

Influence of Temperature Changes on Aquatic Ecosystems: An Interpretation of Empirical Data

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Abstract.—Many mathematical relationships have been used to summarize quantitative information about the effects of temperature on rate processes in ectothermic living systems. One of the more common relationships, which has been used for a century, is here termed the “combined exponential model.” An exponential model, as with a first-order chemical reaction, is used to define a coefficient for a rate at a particular temperature; another exponential relationship (of the van’t Hoff or the Arrhenius form) is then used to relate the coefficients of the rate process to their respective temperatures. The Arrhenius form has come to be preferred over the van’t Hoff form. In ectotherm physiology, the combined exponential model applies when the relevant organism has not evolved means of compensating biologically for the underlying physicochemical dynamics as affected by temperature. Here we assess the applicability of the combined model, of the Arrhenius form, to analogous ecological situations for aquatic ectothermic populations and ecosystems. On an empirical basis, we find that this combined model has some utility in that it permits approximate assessments of some ecosystemic effects of climate warming.

Living systems, at whatever level of organization, must cope with environmental temperatures and temperature changes. As ecologists, we generally do not expect to find that a simple and general mathematical expression will satisfactorily characterize a variety of causal or stimulus-response relationships between, say, measures of some rate processes within a living system and various environmental temperatures to which the system may be subjected. For example, after reviewing many mathematical expressions used with data on rate of fish body weight increase, Ricker (1979) concluded: “To date, the most convenient form for presenting data on growth in relation to temperature or rations is an empirical table of smoothed values, or the corresponding graph.” But some ecologists, including ourselves, have continued to apply relatively simple temperature models for some kinds of ecological processes. We have used them for descriptive rather than explanatory purposes. In this paper we sketch some conceptual bases for such apparently simple models.

Thienemann (1930) and his colleagues applied the Q_{10} convention—which is based on a combination of two simple exponential functions (see below)—to describe the dependency of certain limnological rate processes on environmental temperature. More recently, Woodwell (1983) also applied the Q_{10} concept in terrestrial ecology to suggest some very general ecosystemic effects of

climate change. We have implicitly used other versions of the underlying combined model to describe ecological variables related to fish and fisheries at the level of populations and species associations (Pauly 1980; Schlesinger and Regier 1983). We have also found that the simplest combined model does not apply even approximately to some kinds of ecological rate processes (Schlesinger and Regier 1982), as is also apparent with some physiological processes. In ecological situations in which the combined model seemed appropriate, it was apparently used pragmatically to provide a convenient means of summarizing quantitative information. It was not applied deductively on the basis of some accepted general theory. Here we explore some conceptual underpinnings of what we term the “combined exponential model” as applied to particular types of ecological rate processes.

Unless one is quite familiar with the jargon of a variety of different quantitative conventions, it may not be apparent that particular analysts actually have invoked different versions of the same “combined exponential model,” so we review these conventions to expose the isomorphisms. We propose some general characterizations of the situations in which the combined model might apply. We review some of the many data sets, at several organizational levels of living systems, for which some version of the combined model has been

used. Finally we consider the applicability of the combined model for assessing the ecological effects of climate warming.

Fry (1947) developed concepts such as controlling and limiting factors in the context of physiological ecology, based in part on earlier work by Blackman (1905; see McCombie 1960). We explore the relevance of such concepts for population and ecosystemic phenomena as related to the applicability of the "combined exponential model." We concern ourselves with process rates at lower levels of organization as part of our reductionistic analysis of ecological phenomena. We leave open here the question whether application of the same combined model at different levels of organization may be done only by analogy or by causal connections between levels of organization.

First Exponential Model

Physicists, chemists, physiologists, and ecologists often use the exponential model for particular stages or phases of rate processes when temperature and other "controlling" factors are constant:

$$\frac{dx}{dt} \cdot \frac{1}{x} = k \quad (1)$$

or

$$x_2 = x_1 e^{k(t_2 - t_1)} \quad (2)$$

Here, x is the amount of substance that enters into a reaction, in terms of mass, concentration, etc. Time is denoted by t ; t_1 and t_2 are the beginning and end of a particular time interval. The term k may be variously called the rate constant, specific rate constant, specific reaction rate, relative reaction rate, rate coefficient, exponential coefficient, instantaneous rate, etc. The k coefficient may be greater than zero (with positive sign) with growth processes and less than zero (with negative sign) in attrition and decomposition processes.

In chemistry, this model applies to a special case—the first-order chemical reaction—of a more general expression for the rate of reaction:

$$\frac{dx}{dt} \cdot \frac{1}{x^n} = k.$$

Here, n denotes the "order" of the reaction; when estimated empirically, it is found to be an approximate function of the number of molecules whose concentrations determine the rate of the reaction. The first-order chemical reaction, with $n = 1$, applies ideally, for example, in situations where a chemical substance in dilute aqueous so-

lution reacts with the water to form a different substance. Water is so abundant that its concentration is essentially constant, and the products of reaction are too dilute to slow down or interfere significantly with the reaction as it progresses. The first-order reaction in physics applies in somewhat similar situations: for example, when a radioactive element disintegrates gradually over time, or a substance diffuses through a liquid or a nonliving membrane. These elementary considerations have possible relevance, perhaps only by analogy, to the subsequent discussion of somewhat comparable ecological phenomena.

Models (1) or (2) often appear in a different guise: to characterize the length of time that it takes a particular process to run its course. With an exponential model like this, in theory, a reaction never quite ends, so some cutoff convention must be invoked to apply it—say 50% completion or 99% completion.

Let $t_2 - t_1 = \Delta t$, and $\Delta t_{0.5}$ be the time interval required for 50% completion: a reduction in the original amount of x by 50%. Then

$$\frac{x_2}{x_1} = 0.5 = e^{k\Delta t_{0.5}},$$

and

$$k = \frac{0.693}{\Delta t_{0.5}}.$$

If z specifies the cutoff convention, then in general

$$k = \frac{\log_e(1 - z)}{\Delta t_z}; \quad (3)$$

z specifies the percent completion, and Δt_z the length of time required to achieve that level of completion.

We repeat, equations (1), (2), and (3) are versions of the same model, which is that of the first-order chemical reaction.

Second Exponential Model

Consider a particular kind of first-order reaction observed in several different situations in which all conditions are identical except that the separate reactions occur at different temperatures. We note at the outset that a first-order reaction acts "normally"—it is consistent with the underlying model formulated as (1), (2), or (3) above—only for a limited range of temperature. The reaction has a different outcome at temperatures that are too high or too low. In living systems, the rates drop to zero, but not necessarily monotonically, at temperatures below and above the "normal" range.

