the fact, that the set of all functions more convex than some φ_1 is closed and convex.

So, the results obtained enable us to assert, that the assumption about separation of density-dependent parameters isn't essential for the basic conclusions: adaptation to the Liebig's system of factors makes increase the number of meaningful factors - and this is the shift towards the many factors effect.

Systems with Several Resources

Arguing about systems with several adaptation resources and their independent distribution is, at present, rather of academic interest, for the way to single these resources out in a biological object, aren't clear yet. Therefore, we'll discuss these systems in brief and on simplest models. The conclusions will, in essence, be similar to the above discussed.

Let there be n factors and m resources, each of them might be directed to neutralize any factor, but the efficiency of different resources with respect to different factors differs. In analogy to the one resource case, according to the Liebig's principle arrive at the problem

$$\begin{aligned} \max_i (f_i - \sum_j a_{ij} r_{ij}) \rightarrow \min & \quad (26) \\ \sum_j a_{ij} r_{ij} \leq f_i, \quad \sum_i a_{ij} r_{ij} \leq f_j; \quad f_j \geq 0 \end{aligned}$$

where r_{ij} is the quantity of the j -th resource, distributed to neutralize the i -th factor; $a_{ij} > 0$ is the efficiency of the j -th resource against the i -th factor; r_{ij} is the total stock of the j -th resource.

We can easily see, that solution of problem (26) is achieved at such distributions of r_{ij} , for which at all i the values of $f_i - \sum_j a_{ij} r_{ij}$ coincide. In fact, otherwise, the resources can be redistributed to reduce somewhat the minimal quantities of these values, taking account, probably, of some other quantities.

So, in the case of several resources from the Liebig's principle it ensues, that adaptation leads to polyfactoriality, to the equivalence of various factors.

For the synergistic groups of factors have, in analogy, problem

$$\Phi(f_i - \sum_j a_{ij} r_{ij}, \dots, f_n - \sum_j a_{nj} r_{nj}) \rightarrow \max \quad (27)$$

in the assumption, that the function Φ at assigned f_i is convex on the polygonal of restrictions

$$y \geq 0, \quad \sum_j a_{ij} r_{ij} \leq f_i; \quad \sum_i r_{ij} = r_j \quad (28)$$

The use of equality in the last formula is due to the fact, that the maximum in inequality is achieved only when the total resource

is sufficient to make each argument of Φ (27) vanish. This trivial case is not considered.

The maximum of the convex function is achieved at the vertex of the restriction polygonal. At the vertices part of inequalities from the limits (28) turns to be equalities, hence, some arguments can vanish Φ

$$f_i - \sum_j a_{ij} r_{ij}$$

The structure of the restriction polygonal depends on the matrix. Analysis of this structure is beyond the scope of this work. It can be done by well known methods [11].

So, for the synergistic groups of factors and in the case of several resources the adaptation can make decrease the number of the effective factors.

Arrangement of Systems of Factors and Program for Research

Diversity of different systems of factors (Liebig's and strongly synergistic are the extreme possibilities) raise a question: what are the systems of factors actually adequately describing the effect of the environment on the organism? The complexity of this question is that the notion about the unambiguously determined, existing independent of the researcher system of factors is naive and does not accord to the essence of the problem. Singling out and describing the factors an investigator performs definite work on constructing. Although it is difficult and sometimes impossible to discern the personal contribution and tribute to tradition in such work, still, constructing element is evident.

From this viewpoint the Liebig's principle, loses the status of an assumed law of nature, and acquires a new, methodological meaning, - it acts as a principle of constructing a system of factors. It consists in recognizing as individual effective factors only the indices, capable of limiting survival and reproduction. The system of these factors is constructed for a random organism-environment pair (before adaptation) to have monolimiting. On the other hand, the groups of synergistic factors

often occur in practice. Therefore, it is rightful to ask: to what method of constructing the systems of factors is it reasonable to confine ourselves ?

Possible is an intermediary compromise version: totality of factors on strongly synergistic groups or individual factors and relations between these groups are constructed "according to Liebig". Explain this method of constructing a combined system of factors on a model.

