Thermodynamics and Measures of Ecological Integrity

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1. INTRODUCTION

Over the past decade we have studied the organization of ecosystems using complex systems theory, and in particular non-equilibrium thermodynamics. This study has lead to a set of hypotheses concerning the organizational development of ecosystems, a thermodynamic framework for discussing ecosystem integrity, and a set of measures which reflect ecosystem organization and which aid in the assessment of the impact of environmental change. We present these herein.

Our basic premise is that the organization of an ecosystem represents a tradeoff between the imperatives of survival and the second law of thermodynamics which necessitates the degradation of energy. Ecosystem organization tends to increase degradation of energy. Measures of ecosystem organization should therefore reflect energy usage and degradation in ecosystems. Measures of energy utilization in the ecosystem food web and by the ecosystem are presented.

Integrity of an ecosystem refers to its ability to maintain its organization. Measures of integrity should reflect the organizational state of an ecosystem. Ecosystem organization has two distinct aspects, functional and structural. Functional refers to the overall activities of the ecosystem. Structure refers to the interconnection between the components of the system. Measures of function would indicate the amount of energy being captured by the system and the way in which it is being degraded (for example respiration vs evapotranspiration). Measures of structure would indicate the way in which energy is moving through the system. For example measures of the amount of recycling in the ecosystem, the effective trophic levels of species, and the average specialization of the resource niche all reveal something about how energy is being used in the ecosystem. Examples of the application of these measures to the development of ecosystems and to examine stress effects are presented. How these measures can be used to assess ecosystem integrity is discussed.

2. THE THERMODYNAMIC DEVELOPMENT OF COMPLEX SYSTEMS

The development of self-organizing systems is in accordance with the laws of thermodynamics. The importance of the second law in this regard was first observed by Prigogine and his fellow researchers. (Nicolis and Prigogine, 1977,1989, Prigogine et al., 1972) However to truly appreciate the role of thermodynamics in explaining the behaviour of complex systems it is necessary to understand current thinking in thermodynamics.

What is commonly understood to be thermodynamics was developed in the nineteenth century by Carnot, Clausius, Boltzmann and Gibbs (Kestin, 1976) as a science describing the balance and flow of energy in nature. The common statements of the first and second law are that energy is conserved and entropy increases respectively. Unfortunately entropy is strictly defined only for equilibrium situations. Thus these statements are not sufficient for discussing non-equilibrium situations, the realm of all self-organizing systems including life.

In the mid 1960's Hatsopoulos & Keenan (1965) and Kestin (1966) brilliantly synthesized thermodynamics with a statement that subsumes the 0th, 1st and 2nd Laws: *"When an isolated system performs a process after the removal of a series of internal constraints, it will reach a unique state of equilibrium: this state of equilibrium is independent of the order in which the constraints are removed"*. (This is called the Law of Stable Equilibrium by Hatsopoulos & Keenan and the Unified Principle of Thermodynamics by Kestin.) The importance of the statement is that, unlike all the earlier statements which show that all real processes are irreversible, it dictates a direction <u>and an end state</u> for all real processes. As well it does not depend on the entropy concept and hence is applicable to equilibrium and non-equilibrium situations alike.

We have proposed an extension to this principle. In simple terms it is that systems will resist being removed from their equilibrium state. It should be noted that what drives systems away from equilibrium are externally applied gradients (e.g. the temperature and pressure differences in classical thermodynamic systems). More formally then: *The thermodynamic principle which governs the behaviour of systems as they are moved away from equilibrium is that they will take advantage of all means available to them to resist the applied gradients. Furthermore as the applied gradients increase so will the system's resistance to being moved away from equilibrium.*[1] Thermodynamic systems exhibiting temperature, pressure, and chemical equilibrium resist movement away from their equilibrium states. When moved away from a local equilibrium state a system will behave in a way which opposes the applied gradients and moves it back to its local equilibrium attractor. The stronger the applied gradient, the greater the effect of the equilibrium attractor on the system.

Bénard Cells, tornadoes, autocatalytic chemical reactions and ecosystems are examples of non-equilibrium self-organizing systems whose development is in accordance with this principle. As the applied gradients increase, new structures emerge in these systems. In Bénard cells, when the temperature gradient increases to a critical threshold, hexagonal cell structures emerge. These structures, operating by convection, increase the dissipation of the temperature gradient beyond that possible through conduction. Vortices emerge in fluids as pressure differences increase. More species become part of ecosystems as the available energy increases, thus dissipating the energy gradient. All of these structures have one thing in common, they increase the system's ability to dissipate the applied gradient (hence the term dissipative structures).

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[1] It is this extension to the unified principle which is the relevant statement of the second law for discussing living systems. Throughout this paper when we refer to the second law we mean this.

To summarize thermodynamics tells us that a system subject to inputs of mass and energy which drive it away from equilibrium will resist the change. This resistance can consist of deflecting the inputs, dumping the inputs by increasing throughput, or degrading the quality of the inputs through irreversible processes within the system.

3. A THERMODYNAMIC PARADIGM FOR EVOLUTION AND DEVELOPMENT [1]

Living systems in this biosphere have evolved in accordance with the second law so as to decrease the overall effect of incoming energy by increasing throughput and degrading the exergy content[2] of the mass and energy flow through the system. This is the overall thermodynamic direction of evolution, to dissipate and degrade the energy flowing into the system. This exergy reduction is accomplished via the development of highly organized structures. The cornerstone of the paradigm is to view living systems as the solution to the thermodynamic problem of maximizing the degradation of the incoming solar energy in a changing and sometimes unpredictable environment.