Within the relevant "normal temperature range" for a particular type of first-order reaction, the rate of the process is sensitive to temperature in a way consistent with the exponential model

$$k = ae^{b \cdot RT}; \quad (4)$$

k is defined as in equations (1), (2), and (3) above, and a and b are constants. The term $f(T)$ may be defined in one of two ways (see Cossins and Bowler 1987):

$$\begin{aligned} f(T) &= \text{temperature in degrees Celsius, according to the model of van't Hoff; or} \\ f(T) &= \text{inverse of temperature in degrees Kelvin, according to the model of Arrhenius.} \end{aligned}$$

The Arrhenius model, but not the van't Hoff model, has been validated, theoretically and reductionistically. The Arrhenius model may take the form

$$k_i = Ae^{-E/RT_i}; \quad (5)$$

T_i = absolute temperature in °K, i.e., 273.15 + $T^\circ\text{C}$; A = frequency factor; E = energy of activation of the reaction in joules; and R = gas constant, i.e., 8.309 J/mol·K. The general relevance of these terms to physiological rate processes is discussed in various textbooks in physiology (e.g., Hoar 1966; Cossins and Bowler 1987).

From equation (5), it follows that

$$\begin{aligned} \log_e k_i &= \log_e A - \left(\frac{E}{R}\right)\left(\frac{1}{T_i}\right) \\ &= a - b\left(\frac{1}{T_i}\right). \end{aligned}$$

The coefficients a and b may be estimated by regression methods.

Consider the length of time for a particular stage or "stanza" of a process or developmental sequence, such as occurs in the maturation of an organism, as a function of temperature, according to the Arrhenius model.

We combine equations (3) and (5):

$$\Delta t_{zi} = \frac{\log_e(1-z)}{A} e^{\left(\frac{E}{R}\right)\left(\frac{1}{T_i}\right)} = ce^{b\left(\frac{1}{T_i}\right)} \quad (6)$$

and

$$\log_e(\Delta t_{zi}) = \log_e c + b\left(\frac{1}{T_i}\right).$$

All the terms are as defined above except c , which is a constant.

The van't Hoff version of this second exponential model (see below) is considered to be an empirical generalization that may coincidentally provide an acceptable approximation to the Arrhenius model (Cossins and Bowler 1987). The approximation stems from the arithmetic coincidence that the relationship between temperature in °C and the corresponding temperature in °K is only moderately curvilinear over relatively short ranges of temperature within the range of 0 to 40°C (Cossins and Bowler 1987).

A particular short-hand convention has often been used with the van't Hoff model. The symbol Q_{10} denotes the ratio of the specific rate of a process at two temperatures that differ by 10°C.

The basic model is

$$k_i = ae^{bT_i},$$

with T_i in °C. The ratio is

$$Q_{10} = \frac{k_2}{k_1} = e^{b(T_2 - T_1)} = e^{b(10)},$$

because $T_2 - T_1 = 10^\circ\text{C}$.

Within the van't Hoff model, Q_{10} does not vary with temperature, but it is implicitly limited to the range of temperature over which the process acts normally—i.e., in accordance with the model. With empirical data, it is usually noted that the van't Hoff Q_{10} is not constant over an extended temperature range and thus the model is taken to be a rough approximation of the phenomenon under study.

An "Arrhenius Q_{10} " may be calculated that approximates the "van't Hoff Q_{10} ." The basic model is

$$k_i = ae^{b/T_i},$$

with T_i in °K. The Arrhenius Q_{10} is defined by

$$\frac{k_2}{k_1} = e^{b\left(\frac{1}{T_2} - \frac{1}{T_1}\right)},$$

$T_2 - T_1 = 10^\circ\text{K}$ (or 10°C).

As a mathematical expression, the Arrhenius Q_{10} is not independent of the actual measure of temperature, which compromises its usefulness as a convenient rule of thumb. When an Arrhenius Q_{10} is used, as we have done in Tables 1–3 below, the midpoint or some other descriptor of the relevant 10°K range must be specified.

Combined Exponential Model

The specific rate or k of the first-order reaction (equations 1 to 3) has the dimension mass/(mass·

time). In particular physiological and ecological applications, a variety of functional surrogates of mass may be used such as the concentration of a substance in aqueous solution, the number of entities all implicitly of about the same mass, the amount of a surrogate such as oxygen used in the process that results in a change in mass of the primary substances, heat units produced when the relevant mass is burned, etc. That an exponential model has been invoked implicitly may only become apparent after careful analysis of the "dimensions" of the response variable employed by the analyst (see further below).

The k from equations (1) to (3), itself a coefficient in an exponential function, may in turn be an exponential function of temperature (as with the Arrhenius model) within the appropriate temperature range. If so, the quantitative analytical process usually involves two steps.

(1) Each of several k_i 's are estimated with the aid of a semilogarithmic regression equation of a particular rate process conducted at several temperatures T_i :

$$\log_e \left(\frac{x_{i2}}{x_{i1}} \right) = \hat{k}_i T_i;$$

T_i is in °K or °C, and it does not matter here which temperature scale is used.

(2) The relevant coefficients, a and b , of (say) the Arrhenius model are derived with a semilogarithmic regression equation:

$$\log_e \hat{k}_i = \log_e \hat{a} + \frac{\hat{b}}{T_i};$$

T_i is in °K. The analogous estimation formula for the van't Hoff model is

$$\log_e \hat{k}_i = \log_e \hat{a} + \hat{b} T_i,$$

with T_i in °C. The a and b coefficients of the van't Hoff model differ numerically from the a and b coefficients of the Arrhenius model.

We labor these elementary considerations here in order that the way in which we obtained our estimates for various data sets (see below) is quite clear.

Alternative Model

An empirical model or rule of "thermal sums" or "degree-days," first used by Reamur in 1735, is in wide use in applied ecology such as agriculture and fisheries. Often there is a low-temperature threshold for a particular process of a living system. This threshold is implicitly assigned a val-

ue of 0 on the temperature scale. For each unit of time during the period of the process, the difference in temperature between the average temperature within the time unit and the threshold temperature is estimated. Within time units in which the average temperature is actually less than 0, a value of 0 is used. All the positive temperature differences for all the time units necessary to complete the process are then summed to provide the estimate of "thermal sum" or "degree-days." Thus

$$\text{thermal sum} = \sum_{i=1}^t (T_i - T_0);$$

T_i is the mean temperature in °C during day i , T_0 is the threshold temperature; and $T_i - T_0 = 0$ for all $T_i \leq T_0$.

Belehradec (1930) showed that the Reamur rule is consistent with an empirical generalization by Krogh (1914) in which the rate of reaction of a process is directly proportional to temperature (°C) within the relevant normal range of temperature. Belehradec (1930) proposed a more general relationship of the form

$$\Delta t_i = a(T_i - T_0)^{-b},$$

Δt_i being the time period necessary to complete a process at temperature T_i in °C; here a and b are empirical constants. Belehradec (1930) showed that the Reamur and Krogh relationships were special cases of his relationship, i.e., with $b = -1$.

These models are apparently based on empirical generalizations rather than on reductionistic theory. Complex corrections may be developed to apply the thermal sums model with some accuracy to particular situations in agriculture (Neild et al. 1988). Both the Reamur and Belehradec models are used in fisheries studies. We do not consider them further here because we do not know of any reductionistic theoretical concepts on which they may be based. We imply no criticism of their utility by disregarding them in what follows here.

Controlling and Limiting Factors, Log-Phase Processes

Consider again the first-order reaction of equation (1):

$$\frac{dx}{dt} \cdot \frac{1}{x} = k.$$

In realistic situations, various phenomena can influence the x variable to complicate the process. For example, there may be interference (structural rather than thermodynamic interference) with the supply of x , or products of the process may act to

interfere with the subsequent part of the process. Such scarcity or interference may be termed "limiting" and the corresponding influence a "limiting factor."