Each factor is specified by its own intensity $f_{i,j}$ where i is the number of the synergistic group (or of one factor, if it does not belong to synergistic groups), j is the number of the factor in the group (for individual factors, not belonging to synergistic groups, the index j may take only one value $j=1$).

Corresponding to each i is the generalized index of intensity

$$\Phi_i = \Phi_i(f_{i1} - r_{i1}, f_{i2} - r_{i2}, \dots) \quad (29)$$

where $r_{i,j}$ is the amount of adaptation resource, directed to neutralize the i,j -th factor. As above, taken are the conditions

$$0 \leq r_{i,j} \leq f_{i,j}; \quad \sum_j r_{i,j} \leq r,$$

where r is the total amount of the adaptation resource.

The reproduction coefficient k is represented in the form $k = k_0 + k_1$, where k_1 is the function of numbers independent of $f_{i,j}$, and k_0 is the function of the maximum of Φ_i :

$$k_0 = \Phi(\max_i \Phi_i) \quad (30)$$

The latter generalizes the Liebig's principles.

With respect to the functions Φ_i represented is monotonous increase in each argument, vanishing at zero arguments, and for the groups of several factors at fixed $f_{i,j}$ the convexity at intersection of hyperplanes is the space with the coordinates $r_{i,j}$ assigned by the equations $\sum_j r_{i,j} = \text{const}$ with the definition field Φ_i .

It is also assumed, that Φ is monotonically decreasing functions.

In the situation described, the Haldane's principle gives: the maximum of the reproduction coefficient is achieved in the cases when all Φ_i are equal between each other. At this, within each synergistic group the value of individual factors $f_{i,j} - r_{i,j}$

vanishes. Thus, the adaptation makes earlier distinct groups level relative to each other, and within each group - reduce the number of the effective factors.

Such combined systems of factors, formed out of connected between each other according to Liebig synergistic groups, provide broader scope for modelling, than the Liebig's or synergistic systems separately.

To compare empirically the number of effective factors in different situations proper indices need to be developed. As a result of observation each organism from experimental population is compared to an m -dimensional vector of parameters z . The totality of these parameters forms some cloud of points in m -dimensional space. The differences between the organisms inside the group can be assumed to be connected with one of the following reasons: differences in the values of the effective factors, resistance to them, amount of adaptation resource, in its different distribution (at different stages of the adaptation process). Accepting this hypothesis, we can try to evaluate the number of the effective factors through the dimension of the manifold on which (or in its neighborhood) we can locate the experimental points (the number of essential parameters). As through the finite set of points it is possible to draw a manifold of any dimension, we should introduce additional restriction for the form of the manifold. The simplest such a restriction is the linearity. Setting the accuracy of points' lying on the manifold (distance from it, or the sum of these distances and so on), and finding the manifold of the minimal dimension for this accuracy, have the estimate of the number of the effective factors. But this is additional uncertainty connected with the choice of accuracy.

The problem of comparing various groups of organisms in the number of the effective factors is of no less interest and importance. Here we can get rid of the arbitrary rule of setting the accuracy a priori, leaving the uncertainty in the choice of the index of approximation to the linear manifold. Among them we can point out: the maximum distance, sum of distances, their squares graph of parameters (the sum of reliable coefficients of correlation between the parameters exceeding certain value), it is

also convenient to use the spectral characteristics of the correlation matrix. The number of the effective factors at this may be not estimated, but compared only.

For the Liebig's systems of factors the comparison of the populations in the number of effective factors can serve as a useful tool to study the adaptation. The correlation properties turn out to be much more sensitive to the adaptation stress, than the absolute values of the parameters of the organisms. The approach to study the adaptation based on it and its practical application to prophylactic medical examination of the human populations are called correlation adaptometry.