Using a scenario based on Prigogine et al and Wicken's work (Wicken, 1978, 1979, 1980, 1987) it is argued that the solution to this problem is the development of systems (chemical factories) which are joined together in a supersystem. The supersystem degrades the incoming energy by producing and then breaking down molecular structures. The chemical factories have four common behaviors: a self-construction and death cycle, reproduction, evolution and adaptation.

To be more specific, consider a chemical soup bombarded with solar energy.[3] Wicken's work suggests that the second law[4] dictates the emergence of chemical factories in this soup. The factories would degrade the energy impinging on the soup. Degradation would be accomplished largely by utilizing the available molecules and energy to form new more complex molecules. The formation of new molecules could degrade the impinging available potential energy by transforming it into bond, translational, and vibrational energy, and into heat. Many different types of processes and molecular forms should emerge, as the larger their number the more thoroughly degraded the incoming solar energy.

As time goes on, these systems (the chemical factories) should become stable. That is they would evolve mechanisms to stabilize their internal chemical

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[1] For a more detailed discussion of the material in this section see Kay, 1984, Kay, 1989, Schneider, 1988, Schneider and Kay, 1992

[2] Exergy: A measure of available work content of energy.(Brzustowski and Golem, 1978, Ahern 1980, Moran, 1982) It is a measure of the potential of the energy to drive the system away from equilibrium. It reflects the quality of the energy. Irreversible processes destroy exergy The phrase "energy degradation" is used herein to indicate the destruction of the exergy content of the energy.

[3] Or any other form of high quality potential energy, for example the chemosynthetic energy source found in the submarine hot springs. (Corliss, 1988)

[4] The exergy of the solar energy which is absorbed by the chemical soup will drive the soup away from equilibrium. The appropriate system response, according to the second law, is to destroy the absorbed exergy as thoroughly as possible.

processes and to maintain the functioning of the system in the face of environmental changes. The degradation of the incoming solar energy, as required by the second law, would then be assured. This expectation would be justified by the second law alone, but is reinforced by Prigogine's findings regarding the emergence of stable dissipative structures.

The above argument suggests the emergence of primary producers who would use the incoming solar energy to produce complex molecules and stored energy. These primary producers would be expected to degrade, as much as possible, of the incoming energy into lower quality forms. They would produce only as much stored potential energy (via for example photosynthesis) as is required to fuel the processes necessary for the internal stability of the system. The stored potential energy of the primary producers could be further degraded if used by other chemical factories to fuel more production of complex molecules. Chains of such systems, each system feeding on the stored potential energy of another system, would emerge in accordance with Prigogine's order through fluctuations scenario. The characteristics of these chains is that they would degrade as much of the incoming energy as possible per unit production of complex molecules. Such chains will be referred to as ENERGY DEGRADING CHAINS.

If only energy degrading chains existed, they would quickly run out of material to be used as inputs. Thus if they are to continue functioning, the emergence of consumers who would use the complex molecules and stored energy of the energy degrading chains as inputs to processes which simplify the complex molecules, is necessary. The existence of such MATTER SIMPLIFYING chemical factories would guarantee the supply of simple molecules to be used by the primary producers. These consumers would be expected to simplify the molecules as much as possible per unit of energy flow. These matter simplifiers would allow for the reuse of materials by the energy degrading chains.

The restriction placed on the systems to be either energy degrading or matter simplifying is artificial. There is no reason why one system (chemical factory) cannot degrade the potential energy by forming complex molecules from the available molecules, and at the same time break down some of the available molecules into their components. The two cases described, maximizing energy degradation per unit of complex molecules produced, and maximizing molecular simplification per unit of energy consumed, are extremes. Any system could fit somewhere between the two and would be made up of different processes each of which would correspond to one of the two cases. For this reason it is impossible to constrain the individual systems to be either efficient users of energy or material.

There is no reason to expect the emergence of only a few simple chains, made up of either energy degraders or matter simplifiers. Rather the systems would be expected to be interconnected in a complex web. Each individual system would operate somewhere between the two efficiency extremes. This web would offer many different paths of energy and material flow. A set of interconnected chemical factories will be called a SUPERSYSTEM. Because of the constraints imposed by the principles of matter conservation and the second law of thermodynamics, the supersystem would be expected to emerge in a way which makes it an efficient if not self-contained user of material resources,[1] and a very good degrader of incoming solar energy.

The scenario put forward by Prigogine for the development of such stable dissipative structures requires that each system evolve from a maximum to a minimum specific dissipation state if no catastrophes occur. However the second law dictates that the total degradation of incoming solar energy by the supersystem increase. These two constraints are potentially conflicting. The supersystem and component systems must develop strategies to satisfy both these demands concurrently. Several strategies are possible .

One strategy is for the supersystem to evolve, in a way which compensates for the individual systems evolving according to the maximum to minimum specific dissipation rule. This compensation would be accomplished by continually increasing the number and types of systems which make up the supersystem. In this way the individual systems would become more internally stable (according to Prigogine's criteria), while the supersystem, as a whole, would become a better energy degrader. The increase in the number of types of systems would force the systems to become more efficient at utilizing the available material resources. (Since the material resources are in finite supply.) Systems would only be added if they increased the supersystems degradation ability without decreasing its overall stability.

Another possible strategy is to have as many individual systems as possible in the early stages of development. Since the development process would follow a maximum to minimum specific dissipation rule, the larger the number of systems at earlier stages in their development, the larger the total combined dissipation of these systems.

