Ecological optimum of ectothermic organisms: static-dynamical approach

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During 20th century the majority of researchers interpreted ecological optimum as a certain combination of ambient factors which is optimal for growth, existence and reproduction of an organism. However, it was revealed in many species, that the maximum rates of various processes in an organism are achieved at various combinations of values of different factors, and under variable regimes as opposite to constant regimes. One may state that there is no well defined general concept which takes into account a bulk of data that do not conform the traditional definition of ecological optimum. Here, we show that it is necessary to make distinction between concepts of "static" and "dynamic" optima. It is needed for definition of real ecological optimum and creation of optimum conditions for given factor. We show also that it is necessary to take into account so-called delayed effects of factors. Basing on the analysis of responses of zooplankton to various temperatures and phosphoric load, we show that an optimum has “dynamic” characteristics besides previously known "static" ones, like a range of factor values on tolerance curve or a doze of factor. These "dynamic" characteristics are cyclic and stepwise changes of a factor, a directionality of factor’s dynamics in case of stepwise changes and additionally, we reveal stimulating and inhibiting delayed effects of factors. Our results allow for a more detailed concept of ecological optimum, and also may stimulate investigations of quantitative contribution of various parameters of environmental factors to an ecological optimum of an organism or population.

Ecological optimum - one of the basic concepts of ecology. It was initially introduced by V. Shelford[1] in the beginning of 20th century, and is used in the scientific literature till now practically unmodified. The majority of researchers interpret the optimum as a certain combination of most favorable conditions without more detailed definition of their quantitative characteristics[2,3,4]. At the same time, there is a large quantity of field and experimental data in ecology which do not conform classical definition of the optimum. In our opinion, therefore, a necessity of more precise concepts of ecological optimum has ripened. There was a similar situation concerning other important ecological concept, an ecological niche, when G.E. Hutchinson[5] introduced in 1957 concepts of the fundamental and realized niche, after versatile data had been collected. His work inspired a number of experimental and field studies.

It was shown in many species, that optimum values differ for different physiological functions[6,7] and biochemical processes[8] in the same organism. These values also depend on ontogenetic stage, sex[10,11], body size[12], season of year, time of day[13], satiety[14] and general physiological state[15]. It was shown also, that rates of growth and development differ under various conditions[16]. Consequently, the maximum rates of these processes will be achieved at various combinations of values of different factors.

The effect of acceleration of development at variable temperature has been established in terrestrial insects and aquatic animals. A period of development is reduced and fecundity increases under variable conditions in comparison with constant ones[17,18]. The above allows to ascertain that, for ectotherm organisms, not simply a range of factor’s values on tolerance curve, or a doze of factor provide most favorable conditions for their life, but fluctuations of factor’s values within optimum limits (an astatic regime) are optimal[19]. The idea of optimality of variable regimes of factors was implemented in practice to develop new technologies of fish breeding in ponds and industrial facilities[20]. These technologies are based on the principle of self-regulation of environmental conditions by fish itself[21].

We have conducted chronic experiments to study a thermal biology of zooplankton organisms, using model micro- and mesocosms. The results also show, that the task of habitat optimization could not be reduced only to providing an optimum range of temperatures or even an oscillatory mode within in this range.

For example, results of prolonged cultivation of a mix of zooplankton species (flow-through microcosms, filtered river water, no additional feeding) have shown[22], that *Ceriodaphnia quadrangula* (O.F. Müller, 1785) became one of dominating species at water temperatures 15-25^{o}C. It reached a maximum quantity only after warming water up to 25^{o}C within 7 day with the subsequent decrease down to 20^{o}C (variant VI) (Table 1). A longer cultivation at 25^{o}C (variant VII), as well as the subsequent decrease in temperature down to 15^{o}C (variant IV), led to a sharp decrease of population. In all variants, the rise of temperature from 15 up to 20^{o}C (variants II, III, Y and VIII) resulted in a decrease down to less than 1/3 of initial population after 7 days.