The extent of correlation of the physiological parameters can be estimated by the correlation graph weight, computed as the sum of its ribs' weight (the sum of the respective correlation coefficients):

$$\sigma_{\alpha} = \sum |r_{i,j}| \geq \alpha |r_{i,j}|$$

where $r_{i,j}$ is the coefficient of correlation between the i -th and the j -th parameters. It is possible also to use the functional parameters of the correlation matrix. In the best conformity to the qualitative-physiological pattern are the indices:

$$f_2 = tr(\Lambda) = \sum_{j=1}^k \lambda_j^2; \quad f_3 = \lambda_1/k; \quad f_6 = \sum_{j=2}^k (\lambda_{j-1}/\lambda_j),$$

where $\lambda_1 \geq \lambda_2 \geq \dots \geq \lambda_k = \dots = 0$ - are the eigen-values of the correlation matrix.

Having, thus, a version of ecological-evolutional explanation for the effect of enhancing level of correlation of the physiological parameters under the growing adaptation load, come to the following conclusions.

Conclusions

1. There ways of arrangement of the system of factors affecting the organism have been distinguished: the Liebig's systems, the synergistic systems and combined systems.

2. The models showed, that the adaptation to the Liebig's system of factors leads to the many factors effect, and to the

synergistic one - reduces the number of the effective factors.

3. Peculiarities of adapting to the Liebig's systems of factors formed the basis to propose an approach to comparing populations in the extent of their adaptation - correlation adaptometry.

It is for the first time that the effect of increasing correlations under the adaptation load was obtained for the human populations. However, the general ecological-evolutional explanation allows to conclude its general biological significance. We think it possible to apply the found effect to biological monitoring of the natural environment, which is under discussion nowadays [28].

Supplement. Some Observations Proving the Effect

Works [8,21] present results of investigation of the lipid exchange in the women in birth and healthy mature infants, born in the mid-latitudes of Siberia and the newly come inhabitants of the Extreme North. Comparison of results in the Extreme North and the mid-latitudes vividly shows the elevated level of correlations of indices of the lipid exchange under increased adaptation load.

The lipid exchange indices were compared in healthy mature infants, born in the mid-latitudes of Siberia and in the newly come inhabitants of the Extreme North. The data analyzed were obtained from the whole blood, taken from the newborns on an empty stomach at the same time in the morning hours. The lipids were split into fractions by thin layer chromatography, with prior determination of total lipids by bichromatic method to be followed by densitometry of the chromatographs obtained, to estimate the isolated fractions of lipids and phospholipids qualitatively and quantitatively. The infants were observed in the time history of the first 10 days of their life and in different seasons of the year.

The lipid fractions examined for analysis: free cholesterol (FC), free fatty acids (FFA), triglycerides (TG), cholesterol ethers (CE), phospholipids(PL); phospholipid fractions:

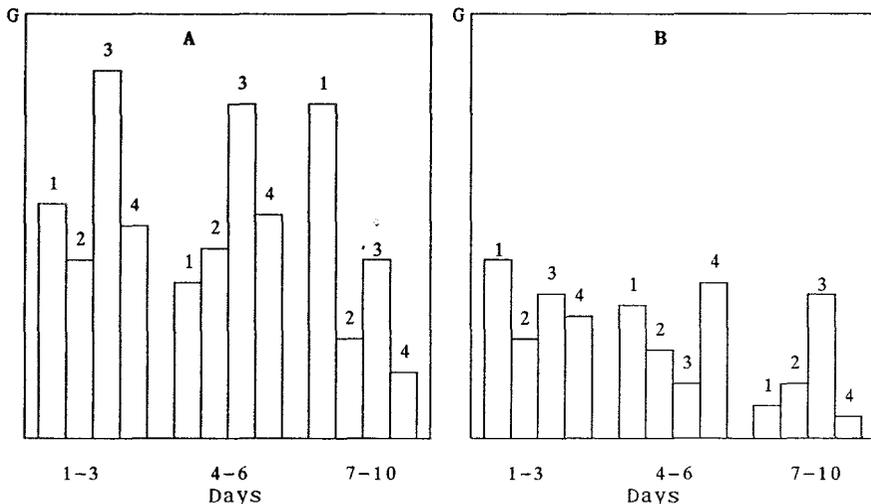


Fig. 1. Time history of correlation graph weight of the new born infants of the newly come inhabitants of Extreme North (A) and new born infants of inhabitants of middle latitudes of Siberia (B) in winter (1), spring (2), summer (3), autumn (4).

lysoiecithin (LL), sphingomyelin and phosphatidylserin (SM+PS), phosphatidylcholine (PC), phosphatidylethanolamine (PEA).