This strategy would be constrained by the availability of material resources to support the early stages of development. This constraint would be alleviated if at some point the mature systems (those which have reached a steady, minimum specific dissipation state) were to cease to functioning (i.e. die), thus making their material content available to new systems.

Such deaths could be highly disruptive to the supersystem. This disruption could be prevented if new systems were to replace the old systems, that is assume the old system's functional role and structural position in the supersystem. This would only work if the old systems survived long enough to allow the new systems to develop sufficiently to replace them. This strategy could satisfy the maximum energy degradation and stability criteria if it involved a GROWTH-DEATH CYCLE of sufficient length and a replacement (i.e. REPRODUCTIVE) mechanism. Because the predictability of the microenvironment of other components must be preserved, the reproductive

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[1] Energy degradation processes depend on a supply of raw materials.

process must produce offspring similar, from the perspective of the supersystems, to the original components. This means that there must be some sort of pre-programming of the development process of the components.

The supersystem proposed above on the basis of purely thermodynamic and system theoretic arguments are manifested as ecosystems in our biosphere. The individual chemical factories are the individual living organisms.The classes of components which make up ecosystems consist of organisms which share the same pre-programming and are the highest level in the system's hierarchy which spontaneously die. Such a class of organisms is a species. The chains of energy degraders would be the grazing chain and matter simplifiers, the detrital cycle.

SOME HYPOTHESES

The FUNDAMENTAL HYPOTHESIS about ecosystems is that they will organize themselves to maximize the degradation of the available work (exergy) in incoming energy. A corollary is that material flow cycles will tend to be closed. This is necessary to insure a continued supply of material for the energy degrading processes.

A SECOND HYPOTHESIS, which is a consequence of the first, is that ecosystems will evolve and adapt to maximize the potential for the ecosystem and its component systems to survive. Such behaviour will assure the continued degradation of incoming energy. This maximization process is subject to the constraint that any evolutionary or adaptive strategy or mechanism which enhances survival, is only justified if its net effect is to increase the energy degradation ability of the ecosystem. That is the thermodynamic cost of the strategy or mechanism must be offset by the gain in energy degrading ability of the ecosystem. Also, each component system will not be able to globally maximize its own survival because it would be done at the expense of other systems. Thus the maximization process is constrained and represents a thermodynamic and systems optimization.

Two hypotheses about species are presented. The first is that an individual of a species will survive long enough to insure the survival of replacement offspring. The second is that the species as a whole will maximize its contribution to the degradation of energy by producing as many offspring as possible, who will survive to reproduce. Each species represents a unique solution to the problem of surviving and reproducing in it's particular microenvironment. These two hypotheses define the goals of individuals and species.

This discussion demonstrates that thermodynamics, particularly in its modern form does inform us about the development of ecosystems. In fact, as is shown later, these hypotheses can be further developed into a set of characteristic changes in ecosystems which occur as succession proceeds. In what follows the implications of this paradigm for discussing and measuring ecosystem development and integrity will be explored.

4. ECOSYSTEM INTEGRITY AND THE EFFECTS OF ENVIRONMENTAL CHANGE

For each set of environmental conditions[1] there will exist at least one system optimum operating point, a point where the functioning of the system represents an optimum tradeoff between the goals driving the system. Self-organization is the process by which the system modifies its internal structure and function so as to move its operating point to the optimum operating point and maintain it there. Any analysis of self-organization must begin by identifying the system and its environment, the components of the system and their microenvironment, and the supersystem. Once these have been established then the goals of the system, and the environmental factors which have an influence on the system's ability to reach these goals, must be determined.

In the context of ecosystems, self-organization is the response of living systems to thermodynamic and environmental pressures. The gradient which drives ecosystem development is the solar energy impinging on the ecosystem. As ecosystems are driven away from equilibrium they become more organized and effective at dissipating solar energy. At the same time as this self-organizing process is occurring in ecosystems, external environmental fluctuations are tending to disorganize the system. The optimum operating point for ecosystems is the point in state space where the disorganizing forces of external environmental change and the organizing thermodynamic forces are balanced. (See Figure 1) The climax community in ecological succession would be an example of an optimum operating point for an ecosystem. The climax community represents a balance between the organizing forces and the disorganizing forces in ecosystems.

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[1] **Environment** is used throughout the paper in its system theoretic sense, that is those things which are not part of the system but which have an effect on it. Thus environment refers to the biotic and abiotic components external to an ecosystem which impact upon it. Humans may be considered as part of the environment of an ecosystem or as part of the ecosystem itself, depending on the context.