Alternatively, there may be phenomena that act directly on the rate, in effect, to alter k independently of any limiting factors. Our second exponential model above—whether in the van't Hoff or Arrhenius version—is a prototypical case involving temperature as a "controlling factor." Other examples of controlling factors, say on the ecological processes of aquatic animals, include effects of alkalinity or salinity or light intensity (Fry 1971).

In physiology and ecology, the phenomenon of "log-phase growth," or "log-phase attrition," is observed in particular circumstances. Explicitly or implicitly the model for the first-order reaction is usually invoked to characterize such a log-phase phenomenon. That this has been done may only be evidenced in the units selected for the particular version of the "specific rate" used. The measure of the specific rate thus estimated is then often described as an exponential function of temperature, etc.

In the simplest situation, a log-phase phenomenon and a good fit with the combined exponential model can be expected with some physiological and ecological processes in which the most important input (resources) or output (wastes) factors are not limiting the rate of progress of the process. When the specific rate of a process at different temperatures is found to be an exponential function of temperature (e.g., the Arrhenius model), other controlling factors are either constant over the temperature range or are themselves exponential functions of temperature of a form generally isomorphic with the Arrhenius model.

Processes that approximate log-phase growth may be noted in early stages of some ecological processes—in the growth in mass of individual fish during the early weeks of life, in the growth in biomass of pelagic algae after spring turnover in a lake, etc. Models of an entire cycle of a living system—of biomass as a function of time, for example—are usually of a sigmoid type in the first "half" of the life cycle, with the "response curve" falling eventually to zero at the end of the temporal cycle. The sigmoid part of such a cycle may start with a stage that is approximately logarithmic or exponential in form. Unconstrained or log-phase growth is eventually superceded by diminishing growth due to internal and external "constraints" typical of maturation within the

growth process, or to "environmental resistance" due to other processes in the larger system; this in turn is superceded by "senescence" and "death."

Natural or cultural perturbations may interfere with "maturation" of a process and tend to contain it within a log-phase state dominated by r -type species (Rapport et al. 1985). Here, r -type species, in contrast to K -type species, have relatively little self-regulatory capabilities at the population level and do not enter into interspecific associations that involve close interrelationships. The turnover phenomena in dimictic lakes, and the resulting pronounced seasonality, may act to maintain such aquatic systems in a state that approximates a log-phase state of development for major periods in an annual cycle; strongly K -type species may be absent or subdominant in such systems (Dobzhansky 1950; Ricklefs 1973). This may provide a partial rationale for the apparent usefulness of the combined exponential model for some ecosystemic processes in lakes, as found by Thiennemann (1930) and as shown here in a subsequent section.

Criteria for Use of the Combined Exponential Model

In the foregoing section, we have reviewed generalizations and abstractions relating to "simple theory" as reflected in the conventional combined exponential model and such concepts as "limiting and controlling factors" and "log-phase growth." Here, we sketch some general features of real-life situations in which the models related to this "simple theory," of only approximate accuracy, may have some usefulness. We seek criteria that apply at various levels of organization, and thus will refer here to "living systems" rather than, say, to cells, organisms, populations, or ecosystems.

A system must have the following properties if it is to resemble a first-order reaction.

(1) The system's rate process of particular interest to the analyst is limited only by dynamic, not structural, phenomena with respect to the availability of necessary inputs or resources, and it is unaffected by the build-up of harmful outputs or wastes.

(2) The system does not possess, or does not exercise, a capability to adjust its rate processes with respect to potentially limiting resources or wastes, at least in the relevant stanza of its overall "life span."

(3) The system is not in an advanced state of maturity, as occurs with aging of a complex organism and attainment of sexual maturity or with

ecological succession of an ecosystem and attainment of dominance by *K*-type species.

(4) The system may be periodically perturbed or stressed by natural or cultural factors that interfere with self-regulatory capabilities and induce some quasi-rejuvenescences. (Perturbations and stresses generally cause greater harm to older organisms within a population and to *K*-species within an ecosystem, thus favoring conditions for log-phase growth of young individuals and of populations of species; see Dobzhansky 1950; Rapport et al. 1985; etc.)

A system characterized by the Arrhenius model has the following properties.

(1) The system does not have, or does not exercise within the life stanzas of interest, a capability to adjust its own temperature, in contrast to the physiological or behavioral influences on processes that organisms can exert. Thus, the system is ectothermic, within the range of temperatures of interest to the analyst, and the process rate of interest is "controlled" by external or environmental temperature.

(2) The system's process rate of interest to the analyst is controlled thermodynamically and is not strongly affected positively or negatively by other controlling processes whose rates exhibit markedly different temperature dependencies.

We note that very small organisms and juvenile, immature, or early successional life stanzas of a living system generally have a lesser capability than do larger organisms and mature states for internal temperature control by physiological, behavioral, or other "self-organizational" means. At the ecosystem level, large *K*-type plant species may act to effect partial "control" on temperatures below the canopy in both terrestrial (Grime 1979) and aquatic systems. Thus the responses to temperature of integrated processes within more "mature" systems are not likely to be characterized well by the Arrhenius model.

Introduction to the Review of Data Sets

We have conducted a search of literature from many sources for information relevant to our issue. We used three main guidelines for selecting information:

- the author(s) had used the exponential model, explicitly or implicitly, for a process that bore some resemblance to a first-order reaction or to log-phase growth at constant temperature;

- the author(s) had used the van't Hoff, Arrhenius, or semilogarithmic model to relate a "specific rate" to different temperatures; or

- the author(s) had explicitly or implicitly used the combined model and had calculated specific rates as a function of temperature for living systems within situations like those sketched in the preceding section.

We have summarized selected data sets of potential interest to ecologists in Tables 1 to 3 and Figures 1 to 12 below. Those presented in the tables and figures do not constitute a biased subset of all the data sets which we examined, so far as we can determine. We used the midpoint of the range of temperatures reported by the original authors as the midpoint of the 10°K range for the Arrhenius Q_{10} ratio. Table 1 and Figures 1 and 2 relate to organismal physiology, Table 2 and Figures 3–8 relate to population dynamics, and Table 3 and Figures 9–12 relate to ecosystem dynamics (*sensu lato*).

The data shown in Tables 1 and 2A and in Figures 1–5 were derived from experiments in which the temperature within different trials was held constant. All the other data are from field observations in which temperatures varied seasonally. For the field observations, we used mean annual temperature as the independent variable. In most cases, mean annual air temperature was used as an estimate of the relevant mean annual water temperature because sufficient data on which to base the mean annual water temperatures were not available (Schlesinger and Regier 1982, 1983).

We recognize that mean annual temperature, whether of water or at nearby air stations, is at best a very approximate measure of what is actually relevant to aquatic ecological processes (e.g., see Pauly 1980; Schlesinger and Regier 1982, 1983). It seems unlikely to us that any single number, however the variable might be defined, would be anything but approximate in such situations. Yet we suggest that a variable like the one we used is better than nothing.

