

## COMMENT

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### Upwelling, clone selection, and the characteristic shape of nutrient uptake curves

I would like to suggest that there is a logical connection between two hitherto intractable problems in phytoplankton ecology, and also to show how these problems may be attacked experimentally without too much difficulty.

1. When rates of nutrient uptake or growth of phytoplankton are plotted against intra- or extracellular nutrient concentrations, an hyperbolalike relationship is frequently observed (*see* any recent issue of this journal). The Michaelis-Menten parameters  $K_m$  and  $V_{max}$  are often used to characterize the shape of these hyperbolalike curves. It is also often suggested that a high value of  $V_{max}$  is advantageous in nutrient-rich environments like upwelling or coastal zones, and that a low value of  $K_m$  (or more exactly a steep slope near the origin) is advantageous in nutrient-depleted environments. The first question is: Are adaptations to these two kinds of environments mutually exclusive? In adapting to a low nutrient situation, for example, does the value of  $V_{max}$  necessarily decrease?

2. Any natural population of a species of phytoplankton, unlike most laboratory cultures—recently isolated cultures, anyway—will consist of many cell lines. Depending on the rate of sexual recombination in the species these cell lines will either be clones or sets of coancestry relationships more or less resembling the pedigrees of human beings and their pets. Adaptation of a phytoplankton population to new nutrient levels, if it occurs, will result in a change in the nutrient uptake curves of the population. Part of the change will be by physiological adaptation of individual cells and part will be by Darwinian selection of cells or cell lines. The second question is: What is the relative importance of physiological adaptation and natural selection in determining the re-

sponse of phytoplankton populations to a changed nutritional environment?

The independent variables in the Michaelis-Menten relationship consist of three rate constants and the concentrations of “enzyme” and substrate. “Adaptation” will be defined, for my purposes, as an increase in reaction velocity (i.e. growth or uptake) at the substrate concentration found in the environment. A little experimentation with a plotting programable calculator shows that four different kinds of changes in the shape of uptake or growth curves can be obtained by manipulating the independent variables in the Michaelis-Menten equation. These changes reduce to two types, namely crossing and noncrossing curves, if adaptation to high and low nutrient levels are *formally* analagous processes with sign reversal. Note, however, that this exhausts the possibilities allowed by the rules of combinations, since any two variables (like initial slope and final value) will either change in the same or opposite directions relative to their starting values. The Michaelis-Menten relationship does not provide any additional constraint on the system so we can dispense with it and deal directly with the curves themselves (Fig. 1). The term “half-saturation constant” will be used instead of  $K_m$  in the rest of the argument.

Figure 1A shows hypothetical, but typical, uptake curves which cross, labeled “before” and “after” to represent one possible kind of adaptation to a period of high nutrient concentration. Figure 1B shows noncrossing curves, the other possible kind of adaptation. There are two “after” curves in Fig. 1B illustrating the fact that in the noncrossing type of response the “after” half-saturation value can be either higher or lower than it was before selection started even though the absolute reaction rate is

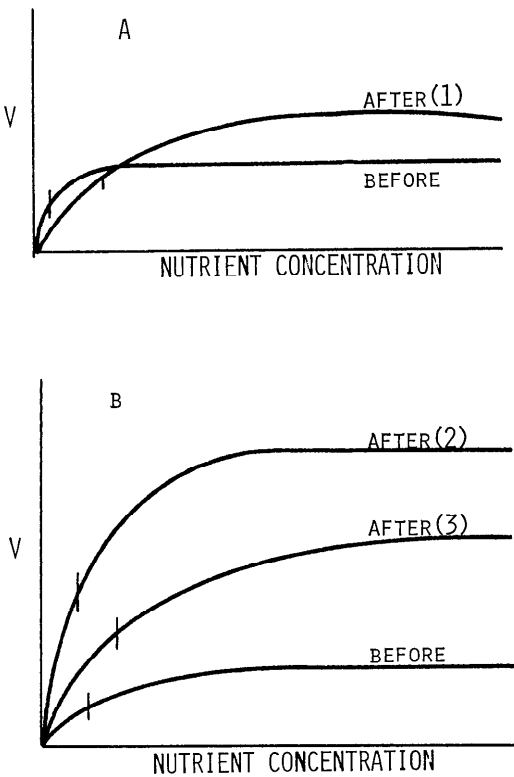


Fig. 1. The only possible changes in hyperbolic nutrient uptake curves during adaptation to changing nutrient concentrations.  $V$  refers to cell division rate or nutrient uptake rate. "Before" and "after" labels refer to selection for increased growth at high concentrations—labels would be reversed in Fig. 1A in the case of adaptation to lower concentrations. The vertical lines represent half-saturation constants.

higher at all points on the curve. In the case of adaptation to a high nutrient level we can see by inspection of Fig. 1 that the half-saturation constant can either rise ("after" curves 1, 3) or fall ("after" curve 2). In the case of adaptation to a low nutrient level  $V_{max}$  can rise ("after" curves in Fig. 1B) or fall (Fig. 1A, with reversal of labels). On purely formal grounds there is no reason to predict the reciprocal, "either-or" adaptation described in question 1. In other words, as far as the Michaelis-Menten formalism is concerned, adapting to a low nutrient concentration does not necessarily imply a decrease in the value of  $V_{max}$ .