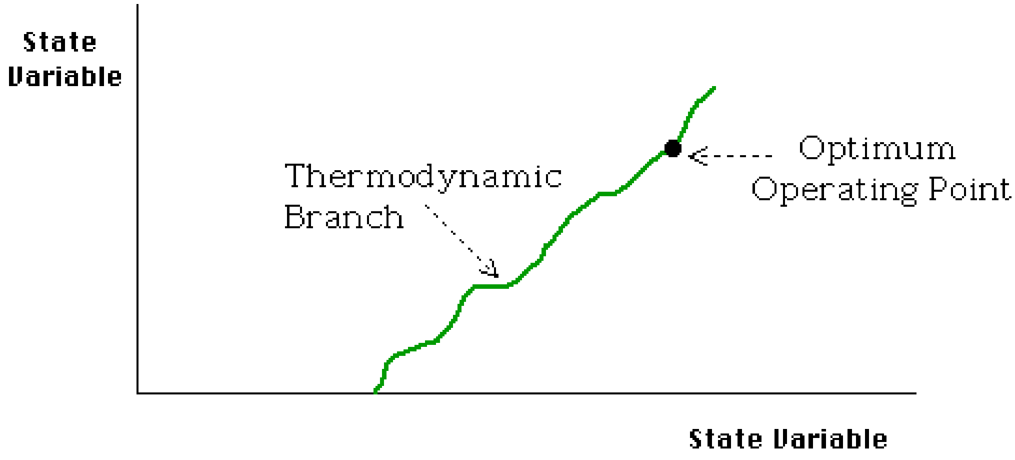

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FIGURE 1: An ecosystem develops along a Thermodynamic Branch (a path in state space) until it reaches an Optimum Operating Point. Examples of state variables could be Net Productivity and Biomass. An environmental variable (axis out of page and not shown) might be annual solar insolation.

In the context of these ideas, our sense of the system as a whole, that is its **Integrity**, has to do with its ability to maintain its organization and to continue its process of self-organization. If a system is able to maintain its organization in the face of changing environmental conditions then it is said to have integrity. If a system is unable to maintain its organization then it has lost its integrity. In essence integrity has to do with the ability of the system to attain and maintain its optimum operating point. Thus measures of integrity should reflect the organizational status of the ecosystem.

Let us assume that the ecosystem has developed along a thermodynamic branch in the way described above and that it has reached its optimum operating point. Suppose some change occurs in its environment. (The change may be short term with the environment returning to its previous condition, or the change may persist.) What effect will this have on the ecosystem's organization and hence its integrity? A series of questions must be asked (See figure 2,3,4 and Table 1 as well):

Will the system be moved away from its optimum operating point?

- If the response is no, then organization and integrity are not immediately affected.
- If the response is yes, then the question becomes:

  Does the system return to its original optimum operating point?

  - If the answer is yes, then there are three issues:
    1) How far is the system moved from its optimum operating point before returning?
    2) How long will it take to return to its optimum operating point?
    3) What is the stability of the system upon its return?

  In any case the system is able to re-organize itself to cope with the environmental change and its integrity for the moment is preserved.

  - If the answer is no, the system does not return to its original optimum operating point, then there are two possibilities; a new optimum operating point exists or it does not. In the latter case the organization breaks down and the system loses its integrity. (Case 0) In the former case there are three possibilities:
    - Case 1: The new optimum operating point is on the original thermodynamic branch.
    - Case 2: The new optimum operating point is on a bifurcation from the original branch.
    - Case 3: The new optimum operating point is on a different thermodynamic branch and the system undergoes a catastrophic re-organization to reach it

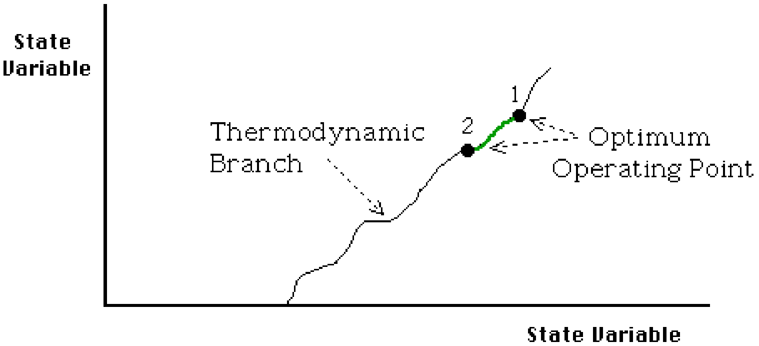

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FIGURE 2: The environmental change causes the ecosystem to move from its original optimum operating point (1) to a new optimum operating point (2). An example of this would be a stress which causes an ecosystem to return to an earlier successional stage.

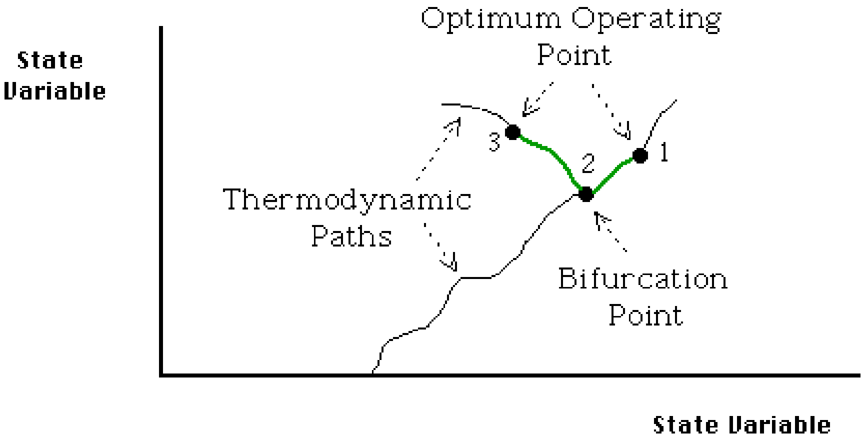

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FIGURE 3: In response to changing environmental conditions the system moves away from the original optimum operating point (1) through a bifurcation point (2) and onto a new path and then to a new optimum operating point (3). An example of this is a stress, such as the hot water effluent from power plants (see section 6.2), which would result in a change in species composition.