Parenthetically, we are exploring complementary approaches to an understanding of the ecological effects of temperature, especially with respect to phenomena in which evolutionary adaptation is apparent. Thus we are exploring the concept of thermal habitat niche for separate species (Magnuson et al. 1979, 1989; Christie and Regier 1988).

The history of the use of the combined exponential model in physiology is well known to some academic physiologists. The corresponding history at the population and ecosystem levels—with respect to the issue of temperature dependence of specific rates—is not well known.

TABLE 1.—Regression equations relating some physiological rates of fish to absolute temperature (T , °K); $\log_e(\text{rate}) = a + b(1/T)$. Egg incubation period extends from fertilization period to 50% hatching. All regression slopes are significant at $P < 0.005$, except an asterisk denotes $P < 0.05^*$. The Arrhenius Q_{10} is specified for the midpoint of the temperature range.

Species	Common name	Regression			r^2	Temperature range (°C)	Q_{10}	Source ^a
		a	b	N				
Standard metabolic rate, mg O₂/(kg·h)								
<i>Oncorhynchus mykiss</i> ^{b,c}	Rainbow trout	23.66	-5,602	5	0.95	5-25	2.0	1
<i>Oncorhynchus mykiss</i> ^d	Rainbow trout	19.48	-4,391	5	0.96	5-25	1.7	1
<i>Oncorhynchus nerka</i>	Sockeye salmon	27.08	-6,519	5	0.96	5-24	2.2	2
<i>Carassius auratus</i> ^e	Goldfish	36.27	-9,295	7	0.95	5-35	2.2	3
<i>Carassius auratus</i>	Goldfish	27.71	-7,076*	4	0.97	10-35	2.3	4
<i>Cyprinus carpio</i>	Common carp	27.04	-6,812	5	0.98	10-35	2.2	5
<i>Salvelinus namaycush</i> ^{e,f}	Lake trout	28.93	-7,020	18	0.81	9-23	1.9	6
<i>Salvelinus namaycush</i> ^{e,g}	Lake trout	40.51	-10,487	14	0.89	9-23	2.5	6
Egg incubation period, d								
<i>Oncorhynchus</i> spp.	Pacific salmon	-31.50	9,928	53	0.90	2.8-12.0	3.5	7
<i>Salmo</i> spp.	Trout	-28.29	9,108	7	0.99	5.2-12.0	3.2	7
<i>Salvelinus fontinalis</i>	Brook trout	-32.58	10,328	41	0.99	1.6-14.8	3.7	8
<i>Salmo trutta</i>	Brown trout	-40.80	12,607	29	0.99	1.9-11.2	5.0	8
<i>Oncorhynchus mykiss</i>	Rainbow trout	-35.58	11,069	23	0.97	3.2-15.5	4.0	8
<i>Salvelinus namaycush</i>	Lake trout	-35.66	11,196	7	0.98	1.8-10.0	4.2	8
<i>Coregonus artedii</i>	Lake herring	-49.66	15,098	14	0.99	0.5-10.0	7.0	9
<i>Coregonus clupeaformis</i>	Lake whitefish	-42.97	13,127	6	0.99	0.5-10.0	5.4	10
<i>Cyprinodon macularius</i>	Desert pupfish	-30.42	9,683	33	0.92	13.0-35.8	2.9	11
Various fish stocks ^h		-26.60	8,015	140	0.83	2.8-29.5	2.5	12

^a Sources of data: 1—Dickson and Kramer (1971); 2—Brett (1964); 3—Fry and Hart (1948); 4—Beamish and Mookherjee (1964); 5—Beamish (1964); 6—Gibson and Fry (1954); 7—Crisp (1988); 8—Emboly (1934); 9—Colby and Brooke (1973); 10—Price (1940); 11—Kinne and Kinne (1962); 12—Pauly and Pullin (1988).

^b Formerly *Salmo gairdneri*.

^c Hatchery-reared fish.

^d Wild fish.

^e Data were converted from cm³ O₂/(kg·h) to mg O₂/(kg·h).

^f One-year-old fish.

^g Two-year-old fish.

^h Dependent variable is the residual from the regression of development time against egg diameter and environmental temperature, and was calculated from the multiple regression as follows: residual = log_e(time period) - 0.5965(log_e[egg diameter]).

Physiological Ecology of Aquatic Ectotherms

The first-order chemical reaction has long been used as a model for catabolic losses under standard conditions, as with the standard metabolic rate (Table 1). Thus Krogh (1914) used the approximation

$$\frac{\Delta x}{\Delta t} \cdot \frac{1}{\bar{x}}$$

Δx was a change in mass due to catabolism or its covariate such as cubic centimeters of oxygen consumed within a time interval such as an hour; the ratio $\Delta x/\Delta t$ was divided by the estimated mean, \bar{x} , of the organism's mass during the time interval of the experiment.

Much of the early discussion in the physiological literature on ectotherms was in terms of the van't Hoff Q_{10} measure. The Arrhenius relationship is now preferred over the van't Hoff by some physiologists such as Hoar (1966) and Winberg

(1971), but the van't Hoff model is still commonly used.

Ecology of Aquatic Ectotherms

Buschkiel (1931), Ruttner (1931), and others used the van't Hoff concept to explain differences in limnological features of tropical and temperate lakes. They applied the concept to the rate of growth of fish and age of maturation, especially of common carp; to the rate of decomposition and mineralization of dead plankters; to the frequency of reproductive divisions and length of the life cycle of plankters; to the rate of ecological production in the trophogenic zone and rate of oxygen depletion in the hypolimnion following stagnation; and even to trophic status.

The authors of the studies summarized in Tables 2 and 3 and Figures 3-12 used a formula for the rate process that was broadly consistent with the model for the first-order reaction (one excep-

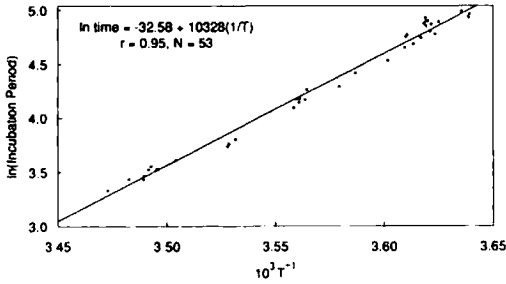


FIGURE 1.—Arrhenius plot of the length of the egg incubation period (days from fertilization to 50% hatch) against the inverse of absolute temperature (T , °K) for brook trout *Salvelinus fontinalis*. Data are from Embody (1934); $\ln = \log_e$. Incubation periods range from 28.0 to 142.5 d and temperatures range from 14.8 to 1.64°C.