At the first stage we examined the time history of the lipid exchange indices, followed by analysis of coefficients of pair correlation for all indices in the groups of new born infants in 1-3, 4-6 and 7-10 days of life in all four seasons of the year. We determined the number of reliable correlations in the totality of correlation coefficients considered and the degree of expressiveness of these correlations. Determined also was the time history of the structure of these connections.

The principal fact established in correlation analysis is that the new born infants of the newly come population of the Extreme North the degree of correlation of the lipid exchange indices is higher, than that of the women in birth and new born infants of the native population of the mid-latitudes of Siberia (Fig. 1, 2).

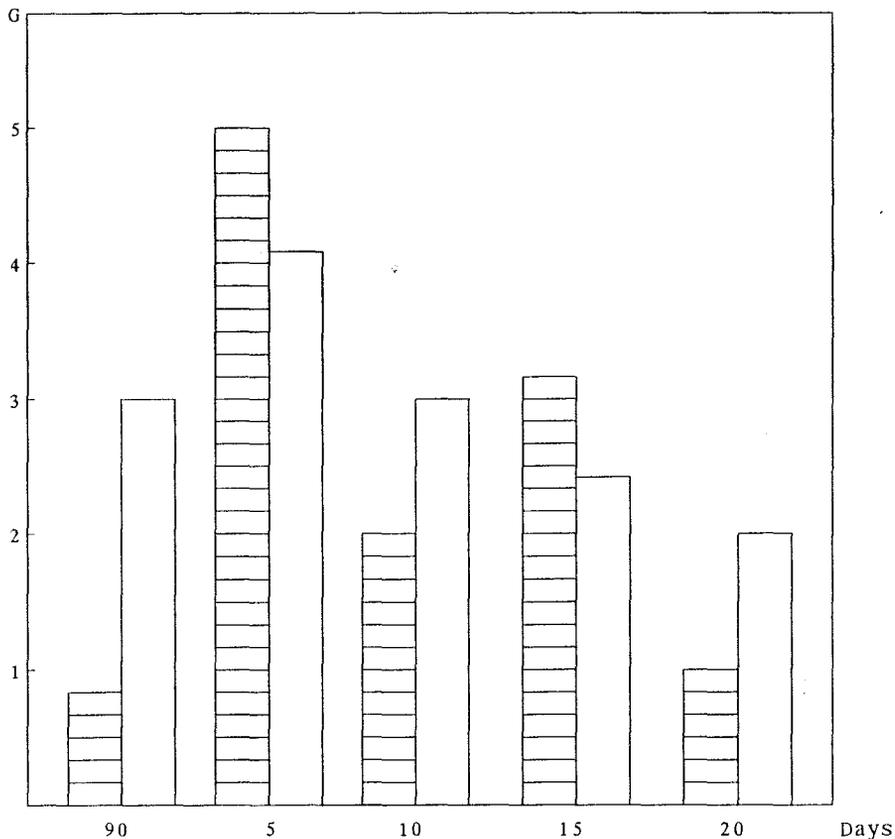


Fig. 2. Degree of correlatedness of indices of leukocyte enzyme activity prior to moving and in the first 20 days after moving into Polar Regions:  - polar night period  - polar day period.

We could trace the tendency of decreasing number or degree of expressiveness of the correlations to the 7-10-th day of life (Fig. 2). The new born infants of the newly come population of the Extreme North showed difference in both degree of expressiveness and the structure of correlation connections depending on the season of the year. In summer, i. e. during the polar day the

correlation graph has the most weight. Ambiguous adaptation responses in different seasons of the year were revealed by different investigators in other metabolism indices, too. A supposition was made, that like many other manifestations of life activity, the population gets tired in cycles, which is due to the solar, seasonal and other natural rhythms. The new born population of the mid-latitudes of Siberia show small dependence of on the season of the year.