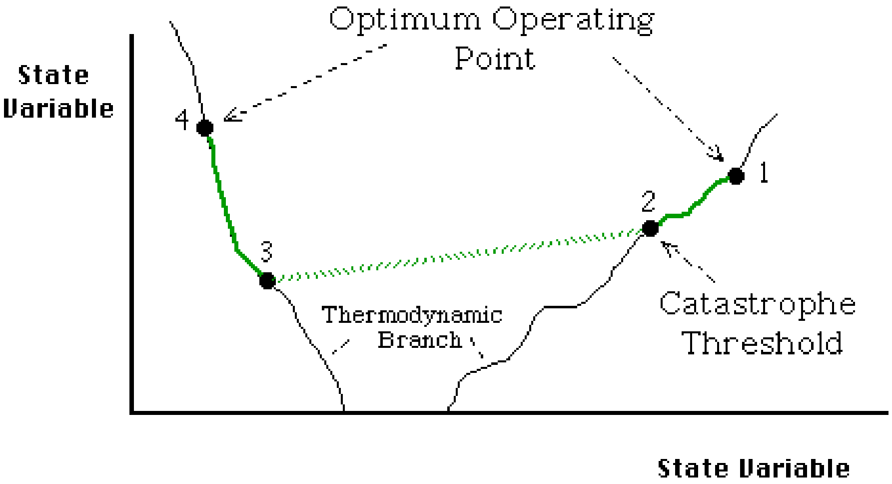

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FIGURE 4: The environmental change drives the ecosystem from its original optimum operating point (1) through a catastrophe threshold (2) to a new thermodynamic branch at (3) and eventually to a new optimum operating point (4). An example is the elimination of fish in lakes caused by acid rain.

TABLE 1: The possible responses of an ecosystem to environmental change. (from Kay, 1991)

a) The ecosystem does not move from its original optimum operating point.

b) The ecosystem moves from its original optimum operating point but returns to it.

> <u>Issues concerning integrity to be considered for this case:</u>
> 1) How far is the system moved from its optimum operating point before returning?
> 2) How long will it take to return to its optimum operating point?
> 3) What is the stability of the system upon its return?

c) The ecosystem moves permanently from its original optimum operating point.

> Case 0: The ecosystem collapses.
> Case 1: The ecosystem remains on the original thermodynamic branch. (See Figure 2)
> Case 2: System bifurcation to a new thermodynamic path.(See Figure 3)
> Case 3: The system moves to a new thermodynamic branch. (See Figure 4)
>
> > <u>Issues concerning integrity to be considered for each of these four cases:</u>
> > 1) How far is the new optimum operating point from the old?
> > 2) How long does it take to reach the new optimum operating point?
> > 3) What is the stability of the system about the new optimum operating point?
> > 4) If the environmental conditions return to their original state, will the system return to the original optimum operating point?

This set of questions, developed from our understanding of the behaviour of complex systems, provides a framework for investigating environmentally induced changes in ecosystem organization. The set of possible ecosystem responses to stress, is far richer than the simple notion of stress temporarily displacing an ecosystem from its climax, to which it will hopefully return. It also frees us from the notion that an ecosystem has a single preferred state which it should be managed for. Ecosystem behaviour is much richer than that of a single dynamical system where the only issue of interest is its stability. It has been shown elsewhere (Kay, 1991) that this framework subsume the notions of stability, resiliency, elasticity, etc.

There are four points of note. First, dissipative systems can respond to environmental change in qualitatively different ways. One response is for the system to continue to operate as before, even though its operations may be initially and temporally unsettled. A second response is for the system to operate at a different level using the same dissipative structures it originally had (for example, a reduction or increase in species numbers). A third response is for some new structures to emerge in the system to replace or augment existing structures (for example, new species or paths in the food web). A fourth response is for a new dissipative system, made up of quite different structures, to emerge. We must be aware of each of these possible responses if we are to anticipate the impact of environmental change on the integrity of an ecosystem.

The second point of note is that if the concept of integrity is to be useful, it must have an anthropocentric component that indicates which changes in the ecosystem are considered acceptable by the human actors. The framework indicates ways in which an ecosystem might re-organize in the face of environmental change, but not which re-organizations constitute a loss of integrity. It could be argued (and often is) that any environmental change which permanently changes the optimum operating point affects the integrity of the ecosystem. In this case there would be four distinct types of loss of integrity. (Cases 0 through 3 above.) It could also be argued that any time that the system can maintain itself at an optimum operating point, it has integrity. In this case, loss of integrity would occur only if the system is unable to maintain itself at an optimum operating point.

In between these two extreme positions there is the possibility of defining some optimum operating points as being undesirable changes in the system, and therefore representing a loss of integrity. This would inject an anthropocentric component into the definition of integrity. Without this anthropocentric component, we are restricted to defining integrity as the ability of an ecosystem to absorb environmental change without any ecosystem change. This would rule out the acceptability of the other three ecosystem responses to environmental change discussed above. This does not seem reasonable to the authors. Ultimately an evaluation of the ecological acceptability of an action will depend on a value judgement concerning which changes in the effected ecosystem are acceptable to the human participants.

A third point follows from the second. From an anthropocentric perspective, a new optimum operating point on a new thermodynamic branch may be preferred over the old optimum operating point on the system's previous branch (e.g a corn field vs an old growth forest). This may be the case even if it implies the catastrophic collapse of the previous ecosystem. The implication is that under some circumstances we might be willing to accept, even require, some degradation in existing ecosystems in order to allow a new one to flourish. The difficulty is that by their very nature bifurcations and flips can be unpredictable. When an ecosystem has been seriously degraded by an environmental change, returning it to its original state may not be the sensible management goal. Rather aiming the system towards a new optimum operating point on a different branch may be the optimum course of action. For example this is the management strategy for Lake Erie's fisheries, to introduce entirely new species and inter species relationships and thus establish a "new" ecosystem.

