

EVOLUTION: TIME, ENERGY, and PERTURBATION

by

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**Evolution: Time, Energy, and Perturbation**

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## ABSTRACT

An investigation of biological energy exchange processes has led to the derivation of an analytic expression pertaining to the energy exchange rates between any given biosystem and its specific environment. The derived expression has been used to define a universally applicable measure of 'efficiency' for any organism, species, or ecosystem. Further, this measure of efficiency has been related to biological 'fitness' and therefore, by implication to biological evolution.

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E.M. Reimer

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"It (evolution) is a general condition to which all theories, all hypotheses, all systems must bow and which they must satisfy henceforward if they are thinkable and true. Evolution is a light illuminating all facts, a curve that all lines must follow."

-from The Phenomenon of Man

Pere Teilhard de Chardin

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## LIST OF SYMBOLS

A	Adaptation Coefficient
C	Energy Content of a Food Particle (Cal/Mole),
$C_e$	Food Particle Concentration in Environment (Mole/Litre)
$C_o$	Food Particle Concentration in Organism (Mole/Litre)
$\underline{E}$	Energy of Egestion or Excretion
E	Energy Loss, (Cal)
$E_g$	Environmental Grade
$\dot{F}, \dot{F}_i$	Food Particle Influx (Mole/Sec)
$\Delta G$	Gibbs Free Energy, (Cals)
$G_A^0, G_X^0$	Standard Free Energy
H	Enthalpy
$\underline{I}$	Ingestion Energy
$J_o$	Energy Flow
K	Constant
$K_m$	Constant (Mole/Litre)
L	Lag-load
M	Metabolic Conversion Efficiency
m	Mean individual Weight
N	Population Number
$\underline{P}$	Production Energy
p	Assimilation Ratio
$\dot{Q}_1$	Gross Energy Influx, (Cal/Sec)
$\dot{Q}_2$	Gross Energy Efflux, (Cal/Sec)
$\dot{Q}_T$	Net Energy Flow, (Cal/Sec)

$\dot{Q}_H$	Heat Dissipation, (Cal/Sec)
$R$	Molar Gas Constant, (Cal/Mole <sup>o</sup> K)
$R_o$	Utilization Ratio
$\underline{R}$	Loss of Respiratory Heat
$\dot{s}$	Energy Loss Rate, (Cal/Sec)
$S, S_A, S_X$	Entropy
$T, T_o$	Temperature, ( <sup>o</sup> K)
$\dot{T}_b$	Maximal Food Ingestion Rate (Mole/Sec)
$U_o$	Performance Index,
$\dot{W}_o$	Gross Metabolic Work Output, (Cal/Sec)
$W_i$	Work Input
$W_n$	Intrinsic Energy, (Cal/Mole)
$\hat{W}$	Optimal Fitness
$\bar{w}$	Mean Fitness
$\dot{Z}$	Useful Work, (Cal/Sec)
$\mu$	Entropic Efficiency, $W_o/W_i$
$\Psi$	System Potential
$\emptyset$	Entropic Dissipation
$\Lambda$	Availability

## I. FITNESS, ENTROPY AND VALUE

The contemporary Neo-Darwinian views on evolution harbour two fundamental inconsistencies which are assiduously ignored. The first of these, as both Waddington (1962) and Eigen (1971) have pointed out, is that Darwin's 'survival of the fittest' is a tautology rather than an explanation. It tells us only that those which survive are the fittest and that the fittest survive. The fact that Darwin's synthesis has been useful as an 'explanation' for many decades now implies that, as individuals, perhaps we already possess some intuitive appreciation of 'fitness' which allows us to apply Darwin's observation in a predictive fashion.

Eigen (1971) has asserted that if we can define some 'value system' by which to assess 'fitness', that is, if we can relate fitness to some physically objective value, then the statement 'survival of the fittest' is no longer a truism. An objective value system as a reference framework on which to evaluate 'fitness' is essential to any prediction of differential survival or differential reproductive success.

The difficulty in establishing such a value system lies partially with the inherent implication that evolution is a goal-directed or teleological process. Although biologists readily recognize that life cannot be the result of entirely random processes (Ayala 1970), they are equally unwilling to accept that life is the result of a goal-directed process. Dobzhansky (1974) has attempted to resolve this difficulty by invoking 'internal teleology': the mechanisms of genetic mutation and of environmental selection are purely mechanistic

but in concert they form a 'creative' system. This, as far as I can see, does not constitute an explanation; it is an intellectual sleight-of-hand which simply obscures the fundamental question.

The second inconsistency in the contemporary view of biological evolution is most frequently encountered in the explanations of biochemical and prebiotic evolution. It is an inconsistency closely related to Erwin Schrodinger's remark to the effect that living organisms feed on 'negative entropy'. The concept of negative entropy or negentropy as related to living organisms was first raised by Schrodinger (1945) and by Wiener (1948). Since that time the concepts behind the idea of negentropy have been central to a longstanding controversy over the status of living organisms in respect to the second law of thermodynamics (Smith 1975). Prigogine and Nicolis (1971) have provided a succinct outline of this issue in their introduction to "Biological Order, Structure and Instabilities":

"In biology or in sociology, the idea of evolution is associated with an irreversible increase of organization giving rise to the creation of more and more complex structures.

In thermodynamics and statistical mechanics, the second law is formulated as the Carnot-Clausius principle. In its modern version, the content of this law is as follows. There exists a function, the entropy  $S$ , which depends upon the macroscopic state of the system...

...Entropy therefore increases irreversibly for an isolated system.

Evolution (of an isolated system) is always directed to a continuous disorganization, i.e. the destruction of structures introduced by initial conditions. The work of Boltzmann has added a new important element: irreversibility in thermodynamics expresses a statistical law of evolution to the 'most probable' state corresponding to the state of maximum disorder.

Ever since its formulation it was realized that the second law of thermodynamics has wide implications. The extension of the thermodynamic concept of evolution to the world as a whole leads to the idea that 'structure' originated in some distant 'golden age' (Whyte et al. 1969). Since then this order is annihilated in a progressive chaos corresponding to the 'most probable' state.

The biological evolution points in precisely the opposite direction. Is it possible to reconcile these two apparently opposite aspects of evolution?"

Many contemporary biologists are adamant that this inconsistency is trivial (Monod 1970, Jacob 1970, Lwoff 1962). They argue that the thermodynamics of living systems as 'open systems' are in no way inconsistent with the second law of thermodynamics. Although a measurable localized entropy reduction (negentropy production) will be associated with the elaboration of relatively unorganized elements of carbon, oxygen, hydrogen, and nitrogen into a highly organized and complex living entity, this elaboration will only be accomplished as the result of the concomitant dissipation of a quantity of energy resulting in a much larger entropy production in the surroundings (i.e. in the universe). In my opinion this view is entirely correct; however, as Prigogine and Nicolis have observed, these general arguments cannot suffice to solve the problem.

Although localized entropy redistributions do not contravene any of the thermodynamic laws, yet these laws do not of themselves constitute an explanation of the events or effects observed in conjunction with living organisms. The events which one could predict on the basis of the second law of thermodynamics would be a progressive disintegration of order. The opposite effect, the spontaneous aggregation of complex living molecular aggregations,

although it is within the realm of possibility, is not within the realm of probability.

Morowitz (1968) has calculated that the probability of the occurrence of a small organism such as Escherichia coli (as a spontaneous fluctuation in an equilibrium ensemble) is roughly  $10^{-10^{11}}$ . Even for a small biomolecule such as hemoglobin, the figure is still  $10^{-40000}$ . The magnitude of these numbers is such that the spontaneous occurrence of such an event during the lifetime of the earth, as a result of random processes, is virtually nil. However, biological organisms and molecules exist in profusion; evidently the probabilities as calculated above on the basis of equilibrium thermodynamics are invalid.

It would be desirable to attribute the occurrence of biological organization to some valid physical principle. Prigogine (1970) (also Prigogine and Nicolis 1971) has approached this task, first of all, by observing that the laws for closed thermodynamic systems may not be valid or directly applicable in the realm of non-linear, non-equilibrium processes (a category which definitely includes living systems). This point, although it may be patently obvious, has nevertheless not been clearly recognized in much of the ongoing discussion of the thermodynamics of living systems. Prigogine and co-workers have set out to derive the principles pertaining to thermodynamics in the non-equilibrium realm.

Eigen (1971), as previously mentioned, has asked for a physical 'value system' as an adjunct to the Darwinian perception of fitness and survival. He has demonstrated that, given such a 'value system', it is possible to rationalize

autocatalytic selforganization of molecules and, by projection, the spontaneous occurrence of life. Prigogine (1947) has provided a possible value system in his 'principle of minimum entropy production' which posits that, for dissipative systems, fluctuations in the structure of the system which result in a reduction of internal entropy production will be self-stabilizing. That is, spontaneous fluctuations of this type will tend to be irreversible. This could be taken to imply that 'fitness' in biological systems (as dissipative systems) would be related to those events or structures which tend to minimize entropy production (Prigogine & Nicolis 1971). The primary principles may be applicable to biological phenomena, to evolution in particular, and that it may therefore be possible to generate a quantitative definition of biological fitness.

Whereas Eigen (1971) has provided an analysis appropriate to molecular interactions, this thesis presents an analysis of life processes on a macroscopic scale in terms of metabolic mass/energy flows and exchanges. This has been done without reference to any arbitrary physical 'value system'. An analytic expression for biological activity in terms of matter and energy flow has been formulated. Biosystem homologues based on this expression have been shown to mimic some of the ordinary characteristics of real biosystems including their evolutionary tendencies.

Since the analytic expression referred to has been constituted in physical terms, as matter and energy fluxes, and since no a-priori criteria or 'values' were built into the expression, it should be possible to identify an underlying physical

principle which is operational when the homologue mimics the processes observed in biological evolution. I have tentatively identified such a principle in Appendix A and have suggested that it is compatible with Prigogine's theorem of minimum entropy production.

One further comment on this thesis is in order. As with Eigen's work on self-organization of matter, I have been concerned with the physical problem of 'value'. But any definition of a value system, though it may be entirely expressed as a physical property of the universe, will ultimately be bound to human social values, mores and aesthetics.

The problem of a value system in connection with biological phenomena, man in particular, has traditionally fallen into the realm of philosophy, metaphysics and religion. A physical solution to the question of 'value', if and when it is found, will constitute, among other things, the formation of a tangible interface between the disparate disciplines of physics and metaphysics. It will see the reversal of a trend in which these two disciplines have been progressively estranged over the past four centuries of Western thought. The current controversy over sociobiological issues is a foreshadowing of this event.



## 2. ENERGETICS

It is one purpose of the present chapter to show, by means of an analysis of the energetics of life processes, that all attributes of a biosystem are amenable to general thermodynamic description, and further, if the various flows of mass and/or energy are divided into a number of carefully defined functional categories that it is possible to define the efficiency of a biosystem unambiguously. The primary novelty in this analysis is the definition of 'useful work'.

### Living Systems

What essential properties distinguish living matter from inanimate matter? It is not sufficient to define 'life' as a steady-state energy processing system, for this would not distinguish living systems from stars, machines, or many other non-animate steady-state processes. This 'steady-state' criterion would, however, distinguish a 'living' from a 'dead' state for a biological organism, as do the common applications of 'live' and 'dead' to a full range of steady-state systems other than the biological when they are respectively in an 'operating' or 'non-operating' state. Thus, if we are only concerned with contrasting 'life' and 'death', it is irrelevant whether we are conceptualizing the processes concerned as biological, chemical or physical.

The essential question is not how to classify the processes but rather to describe them as succinctly as possible. The following description will focus upon the energetics of steady-state processes for biological organisms in particular, but the analysis to be presented should be applicable to steady-state processes in general. In the biological realm, such steady-state considerations

can be applied within boundaries which encompass a range of organizational levels from component cells, tissues and organs to the higher aggregates of family, colony, association or ecosystem.

Living organisms acquire energy actively. Reproduction is secondary to this function; a live organism can be non-reproductive but the converse is impossible. Live plants and animals work to capture nutrients. A dead organism, on the other hand, lacks any potential to do so ('potential' is used here to distinguish dormancy from death).

Could evolution be viewed as a progressive enhancement of this energy accumulating capability? Intuitive assessments of 'improved' fitness involve either an improvement in energy accumulation techniques or in methods of self-preservation (which in the end amounts to the same thing). Often an 'adaptation' will be realized as an improvement in the organisms ability to capture energy and thereby to utilize a less attractive energy source. For instance, the entry of  $C_4$  plants into arid habitats was made possible by the use of the  $C_4$  pathway in fixing carbon (Bjorkman & Berry 1973). This ploy allows plants to function photosynthetically with reduced transpiration losses.

One can intuitively appreciate the notion of 'fitness' but how can it best be quantified so as to make it amenable to quantitative analysis? The gross energy flux through a species or organism is one accessible and relatively important indicator of the state of the organism. Could biosystems be evaluated in terms of gross energy throughput? Van Valen (1976) has suggested that fitness might be defined wholly in terms of 'trophic energy', i.e., in terms of the gross energy flux through the organism or species. (Trophic energy is defined as a

composite of various contributory flows: waste energy, productive energy, structural energy, etc., and each of these must be taken into account separately).

Unfortunately, the concept of trophic energy as a gross measure of fitness is of little use. If one were to choose a particular ecosystem and classify the organisms in terms of 'trophic energy' throughput, the result would not be informative. Photosynthetic plants would rank first, herbivores next, then primary and secondary carnivores. Nevertheless, certain other energy concepts introduced by Van Valen (1976), viz. expansive energy and regulatory energy, appear to have great potential as indicators of fitness; however, Van Valen has not so far been able to elucidate the relationships between these various energy terms and physical thermodynamics. This does not suggest that the relationship does not exist but does suggest that Van Valen's conceptual organization may be amiss; if the behaviour of a system can be described in terms of energy flows then it should be possible to relate those flows to the physical properties of the universe.

The thrust of the ensuing argument will be to organize and conceptualize energy flows in the biosphere in such a way that a thermodynamic analysis becomes possible, i.e. in such a way that all flows of energy in the system can be accounted for in terms of physical forces or accumulations of potential energy.

### An Equation for Organism/Environment Interactions

"Thermodynamics might be called the science of the possible. It offers no mechanistic answers; rather, it plays a legislative role circumscribing the universe of physically admissible phenomena... The great weakness of thermodynamics is that it is fundamentally a black box theory. That is, it addresses itself not to the inner workings of a given system but only to those relationships that must hold between external measurements. But this shortcoming is also the secret of its enduring success as a mathematical model for the physical world. Regardless of the contents of the black box, the input/output relations are constrained by its laws".

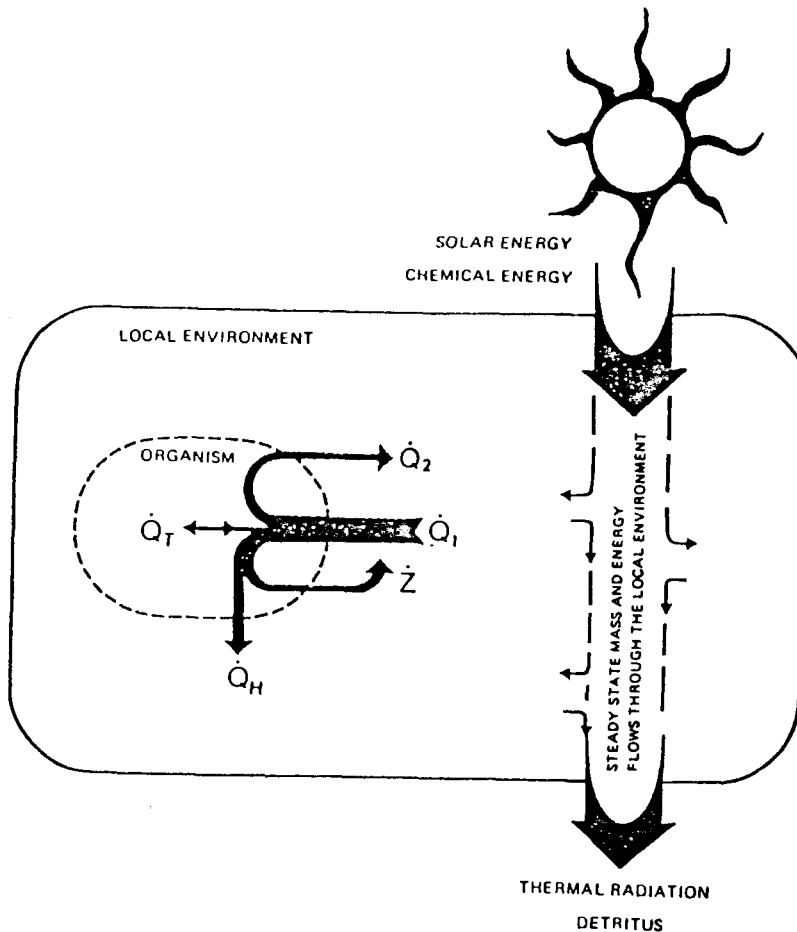
- from IRREVERSIBLE THERMODYNAMICS AND THE ORIGIN OF LIFE, (Oster et al. 1974).