The presence of the effect is proved by investigation of the activity of leukocyte enzymes.

The leukocytic system is of great importance for the performance of adaptive and protective responses. The functional condition of the blood leukocytes considerably determines the organism response. To examine the adaptive changes at the cell level in human adaptation to new ecological conditions we examined 3 groups of practically healthy males 20-40 years old, coming to the polar regions of the Soviet Union from the middle latitudes of the country, from the polar regions and the middle latitudes in the city of Sochi. We examined 411 men in the adaptation time history: in 5, 10, 15 and 20 days after moving. The peripheral blood leukocytes were examined for the enzyme activity - markers of various metabolic ways:

1. Krebs cycle - succinatedehydrogenase (1. 3. 99. 1, SDH).
2. Glycerophosphate by-pass, connecting glycolysis with the Krebs cycle - α -glycerophosphatedehydrogenase (1. 1. 99. 5, α -GPDH).
3. Catabolism - non-specific acid phosphatase (3. 1. 3. 2, CP) and non-specific alkaline phosphatase (3. 1. 3/1, AP).
4. Aminooxidase way of oxidizing the biogenous amines - monoaminooxidase (1. 4. 3. 4, MAO).

In the examination we established some physiological parameters of the people examined (arterial pressure, pulse rate, leukocyte number, leukocytic formula), account was made of the disease rate in the observation period.

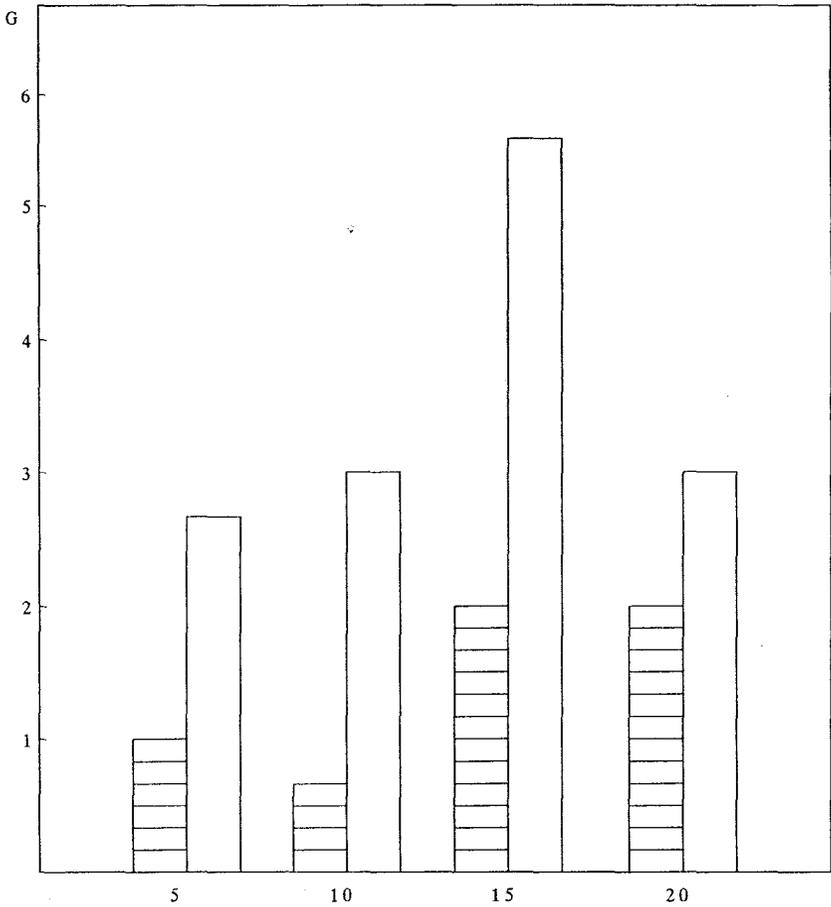


Fig. 3. Degree of correlatednes of indices of leukocyte enzyme activity in people coming to Sochi from Polar Regions (▨) and from the middle latitudes of European part of Russian (□) in the first 20 days after arrival.