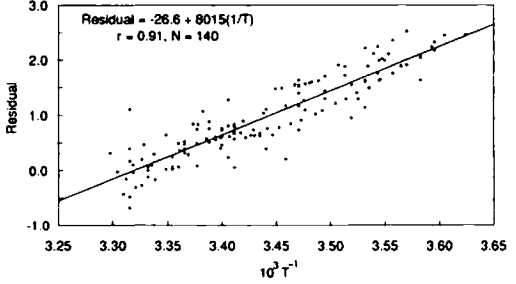


FIGURE 2.—Arrhenius plot of the residuals from the regression of egg development time to hatching against egg diameter plotted against the inverse of absolute temperature (T , °K) for various pelagic marine fish stocks. Residuals were calculated as follows: residual = $\log_e(\text{observed}) - \log_e(\text{expected})$; $\log_e(\text{expected})$ is $\log_e(\text{development time}) - 0.5965 \log_e(\text{egg diameter})$. Data are from Pauly and Pullin (1988). Development times range from 0.38 to 16.0 d and temperatures range from 30.1 to 4.3°C.

tion is mentioned below). With respect to the temperature effects on the specific rates, many recent authors relied on the van't Hoff model, but some have chosen the Arrhenius model; see for example, Goldman and Carpenter (1974) as in our Figure 4, Ivleva (1980), and Tseitlin (1980).

In fisheries, the expression for a first-order reaction has been applied as a rough approximation to certain population processes, notably by Ricker (1975). Thus

$$\frac{dW}{dt} \cdot \frac{1}{W} = G;$$

W is the average mass of individual fish at some point in a stanza of a cohort's life cycle, and G is the instantaneous rate of growth or specific rate of growth. Figure 5 provides an explicit example, and Figure 6 an implicit example.

Similarly,

$$\frac{dN}{dt} \cdot \frac{1}{N} = -M;$$

N is the number of fish and M is the instantaneous rate of natural mortality. Figures 7 and 8 provide examples; see further discussion below.

With appropriate simplifying assumptions,

$$B = Nw;$$

B is the biomass of the cohort.

The simplest model related to fishery yield, Y , is

$$\frac{dY}{dt} \cdot \frac{1}{B} = F;$$

F is the instantaneous rate of fishing mortality.

The simple models sketched above are seldom used now because more realistic and more com-

plicated expressions have been found for growth, mortality, etc. But fish associations that are naturally perturbed or heavily stressed due to intensive fishing or other cultural influences tend to be dominated by young and small fish such as clupeids, as shown in Figure 7. For them, Ricker's (1975) simple models are less unrealistic than they would be for older and larger fish.

Under conditions that are in approximate equilibrium, and with several year-classes of a species contributing to a fishery,

$$\frac{\Delta Y}{\Delta t} \cdot \frac{1}{B} = F;$$

ΔY is the sum of the landings within a relatively short time interval Δt , and B is the equilibrium biomass of fish within the life stanza in which they animals are vulnerable to the fishery. See Pauly (1984) for examples of this application.

Continuing with the rather simplistic theoretical argument, under conditions of maximum sustainable yield, MSY ,

$$F_{MSY} = aM$$

according to Gulland (1971), Beddington and Cooke (1983) and Pauly (1984). Thus

$$\frac{\Delta Y}{\Delta t} \cdot \frac{1}{B} = aM.$$

If the biomass of a fishable stock is evenly distributed over the area of the stock's habitat, then for comparative purposes

$$B = bH;$$

TABLE 2.—Regression equations relating population processes to absolute temperature (T , °K); $\log_e(\text{rate}) = a + b(1/T)$. All regression slopes are significant at $P < 0.05$, except an asterisk denotes nonsignificance ($P > 0.05^*$). The Arrhenius Q_{10} is specified for the midpoint of the temperature range.

Organism	Regression		r^2	N	Temperature range (°C)	Q_{10}	Source ^a
	a	b					
Growth rates, in terms of mass or number							
Algae ^b	30.44	-9.268	0.51	21	10.0-41.0	2.9	1
Algae ^c	22.36	-6.472	0.81	26	13.5-39.2	2.1	2
Protozoa ^d	26.56	-7.542	0.98	4	14.0-26.0	2.4	3
Stonefly nymphs ^e	62.14	-17.127	0.78	18	0.4-10.2	9.0	4
Common carp ^f	25.23	-7.772	0.56	52	15.6-26.4	2.5	5
Developmental period							
Fish stocks ^g	-19.21	6.018	0.35	12	7-28	2.0	6
<i>Stizostedion vitreum</i> ^h	-9.063	3.659	0.75	20	-9.4-20.5	1.6	7
Mortality rateⁱ							
All stocks	14.60	-4.369	0.23	175	5-28	1.7	6
Freshwater fish	20.11	-5.833	0.24	30	5-27	2.0	6
Marine fish	14.99	-4.504	0.26	145	5-28	1.7	6
Scombridae	40.48*	-12.068*	0.11	17	15-28	4.0	6
Clupeidae	15.47	-4.683	0.40	16	8-27	1.7	6
Gadidae	48.00	-13.723	0.42	17	5-12	5.6	6
von Bertalanffy parameters and environmental temperature							
All stocks ^j	$\log_e M = 11.55 - 2,968(1/T) - 0.310 \log_e L_\infty + 0.6266 \log_e K$						6
	$r^2 = 0.73; r_1^2 = 0.04; r_2^2 = 0.03; r_3^2 = 0.65; N = 175$						

^a Sources of data: 1—Fogg (1966); 2—Goldman and Carpenter (1974); 3—Caron et al. (1986); 4—Brittain (1983); 5—Knyazev (1987); 6—Pauly (1979, 1980); 7—Colby and Nepszy (1981).

^b Data represent growth rate constants (per day) for planktonic and nonplanktonic algal populations grown in continuous light that was approximately saturating for photosynthesis.

^c Maximum specific growth rate (doublings/d) for freshwater and marine algae grown in continuous culture experiments. The equation was taken without change from the source.

^d Data are population increases expressed as cell number/d and are derived from experiments on *Phaeodactylum tricornutum*.

^e Data are mean specific growth rates (% mass increase/d) for four species of stonefly (Plecoptera) from a Norwegian mountain lake.

^f Data are specific rates of weight increase for age-0 fish.

^g Data represent longevities of fish stocks approximated by the formula $t_{\max} \approx (3/K) + t_0$; K and t_0 are von Bertalanffy growth parameters (see footnote j).

^h Age at which 50% of female walleyes are sexually mature as estimated from probit paper.

ⁱ Data represent instantaneous natural mortality rates. M .

^j M = instantaneous rate of natural mortality; L_∞ = asymptotic length as determined from Ford-Walford plots; W_∞ = asymptotic weight corresponding to L_∞ ; K = von Bertalanffy growth constant determined from Ford-Walford plots; r_1^2 , r_2^2 , and r_3^2 = fractions of variability explained by independent variables 1, 2, and 3, respectively.

b is the standing crop per unit area of habitat and H is the area of habitat. Hence,

$$\frac{\Delta Y}{\Delta t} \cdot \frac{1}{bH} = aM.$$

If the production processes upon which a fishery depends are roughly analogous in form to a first-order chemical reaction with respect to what is of concern here, and if the relevant specific rates G and M are affected by temperature according to the Arrhenius model, then the following expressions should apply:

$$\begin{aligned} \frac{\Delta Y}{\Delta t} \cdot \frac{1}{bH} &\approx aM \\ &\approx a(Ae^{-E/RT}), \end{aligned}$$

and

$$M \approx Ae^{-E/RT}.$$

The latter relationship is fitted to mortality data from fish stocks in Table 2C and Figures 7 and 8.