Hence, not only absolute values of temperature influence on growth and keeping populations at high level of abundance, but also a duration of influence of either temperature value, and the course of alternation of higher and lower temperatures (directionality of the factor's dynamics) are important. Besides, the delayed stimulating effect of increased temperature is observed.

The similar effect is described for strains of infusorians *Blepharisma*[23] collected in various latitudes zones and consequently adapted for a long time period to 20.0^{o}C. A growth rate of these infusorians increased after temperature was raised shortly up to 30.0 and 40.0^{o}C and then returned to 20.0^{o}C. Also, an ambient temperature during embryogenesis in rotifers *Brachionus calyciflorus*[24] and Cladocera *Daphnia magna*[25] exerts a so-called "trace" effect upon a dependence of growth parameters on temperature during postembryonic period.

Our experimental research of an influence of mineral phosphorus on zooplankton[26] also shows how complicated is the problem of ecological optimum definition. An addition into water the phosphorus in concentrations 0.7-0.8 and 1.4-1.6 mg/l (12-16 and 24-32 times as high as background concentration) in the course of 8 days suppressed the abundance of large Cladocerans *Diaphanosoma brachiurum* (Levin, 1848), *D. dubia* Manuilova and *Daphnia longispina* (Sars, 1862) within subsequent 37 days after the termination of addition. On the other hand, a development of smaller species *Chydorus sphaericus* (O.F. Müller, 1785) and *Bosmina longirostris* (O.F. Müller, 1785) was stimulated. No effect of phosphorus on other Cladocerans, *C. quadrangula, Alona rectangula* (Sars, 1862), *Polyphemus pediculus* (Linne, 1778) and *Scapholeberis mucronata* (O.F. Müller, 1785) was observed.

The inhibitory effect on Daphnids was observed immediately after phosphorus had been added to water (Fig. 1,a). Besides, a smaller concentration of phosphorus suppressed the experimental population growth rate by 25 % with comparison to control. Therefore, a twofold increase in phosphorus concentration led to irreversible population decrease until the end of experiment. In control, a growth of populations proceed in both *Diaphanosoma* species, starting at 36th day until the end of experiment (Fig. 1,б). In variants with phosphoric load, the populations were comprised by several individuals only throughout the observation period. This result points to a delayed inhibitory effects of phosphorus concentrations, applied in our experiments. A stimulating influence on populations of Bosmins and Chidorids was revealed starting from 14 day after the addition of phosphorus had been terminated, i.e. the effect of the delayed action also was observed (Fig. 2).

Thus, it is possible to state that it is not enough to determine only a range of optimum values in order to determine a real ecological optimum for an organism or a population. Moreover, in order to optimize a given factor, it is not enough to keep the factor static or even astatic. It is necessary to consider also other important characteristics of environmental factors described above.

Basing on this, we propose to draw a distinction between concepts of "static" optimum (or static characteristics of an optimum) and "dynamic" optimum (or dynamic characteristics of an optimum) when defining an ecological optimum. The static optimum includes a range of optimum factors' values on tolerance scale and the "doze" of each factor corresponding to requirements of an organism and providing most favorable conditions for its life.

The dynamic optimum includes a set of certain dynamic characteristics which provides optimum conditions for a life of an organism in natural habitats (or are necessary to create such conditions in artificial habitats). At the time being, known dynamic characteristics include optimum parameters of periodic/cyclic changes of a factor (frequency and amplitude), their position within a range of optimum values (at its bottom, middle or top part), presence or absence of stimulating or inhibiting influence of stepwise changes of the factor, duration of influence of either "doze" of the factor, interval between values of "doze" and a directionality of a change of factor. Besides, a presence and character of delayed effects, manifested some time after an action of optimal factor's values starts or even after it is terminated (see the scheme), should be taken into account.

We assume that further investigations will reveal more characteristics and effects which directly determine a real ecological optimum in ectothermic animals. It will allow for a more detailed concept of an ecological optimum, and also make it possible to estimate quantitatively a contribution of various characteristics of environmental factors to formation of ecological optima for organisms and populations.