Biological systems are described in thermodynamic terms as open systems, that is, they are continuously exchanging matter and energy with the surrounding universe. Because of this transient character, attempts at concise thermodynamic description of biosystems have been relatively unsuccessful. Certain partial descriptions of biophysical performance such as 'ecological efficiency' or 'production efficiency' are widely used (Kozlovsky 1967), yet none of these measures constitute a universally applicable index of physical performance.

As the quotation above implies, a detailed internal description of the environment or organism is unnecessary; an enumeration of the flows at the organism/environment interface should be sufficient. Accordingly, if one were to treat a biosystem as a black box and consider only those flows of mass and energy which cross an arbitrary organism/environment interface, it should be possible to make some useful generalizations about the organism/environment interactions.

Imagine a system consisting of one or more organisms in a defined physical environment. These organisms can be enclosed by an arbitrary boundary or interface. The enclosed organism(s) will be characterized by a set of extensive physical properties (volume, mass/energy content, etc). The system as a whole including the enclosed organism will form the environment which will also have a set of characteristic extensive properties.

Figure 2-1 depicts such a system containing both biological and non-biological elements. A boundary has been arbitrarily drawn to encompass a segment of the system containing one or more biological organisms. The combined elements of the system are defined as environment and the segment enclosed by the boundary is defined as organism(s). All flows of mass/energy across the organism/environment interface have been enumerated in terms which will lend themselves to the ensuing analysis. The diagram also shows a flux of solar energy, mass, chemical energy and thermal radiation into and out of the environment. These flows will not enter into the ensuing analysis but are depicted here as implicit to any discussion of an 'environment' since it is also an open system.



**Figure 2-1:** A depiction of the mass and energy flows in a biosystem and its environment. Briefly,  $\dot{Q}_1$  represents the rate of mass/energy flux into an organism (or group of organisms);  $\dot{Q}_2$  represents mass/energy losses from the enclosure; while  $\dot{Z}$  and  $\dot{Q}_H$  represent energy losses or outputs from the enclosure. The term  $\dot{Z}$  is differentiated from other energy losses since it represents the 'useful' work output from the enclosure.

The flux of mass/energy across the larger environment boundary is included as an indication that the environments in which biosystems function are also open systems.

The various mass/energy flows in Fig. 2-1 are defined as follows: (the dot above a term indicates that it is a rate,

$$\text{e.g. } \dot{Q}_T = dQ_T/dt$$

- $\dot{Q}_1$  The gross energy input or food flux into the organism(s).
- $\dot{Q}_2$  The gross energy flux out of the organism(s) as tissue, feces, metabolites, etc.
- $\dot{Q}_T$  The net flow of mass or energy across the organism/environment interface as opposed to the gross flow represented by  $\dot{Q}_1$ . This quantity will reflect a net loss or gain in the biomass of the organism(s) and can be intuited as a 'storage' term. This quantity is roughly equivalent to Van Valen's 'expansive energy'.
- $\dot{Z}$  The useful work output from an organism; its meaning is highly restricted.  $\dot{Z}$  includes only that portion of the work output of an organism which results in net changes to the potential energy of the environment, specifically to those particular resources upon which the organism may be dependent. Any other work outputs will be considered to be dissipated as heat and will be included in the following term  $\dot{Q}_H$ . (At first glance it might appear to be rather difficult to discriminate 'useful work' from other organismic work outputs. The process would appear to involve an evaluation of the ultimate purpose of each movement. I will attempt to show however, that such a discrimination can be made on purely thermodynamic grounds. This term and its definition is the key element in the entire analysis.)
- $\dot{Q}_H$  The energy dissipation from the organism in the form of heat.

All of the above flows are expressed as energy equivalents (calories). For the purposes of the deliberations to follow, mass and energy are considered to be identical; for example, an increase in biomass would be expressed in calories. This is a simplification since the chemical energy content of various tissues does differ. However, the general validity of the equations is not jeopardized (only the immediate precision).

A simple energy balance equation for the situation depicted in Fig. 1 can be written as:

$$\dot{Q}_1 = \dot{Q}_2 + \dot{Q}_T + \dot{Q}_H + \dot{Z} \quad (2-1)$$

The energy influx into the organism ( $\dot{Q}_1$ ) is dispersed in several ways. A proportion will be lost in tissues or unassimilated food ( $\dot{Q}_2$ ), some may be sequestered as tissue ( $\dot{Q}_T$ ), and the remainder will be transformed into the useful work output ( $\dot{Z}$ ) at some finite efficiency. The energy conversion losses appear as  $\dot{Q}_H$  which includes all of the heat loss from the organism plus any work output which is not 'useful'. The quantity of energy potentially available for 'conversion' to  $\dot{Z}$  will be proportional to  $(\dot{Q}_1 - \dot{Q}_2 - \dot{Q}_T)$ . The sense of  $\dot{Q}_T$  is positive if the organism is gaining mass and negative if it is losing mass. The conversion of  $(\dot{Q}_1 - \dot{Q}_2 - \dot{Q}_T)$  into work will be characterized by some finite efficiency. It is expedient to define two separate coefficients of performance for this conversion.



(a)  $M$ , the metabolic conversion efficiency

$$M = \frac{\dot{W}_O}{(\dot{Q}_1 - \dot{Q}_2 - \dot{Q}_T)} \quad (2-2)$$

where  $M$  represents the conversion of assimilated energy into gross metabolic work ( $\dot{W}_O$ ) which includes such things as muscular work, chemical synthesis, osmotic work, etc. (The conversion efficiency for many common metabolic processes seems to average about 30%-50%, e.g. glycolysis, photosynthesis.)

(b)  $A$ , the adaptation coefficient reflects the adaptation of an animal to its normal range of activities, foraging in particular. An animal may have claws enabling it to capture a particular kind of prey with great efficiency yet it may be incapable of capturing other prey with anything like the same efficiency. The 'useful' work  $\dot{Z}$  accomplished in capturing prey is independent of the predator. Thus the adaptation coefficient,  $A$ , reflects the ratio of useful work to energy expended as gross metabolic work  $\dot{W}_O$ .

$$A = \frac{\dot{Z}}{\dot{W}_O} \quad (2-3)$$

Since only a proportion of  $\dot{W}_O$  will actually be expended on the environment in the explicit capture of mass/energy,

$$\dot{Z} = \dot{W}_O A = AM (\dot{Q}_1 - \dot{Q}_2 - \dot{Q}_T) \quad (2-4a)$$

and from (2-1)

$$\frac{\dot{Z}}{AM} = (\dot{Q}_1 - \dot{Q}_2 - \dot{Q}_T) = \dot{Z} + \dot{Q}_H \quad (2-4b)$$

The definition of  $\dot{Z}$ , 'useful' work done on the environment is central to the validity and utility of this equation. The essential task of any foraging organism is to locate food particles in the environment and to alter the distribution of these particles by consuming them. The work accomplished can be assessed quantitatively by computing the potential energy and entropy change to the environment resulting from that redistribution. The rate of this narrowly defined work output is  $\dot{Z}$  and its static equivalent, that is, the work done per mole of food particles captured ( or 'rearranged') will be represented by  $W_n$ , the intrinsic work requirement per mole of 'food particles' captured.  $W_n$  can be evaluated by determining the energy change in the environment resultant to the 'capture' of a 'food particle'. (A specific example is presented in Appendix D for a situation in which  $W_n$  can be computed from the Gibbs free energy change).

A simple example of the above may be seen in the adaptation of animals to specific foraging tasks. An animal with special adaptations can capture a given prey with a much smaller gross energy expenditure ( $\dot{W}_0$ ), than can a non-specialized animal, yet the measureable work done on the environment,  $\dot{Z}$ , may be the same in both cases. The corollary to this is the observation that it is not possible to do more work on the environment in capturing a food particle than is determined by the nature of the particle/environment itself. For example: in the case of a bacterium extracting glucose from the surrounding medium, the actual work done on the environment is determined by computing the Gibbs free energy change of the glucose (regardless of the efficiency or

nature of the pumping mechanism which the bacterium uses). Since the glucose remains a part of the environment as a whole, the only net change to the system is in the distribution of the molecules, i.e. the entropy of the environment will be reduced by perturbing the random distribution of glucose molecules.

Although equation (2-1) may not at first glance appear to be significantly different from the classical energy exchange equation,

$$\underline{P} = \underline{I} - \underline{E} - \underline{R} \quad (\text{Kendeigh 1974})$$

where  $\underline{P}$  = production energy

$\underline{I}$  = ingestion energy

$\underline{E}$  = energy of egestion or excretion

$\underline{R}$  = loss of respiratory heat

It is different in that it takes into account 'useful work' ( $Z$ ). I will attempt to show that this apparently minor modification is of major significance.

The traditional approach to establishing an 'energy budget' for a living system has been to ignore the 'work' output from an organism or a group of organisms as it appears to be a negligible fraction of the total energy exchange process (Wiegert 1968). Work output is usually lumped in with metabolic heat production as in the equation above where  $\underline{R}$  is considered to account for both internal and external work (Koslovsky 1968). In the cases where work outputs are considered, (Brody 1945), the interest has been in the gross work output ( $W_o$ ) rather than the 'useful work'. Although it is true that the work outputs from an organism may be rather small, (particularly if defined as  $Z$  in which only a fraction of the gross work output is considered), to ignore such a factor in the

description of an autocatalytic ensemble (if I may apply such a term to living systems) is to ignore the 'feedback' term in a homeostatic system. The applicability of any descriptive endeavour which ignores such a term must be severely limited. On the other hand, the inclusion of a term such as  $\dot{Z}$  which is determined by the physical properties of the environment brings an energy balance equation into a larger perspective. The energy flows at the organism/environment interface are not only determined by the specific properties of the organism and the environment but these flows can also influence the controlling properties. The ramifications of this 'feedback loop' can be more explicitly expressed by rearranging equation (2-1) into a format in which the environmental components of the equation are separated from the organismic components.

Define  $E_g$  as the environmental grade

$$E_g = \frac{\dot{Z}}{\dot{Q}_1} = \frac{W_n}{C} \quad (2-6)$$

The environmental grade will be the ratio of the intrinsic energy required to capture a food particle ( $W_n$ ) to the energy available from the food particle (C). Again in the example of the bacterium, if the energy value of glucose were about 680 kcal/mole as would be the case for aerobic metabolism and if the alteration to the entropy of the environment were about 1 kcal/mole of glucose ingested, then the 'grade' would be relatively shallow, i.e. about 1/680.

On comparison, if the bacterium were an anaerobe, the 'energy content' (C), of the glucose may be only ~30 kcal/mole, so that  $E_g$  would be ~1/30, a considerably 'steeper' grade.

Environmental grade,  $E_g$ , reflects the 'quality' of the environment as experienced by the organism; that is, it will indicate the general availability or cost of the particular resources on which the organism depends. The environmental grade or 'quality' sets a lower limit to the efficiency with which an organism can operate in a given circumstance. In the case of the anaerobe in the example above, the bacterium must convert the energy gained via glucose ingestion into 'useful' work with an efficiency of at least 3.3% in order to 'break even'. The grade can only be altered by changing the nature or dispersion of resources, i.e. by changing the environment itself. But this is exactly the type of change which will be effected by the 'useful work' output of the organism.

If  $E_g$  is defined in terms of the instantaneous flows in the system, that is as  $E_g = \dot{Z}/\dot{Q}_1$ , then using equation (2-4a) we get:

$$E_g = \frac{\Delta M (\dot{Q}_1 - \dot{Q}_2 - \dot{Q}_T)}{\dot{Q}_1} \quad (2-7)$$

Equation (2-7) has several useful properties which will become clearer if some of the terms are condensed.

$$R_o = \frac{\dot{Q}_1 - \dot{Q}_2}{\dot{Q}_1} \quad (2-8)$$

$R_o$  is defined as a utilization ratio. It is almost identical to the 'assimilation ratio' which physiologists assign to the efficiency of food digestion for animals. It differs, however, in that the term  $\dot{Q}_2$  includes tissue losses (e.g. hair, fingernails, or the loss of whole bodies in the case of populations ['production'] as well as faeces).

Equation (2-7) can now be written as:

$$E_g = AMR_o - AM \left( \frac{\dot{Q}_T}{\dot{Q}_I} \right) \quad (2-9)$$

and defining  $U_o$  as the product  $AMR_o$

$$U_o = AMR_o = \dot{Z} + \frac{AM\dot{Q}_T}{\dot{Q}_I} \quad (2-10)$$

where  $U_o$  represents the apparent overall efficiency or 'performance index' of the organism(s), being the product of assimilation ratio, metabolic efficiency, and the adaptation coefficient.

Equation (2-9) therefore becomes:

$$E_g = U_o - AM \left( \frac{\dot{Q}_T}{\dot{Q}_I} \right) \quad (2-11)$$

where the left-hand side represents environmental characteristics only and the right-hand side represents the characteristics of the organism only. Then (2-11)

can be rearranged as:

$$\dot{Q}_T = \frac{\dot{Q}_I}{AM} (U_o - E_g) \quad (2-12)$$

$\dot{Q}_T$  will reflect the biomass variation for the organism(s) in question. The magnitude and direction of the flow  $\dot{Q}_T$  will be determined by the difference  $(U_o - E_g)$ , that is, by a comparison between the performance index (or 'efficiency') of the organism(s) and the grade (or 'quality') of the organism(s) and the grade (or 'quality') of the environment.

In this form (which corresponds to the typical form of a population equation) equation (2-12) is useful in the prediction of the responses and range of behaviours available to organisms in the face of either an environmental or a physiological change. For stable populations, or mature individual organisms, equilibrium conditions (or stationary states) would occur when the average biomass remains constant, i.e., when on the average  $\dot{Q}_T = 0$ . This will be the case when  $U_o = E_g$ , i.e., when the environmental grade is exactly matched by the performance index of the organism(s). If such a situation is perturbed by a change in either  $E_g$  or  $U_o$ , the resulting 'mismatch' will necessitate that  $\dot{Q}_T \neq 0$ . The result will be a continuous net transfer of mass/energy across the environment/organism(s) interface and either a growth or decline in the biomass of the population.

As defined above, the sense of  $\dot{Q}_T$  is positive when the net flow of biomass/energy moves into the organism. Thus when  $U_o > E_g$  then  $\dot{Q}_T > 0$ , that is, if the performance index of the organism exceeds the intrinsic requirements imposed by the grade of the environment, growth will take place. A  $\dot{Q}_T < 0$  would imply loss of mass for an individual or a loss of numbers for a population.

There is a further implication: the net transfer of mass to or from the environment can affect the character of the environment as expressed in  $E_g$ . The flow  $\dot{Q}_T$  represents the flow of mass (or chemical potential energy) which will alter the local resource concentration, hence  $E_g$ . If the local conditions are appropriate,  $\dot{Q}_T$  will eventually result in an alteration to  $E_g$  such that  $E_g = U_o$  and  $\dot{Q}_T = 0$ . The rate of this equilibrium is dependent upon the

magnitude of  $\dot{Q}_1/AM$  as well as on the magnitude of the mismatch between  $U_o$  and  $E_g$ . (The term  $\dot{Q}_1/AM$  can be regarded as a rate parameter). Returning momentarily to the classical energy balance equation  $\underline{P} = \underline{I} + \underline{E} + \underline{R}$ , it is now possible to appreciate the importance of the 'useful work' term  $\dot{Z}$ . The inclusion of 'useful work' in equation (2-1) allows the definition of an environmental grade  $E_g$  which is a measure of the environmental 'quality'. As  $E_g$  can only be evaluated by a continual assessment of the extent and availability of environmental resources, a 'quality' factor has been directly incorporated into the energy balance equation.