Growth rate in phytoplankton, like fe-

cundity and viability in animals, is a major component of fitness as this term is used by quantitative geneticists. Here it means, essentially, very important to population survival. The absolute velocity of nutrient uptake is a secondary character positively correlated with absolute cell division rate at all substrate concentrations. Let us define cell division rate (or nutrient uptake rate) at low and high concentrations as two distinct, biological characteristics and then consider the nature of the correlation between them. Whether one prefers to attribute any such correlation to the independent Michaelis-Menten rate constants or directly to the complex behavior of biological membranes, pools, and so on does not affect the argument.

In populations exposed to fluctuating nutrient conditions, for example during spring mixing or an episode of upwelling, rapid cell division both at low and high nutrient concentrations will be selected for, although not at the same time. Over the course of many years and many geographical regions there will be alternating periods of high and low nutrient concentration in the history of most, if not all, phytoplankton species. This alteration will be accompanied by natural selection so drastic that the species may seem to disappear entirely at times. In any organism, when two or more characters are selected simultaneously or alternately in this way, the genetic correlation between them can eventually be expected to become negative. The explanation for this involves the complex and incompletely understood consequences of linkage and pleiotropism in polygenic systems—matters too difficult to undertake even briefly in this note. The essence of the argument can be found in the well-known text by Falconer (1965, p. 328):

Those genes that affect both characters in the desired direction will be strongly acted on by selection at all times and brought rapidly towards fixation. (Fixation of a gene means that it attains a relative frequency of 1.0.) They will then contribute little to the variances or covariances of the characters. [The two characters in this case are growth

rate at low and at high nutrient levels.] The genes which affect one character favourably and the other adversely will, however, be much less strongly influenced by selection and will remain longer at intermediate frequencies. Most of the remaining genetic covariance of the two characters will therefore be due to these genes, and the resulting genetic correlation will be negative.

Turning to Fig. 1 we consider the case of a population while it is being selected for maximum growth at high nutrient levels. I suggest that any genes involved in the kind of response to selection exemplified by Fig. 1B will have been fixed, or nearly fixed, because they are selectively advantageous under all conditions. They will therefore contribute little to the genetic variance between cell lines. Most of the variation on which selection can act to improve the performance of the population will be of the type exemplified by Fig. 1A. Inspection shows that if  $V_{\max}$  rises as the result of changes in the frequencies of these genes, the half-saturation constant will also necessarily rise. Similarly, in the case of selection for low nutrient levels, only genes giving rise to Fig. 1A will be available to provide a selection response, and  $V_{\max}$  will necessarily fall. The overall conclusion is that we may indeed expect to find a negative correlation between adaptation to high and low nutrient levels, *insofar as this adaptation takes place by natural selection of cells or cell lines*. Furthermore, if this mode of adaptation exists, it should be possible to predict the direction of changes in the values of the empirical  $V_{\max}$  and half-saturation constants.

As corollary it follows that observations on the half-saturation constants and  $V_{\max}$  at the intraspecific level can be used to discover whether natural selection is of widespread importance in determining the response of phytoplankton populations to nutrient fluctuations. There are basically two types of experiments that might be done:

1. Determine the mean uptake curves of a population before and after an episode of nutrient enrichment or depletion in nature. To do this, isolate a number of cells

of a given species at the height of a phytoplankton bloom, grow them up individually in flasks, pool equal numbers of cells from each flask, and work out the uptake kinetics of the pooled material. The number of cells isolated would have to depend on the sizes of the experimental errors and desired standard error of the estimates—twenty cells might be satisfactory. Except for mutations occurring during the experiment, this will give an estimate of the mean kinetic properties of the original isolates. Repeat the experiment with a new sample of cells collected when the population has declined and see whether the uptake curves have changed and, if so, whether they cross the old curves.

2. Determine the genetic covariance of the half-saturation constant and  $V_{\max}$  at some one time and place. Again, clone cells and grow them up individually, but instead of pooling them measure the uptake parameters separately on each clone and look for a negative correlation coefficient between  $V_{\max}$  and the half-saturation constant.

Adopting a genetic approach to the two problems posed at the beginning puts them into a perspective in which they can be seen to be closely related. If the underlying genetic variance in the population is of the type usually characterizing major components of fitness, then the covariance of  $V_{\max}$  and the half-saturation constant will, in general, be negative. If natural selection acts on this variance in such a way as to change the genetic composition of a population during episodes of local enrichment or depletion, then the hyperbolalike uptake curves representing the mean properties of the population before and after the episode will, in general, cross each other.

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#### Reference

FALCONER, D. S. 1965. Introduction to quantitative genetics. Ronald.