The terms a and b in the preceding four equations are empirical proportionality coefficients specific to the particular application; these terms are not as defined in equation (4) above.

Further to Figures 7 and 8, Pauly (1980) presented two empirical models for estimating the exponential natural mortality coefficients of fish stocks from their von Bertalanffy growth parameters and environmental temperature. We fitted the Arrhenius relationship to his data set (Table 2). When we divided Pauly's (1980) data set into marine and freshwater stocks and families, the results (Table 2) were similar to those of all stocks

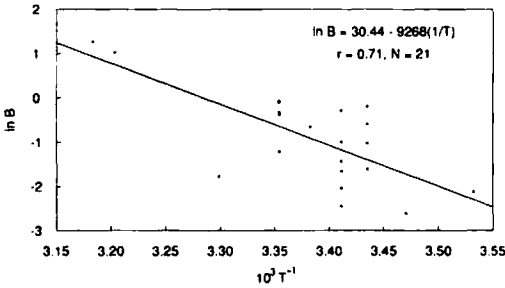


FIGURE 3.—Arrhenius plot of algal growth rate constants (B) from populations grown in continuous light that was approximately saturating for photosynthesis against the inverse of absolute temperature (T , °K). Data are from Fogg (1966); $\ln = \log_e$. Growth rate constants range from 0.087 to 3.55 and temperatures range from 41 to 10°C.

combined. The Arrhenius relationships were statistically significant in all cases except for the Scombridae. The total variability explained by temperature (23–43%) within this set of relationships is considerably less than in the other sets that we have examined; this may be due to the wide range of fish sizes in Pauly's data set, and to the empirical observation that M is strongly correlated with size. Results of the analysis shown in Table 2 and in Figure 8 are consistent with this hypothesis.

Yields for individual species at different temperatures apparently do not fit the Arrhenius model well (Schlesinger and Regier 1983). The Arrhenius relationship should, we suggest, be applicable to combined yield or production from a set of different species of a lake that are somewhat similar ecologically but with different temperature optima; this was found to be so with the four ecolog-

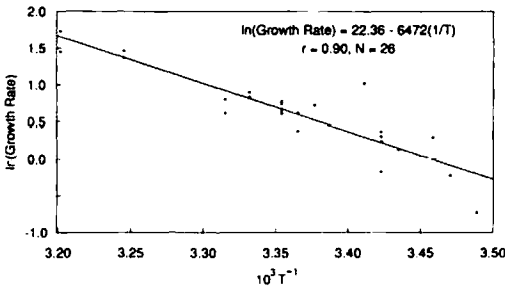


FIGURE 4.—Arrhenius plot of population growth rates (doublings/d) of freshwater and marine algae grown in continuous culture against the inverse of absolute temperature (T , °K). Data are from Goldman and Carpenter (1974); $\ln = \log_e$. Specific growth rates varied from 0.48 to 5.65 and temperatures ranged from 39.2 to 13.5°C.

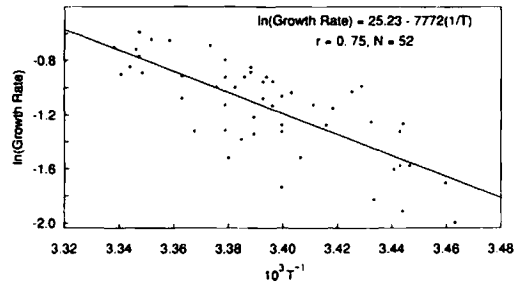


FIGURE 5.—Arrhenius plot of the specific rate of weight increase of age-0 common carp against the inverse of absolute temperature (T , °K). Data are from Knyazev (1987); $\ln = \log_e$. Rate data vary from 0.136 to 0.555 and temperatures range from 26.4 to 15.6°C.

ical groups in Table 3 and shown in Figures 9–12. In such cases, the niches of the species overlap so that some interspecies compensation can occur within the range of temperature.

Zooplankton biomass was used as a surrogate measure of production because production has been found empirically to be a semilogarithmic function of standing crop (Morgan et al. 1980). (This was the exceptional case flagged in the earlier discussion above.) Mean annual air temperatures for the phytoplankton and shrimp data sets were taken from Wernstedt (1972).

The Arrhenius relationship provided statistically significant fits to data sets for four distinct ecological groups in Table 3. Both the shrimp and fish equations are reparameterizations of relationships provided by Schlesinger and Regier (1982) and Turner (1977), respectively. The fits (based

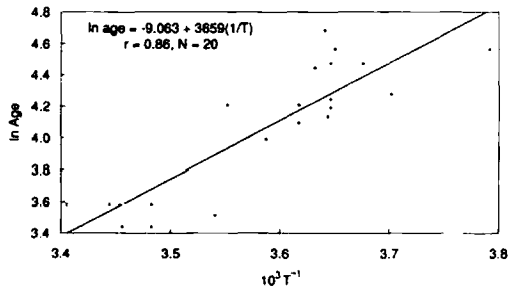


FIGURE 6.—Arrhenius plot of the age of sexual maturity of female walleyes against the inverse of absolute mean annual air temperature (T , °K). Data represent age at which 50% of the females in a given population are sexually mature, as estimated by probit analysis of Colby and Nepszy's (1981) data; $\ln = \log_e$. Age data vary from 31.2 to 108 months and temperatures range from 20.5 to -9.4°C.

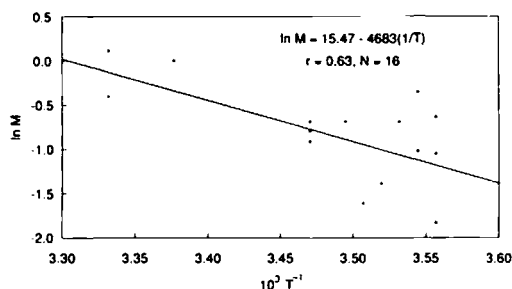


FIGURE 7.—Arrhenius plot of the instantaneous natural mortality rate (M) of some species of Clupeidae against the inverse of absolute environmental temperature (T , °K). Data are from Pauly (1980); $\ln = \log_e$. Mortality rates range from 0.16 to 1.12 and temperatures vary from 27 to 8°C.

on r^2 values) to the shrimp and fish data sets are slightly better based on the Arrhenius formulation than the fits based implicitly on the van't Hoff approximation as reported by Schlesinger and Regier (1982). Mean annual air temperatures were not significantly correlated with zooplankton biomass but mean epilimnion temperatures given by Patalas (1975) were significantly correlated; this may account for the greater total variability explained by temperature in the zooplankton data set.

Attempts to relate rates of primary production in natural water bodies to external environmental factors have shown that such rates are related statistically to both insolation and temperature (Brylinsky and Mann 1973; Brylinsky 1980). The separate roles of these two factors have long been of interest (e.g., see Blackman 1905). We have not found a study in the literature in which the separate effects of temperature and insolation operating in the field have been clearly distinguished with respect to photosynthesis in natural aquatic systems. Careful laboratory studies with particular species have been reported (e.g., Schlesinger 1980; Schlesinger et al. 1981). Part of the problem in attempting to explicate primary production in the field concerns the rapid seasonal succession that occurs within water bodies, different algal species being adapted to different ranges of insolation and temperature.