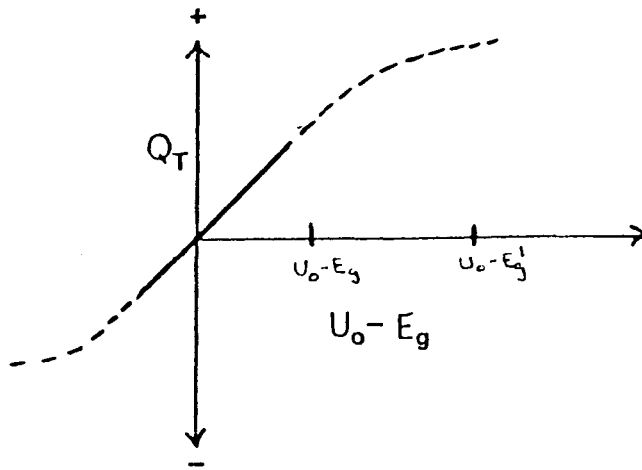
### Functional Implications

The energy balance equation (2-1) is no more than an enumeration of arbitrarily defined variables  $\dot{Q}_1$ ,  $\dot{Q}_2$ ,  $\dot{Q}_T$ ,  $\dot{Q}_H$ , and  $\dot{Z}$ . The relationship between  $\dot{Z}$  and  $\dot{Q}_1$  has been defined as  $E_g$ , an environmental quality factor. Further, equation (2-12) has been used to define  $\dot{Q}_T$  in terms of  $U_0$ ,  $E_g$  and  $\dot{Q}_1/AM$  where  $AM$  can be defined as a product of two separate efficiency terms. The absolute magnitudes of  $\dot{Q}_1$  and  $\dot{Q}_2$  are unspecified. Ultimately we are interested in population growth and in fitness which are related to  $\dot{Q}_T$  and  $U_0$  respectively. These terms can be evaluated only for specified values of  $\dot{Q}_1$  and  $\dot{Q}_2$ . Although definition methodologies specific to the physiology of a given species are presented in Appendix D the current interest is to examine the interplay between these parameters in a more general context.

Consider some organism with a specified set of functional parameters,  $A$ ,  $M$ ,  $\dot{Q}_1$ ,  $\dot{Q}_2$ , in an environment  $E_g$ . The system is in steady state, i.e.  $\dot{Q}_T = 0$ ,  $U_0 = E_g$ . What will happen if the system is perturbed?

Let  $E_g \rightarrow E'_g$  where  $E'_g < E_g$ . (Fluctuations in the quality of the environment appear to be a common place phenomenon.) This change will affect the organism in that the useful work output  $\dot{Z}$  required to maintain the energy influx  $\dot{Q}_1$  will be reduced. What is the range of responses available to the organism?

According to equation (2-12) the immediate natural response will be to increase  $\dot{Q}_T$ , the rate of tissue accumulation or population growth, to some finite positive value (assuming  $\dot{Q}_1$  is invariant).



This appears to be reasonable for small fluctuations in the vicinity of  $U_0 = E_g$ . However,  $\dot{Q}_T$  is not an infinitely variable parameter; there will be physiological limits on both anabolic and catabolic metabolism and on reproductive rates for any given species. (A population presented with an overabundant food supply can only achieve a limited growth rate regardless of the ease in obtaining food). What other response mechanisms might be possible within the constraints of equation (2-12)?

An alternate response in the case above might be to reduce performance index  $U_0$  when  $\dot{Q}_T$  reached some limiting value (again assuming  $\dot{Q}_1$  is invariant).

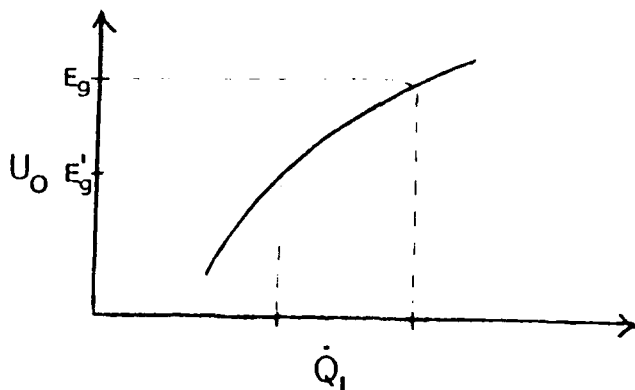
Recalling that  $U_0 = AMR_0$  where A and M determine the efficiency for the conversion of energy to  $\dot{Z}$ ; it would be possible for an organism to 'burn off' excess energy through non-functional activity. Similarly  $R_0$  could be reduced by increasing  $\dot{Q}_2$ . In both instances the organism would be deliberately reducing its performance index in order to match the lower environmental grade.

The foregoing responses all assumed a constant energy ingestion rate of  $\dot{Q}_1$ . A simpler and more direct expedient in the case of sudden fluctuations in  $E_g$  would be to reduce  $\dot{Q}_1$  in accordance with normal metabolic needs and reproduction rates.

Recalling that  $\dot{Q}_H$  and  $\dot{Q}_2$  both can involve fixed losses (e.g. basal metabolism, tissue losses etc.) and recalling equations (2-1), (2-10), and (2-8), the performance index of an organism can be defined as:

$$U_o = AMR_o = 1 - \frac{\dot{Q}_H}{\dot{Q}_1 - \dot{Q}_2 - \dot{Q}_T} = 1 - \frac{\dot{Q}_2}{\dot{Q}_1}$$

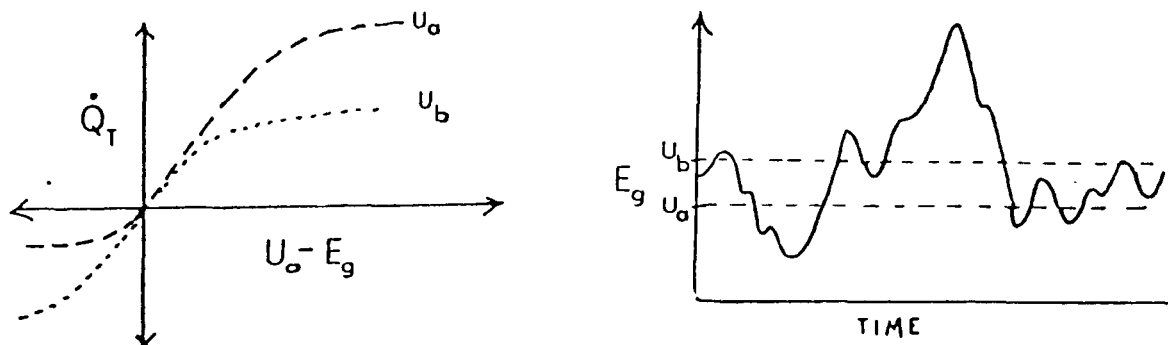
If it is assumed that  $\dot{Q}_H$  and  $\dot{Q}_2$  are constant and that  $\dot{Q}_T = 0$ , then it is possible to define a correlation between  $U_o$  and  $\dot{Q}_1$ .



It is possible to maintain a balance between  $U_o$  and  $E_g$  by reducing  $\dot{Q}_1$  while maintaining constant normal energy expenditures (which effectively reduces the performance index  $U_o$ ). In terms of familiar biological behaviour patterns this is the one which is most common for short term fluctuations in food availability, i.e. reduce food intake to match actual metabolic needs.

Any combination of the responses discussed above is also possible. In the limiting case (i.e. over the long term) where  $U_o = E_g$  these are reasonable responses. If on the other hand  $U_o$  is greater than  $E_g$  consistently, the organism which is able to maximize  $\dot{Q}_T$  will have a reproductive advantage over other species.

In an environment subject to consistent spatial and temporal fluctuations in  $E_g$ , species with differing values of  $U_o$  can co-exist by utilizing different reproductive strategies.



In the diagram above  $U_A$  is an opportunist with a high potential reproductive rate ( $\dot{Q}_T$ ) and a low loss rate when  $E_g$  is greater than  $U$ .

Organism  $U_B$  has a high performance index and functions at low growth rates through most environmental extremes. The organisms in an ecological succession might be taken as an example of this type of co-existence.

Whereas the energy balance equation can suggest a range of different short term and long term behaviours depending upon the size or capacity of the environment in relation to the particular species and the nature of its adaptation, it will not predict specific behaviours. It will indicate a range of possible alternatives, any of which appear to be plausible or familiar.

In many situations,  $E_g$  will constantly fluctuate with the seasons and other external influences. All species must maintain an appropriate level of resilience in their behaviour or physiology in order to accommodate the full range of normal fluctuations in the grade of the environment. In mammals the primary recourse with respect to short term variations (less than year) is usually a net gain or loss of mass. Photosynthetic organisms accommodate diurnal variations in light intensity by accumulating energy ( $\dot{Q}_T$  positive) when sufficient light is available and by consuming this energy during dark periods ( $\dot{Q}_T$  negative); the condition for survival is only that the cumulative  $\dot{Q}_T$  is equal to or greater than zero. The hibernation strategy of bears in temperate or subarctic climates provides another illustration of this principle. During the summer, tissue (fat) is accumulated when food is abundant ( $\dot{Q}_T$  positive) but in winter these fat deposits are catabolized ( $\dot{Q}_T$  negative).

It is probably rare for the instantaneous  $\dot{Q}_T$  of an individual organism to be actually equal to zero; however the average  $\dot{Q}_T$  over some long time span will be zero for any species with a stable population. It is evident that organisms in a fluctuating environment must maintain a margin in their biomass and/or performance index sufficient to accommodate temporary variations in environmental grade without disastrous results. For example, a healthy human being can tolerate many months of starvation with the accompanying catabolism of as much as 50% of his body tissue. This certainly provides a margin of flexibility for dealing with an extreme environmental challenge that might spell disaster for a more 'finely tuned' organism.

An excellent example of alterations in environmental grade actually resulting from competition between species can be seen in the case of  $C_3$  and  $C_4$  plants. With full sunlight and adequate mineral nutrition, the limiting nutrient for photosynthesis is  $CO_2$ . Four-carbon ( $C_4$ ) plants are adapted to accumulate  $CO_2$  at much lower partial pressures than are  $C_3$  plants. As a consequence, in a bell jar,  $C_4$  plants are able (by lowering the  $CO_2$  partial pressure in the atmosphere) to raise the environmental grade to such an extent that  $C_3$  plants are unable to photosynthesize and must resort to respiratory metabolism ( $\dot{Q}_T$  negative). As a result there is a net transfer of mass/energy from the  $C_3$  plants to the  $C_4$  plants which are thus able to maintain a positive  $\dot{Q}_T$ .

The preceding illustrations have been oversimplified. The intent has been to show that a black-box type of analysis can be used to define a set of bounds for behaviour, and that for the analysis presented these bounds appear to encompass familiar response patterns.

If the definition of useful work  $\dot{Z}$  is valid then the variously defined efficiencies, lumped together as a performance index  $U_0$ , should be useful in the definition of biological fitness. The ensuing chapter examines this measure of efficiency in relation to fitness.

### 3. FITNESS

Maynard-Smith (1976b) has defined lag-load,  $L$ , as

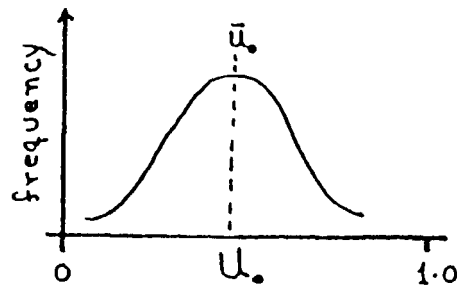
$$L = \frac{\hat{W} - \bar{W}}{\hat{W}}$$

where  $\bar{W}$  is the mean fitness of a population and  $\hat{W}$  is the fitness of the fittest possible genotype. Maynard-Smith has suggested that the intensity of selection can be related to this quantity. The difficulty with the lag-load concept lies in its inability to deal with both exogenous environmental change and the endogenous changes resulting from selection acting on the organisms which constitute the environment. It is possible through the use of equation (2-12) to define a measure of fitness which will reflect selection intensity in such a way as to accommodate both exogenous and endogenous influences.

If fitness is defined as the term  $(U_o - E_g)$ , that is as the relative match between the performance index of the organism and the quality or grade of the particular environment, then it is logical to define 'optimal fitness' as  $(U_o = E_g)$  and any positive or negative values of fitness as 'supra' and 'sub' optimal respectively. Thus, any organism with an optimal fitness will be in a steady state whereas a population with either supra- or sub- optimal fitness will experience either a growth or decline in numbers in some proportion to the numerical value assigned to its fitness. The  $(U_o - E_g)$  mismatch, designated as fitness, will directly reflect selection intensity on the basis of both exogenous and endogenous factors.

It should be possible to assess differential survival or reproductive success in terms of the performance index of the individuals of a species. Consider a group of contiguous organisms, that is, organisms which are dependent on the

same environmental resources, and some delineated environment which is more or less homogeneous with respect to the resource needs of these organisms. Assuming that there is some genetic and phenotypic variation in the group, each individual will have some characteristic performance index  $U_o$  and the group as a whole will have some mean or aggregate index  $\bar{U}_o$ .



The grade of the environment will also have some characteristic value  $0 < E_g < 1$  such that the net growth or decline of the population will be determined by  $(\bar{U}_o - E_g)$ . If  $E_g = \bar{U}_o$  the population will be in steady state. In the steady state situation individuals with  $U_o < \bar{U}_o$  will experience a negative  $\dot{Q}_T$  and therefore will have a declining representation in a more or less constant population whereas those with  $U_o > \bar{U}_o$  will have  $\dot{Q}_T > 0$  and therefore will gain in proportionate representation in the population. Further, even in the cases where  $\bar{U}_o \neq E_g$ , whether the population as a whole is in a state of growth or decline, those organisms with the higher  $U_o$  values will steadily gain in proportionate representation with the passage of time. As long as the metabolic processes of the population are ongoing it is inevitable that those organisms with the higher  $U_o$  values will be favoured (i.e. selection of the 'most fit' is a spontaneous process which will continually increase the  $\bar{U}_o$  of the system as a whole).



In the situation above an inevitable consequence of ongoing selection will be a gradual rise in the aggregate performance index,  $\bar{U}_0$ . Therefore if the initial situation is  $\bar{U}_0 = E_g$ , the situation must eventually become  $\bar{U}_0 > E_g$  (as long as external influences do not perturb the situation to any large extent). The consequence of a situation with  $\bar{U}_0 > E_g$  would be a population growth proportional to  $\dot{Q}_T$  which could eventually also alter the value of  $E_g$  (depending upon the size of the environment in relation to the value of  $\dot{Q}_T$ ). In the absence of any perturbation to the system the ultimate result of such a feedback situation might be a population with a single unique  $\bar{U}_0$  value in equilibrium with an environment with a unique, high grade. This utopian situation does not appear to be a likely one. Mutation will continually generate a spread in the  $U_0$  values of the population but perhaps more significantly, the environment is not likely to be invariant. Not only do most environments vary in a cyclic manner, but their characteristics are spatially non-uniform as well as temporally variable in a random fashion. As previously discussed, this type of environmental variation should allow the existence of organisms with differing  $U_0$  and differing reproductive strategies.

It is useful to distinguish between the rate of mutation and the rate of selection or fixation of new adaptations. Mutations may arise spontaneously as a stochastic process whereas selection operating on the mutations is a result of the divergence of the performance index of the mutated organism from 'optimal fitness'. The existence of a mismatch will result in selection for or against certain organisms in direct proportion to the magnitude of the mismatch.

However, this selection is an equilibration process which tends to reduce the mismatch. Suboptimal mutations are eliminated from the population by attribution while supraoptimal mutations tend to take over and raise the general  $\bar{U}_o$  and  $E_g$  values. The trend is deterministic although the specific events or perturbations giving rise to the trend are wholly random.

### Summary

The introduction of the concept of  $\dot{Z}$ , 'useful work' output into an otherwise conventional energetic description of biological systems, makes it possible not only to define fitness in terms of a performance index  $U_0$  but also to define the relationship of fitness to the local environmental grade  $E_g$ . The relationship between these two parameters can be used to evaluate differential reproductive success.

Since the definition of these parameters is based on quantitative physical characteristics, the door has also been opened for an examination of differential reproductive success in thermodynamic terms. The ensuing appendix (A) is presented as a speculative exploration of this possibility.

## APPENDICES

APPE NDIX A

## EVOLUTION AND ENTROPY

Although the notion of entropy and order in relation to biological phenomena has been broadly discussed over the past two decades, (Lwoff 1962, Schrodinger 1967, Morowitz 1968, and Gatlin 1972) it appears that a functional thermodynamic description of biosystems has not yet been formulated (as discussed in the introductory chapter). The development of an energetic description of biosystems would appear to be contingent upon the prior solution of certain fundamental problems in non-equilibrium thermodynamics. Considerable progress has been made in this difficult field, particularly by Prigogine (1947, 1970) with the development of the 'law of minimum entropy production' which states that, for a steady state dissipative system, fluctuation in the on-going processes can result in instability and an eventual reduction in the steady state entropy production. Eigen (1971, 1977) has related such instabilities to the selective growth and evolution of autocatalytic systems on the molecular level. Even with these steps, however, the conceptual tools for the application of thermodynamic principles to biosystems as a whole do not yet appear to be available (Smith 1975). This appendix presents a simple heuristic device which may be used for more effectively bringing thermodynamic principles to bear on biological systems.