Analysis of the degree of correlations physiological parameters (enzymatic activity) revealed enhanced correlations and their elevated number when moving into the areas with extreme conditions. Analysis of the correlation graph when moving from Krasnoyarsk to Norilsk showed the following. In summer the value of the correlation graph is the highest on the 5-th day after moving reducing to the 15-20-th day. Similar tendency was observed in winter, but enhancement of correlations of enzyme activity indices on the 5-th day after moving is sharper, compared to examination in Krasnoyarsk. The weight of the correlation graph goes down towards the 20-th day after moving wavewise: reduces on the 10-th day, elevates on the 15-th day and considerably reduces again on the 15-th day.

Analysis of the correlation graph weight in the groups of people coming from the polar regions and from the middle latitudes in the Soviet Union to Sochi yielded the following results: in all observation days the correlation of the leukocyte enzyme activity indices of Norilsk inhabitants was higher; the weight of the correlation graph reaches its highest on the 15-th day at the Black Sea towards the 20-th day it gets to its original level in the inhabitants of the polar regions (Fig. 2).

Fig. 3 shows the general pattern of the behavior of the correlation graph weight when moving to the areas with contrast climatic conditions during the short time adaptation periods.

It was of interest to compare the correlation of leukocyte enzyme activity indices in the groups of people who were ill during the short time adaptation period and people, who didn't see the doctor in the same time: the weight of the correlation graph in the ill persons was three times as great (Fig. 4).

Analysis of the correlations of leukocyte enzyme activity indices is in good agreement with the conclusions of some authors, that one of the factors making possible to adapt to the ecological conditions of the polar regions is the high level of energy exchange [12, 17].

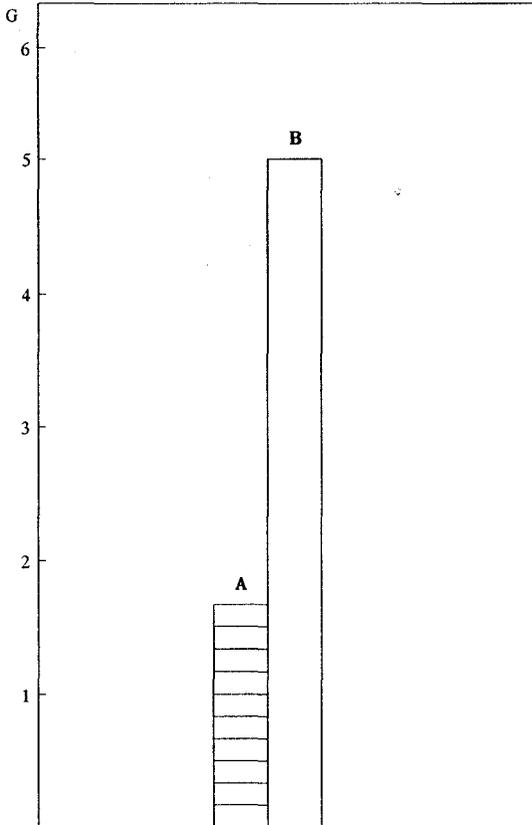


Fig. 4. Degree of correlatedness of indices of leukocyte enzyme activity in the first 0.5 year after moving to Polar Regions: A - people, not falling ill, B - people, ill in the beginning of adaptation period.