In our opinion, the approach outlined here, could be especially productive for an introduction of new species into an aquaculture, as well as for an optimization of cultivation regimes for aquatic and terrestrial ectothermic organisms.

Methods Summary

Temperature reactions *of Ceriodaphnia quadrangula* were studied in chronic experiments (30 days) in 20 l aquaria filled with river water[22]. Water was changed once for three days. Aquariums were kept under a diel LD 16:8 photoperiod. The initial density of zooplankton was equaled its density in the pond. A pre-defined temperature regime was maintained in the each aquarium according to an experimental design. Deviations of a temperature from preset values do not exceed ±0.5-1.0^{o}C. A suspension of algae *Chlorella vulgaris* was introduced to a aquarium at every change of water to maintain a sufficient food density (1*10^6 cells/ml) between changes, so an algae density always remained above an "initial limiting level"[30]. Measurements of the density was made during a change of water. 271 samples of zooplankton were collected in the course of experiments. Samples were taken every 3-4 days using a 0.5 l sampler, and then concentrated and fixed with 4 % formalin solution. The subsequent processing of samples was conducted using techniques described elsewere[31,32].

Responses to mineral phosphorus were studied in chronic experiments (61 days) in 600 l aquaria, which were kept indoor and thermostated[26]. Phosphorus was introduced in the form of phosphoric acid (KH_2PO_4) in concentrations 0.70-0.82 and 1.45-1.60 mgP/l (natural background - 0.05-0.06 mgP/l) during 11 to 18 days of experiment. The phosphorus content in water was measured every 3-4 days. On day 19th , phosphorus content in water was diminished to a natural level by a change of water. A dry product of chemical processing of *Chlorella* (cells processed by enzymes which destroy cellulose and split proteins into amino acids) was used as a food. The river water filtered from algae was used to reduce a possible uptake of phosphorus by algae. All variants of experiments were repeated 5 times.

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Competing interests statement The authors declare that they have no competing financial interests.

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Authors Contributions V.B.V. planned the study, analysed data, interpreted the results and wrote the paper. V.B.V. and T.I.V. developed stimuli and gathered experimental data.

Table 1. **Influence of various temperature regimes on abundance of *C. quadrangula***