The fourth point is that an environmental change has implications for the ability of an ecosystem to respond to future environmental changes, even though the current change may have no immediate impact on the ecosystem. An example is the Fenitrothion spray of forests to control spruce budworm. This has no immediate impact, but interferes with the ability of the forest to regenerate itself in the face of other environmental changes. Similarly, forest fire suppression now appears to interfere with the ability of the forest to cope with fires at later times. Put another way, the response of an ecosystem to environmental change is a function of both the immediate environmental change and changes the ecosystem has been subjected to in the past. Historical environmental change can have both positive and negative implications for the ability of the system to cope with current changes.

This discussion of integrity using the notions of state spaces and operating points begs two questions: What are the state variable, that is what should we measure? What characteristic changes in the state variables are associated with ecosystem development? We address these issues forthwith.

5. A THERMODYNAMIC ANALYSIS OF ECOSYSTEM ATTRIBUTES

Ecosystems display the influence of thermodynamic principles in their patterns of growth and development. A thermodynamically based theory of ecology holds the promise of raising ecology from a descriptive to a theoretical science. Ecosystems are the result of the biotic, physical, and chemical components of nature acting together as nonequilibrium dissipative structures which develop in a way that increases their energy degradation potential as necessitated by the imperative of the second law. This hypothesis can be tested by observing the energetics of ecosystem development during the successional process or by determining their behavior as they are stressed or their boundary conditions are changed.

As ecosystems develop or mature they increase their total dissipation, they develop flow networks with higher mutual information (i.e.. they have a more highly articulated energy flow network) and develop more complex structures with greater diversity and more hierarchical levels. Species which survive in ecosystems are those that funnel energy into their own production and reproduction and contribute to autocatalytic processes which increase the total dissipation of the ecosystem. In short ecosystems develop in a way which systematically increases their ability to degrade the incoming solar energy, that is to dissolve the potential for the energy to produce gradients and cause dis-equilibrium.

In this sense the development of ecosystems through succession is the result of the system organizing itself to dissipate more incoming energy with each stage of succession while maintaining its ability to survive. Thus one would expect successional processes to result in ecosystems with the following functional and structural attributes:

ECOSYSTEM FUNCTION:

1. Better degradation of the available energy resources.

$$\text{Total exergy destroyed} = \frac{\text{exergy destruction}}{\text{unit of energy captured}} \times \text{total energy captured.}$$

Thus there are two aspects which would change with succession:

   a) The first is a proportional increase in low quality energy outputs relative to higher quality outputs. For example, tropical rain forests output relatively more of their energy as evapotranspiration (as versus infrared radiation and heat flux) than other types of terrestrial ecosystems. (Sato et al. 1989) In aquatic ecosystems the respiration rate would increase.
   b) The second is an increase in the total energy flow through the system.

2. Ecosystems will develop networks for breaking down and recycling nutrients. The detrital activities of the ecosystem will increase. It will become less leaky. The reason for this is that the exergy destroying process, as discussed earlier, are matter organizing and hence need a continuous supply of matter in a simple molecular form.

ECOSYSTEM STRUCTURE:

The thermodynamic principle underlying the following is that every additional step in the foodweb which can be supported by the ecosystem will result in more exergy destruction. In terms of the classical second law, every time you add a mass-energy transformation you produce more entropy.

1. More and longer cycles in the food web. Cycles are necessary to close material flows in the ecosystem. More and longer cycling will allow more opportunity for energy degradation at each step as the energy goes around the cycle.
2. The effective number of trophic levels will increase. Again, this will allow more opportunity for thorough degradation of the energy. Energy that is passed higher up the food chain will be degraded further than energy that is shunted immediately into the detrital subsystem. In order for more trophic levels to exist the efficiency of each tropic level must increase.
3. There will be more and narrower resource niches in the ecosystem. Again, this allows more pathways for energy degradation. This will manifest itself as more specialized species and more species diversity.

In short, the structure of the ecosystem will become more articulated as has been shown by Ulanowicz. (Ulanowicz, 1979,1980,1986)

This discussion of ecosystem attributes shows how the paradigm presented in Section 3 can be used to generate specific hypotheses about ecosystem development. These hypotheses inform us about what to measure in order to monitor changes in ecosystems. In the next section we examine two examples which illustrate what to measure, how these measures change, and what these changes tell us about ecosystem integrity. Finally, it should be noted that this discussion can be extended to similar hypotheses concerning individual species.

6. SOME EXAMPLES

6.1 FLOW ANALYSIS

When E. Odum elaborated the concept of an ecosystem, it was in the context of the mass and energy flowing through the system. H.T. Odum developed this idea further and introduced the familiar energy flow diagrams. (See Figure 5) Hannon and later Patten and Ulanowicz applied the mathematical framework of Leontief's and Augustinovics' economic input/output analysis to such flow networks. A set of measures have been developed which characterize the energy/mass flow network in ecosystems. (See Kay et al. 1989 and Ulanowicz 1986 for details.) These measures describe important functional attributes of ecosystems such as the amount of recycling being carried out, the use of nutrients and energy by the system, the amount of throughput, etc.. As well, structural attributes such as the degree of interconnection between the components, a component's effective trophic level, and the number of trophic levels in the ecosystem can be calculated. These have been successfully applied to a variety of ecosystems in the context of evaluating their development and health. (See Wulff et al, 1989) Examples of such an analysis follow below.