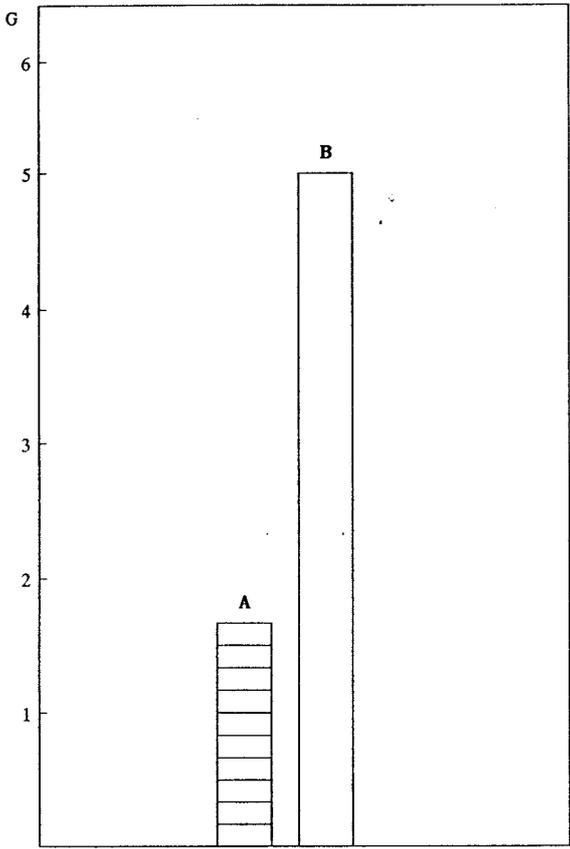


Fig. 5. Degree of correlatedness of indices of leukocyte enzyme activity in school-children: A - born in the Polar Regions, B - Having moved to the Polar Regions.

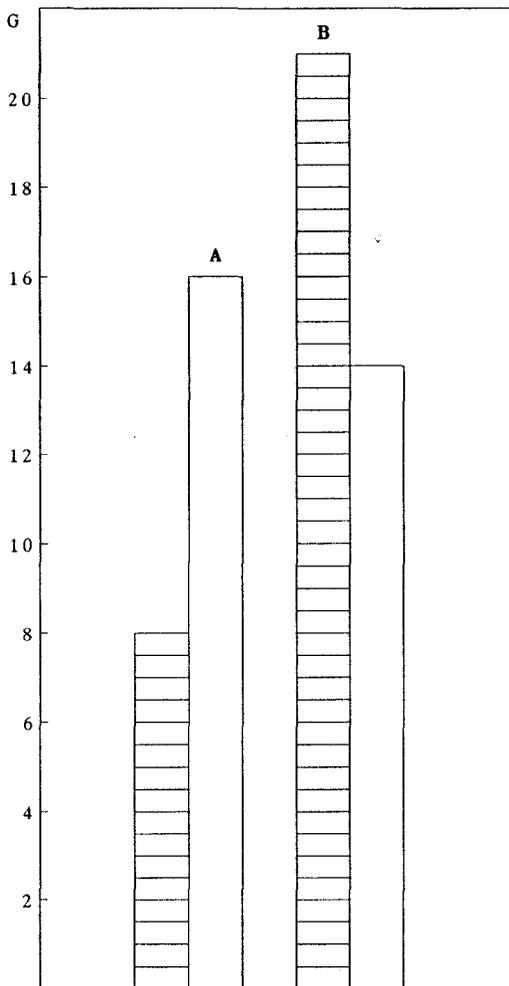


Fig. 6. Degree of correlatedness of indices of enzymatic status of leukocyte in junior schoolchildren: A - middle Latitudes of European part of Russian, B - Polar Regions; ▨ - children going in for sports intensively; □ - children, not going in for sports.

The method of correlation adaptometry was tested for the case, when increased adaptation load isn't evident - in analysis of comparative examination of enzymatic condition of leukocytes in pupils of elementary school in polar areas and in the middle latitudes of Siberia with different level of sports condition (118 children 8-10 years old). Comparison was made between the children

not going in for sports and the children regularly attending training sessions at the swimming pool. Correlations of enzyme activity indices in the young swimmers was considerably higher, than in the children not attending sport sessions of Siberia - on the contrary - regular swimming lessons reduce the correlations of indices compared to the children with the lower level of sports training (Fig. 6). Analysis of correlations of enzyme activity indices helps conclude, that regular training in the swimming pool in the North is the cause of additional strain.

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