The first step is to reexamine the properties of equation (2-12) as a description of a steady state (non-equilibrium) system. The second step will be to introduce a theorem which is no more than a simple observation as to the nature of 'engines' as non-equilibrium systems. This theorem pertains to the type of fluctuations which can lead to minimum entropy production. The theorem suggests that fluctuations which minimize entropy production by increasing the

operating efficiency of an engine also have the effect of reducing the potential energy of the system which contains the engine. The implication is that certain 'alterations' to the 'design' of an operating engine will be favoured by energetic considerations which can be evaluated using thermodynamic arguments.

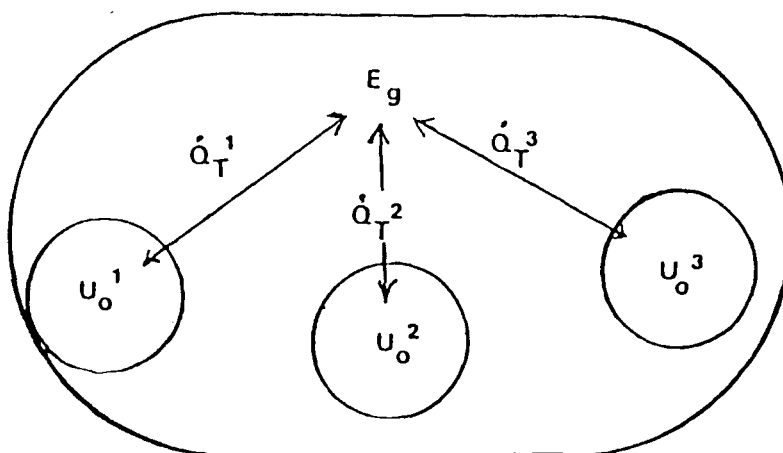
### Evolution

Equation (2-12) is nothing more than a statement of constraint, a definition of the relationship between organism and environment. Indeed, in a system in which identical organisms occur in an otherwise abiotic environment, the equation defines symmetrical or reversible properties. In such special circumstances, any net flow  $\dot{Q}_T$  resulting from a change either to the environment or to the organism could be reversed by returning the system to its initial conditions. Accordingly, if a series of random perturbations were to end with  $U_o$  and  $E_g$  at the original values, the final state of the system would be indistinguishable from its original state.

However, in a multi-organism environment, i.e., an environment which admits fluctuations in the characteristics of several individuals, the processes defined by the equation are likely to create an asymmetry; it may not be possible to reverse a sequence of events or flows ( $\dot{Q}_T$ ) by reversing the sequence of applied fluctuations or by re-establishing the original characteristics of the environment. The result of the net mass/energy flows between resource pools in this situation may have irreversible characteristics. Any random sequence of variations to the performance index of the organism(s), applied at random to the individuals involved, will result in a net transfer of mass/energy

$(\dot{Q}_T)$  to those organisms with the highest  $U_o$  values. Both the environment and the organisms with the lower  $U_o$  values contribute mass. If unique organisms are removed by extinction then it may be quite impossible to reverse these changes by returning  $E_g$  and  $U_o$  of the remaining organisms to their original values or by reversing the sequence of events.

Consider the example of a small ecosystem with three 'organisms' competing for one mutual resource. Only the net mass/energy flows are shown  $(\dot{Q}_T^1, \dot{Q}_T^2, \dot{Q}_T^3)$ .



Assume an initial equilibrium state in which  $E_g = U_o^1 = U_o^2 = U_o^3$ . Consequently the  $\dot{Q}_T$ 's will be zero. If the  $U_o$  values are subjected to random perturbation, the following pattern of events will ensue. The first perturbation will either increase or decrease the performance index of one of the organisms. If an increase occurs in  $U_o^1$  the result will be a net mass/energy flow  $\dot{Q}_T^1$  into organism 1. Eventually the value of  $E_g$  will be affected by this flow of mass/energy (depending on the size of the environment in relation to the flow  $\dot{Q}_T^1$ ). The loss of resource material must increase the value of  $E_g$  but this in turn will cause a mismatch



between the environmental grade and the performance indices of the other two organisms, i.e.,  $E_g > (U_o^2, U_o^3)$ . If the system is free from further perturbations for a sufficient length of time, organisms 2 and 3 will lose all of their mass/energy to the environment and will in effect die or become extinct.

On the other hand, if the initial perturbation had been a decrease in  $U_o^1$  the opposite sequence of events would have transpired; organism 1 would have lost mass/energy steadily and would eventually have become extinct if no further perturbations occurred.

A sequence of random perturbations to all three organisms would always have the predictable result that mass/energy would be continually shifted, via the environment, to those organisms with the largest performance indices. In a more realistic biosystem there would be a finite probability that those organisms with the lowest performance indices would become extinct if their mass/energy content (i.e. their population) became small enough.

The net result of a long sequence of random perturbations, in a large multi-organism environment, allowing time for equilibrium to take place after each perturbation ( $\dot{Q}_T = 0$  at equilibrium), will be a net increase in the average value of  $U_o$  and an increase in environmental grade  $E_g$ . Even if the perturbations were to take place much more rapidly than the equilibrium time for the system, there would be a gradual, overall displacement of mass/energy into the organisms with the highest  $U_o$  values. This 'evolutionary' effect has been demonstrated in a computer model in which large numbers of discrete organisms were simulated. The typical result of a simulation based on the model developed in Appendix D is presented in Fig. A-1 and Fig. A-2.

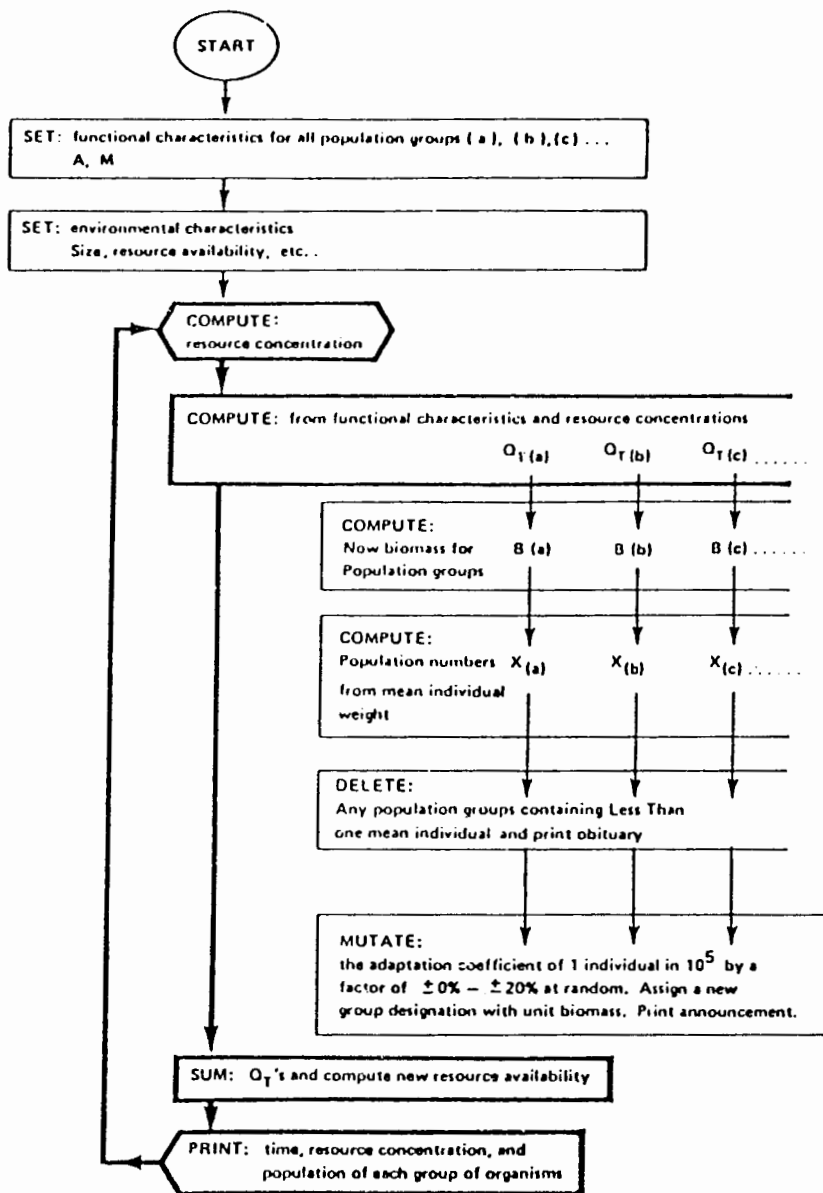


Fig. A-1

A general algorithm for a computer program in which equation (D-9) was used as a population equation for a demonstration of population response and mutation effects. The symbols A & M refer to adaptation coefficient and to metabolic conversion efficiency respectively.  $Q_T(a)$  is the net energy flux as previously discussed while B(a) and X(a) simply refer to the total population biomass and a population number computed on the basis of a unique individual weight or mass for each population group. The program creates new population types by random mutation (variation in A) and allows the populations to grow or decline to extinction on the basis of their own functional characteristics in relation to a single mutual resource pool which is renewed at a fixed rate. Populations which reach a size of less than one individual are deleted from the record.

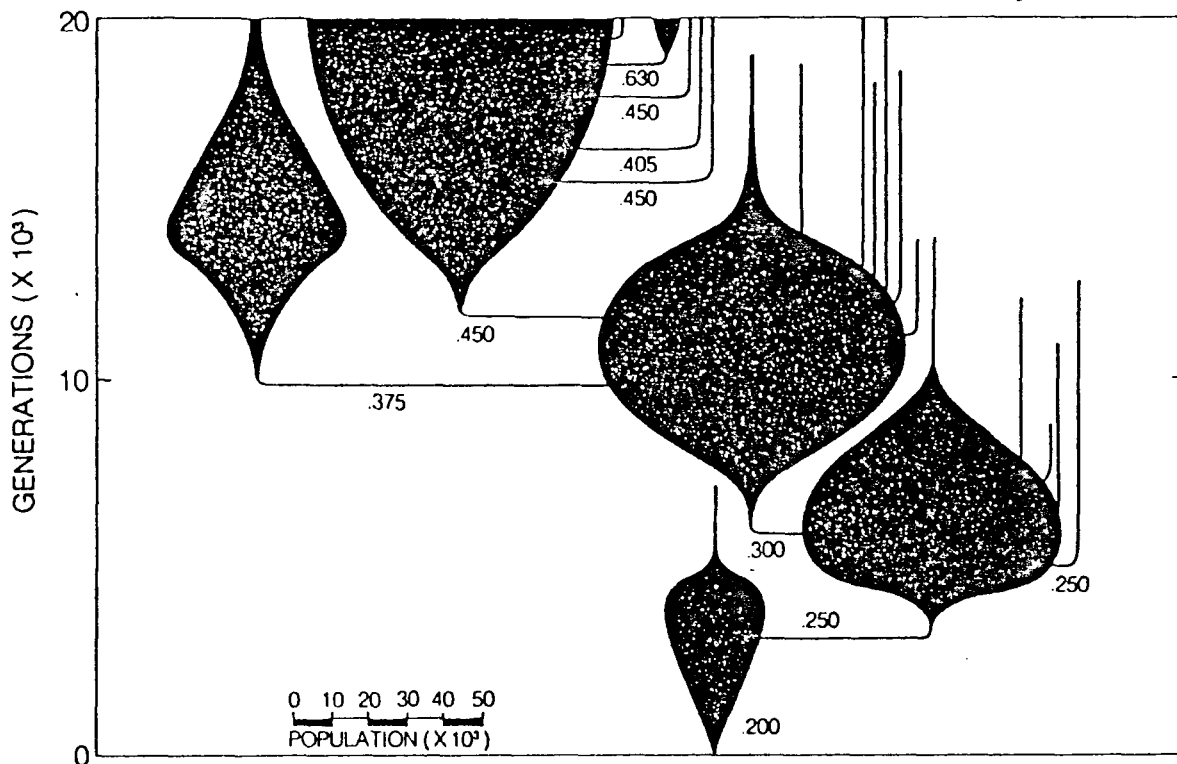


Fig. A-2 A typical 'phylogeny' generated by the algorithm shown in Fig. A-1 in which a multitude of organisms distinguished by differing  $A$  values was programmed to multiply, differentiate further by mutation and to compete for a single limiting resource. Monte Carlo techniques were used to generate random 'mutations' to the functional parameter  $A$  of the model organism. The decimal notations on various branches refer to the value of the adaptation coefficient  $A$ . Mutations which produced an organism with less than viable values of  $A$  are not recorded in this phylogeny. The apparent value of  $A$  increases monotonically; there is also a modest increase in total population numbers with the passage of generations.

It demonstrates a trend toward higher  $U_0$  values for a system containing many individual organisms with differing  $U_0$  values. All the variation generated was initiated by random 'mutation' (perturbation of A values where  $U_0 = AMR_0$ ). The net result of a long series of mutations, combined with the ongoing modelled life processes of the organism concerned is presented as a phylogeny. It is evident in this case that the variable A, the adaptation coefficient, which was subject to small random perturbations, steadily increased in average value. Since  $U_0 = AMR_0$  and since M,  $R_0$  were fixed, the value of  $U_0$  increased monotonically during a sequence of several thousand random 'mutations'. The generation of a realistic looking 'phylogeny' is in itself not an indication of selective or non-random processes. Raup (1977) has demonstrated that very typical-looking phylogenies can be generated by Markov processes. On the other hand the tendency for  $U_0$  to increase, as was consistently observed in all simulations, cannot be attributed to random processes.

It does not seem likely that this asymmetrical property of models based on the energy balance equation could be entirely fortuitous. Where one finds trends it is rational to seek a 'causal mechanism'. Can the asymmetrical properties of these models be justified on some broad level and can this same justification be applied to real living systems?

Equation (2-1) appears to be a simple energy conservation statement; could it have the properties which would be required for the generation of defined trend in response to a truly random sequence of perturbations?

Before concluding that a causal mechanism or a 'driving force' must be present, it would be reasonable to ask whether or not the observed asymmetry in this demonstration could be attributed to any of the particular constraints introduced in the simulations themselves rather than to some property inherent in the energy balance equation.

Two factors in these programs can be isolated as mechanisms which are instrumental in the generation of the observed asymmetries:

a) 'Death' or extinction of species or groups of organisms could occur under certain circumstances. Such events were not reversible in any of the simulations presented, that is to say, spontaneous generation of new life on the time scale of these programs was not assumed to be possible. This is the first source of asymmetry: deaths and extinctions of unique organisms are probable, but de novo creations are not. Only modifications of existing organisms can be created by mutation effects.

b) Mutation events were assumed to be initiated in individuals of the population. The reversal of a given mutation by a back mutation, although it was an equally likely single event, could also only affect a single individual. If the mutation had been incorporated into a large number of individuals the probability that such a mutation could be 'undone' by random back mutation became vanishingly small.

It will be recognized that, although the mechanisms above are instrumental, they are not casual; without some selection agent these mechanisms cannot generate trends. Particularly in the case of b) it is evident that asymmetries can only result if mutations of one kind proliferate and others do not; some 'value system' or selection criterion is implied.

I will claim that this selection criterion is an inherent property of the universe as well as a property of this energy balance equation. Although equation (2-1) is no more than an enumeration of flows through the system, there are thermodynamic constraints on the interrelationships of these flows. These constraints can most easily be appreciated as the dimensionless coefficients  $E_g$  and  $U_o$  in equation (2-12) which are, in effect, efficiency terms.

The vindication of the claim above entails an argument to the effect that the internal potential energy of a non-equilibrium system is related to the efficiency of that system where the efficiency is defined as the ratio of work output to work input. The argument follows in the form of a theorem plus corollaries which are intended to apply to the energetics of dissipative systems which can be viewed as 'engines'. The theorem suggests that the entropy of a system can be altered by altering the efficiency of an operating engine contained within that system.

### System Potential

"A system is in a state of equilibrium if a change of state cannot occur while the system is not subject to interactions. Equilibrium states may be of different kinds--namely, stable, neutral, unstable and metastable".

from Hatsopoulos and Keenan (1965) pp. 30

By definition a reversible process is a quasi-static process in which the sequence of equilibrium states through which the system passes can be caused to occur identically but in the reverse order (Giedt 1971). A reversible process is

therefore a limiting case which takes place infinitely slowly without friction, acceleration or heat transfer through finite temperature gradients. The reversible system only exists in a series of equilibrium states.