In general with respect to the relationships included in Table 3, the coefficients that relate some form of ecological production to temperature likely also include effects due to insolation. The data set for each of the four relationships covers a range of latitudes and hence reflects differences in temperature and insolation (as well as other factors).

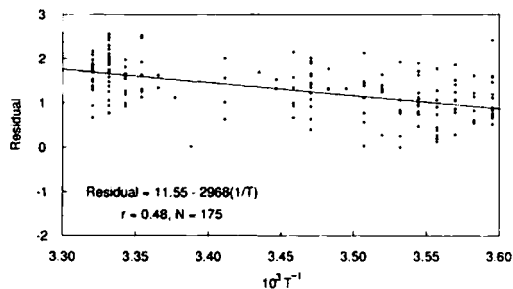


FIGURE 8.—Arrhenius plot of the residuals from the regression of mortality rate (M) against von Bertalanffy growth parameters (L = length; K = growth coefficient) plotted against the inverse of absolute environmental temperature (T , °K). Residuals were calculated as follows: residual = $\log_e(\text{observed}) - \log_e(\text{expected})$; $\log_e(\text{expected})$ is $\log_e M + 0.3101 \log_e L - 0.6266 \log_e K$. Data are for marine and freshwater stocks from Pauly (1980). Temperatures range from 28 to 5°C.

We have searched without success for data on aquatic ecosystems at different altitudes (and hence at different temperatures) within a small geographic region (and hence at approximately constant levels of insolation). We expect that a coefficient based on field data but strictly limited to temperature effects will be smaller than a coefficient within which differential insolation effects are also contained. Hence we judge that the numerical values of the temperature coefficients of the expressions in Table 3 are biased upwards by the hidden insolation effects.

Comments About the Combined Exponential Model

Our paper focuses on certain ectothermic phenomena in freshwater ecosystems; for whatever reasons, these phenomena do not reflect a capability by the system to compensate for temperature change. For measuring growth or attrition of the biomass, or of some surrogate measure of biomass of a living system, biologists often estimate a rate or coefficient of the general form

$$\frac{dx}{dt} \cdot \frac{1}{x} = k.$$

Among biologists, laboratory-oriented physiologists are generally informed as to the situations in which the combined model may have some approximate realism, as are field-oriented physiological ecologists. Comparable competence among ecologists seems to be rare by comparison; perhaps ecologists do not look for real-life situations or conceptual simplifications in which such

TABLE 3.—Regression equations relating ecological rates to absolute temperature (T , °K).^a All regression slopes are significant ($P < 0.001$). The Arrhenius Q_{10} is specified for the midpoint of the temperature range.

Group	Equation	Q_{10}	Source ^b
Temperate freshwater fish yield	$\log_e \text{MSY} = 29.74 - 8,115.4(1/T) + 0.4895 \log_e \text{MEI}_{25}$ $r^2 = 0.83; r_1^2 = 0.74; r_2^2 = 0.09; N = 43$ Temperature range: -5.2-25.6°C	2.6	1
Penaeid shrimp yield	$\log_e \text{SCSY} = 52.00 - 14,312(1/T)$ $r^2 = 0.34; N = 27$ Temperature range: 16.9-28.3°C	5.3	2
Phytoplankton production	$\log_e 1^\circ = 44.40 - 11,308(1/T) + 0.2908 \log_e \text{MEI}_{25}$ $r^2 = 0.58; r_1^2 = 0.51; r_2^2 = 0.06; N = 32$ Temperature range: -16.2-15.3°C	3.7	3
Crustacean plankton biomass	$\log_e \text{ZB} = 40.91 - 12,074(1/\text{EPTEMP}) + 0.4080 \log_e \text{MEI}_{25}$ $r^2 = 0.92; r_1^2 = 0.89; r_2^2 = 0.03; N = 14$ Temperature range: 4.0-23.5°C	4.0	4

^a Symbols and units as follows: MSY = maximum aggregate sustainable yield in kg/(hectare · year); SCSY = stabilized commercial shrimp yield, kg/hectare of intertidal vegetation; 1° = primary production in g C/(m² · year); ZB = zooplankton biomass during the summer in wet weight mg/L; T = absolute mean annual air temperature, °K; EPTEMP = absolute mean epilimnion temperature, °K; MEI₂₅ = morphoedaphic index for maximum mean depth of 25 m; r_1^2, r_2^2 = fractions of variability explained by the first and second independent variables, respectively.

^b Sources of data: 1—Schlesinger and Regier (1982); 2—Turner (1977); 3—Oglesby (1977); 4—Patalas (1975).

reductionistic models might apply. But some ecologists have reported studies in which they have implicitly used empirical conventions consistent with the first-order reaction model and the van't Hoff or Arrhenius models (see Tables 2 and 3).

When we found data on rate processes broadly consistent with a first-order reaction model summarized as a van't Hoff function of temperature, we fitted the Arrhenius model and generally obtained a closer fit to the data.

We have summarized above some empirical information that is consistent with the limnological generalizations of Thienemann (1930) and his col-

leagues. Also our data on aquatic rate phenomena are broadly consistent with generalizations concerning terrestrial ecological processes by Woodwell (1983). Our approach is related conceptually to the physiological ecology of Fry (1947), the r and K concepts of Dobzhansky (1950), and the population dynamics of Ricker (1975), the latter as extended by Pauly (1980). The combined exponential model provides a kind of null hypothesis in that it assumes the absence of biological organization beyond the underlying chemical (or biochemical) processes, at least with respect to temperature factors.

We propose three tentative generalizations that may be tested by theoretical ecologists and used with due caution by applied ecologists.

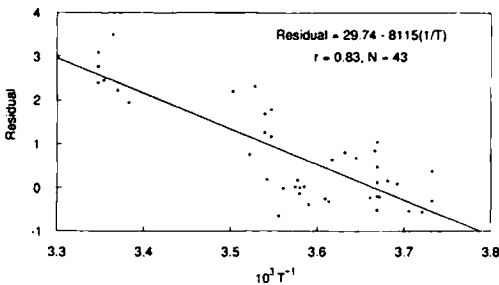


FIGURE 9.—Arrhenius plot of the residuals from the regression of mean annual (maximum sustainable) fish yield (MSY, kg/[hectare · year]) against the morphoedaphic index for a maximum mean depth of 25 m (MEI₂₅) plotted against the inverse of mean annual air temperature (T , °K). Residuals were calculated as follows: residual = $\log_e(\text{observed}) - \log_e(\text{expected})$; $\log_e(\text{expected})$ is $\log_e \text{MSY} - 0.4898 \log_e \text{MEI}_{25}$. Data are from Schlesinger and Regier (1982). Temperatures range from 25.6 to -5.2°C.

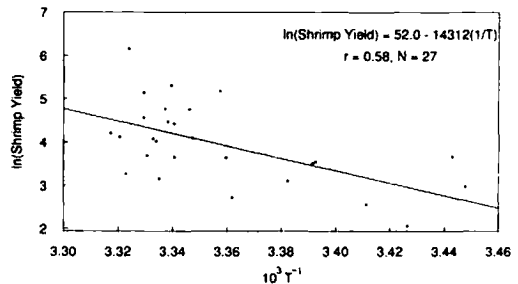


FIGURE 10.—Arrhenius plot of penaeid shrimp yield (kg/hectare of intertidal vegetation) against the inverse of mean annual air temperature (T , °K). Data are from Turner (1977) and Schlesinger and Regier (1982); $\ln = \log_e$. Shrimp yields range from 7.86 to 472 kg/hectare and temperatures vary from 28.3 to 16.9°C.