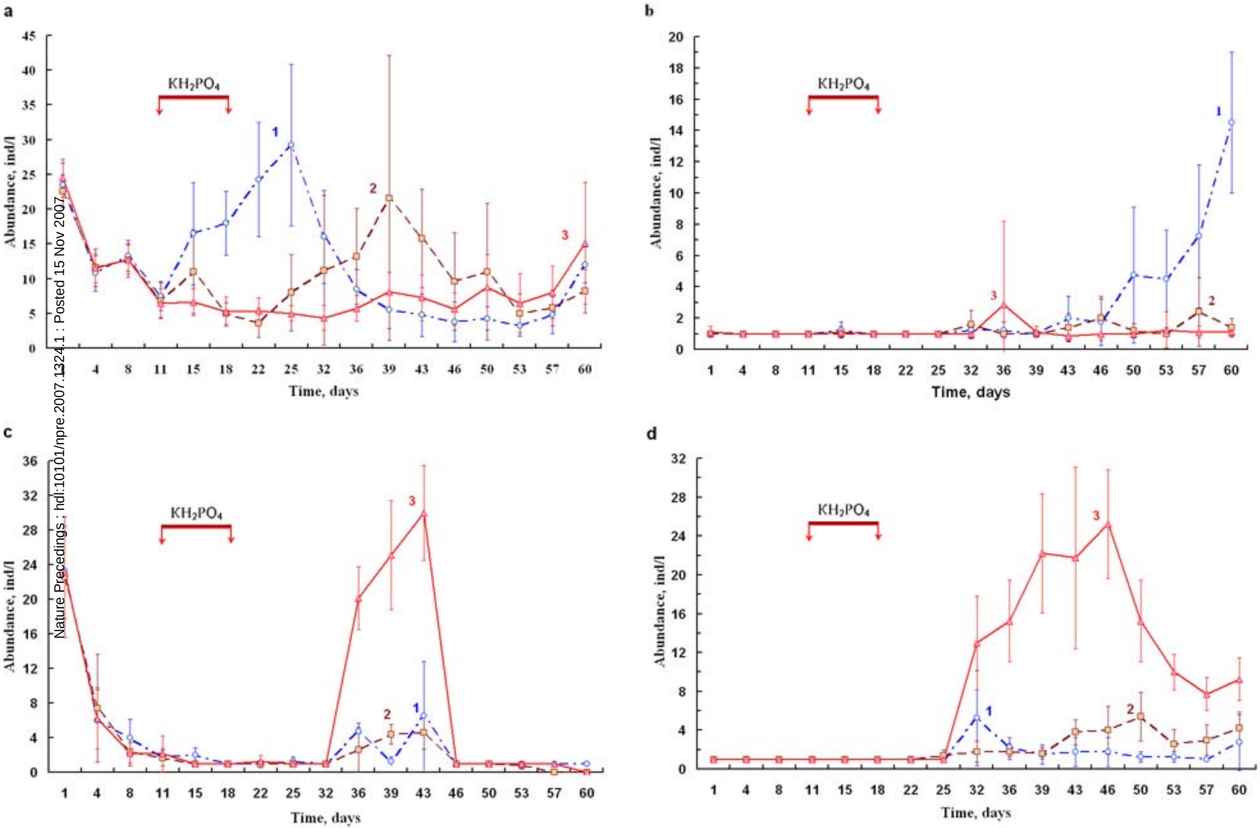
Variant	Days			
	1-7	8-14	15-21	22-30
	Temperature, ^{o}C / Abundance*, ind/l			
I	15 / 67.4 ± 6.4	15 / 15.5 ± 3.5	15 / 10.7 ± 2.8	15 / 7.8 ± 2.3
II	15 / 67.0 ± 4.6	20 / 6.6 ± 3.3	15 / 5.0 ± 1.8	15 / 2.8 ± 2.0
III	15 / 67.0 ± 4.0	20 / 9.5 ± 3.6	20 / 8.2 ± 6.5	15 / 2.1 ± 1.4
IV	15 / 69.2 ± 6.1	25 / 41.5 ± 13.9	15 / 14.3 ± 2.8	15 / 17.6 ± 5.2
V	15 / 71.0 ± 6.4	20 / 9.2 ± 5.0	20 / 5.8 ± 2.1	20 / 10.9 ± 5.1
VI	15 / 68.0 ± 4.7	25 / 36.0 ± 15.2	20 / 27.3 ± 8.3	20 / 62.7 ± 12.4
VII	15 / 69.4 ± 4.8	25 / 49.7 ± 22.7	25 / 40.6 ± 6.9	15 / 18.3 ± 7.3
VIII	15 / 71.8 ± 5.6	20 / 11.6 ± 8.3	25 / 5.9 ± 6.3	25 / 6.7 ± 3.2

The note: * mean ± s.d.

Figure captions for V.B.Verbitsky's article: Ecological optimum of ectothermic organisms: static-dynamical approach.

Fig. 1. Dynamics of population of *Daphnia longispina* (a), *Diaphanosoma brachiurum* (b), *Bosmina longirostris* (c) and *Chydorus sphaericus* (d). 1 - phosphorus concentration 0.05-0.06 mgP/l (control), 2 - 0.70-0.82 mgP/l, 3 - 1.45-1.60 mgP/l. Mean±s.d. is shown for each value of abundance.

 –period of addition of phosphorus into microcosms.


a
b
c
d
KH₂PO₄
Abundance, ind/l
Time, days
1
2
3
1 4 8 11 15 18 22 25 32 36 39 43 46 50 53 57 60