Hatsopoulos and Keenan (1965) suggest that reversible processes are outside the bounds of human experience; reversibility is an intellectual device which allows more precise definition of work and heat interactions than is possible for any observable process. An engine based on a (reversible) Carnot cycle is the classic example of a perfect engine which cannot be realised in practice.

Gibb's principle of generalized inertia can be invoked as an explanation of the inattainability of actual reversibility. The principle states that a sudden discontinuous alteration from a finite rate of change to a zero rate of change cannot occur without a finite alteration in circumstances no matter how small the order to change (Hatsopoulos & Keenan 1965). Effectively there is no way to cause a reversible engine to pass through its sequence of equilibrium states without external influence, i.e. without introducing disequilibrium. The definition of equilibrium can be restated succinctly as:

"A system is in a state of equilibrium if a finite change of state of the system cannot occur in a finite time without some finite change of state of the environment, either temporary or permanent".

- Hatsopoulos and Keenan (1965), p. 360

Therefore by the accepted definitions of reversibility and of equilibrium any system which is an engine operating reversibly will be indistinguishable from an equilibrium system. This is a useful conclusion in that it provides an analytical

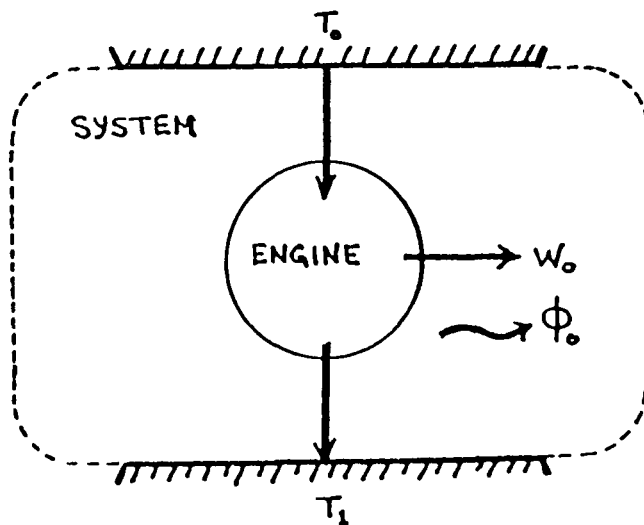
tool which can be used to examine the internal state of some non-equilibrium systems. The argument follows as a theorem and proofs.

THEOREM: Any system which is an engine operating reversibly will be indistinguishable from an equilibrium system.

Alternate Statement: Any heat engine in contact with a thermal source and sink of differing potentials (i.e.  $T_0 \neq T_1$ ), will be in equilibrium if it is a Carnot engine.

Proof: If a net flow of mass or energy were observed anywhere in the system it would be possible to extract further work from the system and thereby to exceed the maximum possible work output.

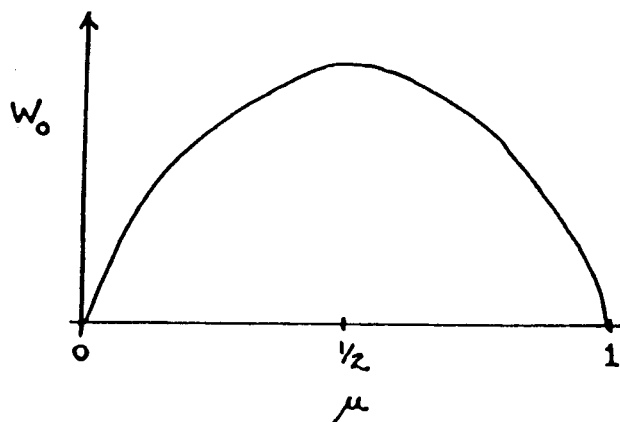
Alternate Proof: Consider the heat engine illustrated below. The following system will be in equilibrium as defined above if  $T_0 = T_1$ .





Under this circumstance the engine can have no finite work output and there will be no net flow of energy through the engine. Therefore the system meets the criterion for equilibrium as established in the definition above.

Now consider the case where  $T_0 > T_1$  and the heat engine is a Carnot engine, i.e. it is operating reversibly. Traditionally a Carnot engine must operate by quasi-static processes in order to extract work from a heat source/sink in a reversible manner. Although it is possible, in theory, to integrate the infinitesimals of this process in order to demonstrate the work output, this integration must be carried out over the interval from  $t = 0$  to  $t = \infty$ . Over any finite time interval no work output can be demonstrated; a Carnot engine (or any other reversible engine) has no work output in real time. This fact has not gone unappreciated by scientists and engineers over the past century. The rate of work output for an engine as a function of efficiency is zero at efficiencies of one and zero, and reaches a maximum when efficiency,  $\mu$ , equals one half (Odum & Pinderton 1953, Gabriel 1967). (In the case of heat engines,  $\mu$  refers to the partial efficiency namely  $\mu/\mu_0$ . This is implied in all further references to the efficiency of heat engines).



As can be seen from the diagram above the real power output from any engine approaches zero as efficiency approaches unity.

Therefore it must be concluded that the Carnot engine depicted above with  $T_0 > T_1$  cannot perform any work over a finite time interval. Since it cannot perform work there cannot be any net flow of heat through the system over any finite time interval. By the definition of equilibrium above, this system must be in equilibrium.

It remains to be shown that the equilibrium state defined for reversible engines falls within the definition of stable equilibrium from which the second law of thermodynamics can be derived. If this is the case then any system which is an engine operating reversibly is at a state of maximum entropy. This statement, if proven, will allow determination of changes of state in a system resulting from changes of efficiency.

THEOREM: A system which is an engine operating reversibly in contact with a source of potential energy (such as a heat source and sink with  $T_0 > T_1$ ) will be at a minimum energy state when it is operating reversibly. (Its entropy will be maximal.)

Proof: According to the foregoing definitions a reversible process represents a neutral equilibrium state where:

"A system is in neutral equilibrium if some finite change of state of the system can take place by means of a finite temporary change of the state of the environment but a finite rate of change cannot be established without a finite permanent change of state of the environment".

Hatsopoulos & Keenan, p. 362.

The reversible engine can be moved from one equilibrium state to the next only by some temporary change in the environment (of arbitrarily small

order). A finite rate of change however can only be established with the loss of reversibility (i.e. finite motion, thermal gradients, etc.). Therefore a reversible process correctly qualifies as a state of neutral equilibrium.

A stable state (of equilibrium) can include any number of neutral equilibrium states. Therefore it is sufficient to state that a system is in a stable state of equilibrium if a finite rate of change cannot be established without a finite permanent change of state of the environment. (Hatsopoulos & Keenan, p. 364.) But this is a statement of the second law of thermodynamics. Therefore it is established that the entropy of a system is maximal when it is an operating reversible engine.

It is now possible to consider a less than perfect system operating irreversibly.

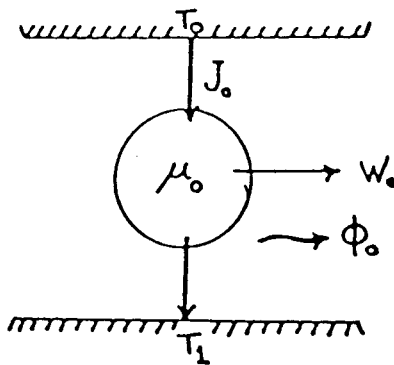
Corollary II: Any alteration to the structure of an operating engine (as a dissipative system) which results in an increase in the operating efficiency will result in a reduction of the net potential gradients (unbalanced potentials) within the system and a corresponding release of energy from the system, i.e., the entropy of the system (engine plus surroundings) will be increased.

Proof: This corollary follows from the second theorem; however it is my intention to show that the energy content of a system can be concisely defined as a function of the actual efficiency.

Return to the heat engine operating between the reservoirs  $T_0$ ,  $T_1$  where  $T_0 > T_1$ . If the efficiency  $\mu$  is zero, the net potential gradient within the system will be equivalent to the externally applied potential gradient  $X_0$

where  $X_o = (T_o - T_1)$ . Consequently it should be possible to describe the 'disequilibrium' of the system as proportional to this externally applied gradient  $X_o$ . On the other hand when  $\mu = 1$  the system must be in equilibrium (by the theorem above). Therefore the net potential gradients within the system must be zero even though an externally applied gradient  $X_o$  may still be observed. It would be desirable to define the situation for the intermediate states where  $0 < \mu < 1$ . This may be done as follows:

Take some engine with efficiency  $0 < \mu_o < 1$ , work output  $W_o$ , energy flow  $J_o$ , entropy production  $\phi_o$ , and the equations of state shown below



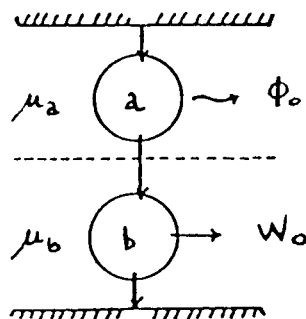
$$X_o = T_o - T_1 \quad (A-1)$$

$$W_o = \mu_o (J_o X_o) \quad (A-2)$$

$$\phi_o = J_o X_o - W_o \quad (A-3)$$

$$W_i = J_o X_o \quad (A-4)$$

For the sake of the analysis this system can be decomposed into two ideal engines in series, one with a minimal efficiency  $\mu_a = 0$ , and the other with a maximal efficiency  $\mu_b = 1$ .



The only output from  $\mu_a$  will be  $\phi_o$  and the only output from  $\mu_b$  will be  $W_o$ . The effective temperature intermediate between the two engines is represented by  $T_x$ . Since  $\mu_a = 0$  the internal potential gradient across this part of the system will be the full quantity  $T_o - T_x$  and the entropy production will be:

$$\phi_o = J_o (T_o - T_x) \quad (A-5)$$

Engine B with its ideal efficiency will have a work output  $W_o$  with:

$$W_o = J_o (T_x - T_l) \quad (A-6)$$

Since it is operating reversibly the net internal potential gradient across this segment of the system must be zero (as per theorem presented above). Therefore the total potential gradient within the combined A/B system must be equal to  $(T_o - T_x)$ , the gradient in segment A. Recalling that the efficiency of an engine is defined as:

$$\mu_o = W_o/W_i \quad (A-7)$$

and recalling (A-4) and (A-6) we can define  $\mu_o$  for the system as

$$\mu_o = \frac{J_o (T_x - T_l)}{J_o X_o} \quad (A-8)$$

which reduces to:

$$(T_x - T_l) = X_o \mu_o \quad (A-9)$$

By subtracting  $X_o$  from both sides and recalling (A-9) we get

$$(T_o - T_x) = X_o (1 - \mu_o) \quad (A-10)$$

where  $T_o - T_x$  will be recognized as the net potential gradient within the system A/B. Equation (A-10) can be rewritten as

$$\psi = X_o (1 - \mu_o) \quad (\text{A-11})$$

where  $\psi$  will be called the system potential.  $\psi$  can be conceptualized as the net driving force or disequilibrium in the system. Equation A-11 can also be derived by arbitrarily defining system potential as  $\psi = \frac{\phi_o}{J_o}$  and substituting into equation A-3 which is a general description for any operating engine. The units of  $\psi$  in the case of a chemical system would be calories/mole. For reactions at standard temperatures and pressures, system potential is equivalent to Gibbs free energy (See Appendix B).

In equilibrium thermodynamics, availability,  $\Lambda$ , denotes the maximum amount of work which can be spontaneously extracted from a given system by bringing it to equilibrium (regardless of pathway). For a system in stable equilibrium  $\Lambda = 0$ . The system potential, on the other hand, denotes the maximum amount of work which can be spontaneously extracted from a given non-equilibrium system (an engine) by bringing it to a state of stable equilibrium with  $\mu = 1$  ( $\psi = 0$ ). In other words it represents the net unbalanced potential gradients within the system.

For chemical systems under standard conditions  $\Lambda = \Delta G \equiv \psi$ . The reasons for this congruence is that chemical reactions involve processes with precisely defined pathways in which 'work outputs' such as a coupled reaction are a defined part of the pathway and  $\Delta G$  represents the net unbalanced potential in the system. (This is discussed further in Appendix B). At equilibrium a chemical reaction system becomes a reversible process.

It will be seen that the system potential goes to zero as efficiency goes to unity and, since the disequilibrium of a system is proportional to  $\psi$ , corollary II is justified. The entropy of the system is maximal when  $\psi$  is minimal; when the system potential is zero no further internal energy is available.

Corollary III: Given a dissipative system in which perturbations occur in sufficient magnitude to rearrange local structural features, that is, where rearrangements to the state of the system can occur spontaneously, stable dissipative systems with  $\mu > 0$  can occur spontaneously.

Proof: Any spontaneous transition which results in a positive increment to the  $\mu$  of a system will reduce  $\psi$  and thus increase the entropy of the system; on the other hand perturbations which tend to decrease  $\mu$  would entail a negative entropy change; the occurrence of such events on a macroscopic scale would be a violation of the second law.

For example: in the very simple situation of the onset of convection in a fluid, temperature gradients result in density gradients which, in the presence of a gravitational field, result in small pressure gradients. If the pressure gradients in the system are of sufficient magnitude to overcome the viscous forces of the fluid (reflected by the Reynolds number) the system will be unstable and minor perturbations can result in the onset of convection. A convective cell can be viewed as a heat engine in which the work output appears as movement of the fluid (which is dissipated by viscous forces and friction). Since the system has some measurable work output,  $\mu$  will be a non zero term; thus it can be concluded

that, at the onset of convection, the system potential  $\psi$  has been reduced and the entropy of the system has increased.  $\psi$  in this instance would reflect the net pressure gradients in the system, which would be relaxed at the onset of convection.

The corollary III should be applicable to the evolution of any dissipative system. I am interested specifically in its application to the 'fitness' and evolution of biosystems.

### Living Systems

The theorems presented in this Appendix should be applicable to engines of any kind. I will propose one further corollary to bring the matter into focus for biosystems.

Corollary IV: Any mutation which increases the efficiency of a living organism can potentially effect an increase in the entropy of the system (consisting of organism plus environment).

Proof: The mutation, if expressed, will reduce the system potential for the organism(s) in which it is found. It follows from the discussion of  $\psi_0$  (above) that this will reflect a reduction in the potential energy content of the organism. Therefore the entropy of the system must be increased.

Lemma: Biological evolution as 'survival of the fittest' through 'differential reproductive success' has a demonstrable driving force, namely the increasing entropy of the organism/environment system if and only if 'fitness' can be equated to 'efficiency'.

I do not believe that rigorous proof of this lemma is possible. On the other hand, it may be possible to show that the energy balance equation



presented in (2-1) is a close homologue to overall bioenergetic processes and as such has potential utility as an explanatory analogue. I have attempted to provide some demonstration of this potential in the earlier parts of this thesis.

### Competition: Survival of the Most Efficient

Darwin's phrase 'survival of the fittest' has been replaced with the phrase 'differential reproductive success' by contemporary evolutionists. The preceding lemma implies that, given an appropriate energetic description, this could be interpreted as 'survival of the most efficient'. How does efficiency relate to reproductive success? In chapter 2 fitness was defined as a function of the difference between  $U_o$  and  $E_g$ . The growth rate of the population (or individual)  $\dot{Q}_T$ , was shown to be proportional to this difference (in the vicinity of  $U_o = E_g$ ).

Earlier in this appendix I suggested that the asymmetrical properties of equation (2-1) must correspond to a demonstrable thermodynamic driving force. Equation (2-12) specifies the value of a net mass/energy flow  $\dot{Q}_T$  across the organism environment interface on the basis of  $E_g$  (a property of the environment), and  $U_o$  (a property of the organism) modulated by  $\dot{Q}_I$  which can be viewed as a rate parameter reflecting the magnitude of the organisms metabolic activity. In order to demonstrate a driving force it must be shown that the flow  $\dot{Q}_T$  represents an equilibrium process which maximizes the entropy of the system as a whole.