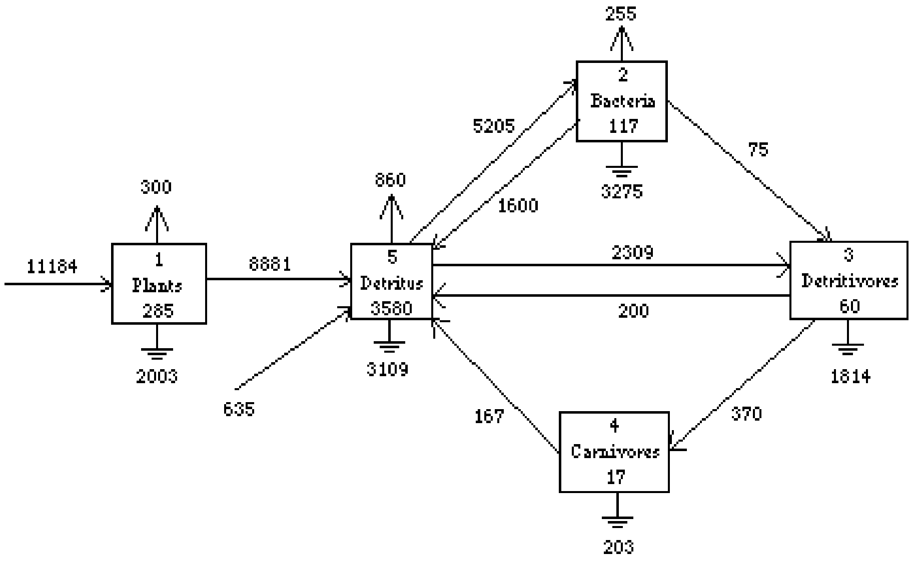

FIGURE 5: The diagram depicts a simple weighted flow network representing the five components of the Cone Spring ecosystem. Flows of energy (kcal/m^2/yr) are indicated by the values that appear on the arcs, while standing stocks (kcal/m^2) are indicated inside the boxes that represent the nodes. There are two inputs that originate outside of the system. The arcs that terminate outside the system represent exports of energy in a form that can be used by other systems. The special ground symbols (^{r}) represent energy that is dissipated through respiration. This energy is lost by the system and is unusable by any system at the same scale (after Kay and others, 1989).

6.2 COMPARISON OF A STRESSED AND CONTROL ECOSYSTEM

If an ecosystem has developed into dynamic quasi-stable state, one would expect it to respond to changes in environmental conditions that perturb these states by retreating to configurations with lower energy degradation potential. We have recently analyzed a data set of carbon-energy flows collected from two tidal marsh ecosystems adjacent to a large power generating facility on the Crystal River in Florida.[1] The ecosystems in question have identical environmental conditions except that one is exposed to hot water effluent from the nuclear power station. The effluent results in an maximum 6° C water temperature increase. The objective of the analysis was to determine the effects of the changes in environmental conditions on these otherwise identical ecosystems.

Table 2 summarizes a set of ecosystem indicators. The Input/Output (I/O) measures indicate various aspects of the flows through the ecosystem. In absolute terms all the flows have dropped in the stressed ecosystem. Overall the drop in flows is about 20%, in particular the imported flows (that is the resources available for consumption) drops by 18% and the TST (the total system throughput, the total flow activity in the system) drops by 21%. The biomass drops by about 35%. These numbers indicate that in terms of biomass, consumption of resources, and ability to degrade and dissipate incoming energy the ecosystem's response to the stress has been to shrink in size.

If the flows are scaled by the import to the ecosystem from the outside, the resulting numbers indicate how well the ecosystem is making use of the resources it does capture. The most substantial change in the total scaled flow rates (See Table 2and Figure 6) is that the stressed ecosystem is exporting more (12%). In other words, it is losing the material it does captures more quickly than the control ecosystem. It is a leaky ecosystem.

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[1] This evaluation is at the ecosystem level only. To completely evaluate the impact it is necessary to examine species level impacts (the next hierarchical level down) and the broader regional impacts (the next hierarchical level up).