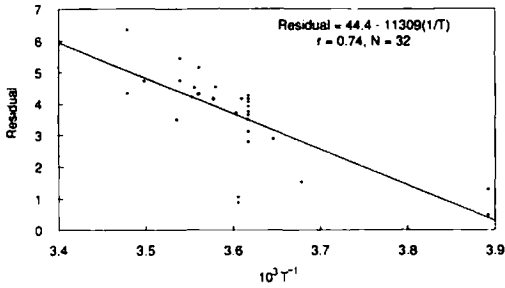


FIGURE 11.—Arrhenius plot of the residuals from the regression of phytoplankton primary production ($g\ C/(m^2 \cdot y)$) and the morphoedaphic index for a maximum mean depth of 25 m (MEI_{25}) plotted against the inverse of mean annual air temperature ($T, ^\circ K$). Residuals were calculated as follows: residual = $\log_e(\text{observed}) - \log_e(\text{expected})$; $\log_e(\text{expected})$ is $\log_e(\text{primary production}) - 0.2908 \log_e MEI_{25}$. Data are from Oglesby (1977). Primary production ranges from 4.1 to 3,285 $g\ C/(m^2 \cdot y)$ and temperatures vary from 15.3 to $-16.2^\circ C$.

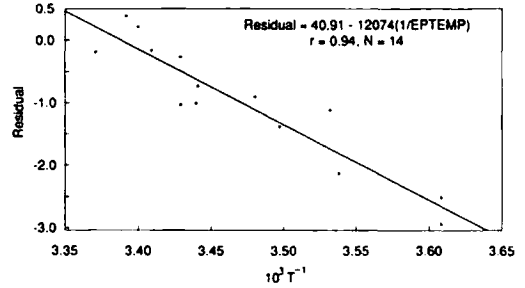


FIGURE 12.—Arrhenius plot of the residuals from the regression of zooplankton biomass (wet weight, mg/L) and the morphoedaphic index for a maximum mean depth of 25 m (MEI_{25}) plotted against the inverse of mean epilimnion temperature ($T, ^\circ K$). Residuals were calculated as follows: residual = $\log_e(\text{observed}) - \log_e(\text{expected})$; $\log_e(\text{expected})$ is $\log_e(\text{zooplankton biomass}) - 0.408 \log_e MEI_{25}$. Data are from Patalas (1975). Zooplankton biomass ranges from 0.07 to 3.81 mg/L and temperatures vary from 23.5 to $4.0^\circ C$.

- (1) At all levels of organization, from an enzyme-driven chemical reaction in a cell (data not shown above) to ecological production in an ecosystem, systemic situations occur in which the first-order reaction model combined with the Arrhenius model is useful (perhaps only as an analogue).
- (2) The higher the frequency of strong natural perturbations or strong cultural stresses in ecosystems, the more frequent or general will be the situations in which the combined model is likely to apply. The greater the amplitude of natural temperature-related perturbations in a system, the stronger the systemic responses are likely to be, and the greater the scope for application of the combined model.
- (3) When the combined exponential model applies, we expect that the underlying ecological process is consistent with r -type dynamics; hence K -type processes (and the relevant species, etc.) must be subdominant to the r -type processes.

Application to an Assessment of Climatic Warming

According to presently available scenarios, temperature changes due to the greenhouse effect will be smallest at the tropics and greatest near the poles (Hansen et al. 1988; Hengeveld 1990, this issue). The ecological effect, with respect to rate processes of the kind discussed above, should be approximately an exponential function of temperature change. For such processes, we may expect minor changes near the tropics, moderate

changes in midlatitudes, and quite pronounced changes in high latitudes.

Whether the increase in r -rates will lead to a corresponding increase in ecological production of the type valued by humans is, as yet, uncertain. It should do so in ecosystems in which r -processes are now dominant over K -processes, and in which all materials of primary importance to the ecological production process are charged into the ecosystem at comparable advanced rates with climate warming. The general assessment by Woodwell (1983) may presuppose that terrestrial ecosystems will do so, though there is concern that photosynthetic and hence anabolic processes may respond to a lesser degree than some catabolic processes to climate warming (Houghton and Woodwell 1989).

Comparative studies of similar aquatic ecosystems across a wide range of latitudes, as reported here, provide results that are consistent with a general increase with climate warming of all major productive processes that contribute to primary, secondary, and tertiary ecological production. But little confidence can now be placed on such an "optimistic" assessment; the relevant science is at a very immature stage.

Much of any increase in production due to climate warming may occur because of a shift of dominance among the native species in favor of those that are adapted to warmer conditions. Invasions of warm-adapted species from elsewhere may also occur and some native cold-adapted species will likely be extinguished locally (Man-

drak 1989). Further, if the climate warming will lead to greater temperature fluctuations seasonally, *r*-type species may be favored over *K*-type species.

Within the ecological seasonal succession that occurs after the spring overturn of the water mass, the tempo with which the relatively more thermophilic species succeed the more thermophobic species may increase with climate warming. The summer stagnation period may be longer. If climate warming leads to a reduction in the rate of flow of water from lakes, the effect on the trophic status would be in the direction of eutrophy (Vollenweider 1968). Plankters that drop out of the trophogenic zone may be decomposed faster, and oxygen depletion of the hypolimnion may occur earlier and persist longer in basins of the appropriate morphometry and water renewal rates (Vollenweider 1968). Anaerobic decomposition may then proceed more rapidly in the appropriate anoxic limnological situations, leading to production of harmful gases such as methane and hydrogen sulfide. These rather speculative assessments are consistent with comparative generalizations by Thienemann (1930) and his colleagues.

We suggest that climate warming may have a general effect in some "vulnerable" waters that superficially resembles eutrophication caused by nutrient enrichment. This "eutrophogenic phenomenon" joins a number of others, such as a reduction in mean depth of the water body, a reduction in the rate of flow of water through the water body, a shift in dominance of organisms from the larger *K*-type species to the smaller *r*-type species, and so on (Vollenweider 1968; Ryder et al. 1974; Rapport et al. 1985; Regier et al. 1988). If any of these other factors change in a "vulnerable" water body during the onset of climate warming, the overall ecosystemic effect of climate warming will need to be distinguished carefully from the interactive effects of these other eutrophogenic factors.

We conclude that the rather simple "combined exponential model" discussed in this paper may provide helpful clues as to some ecological effects that might be expected in aquatic ecosystems as a result of climate warming. Aquatic ecosystems of temperate waters or that are dominated by ectothermic *r*-type species appear to possess relatively little self-organizing capability to compensate for climate warming. As with other living systems at lower "levels of organization" that have not evolved internal ways to temper external temperature fluctuations, certain ecosystem processes may

adapt to climate warming approximately as indicated by the combined exponential model.

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