Consider the consequences of a net flow of  $n$  moles of 'food particle' from environment to organism, keeping in mind that any net flow  $\dot{Q}_T$  will result in an increase or decrease in the standing biomass of the organism or population. The chemical potential energy ( $C$ ) of each particle as it is transferred into the organism will be increased by  $W_n$ , the work done on the particle. However, the internal chemical potential of the particle as a part of the organism will be reduced in proportion to the efficiency of that organism as has been established in the definition of system potential. If  $\delta E$  is the apparent loss of potential energy from a particle as it is incorporated into an organism then

$$\delta E = C - \psi_o - W_n \quad (A-12)$$

But  $C$  and  $X_o$  are functionally equivalent since  $C$  represents the apparent externally measured calorific content of a food particle and  $X_o$  is the more generalized potential associated with a flow  $J_o$ . It is possible to substitute (A-11) into (A-12) using  $C$  in the place of  $X_o$  for this specific biological application.

$$\delta E = -C(1 - \mu_o) + C - W_n = -C\mu_o - W_n \quad (A-13)$$

Since the performance index  $U_o$  of an organism is an expression of its operating efficiency, (A-13) can be rewritten as

$$\delta E = CU_o - W_n \quad (A-14)$$

By multiplying  $W_n$  by  $C/C$  and recalling the definition of  $E_g$  in (2-6), equation (A-14) becomes:

$$\delta E = CU_o - C(W_n/C) = C(U_o - E_g) \quad (A-15)$$

where the sense of  $\delta E$  is defined for 'food' flows from environment to organism ( $\delta E$  will be negative when energy is liberated by the process). This apparent liberation of energy should constitute a thermodynamic driving force for the net mass/energy flow  $\dot{Q}_T$ . When  $E_g = U_o$  there is no potential energy change to the system for net transfers of mass in either direction. Therefore the expected spontaneous net flow  $\dot{Q}_T$  will be zero.

On the other hand when  $E_g \neq U_o$  a disequilibrium exists. The spontaneous direction for any  $\dot{Q}_T$  would be such that the net potential of the system is minimized or, in other words, the entropy maximized. If  $E_g > U_o$  a flow from organism to environment would release energy at a rate specified by equation (A-15). If the size of the system is known, the total energy change from initial conditions to final 'equilibrium' conditions can be computed.

In a similar way, if two organisms a and b occupying the same environment have differing performance indices such that  $U_a > U_b$ , it can be shown that the net transfer of mass from organism (b) to organism (a) would result in a reduction of the total potential energy in the system, where

$$\delta E = C(U_a - U_b) \quad (A-16)$$

Therefore there would appear to be a thermodynamic basis for competition and the process of Darwinian evolution: viz. the second law of thermodynamics.

### Comment

It appears that some of the preceding discussion is relevant to analyses which seek to treat biological systems as 'information systems'. Since the foregoing derivations have been treated entirely as a problem in energetics, a detailed discussion in relation to information theory would be better left for another document. Appendix C presents a brief speculative discussion relating information to system potential.

### Summary

The questions of value and fitness were addressed in the body of this thesis with a resulting conclusion that fitness could be directly related to a performance index or measure of efficiency of an organism in relation to an environmental quality factor. Because the definition of performance index was based on a complete description of energy flows through a 'black box' organism, the possibility of finding a thermodynamic interpretation for 'differential reproductive success' also presented itself. The analysis presented in this appendix indicates that the second law can indeed be used in a predictive mode with respect to evolution, but it requires the definition of the internal energetic state of non-equilibrium systems. This has been provided in the form of  $\psi$ , the system potential which can be used to define a potential difference between organisms.

'Survival of the fittest' in its present day interpretation as differential reproductive success is an intuitive recognition that potential differences can exist between organisms. Superficially we might observe that a more fit

organism has the potential to take over a 'niche' from a less fit organism. The meaning of potential in this case can be quantitatively defined. Any given 'niche' can be occupied by one or more species which will have some characteristic biomass and a measurable system potential. If a more fit organism is introduced into this 'niche', (as previously established, more fit or more efficient implies a species with a lower system potential), the biomass of the former species will then have a defined potential energy with respect to the latter species (vide eqtn. A-16). This potential energy difference,  $\delta\psi$ , can result in the displacement of biomass from the original species into the introduced species with an accompanying energy release  $\delta E$ .

The long term consequences of such inter-species and even intra-species potential gradients will be the gradual displacement of organisms with high system potentials in favour of organisms with low potentials. The system potential as defined in eq. (A-11) is a reflection of the performance of index,  $U_o$ , or the thermodynamic efficiency of an organism. Therefore 'selection' on the basis of system potentials should result in the evolution of more efficient organisms.

The concept of efficiency as a measure of evolutionary progress is not new; it has been proposed and rejected more than once in the past. Sahlins and Service (1960) discussion of the idea is typical:

"But an organism's thermodynamic efficiency is not a measure of its general evolutionary status. By efficiency we usually mean some ratio of input to output... a measure of the thermodynamic efficiency of a living thing would be the amount of energy captured and used relative to the organism's own expenditure in the process of taking it."

They go on to point out the perceived inconsistencies in this idea of efficiency as related to progress:

"But suppose we know the efficiency of an organism as an energy capturing machine; the use to which the efficiency is put remains unknown. Is it put into the build-up and maintenance of its organization? Not necessarily. As pointed out before, the energy can be put into the build up of higher structures or into more numerous offspring, each of which concentrates a relatively low amount of energy. The implication is inescapable: an organism can be more efficient than another and yet remain less highly developed."

In my view these inconsistencies only arise as a result of the failure to define the energetics of the situation rigorously. Ultimately, the efficiency of transformation of captured energy into work must include all of the necessary life functions from communication to reproduction; all of these uses of energy are, in the final analysis directed toward the ongoing capture of energy. If the efficiency is arbitrarily defined as the efficiency in converting energy income into further energy income, i.e., as the performance index, these ambiguities can be avoided. Organisms are continually pitting the efficiency of their total life processes against the properties of their energy source or environment. The work output,  $\dot{Z}$ , is determined by the properties of an inconstant environment.

The solutions to the problem of survival appear to be many and are rarely enduring.

The only phyla to 'survive', ironically, are those which change. In the long term, continued existence requires a constant reassessment and the synthesis of new solutions to the problem(s) of primary homeostasis. This latter point has long been recognized in the realm of human endeavour; as Machiavelli wrote in his survival manual for that rare species, 'The Prince':

"Yet were he to alter his character according to the times and circumstances, Fortune would not change."

### Concluding Remarks

An attempt has been made to assign a universal, quantitative value to 'fitness'; further it has been suggested that on the basis of this definition of fitness, evolutionary phenomena can be predicted using thermodynamic arguments. Interpreting this 'value' vis a vis the real world in terms of physiology or behaviour remains. Particular 'solutions' to the problem of survival cannot be extracted from the type of analysis which has been made here.

The development of a quantitative evolutionary theory in biology is an advance which is being anticipated in many other disciplines. Thorson (1970) perceives an unparalleled benefit to the so-called 'soft sciences'.

"... taking time and evolution seriously can open the door to a genuine science of society, one which is capable of grasping the whole phenomenon of man. This is science not because of what it can be made to look like by the clever mimic, but because it is fundamentally compatible with - indeed a natural and logical extension of - biology, chemistry, and physics."

## APPENDIX B





It appears to be possible to define the Gibbs free energy for an open system in terms of the efficiency of that system. But what is the meaning of efficiency with respect to a simple chemical reaction?

Consider the reaction system:



The transition of molecules from A to B will release an amount of energy  $G_A^{\circ}$  plus the entropy of dilution resulting from the removal of A from the system. If the work input to the system ( $W_i$ ) is defined as all of those events or processes which decrease the chemical potential of the system, and the work output,  $W_o$  (congruent with the previous usage of this term), is defined as those events which increase the chemical potential, then:

$$W_i = G_A^{\circ} + T_o S_A \quad (\text{B-4})$$

where  $S_A$  is the entropy of dilution for A. If the work output of the system,  $W_o$ , will be the entropy change for compound B resulting from the addition of new members to B, then

$$W_o = -T_o S_B \quad (\text{B-5})$$

Rewriting (B-3) and recognizing that, for this case, the applied potential,  $X_o$ , will be proportional to  $W_i$  since  $W_i$  has been defined above as the potential energy release per mole, it can be concluded that:

$$\Delta G = X_o(1-\eta) = W_i \left(1 - \frac{W_o}{W_i}\right) = W_i - W_o \quad (\text{B-6})$$

and using (B-4) and (B-5):

$$\Delta G = W_i - W_o = G_A^{\circ} + T_o (S_A + S_B) \quad (\text{B-7})$$

which is the familiar expression for the free energy change of a chemical reaction. If the state of the system is such that the efficiency  $\eta = 1$  then by definition,  $W_o = W_i$

and therefore:

$$G_A^0 + T_0 S_A = -T_0 S_B \quad (\text{B-8})$$

which is the usual condition for chemical equilibrium.

The efficiency of the reaction system can be written as:

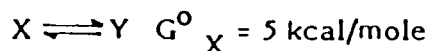
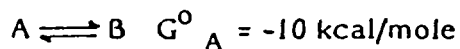
$$\mu_0 = \frac{W_o}{W_i} = \frac{-T_0 S_B}{G_A^0 + T_0 S_A} \quad (\text{B-9})$$

Thus chemical equilibrium can be interpreted as an energy conversion process functioning reversibly with unity efficiency. Although there may be a continuous exchange of energy in the system, there is no net observable change in the system.

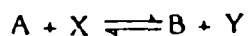
Note that the definitions above for  $W_i$  and  $W_o$  are dependent upon the direction of the process. If  $W_o$  were to exceed  $W_i$ , the efficiency in equation (B-6) would have a value  $\mu_0 > 1$  which in this case would have to be interpreted as an indication that the spontaneous direction for the process was opposite to the polarity chosen for the definitions of  $W_o$  and  $W_i$ .

It might be argued that  $W_o$  and  $W_i$  have been arbitrarily defined in order to obtain this particular result. I will attempt to demonstrate that these definitions are quite universal by looking at a more complex example in which the definitions should make more intuitive sense.

Consider two reactions:



which are coupled in an overall reaction.



By the previous conventions, gathering all events which increase the entropy of the system as  $W_i$  and all events which decrease entropy as  $W_o$ :

$$W_i = G_A^{\circ} + T_o (S_A + S_X) \quad (\text{B-10})$$

$$W_o = -G_X^{\circ} - T_o (S_B + S_Y) \quad (\text{B-11})$$

Therefore:

$$\Delta G = (G_A^{\circ} + G_X^{\circ}) + T_o (S_A + S_Y + S_B + S_X)$$

which under standard conditions reduces to

$$\Delta G = (G_A^{\circ} + G_X^{\circ}) = -5 \text{ kcal/mole}$$

The efficiency, on the other hand, will be expressed by

$$\mu = \frac{-G_X^{\circ} - T_o (S_B + S_Y)}{G_A^{\circ} + T_o (S_A + S_X)} \quad (\text{B-12})$$

I posed the question a few pages back as to the meaning of efficiency with respect to a chemical reaction system. In expressions (B-12) or (B-9) it becomes evident that the efficiency term reflects the relative energetic state of a reaction system. Efficiency is, in this case, an intensive state parameter (as opposed to  $\Delta G$  or  $\psi$  which are extensive parameters) which is related not only to the standard free energy of the components and to their relative concentrations but also to the absolute concentrations. In the case above, if the substances involved are 'pure', the entropy terms in equation (B-12) will be small and the 'efficiency' of the reaction will approach the ratio  $G_A^{\circ}/-G_X^{\circ}$ . On the other hand if the substances are greatly diluted the entropy terms will dominate expression (B-12) and the 'efficiency' of the reaction will approach unity even though the Gibbs free energy may remain at some finite value. This makes intuitive sense since at great dilution the effective potential energy of the system will approach zero despite the finite potential indicated by  $\Delta G$ . The efficiency term as an intensive state parameter in this instance indicates that the system is close to an equilibrium state even though the extensive state parameter,  $\Delta G$ , may indicate a general disequilibrium.

## APPENDIX C

## INFORMATION

The preceding discussions make only a single oblique reference to information theory. Yet it is fair to say that the conceptual developments in information theory have had a considerable influence on the ideas put forth here.

Analytical techniques for the treatment of information transmission systems were developed during the 1940s principally by C. E. Shannon, whose analytical forms (Shannon and Weaver, 1964) were identical to the treatments developed earlier in the century for the treatment of thermodynamics in the field of statistical mechanics. This tantalizing congruence of form has reinforced the idea that there must be some direct relationship between information and energy. (The idea dates at least as far back as Maxwell's notorious demon who, with the aid of information, was able to reduce the entropy of a system.)

L. Gatlin has been prominent among theoreticians who have attempted to apply information theory concepts directly to biological systems (on the tacit assumption that the energy-information relationship does exist). Gatlin (1972) has elaborated some interesting and potentially useful ideas such as 'second theorem selection' which relate to the efficiency of information coding mechanisms. However, the question of 'meaning' eluded Gatlin; without a methodology for evaluating the 'effect' or 'value' of information, it is not possible to assign it an energetic equivalent.

Weaver (Shannon and Weaver, 1964) suggested that communication problems could be considered on three levels

Level A How accurately can the symbols of communication be transmitted?

Level B How precisely do the transmitted symbols convey the desired meaning?

Level C How effectively does the received meaning affect conduct in the desired way?

Weaver further contended that although information theory (as developed by Shannon et al) ostensibly only deals with Level A, the technical problem, it may have implications for Levels B and C; i.e., meaning and effect.

The question of meaning or effect in information theory is identically the questions of a physical 'value system' as discussed in the introductory chapter of this thesis. At the outset of this investigation in 1976, it did not appear that any direct answers were available in information theory and a deliberate decision was taken to proceed with a bioenergetic analysis of the problem.

However, since the thesis proposes an answer to the problem of 'value', the reader might well ask whether that same answer is pertinent to the question of 'meaning' and 'effect' in information theory? The answer appears to be "Yes", and I will present the case as speculation for those readers with an interest in information theory.

If the phrase 'the information content of a' is substituted for the word 'structure' throughout Appendix A, the various theorems and corollaries come out suggesting that information is a property of the architecture of operating engines (steady state autocatalytic energy processing systems). The 'effect' of information is to alter the structure or architecture of the engine in some way which affects the thermodynamic efficiency of the engine. The 'effect' or 'value'

of information can then be directly equated to the change which it produces in the system potential,  $\psi$ , of the engine. Thus, the 'value' of information to any specified 'receiver' (engine) can be exactly specified as a quantity of energy  $\delta\psi$  released by the receiver as an effect of the information.

It is salient to note that  $\delta\psi$  can attain any value. A message may have a positive value, no value or a negative value.

information  $\delta\psi > 0$

no information  $\delta\psi = 0$

disinformation  $\delta\psi < 0$



APPENDIX D

## A POPULATION EQUATION

In addition to its application to questions of fitness, it is possible to use equation (2-1) as a generalized population growth equation. There are two primary assumptions implicit in the equation which are more in the nature of statements of biological fact rather than idealizations in the name of analytical convenience:

- a. Organisms must work in order to capture food or energy.
- b. Organisms convert captured food/energy into work with some finite efficiency ( $0 < \mu < 1$ ).

The form in which the equation is used in the following discussion does assume for 'analytical convenience' that: the age structure of the populations is invariant, and that the net immigration/emigration is zero. Neither of these assumptions, however, is implicit to the fundamental structure of the equation; appropriate terms could have been inserted to account for such effects without altering the basic structure.

Weigert (1974) has noted that logistic growth equations suffer from two deficiencies:

1. the maximum specific rate of increase is achieved only at zero population density; and
2. the carrying capacity ( $K$ ) does not incorporate the effects of both renewable and non-renewable resources.

The analysis to be presented avoids the first deficiency altogether and is formulated in such a way that any renewable/non-renewable resource situation may be readily accommodated. Biomass increase rates are determined by feeding; reproductive kinetics, in relation to resource density. The carrying

capacity of the system at any time does not depend upon some predetermined factor but is the result of a dynamic balance between current resource availability and the instantaneous requirements of the population.

Although equation (2-1) differs only slightly from other population equations in form, it is fundamentally different in that it represents an integral thermodynamic analysis rather than an admixture of arbitrary equations and energy flow terms such as the analysis presented by Timin and Collier (1970).

Equation (2-1) can be set in the standard format of a growth equation:

$$\frac{1}{N} \frac{dN}{dt} \propto \dot{Q}_T = \dot{Q}_1 - \dot{Q}_2 - \frac{\dot{Z}}{AM} \quad (D-1)$$

Although equation (D-1) provides a complete account of the energy flows through an organism, species, or ecosystem (neglecting immigration/emigration), in the form given it is much too general to be of practical value. It is possible to expand the equation by substituting particular values for each of the variables in order to appropriately 'fit' the equation to the particular species or type of organic system under attention. The following expansion has been made for a population with a continuous age structure which feeds on molecular nutrients (e.g., bacteria feeding on hypotonic glucose).

### A Typical Expansion

This ensuing analysis applies to a population feeding on molecular nutrients and is expressed as a rate per individual of the population.

$\dot{Q}_1$  Energy Ingestion Rate

The rate of energy intake can be expressed as

$$\dot{Q}_1 = \dot{F}C \quad (D-2)$$

where  $F$  refers to a flow of food particles (moles/second) and  $C$  to the energy content of the particles (calorie/mole). However, the flow of food,  $\dot{F}$ , must be dependent on the feeding behaviour of the organisms in question. Is the feeding rate dependent on food concentration? Is it saturable?

Figure D-1 illustrates two possible types of feeding kinetic. The Lotka-Volterra linear feeding kinetic is unrealistic for any organism; there must be some limit to an organism's ingestion capacity regardless of food availability (c.f. Bazin et al., 1974). The "Monod" type saturation kinetic seems appropriate for this case since molecular ingestion is often enzyme mediated.

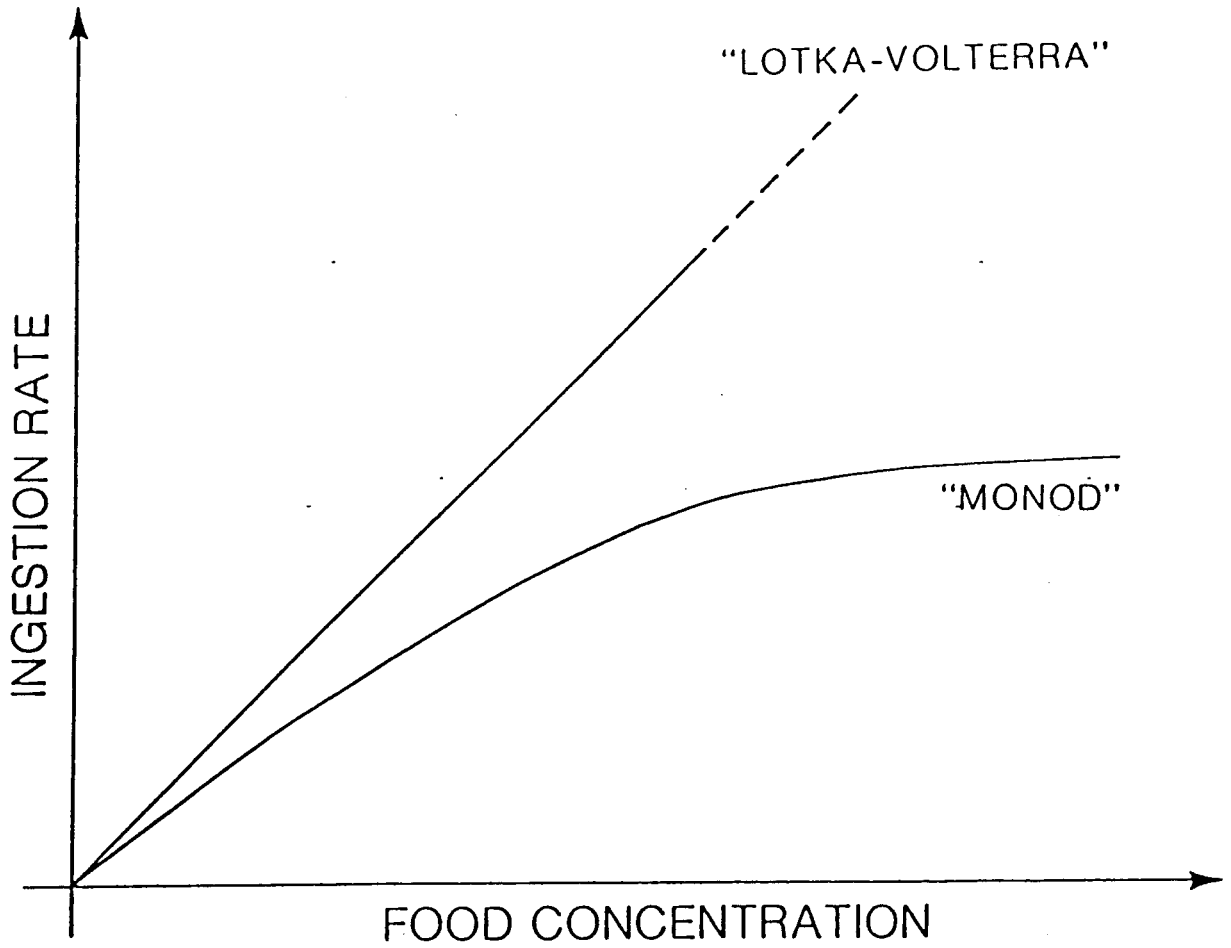


Figure D-1: An illustration of two possible type of feeding kinetic. (Bazin et al., 1974.)

Thus:

$$\dot{F} = \frac{\dot{T}_b C_e}{C_e + K_m} \quad (D-3)$$

where  $\dot{T}_b$  = maximal individual ingestion rate (moles/second)

$C_e$  = food particle concentration (moles/litre)

$K_m$  = concentration at which  $\dot{F}$  is half maximal (moles/litre)

Therefore (D-2) can be rewritten as

$$\dot{Q}_1 = C \left[ \frac{\dot{T}_b C_e}{K_m + C_e} \right] \quad (D-4)$$

Note that this type of feeding kinetic could be applied to plants as well as animals. In the case of plants with adequate mineral nutrition in full sunlight, the limiting nutrient is often  $CO_2$ . The fixation of  $CO_2$  is enzyme mediated and has the characteristic saturation kinetic of enzymatic reactions. Whether or not  $CO_2$  is the source of energy, its absorption kinetic faithfully reflects the actual energy intake by the plant under these conditions. This rate limiting effect is very general and may be applied to a wide range of organisms.

$\dot{Q}_2$  - Energy Egestion Rate

The primary vector for chemical energy loss (as mass) from animals will be through feces, whereas tissue losses will predominate for plants (although guttation and leaching may be significant). Most animals can be characterized by an assimilation ratio,  $p$ , which reflects the efficiency of nutrient assimilation

from ingested foods (as opposed to  $R_o$  which includes tissue losses). Thus some part of  $\dot{Q}_2$  will be directly proportional to  $\dot{Q}_1$ .

$$\dot{Q}_2 = \dot{Q}_1 (1 - p) + \dots \quad (D-5)$$

Biomass loss from a population is also part of  $Q_2$  since tissue losses include the losses of whole organisms from the population through deaths as well as sloughing of tissue, hair, etc. If  $s$  is defined as the biomass loss rate in calories per individual, then:

$$\dot{Q}_2 = \dot{Q}_1 (1 - p) + \dot{s} \quad (D-6)$$

### $\dot{Z}$ - Foraging Work:

As previously discussed, the primary task of foraging organism is to locate food particles in the environment and to alter the distribution of these particles by consuming them. A measure of the work accomplished can be computed from the change in the distribution of food particles in the environment. The Gibbs free-energy change resulting from the rearrangement from some initial environmental nutrient molecule concentration ( $C_e$ ) to some final organismic concentration ( $C_o$ ), where  $R$  is the molar gas constant and  $T$  is the temperature in degrees Kelvin, will be:

$$\Delta G = -RT \ln \frac{C_e}{C_o} \quad (D-7)$$

Since the final concentration ( $C_o$ ) may be considered as more or less constant, and utilizing equation (2-4b),  $\dot{Z}$  can be defined as:

$$\dot{Z} = \dot{F} (-RT \ln [C_e] + k) \quad (D-8)$$

where  $k$  is a constant. Note that  $\Delta G$  could also have been computed from the

entropy of dilution for the food particle, thus avoiding any questionable assumptions about the final concentration  $[C_o]$ .

It is now possible to merge equations (D-4), (D-6), and (D-8) to provide an expanded version of equation (D-1):

$$\dot{Q}_T = \frac{\dot{T}_b C_e}{C_e + K_m} \left[ \frac{C_p - (k - RT \ln[C_e])}{AM} \right] - \dot{s} \quad (D-9)$$

It will be noted that  $\dot{Q}_T$  is not directly equivalent to the population growth. This is because  $\dot{Q}_T$  represents the instantaneous gain or loss of biomass which will show up as a per capita change in the standing mass of the population but may not correspond directly to a change in population numbers. It is a more flexible measure than  $(1/N)(dN/dt)$  in that it directly reflects both catabolic and anabolic processes at a population level.

If it is assumed that the mean weight of the individuals in a population is regulated about some value ( $m$ ), then  $\dot{Q}_T/m$  can be assumed to be equivalent to  $(1/N)(dN/dt)$ . In many cases,  $\dot{Q}_T$  can be a more accurate representation of the state of a population since, for many organisms with discontinuous reproductive patterns, tissue is accumulated as an energy resource which is intermittently converted into progeny. Thus  $dN/dt$  must be based on discontinuous processes (especially in the case of seasonal breeding patterns), whereas  $\dot{Q}_T$  is a more continuous reflection of the state of the population.

As mentioned previously,  $\dot{Q}_T$  can be negative; that is, it can reflect the net catabolic processes which will occur when resources are insufficient to meet the energy needs of the population. A negative  $\dot{Q}_T$  would reflect the



conversion of tissue to energy and a net reduction in the biomass of the population.

When  $\dot{Q}_T = 0$ , the population biomass will be at a steady state where tissue losses ( $s$ ) will be exactly compensated. (This type of continuous function is not as easily applied to populations which experience sudden variations in age structure and biomass; i.e., spawning salmon.)

### Reproductive Capacity

Nowhere in these equations has the reproductive capacity of the population been referred to directly; it is an integral part of the feeding kinetic. As Schoener (1973) has pointed out, animals should restrict their feeding behaviour in accordance with reproductive capacity. The maximal value which  $\dot{Q}_T$  can attain (that is, the maximal rate of increase of the population biomass per capita) is determined by  $\dot{T}_b$ , the saturation feeding rate. (See equation D-3.) This arrangement corrects for the first of Weigert's listed deficiencies in that the maximum intrinsic rate of increase will be determined by the reproductive capacity and by the abundance of resources rather than by some arbitrary measure of population density.

Another implication of the present analysis concerns the concept of carrying capacity which is used in many population equations. This is an unnecessary concept with respect to equation D-9. A population limit will be achieved when the availability (concentration) of renewable and non-renewable resources is such that energy requirements of the population are just met; i.e., when  $U_o = E_g$ . This will be a dynamic balance and will not lead to the properties of a fixed parameter such as carrying capacity.

## Resources

The previous discussion of foraging work,  $\dot{Z}$ , was limited to a single, presumably renewable, resource. Some further attention should be given to  $\dot{Z}$ .

The growth rate of an organism should be proportional to food intake minus various costs:  $\dot{Q}_T = f(\dot{Q}_I - \text{basal metabolism, foraging, reproduction, defence, etc.})$  In equation (D-9), all of these costs were represented by  $\dot{Z}/AM$  which, although it may be an accurate representation of the net behaviour of a population over time, does not represent individual circumstantial behaviour. The term  $\dot{Z}/AM$  can be broken up into several factors. Some of these cost factors may be invariant and others, such as foraging, may be resource dependent. Thus:

$$\frac{\dot{Z}}{AM} = (\text{constant costs}) + (\text{variable costs})$$

NOTE: Constant costs such as basal metabolic rate and variable costs (which are independent of feeding activity) will appear in equation (D-9) outside of the brackets along with the term  $\dot{s}$ .

Assume that  $w_n^i$  is the cost of collecting resource  $i$ .  $A_i$  is the adaptation of the organism to that function, and  $F_i$  is the ingestion or turnover rate of that resource. Then:

$$\frac{\dot{Z}}{A_0 M} = \frac{F_i}{M} \sum \frac{w_n^i}{A} \dots \quad (D-10)$$

where  $w_n^i$  will reflect the cost characteristic for that resource.  $w_n^i$  might be determined as in equation (D-7) by the resource density. (i.e.,

$$\Delta G = -RT \ln [C_e] + k).$$

The cost of obtaining a given resource,  $i$ , is presented above as a characteristic of that resource concentration. Population densities (space limitations) might interfere with some resource related activities for some organisms and for others they might not be significant. Some careful consideration is necessary in the analysis of each case.

For example, for a given group of plants, if nitrogen is the limiting resource, these plants may be in direct competition for the available nitrates. But the cost of accumulating a given quantity of nitrate will depend only on its concentration in the soil. The presence or absence of competing plants in determining that concentration is irrelevant unless there is actual physical interference between the plants.

In the first instance:

$$\frac{\dot{z}}{A_0 M} = \frac{\dot{F}}{M} \sum \frac{(-RT \ln [N] + k)}{A} + \dots \quad (D-11)$$

In the second case, physical interference between plants may be realized as a reduction in  $A_i$ , the adaptation of the plant to the particular task. Therefore:

$$\frac{\dot{z}}{A_0 M} = \frac{\dot{F}}{M} \sum \frac{(-RT \ln [N] + k)}{A_x} + \dots \quad (D-12)$$

where  $A_x$  is some function of  $A_i$ , the optimal adaptation.  $A_x$  may be sensitive to population density or crowding, but the particular characteristics of the function will be entirely species dependent.

Although some determining function for  $A_x$  can easily be written into an analysis, it must be arbitrarily matched to the observed characteristics of the species being modelled.

### Applications: Resource Limited Situations

Two simple applications of the preceding analysis will be demonstrated in the ensuing paragraphs. Each example has been based on equation (D-9) representing the circumstances of a small organism with a continuous population structure, feeding on a molecular nutrient continuously and uniformly perfused into the environment at some predetermined rate (a typical chemostat situation). Both examples were programmed on a digital computer as a continuous iteration process in which the growth equation was solved at constant intervals using the biomass and resource levels which had been established at the end of the previous interval. The operator was able to perturb the situation by altering the population level, the resource renewal rate, etc.

- a. Response of a homogenous population to fluctuations in the availability of a single limiting renewable resource.

Figure (D-2) illustrates the population biomass response to abrupt changes in the availability of a single renewable resource. Response was computed by a continuous iterative integration of  $\dot{Q}_T$  and its effect on the population biomass and the resource concentration.

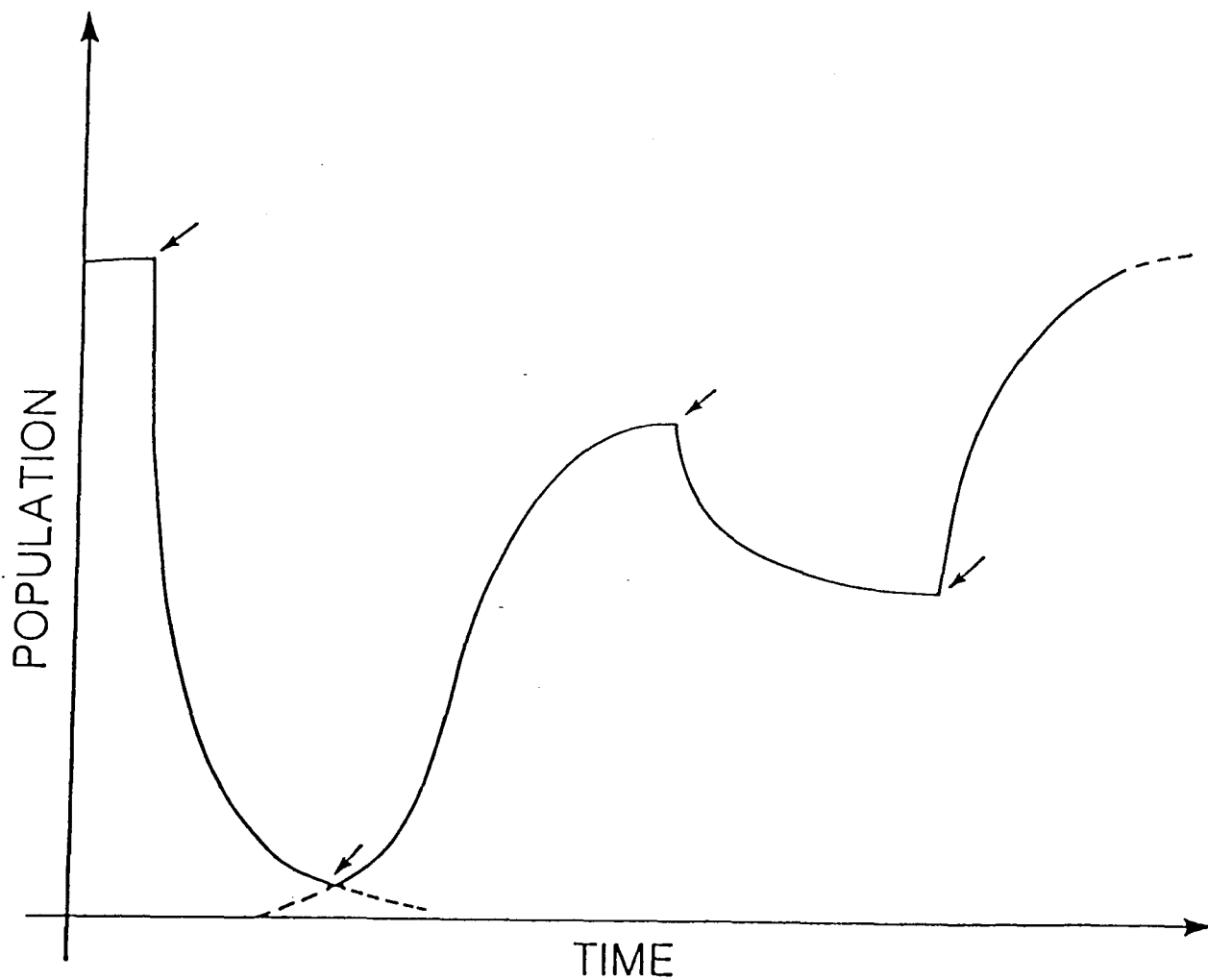


Figure D-2 The response of population biomass to abrupt changes is the availability of a single renewable resource. The population was modelled using equation (D-9). The response was computed by iterative integration of  $\dot{Q}_T$  flows as they affected the resource base and the population biomass. Oblique arrows indicate the points at which the resource base was abruptly altered by the operator. The program algorithm was similar to that shown in Figure A-1 except that there was only one species and no mutation.

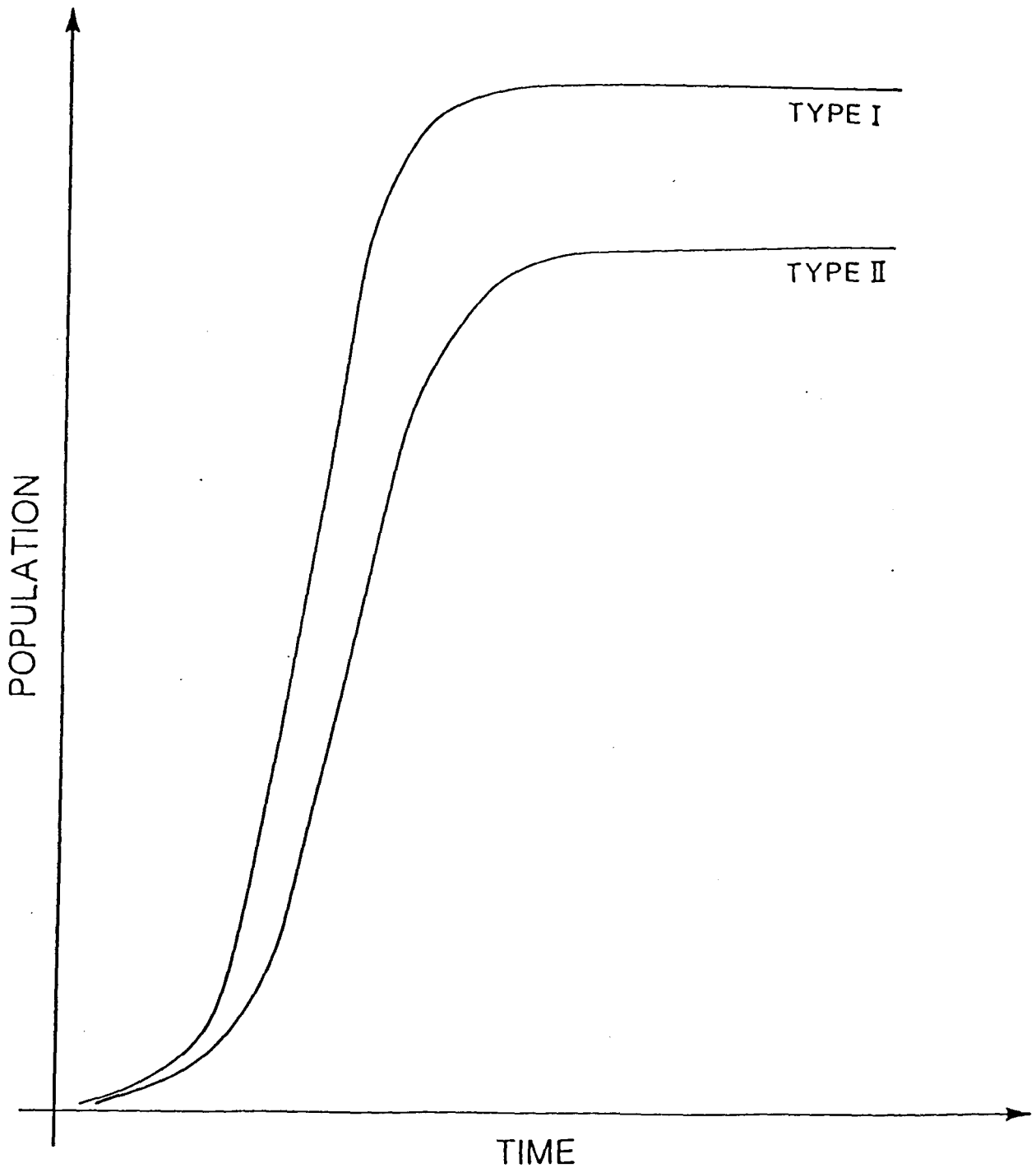


Figure D-3 Population growth curves for two simulated species grown in separate cultures. The curves were determined by a computer integration of equation (D-9) in which all species characteristics but the adaptation coefficient were identical.

For Type I,  $A = 0.1612$ ; for Type II,  $A = 0.1610$ .

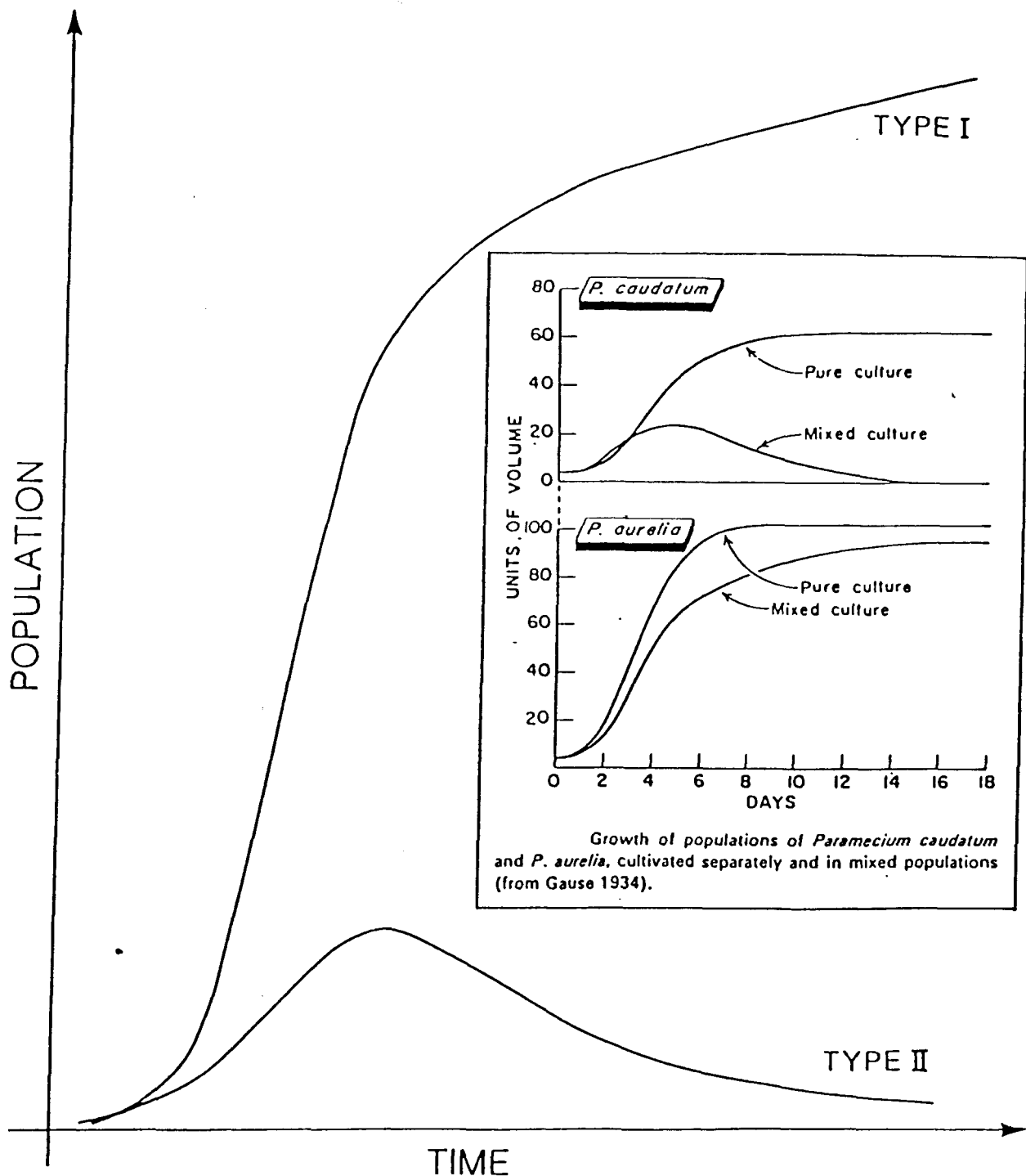
In this case, the maximal growth rates were achieved at the initiation of a perturbation, the growth curves approached their limiting value smoothly. These curves are typical of logistic solutions. The performance index  $U_0$  for the species was invariant in this example.

#### b. Interspecific Resource Competition

Again, using equation (D-9), two separate populations were 'tuned' to show the growth response depicted by the curves in Figure D-2 when grown separately. When the two simulated population types were initiated in a mixed culture, competing for the same renewable resource (accomplished by simultaneous iterative integration), one of the groups soon failed. (See Figure D-4.)

These simulations appear to correspond closely to Gause's (1934) competition experiments with *Paramecium*, *P. Caudata*, and *P. Aurelia*. (See inset in Figure D-4.)

Because equation (D-1) is based on characteristics which are common to all biosystems (e.g., energy flows) it is easily adapted to a large variety of situations. As a population equation, it may not have any general advantage over any one of the equations currently in use; however, because of its thermodynamic correlates, it may offer advantages where the analyst is particularly concerned with energy budgets.



**Figure D-4** The computed growth curves for the species Types I and II (as modelled in Figure D-3), when simulated growth was initiated in mixed culture. The calculation was a simultaneous iterative integration of the two species models in competition for single limiting resource. The inset shows the experimental results as determined by Gause (1934).



LIST OF EQUATIONS

$$\dot{Q}_1 = \dot{Q}_2 + \dot{Q}_T + \dot{Q}_H + \dot{Z} \quad (2-1)$$

$$M = \frac{\dot{W}_o}{(\dot{Q}_1 - \dot{Q}_2 - \dot{Q}_T)} \quad (2-2)$$

$$A = \frac{\dot{Z}}{\dot{W}_o} \quad (2-3)$$

$$\dot{Z} = \dot{W}_o A = AM(\dot{Q}_1 - \dot{Q}_2 - \dot{Q}_T) \quad (2-4a)$$

$$\frac{\dot{Z}}{AM} = (\dot{Q}_1 - \dot{Q}_2 - \dot{Q}_T) = \dot{Z} + \dot{Q}_H \quad (2-4b)$$

$$E_g = \frac{\dot{Z}}{\dot{Q}_1} = \frac{W_n}{C} \quad (2-6)$$

$$E_g = \frac{AM(\dot{Q}_1 - \dot{Q}_2 - \dot{Q}_T)}{\dot{Q}_1} \quad (2-7)$$

$$R_o = \frac{\dot{Q}_1 - \dot{Q}_2}{\dot{Q}_1} \quad (2-8)$$

$$E_g = AMR_o = AM(\dot{Q}_T/\dot{Q}_1) \quad (2-9)$$

$$U_o = AMR_o = \frac{\dot{Z} + AM\dot{Q}_T}{\dot{Q}_1} \quad (2-10)$$

$$E_g = U_o - AM(\dot{Q}_T/\dot{Q}_1) \quad (2-11)$$

$$\dot{Q}_T = \frac{\dot{Q}_I}{AM} (U_o - E_g) \quad (2-12)$$

$$X_o = T_o - T_l \quad (A-1)$$

$$W_o = \mu_o (J_o X_o) \quad (A-2)$$

$$\phi_o = J_o X_o - W_o \quad (A-3)$$

$$W_i = J_o X_o \quad (A-4)$$

$$\phi_o = J_o (T_o - T_x) \quad (A-5)$$

$$W_o = J_o (T_x - T_l) \quad (A-6)$$

$$\mu_o = W_o / W_i \quad (A-7)$$

$$\mu_o = \frac{J_o (T_x - T_l)}{J_o X_o} \quad (A-8)$$

$$(T_x - T_l) = X_o \mu_o \quad (A-9)$$

$$(T_o - T_x) = X_o (1 - \mu_o) \quad (A-10)$$

$$\psi = X_o (1 - \mu_o) \quad (A-11)$$

$$\delta E = C - \psi_o - W_n \quad (A-12)$$

$$\delta E = -C(1 - \mu_o) + C - W_n = -C\mu_o - W_n \quad (A-13)$$

$$\delta E = CU_o - W_n \quad (A-14)$$

$$\delta E = CU_o - C(W_n/C) = C(U_o - E_g) \quad (A-15)$$

$$\delta E = C(U_a - U_b) \quad (\text{A-16})$$

$$\delta \Psi = \psi_a - \psi_b = X_o (\mu_b - \mu_a) \quad (\text{B-1})$$

$$\psi_o = H - T_o S \quad (\text{B-2})$$

$$G = X_o (1 - \mu_o) \quad (\text{B-3})$$

$$W_i = G_A^o + T_o S_A \quad (\text{B-4})$$

$$W_o = -T_o S_B \quad (\text{B-5})$$

$$\Delta G = X_o (1 - \mu_o) = W_i \frac{(1 - W_o)}{W_i} = W_i - W_o \quad (\text{B-6})$$

$$\Delta G = W_i - W_o = G_A^o + T_o (S_A + S_B) \quad (\text{B-7})$$

$$G_A^o + T_o S_A = -T_o S_B \quad (\text{B-8})$$

$$\mu_o = \frac{W_o}{W_i} = \frac{-T_o S_B}{G_A^o + T_o S_A} \quad (\text{B-9})$$

$$W_i = G_A^o + T_o (S_A + S_X) \quad (\text{B-10})$$

$$W_o = -G_X^o - T_o (S_B + S_Y) \quad (\text{B-11})$$

$$\mu = \frac{-G_X^o - T_o (S_B + S_Y)}{G_A^o + T_o (S_A + S_X)} \quad (\text{B-12})$$

$$\frac{1}{N} \frac{dN}{dt} \dot{Q}_T = \dot{Q}_1 - \dot{Q}_2 - \frac{\dot{z}}{AM} \quad (\text{D-1})$$

$$\dot{Q}_1 = \dot{FC} \quad (\text{D-2})$$

$$\dot{F} = \frac{\dot{T}_b C_e}{C_e + K_m} \quad (D-3)$$

$$\dot{Q}_1 = C \frac{T_b C_e}{K_m + C_e} \quad (D-4)$$

$$\dot{Q}_2 = \dot{Q}_1 (1 - \rho) + \dots \quad (D-5)$$

$$\dot{Q}_2 = \dot{Q}_1 (1 - \rho) + \dot{s} \quad (D-6)$$

$$\Delta G = -RT \ln \left[ \frac{C_e}{C_o} \right] \quad (D-7)$$

$$\dot{z} = \dot{F} (-RT \ln [C_e] + k) \quad (D-8)$$

$$\dot{Q}_T = \frac{\dot{T}_b C_e}{C_e + K_m} \left[ C_p \frac{-(k - RT \ln [C_e])}{AM} \right] - \dot{s} \quad (D-9)$$

$$\frac{\dot{z}}{A_o M} = \frac{\dot{F}_i}{M} \sum \frac{w_n^i}{A} \quad (D-10)$$

$$\frac{\dot{z}}{A_o M} = \frac{\dot{F}}{M} \sum \frac{(-RT \ln [N] + k)}{A} + \dots \quad (D-11)$$

$$\frac{\dot{z}}{A_o M} = \frac{\dot{F}}{M} \sum \frac{(-RT \ln [N] + k)}{A_x} + \dots \quad (D-12)$$

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