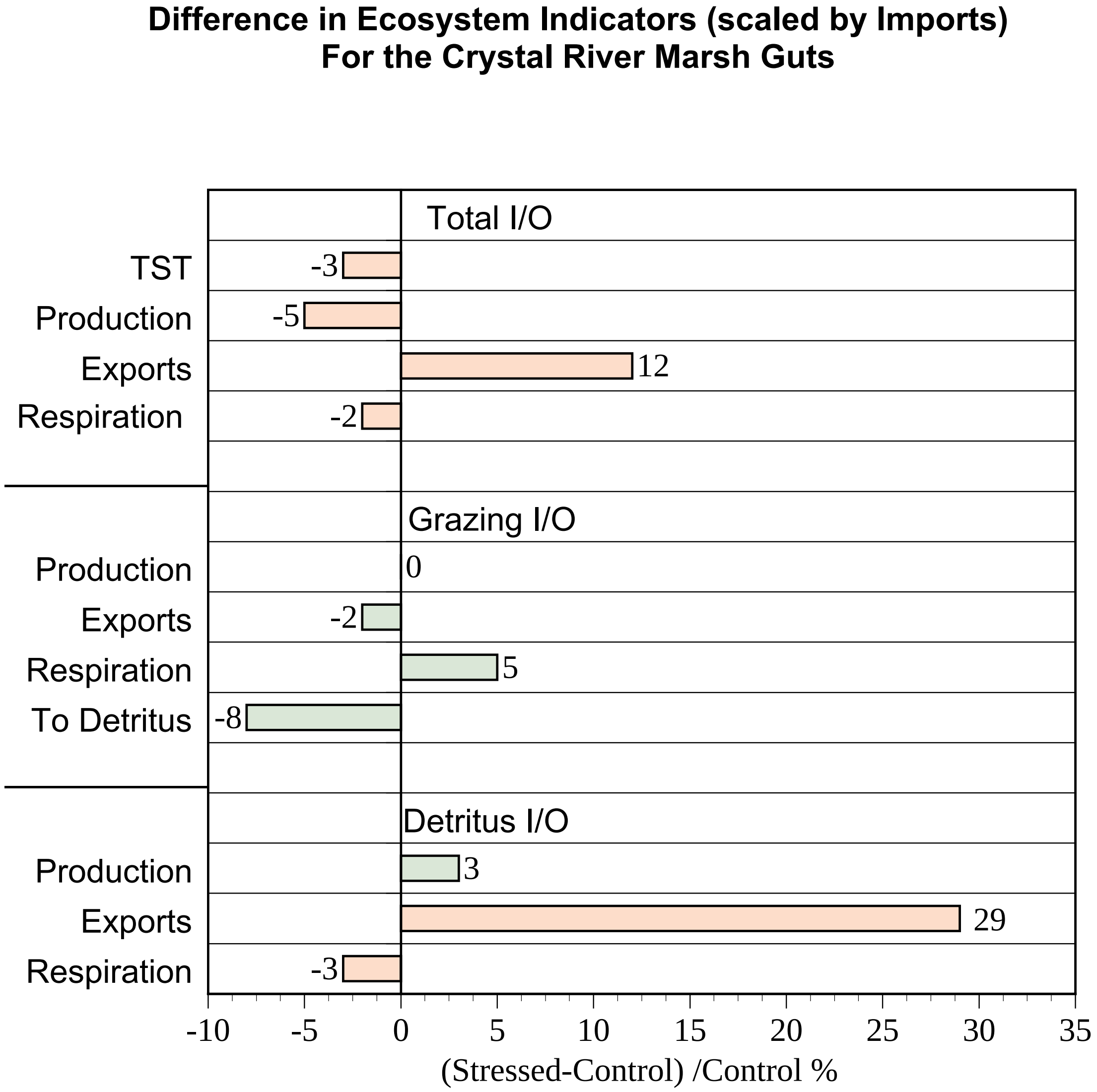

Figure 6: The differences between Ecosystem Integrity measures for a stressed and unstressed ecosystem. The measures are scaled by total imports. See Table 2 for details

TABLE 2: Ecosystem Indicators for the Crystal River Marsh Gut ecosystems. Definitions of all the measures can be found in Kay et al.(1989). The Δ% is the difference between the control value and the stressed value divided by the control value.

Crystal River	**Mg/Sq m/day**			**Scaled by Import**		
	Control	**Stressed**	**%**	**Control**	**Stressed**	**%**
Total I/O						
Imports	7,347	6,018	-18%			
TST	22,768	18,055	-21%	3.10	3.00	-3%
Production	3,292	2,574	-22%	0.448	0.428	-5%
Exports	952	872	-8%	0.130	0.145	12%
Respiration	6,400	5,148	-20%	0.871	0.855	-2%
Grazing I/O						
Production	400	326	-18%	0.054	0.054	-0%
Exports	316	253	-20%	0.043	0.042	-2%
Respiration	3,566	3,078	-14%	0.485	0.511	5%
To Detritus	5,726	4,315	-25%	0.779	0.717	-8%
Detritus I/O				**Scaled by Detritus Inputs**		
from Grazing	5,726	4,315	-25%			
Production	2,893	2,248	-22%	0.505	0.521	3%
Exports	636	619	-3%	0.111	0.144	29%
Respiration	2,834	2,070	-27%	0.495	0.480	-3%
Food Web						
Cycles	142	69	-51%			
Average Cycle Length	4.72	4.39	-7%			
Nexuses	49	36	-27%			
Finn Index	10.20%	9.34%	-8%			
Trophic Levels	5	5	0%			
Average trophic level	2.27	2.20	-3%			
Ascendency	28,499	22,397	-21%			
Other						
Biomass	1,157,136	755,213	-35%	157.498	125.492	-20%
Production/Biomass	0.00284524	0.003408178	20%	3.87E-07	5.66E-07	46%

Looking at the scaled flow rates for just the living components, the largest changes are an increase in respiration (5%) and a decrease in flow to the detritus (8%). There is a small decrease in exports (2%). These changes indicate that the living components are compensating for the stress by making more effective use of the resources they consume. It also indicates the species are stressed.[1] Looking at the detrital components, a different picture emerges. There is a slight increase in production (3%) and a small decrease in respiration (3%) and a very large increase in exports (30%). This analysis of the scaled flow rates indicates that the living components are somewhat stressed but that more importantly, there is a substantial break down in the ability of the ecosystem to recycle material through the detritus and thus retain its resources.

Examining the Food Web data further confirms this. The number of cycles in the stressed ecosystem is 51% of the number in the control. Furthermore overall these cycles are shorter in length. (See Figure 7). Looking at the effective grazing chain (Figure 8), the number of trophic levels has not changed. However the trophic efficiencies of compartments III and IV have changed dramatically, by a factor of 4 in the former case and 2 orders of magnitude in the latter. The flow to the top trophic levels has changed similarly. These are all indicators of a stressed ecosystem.

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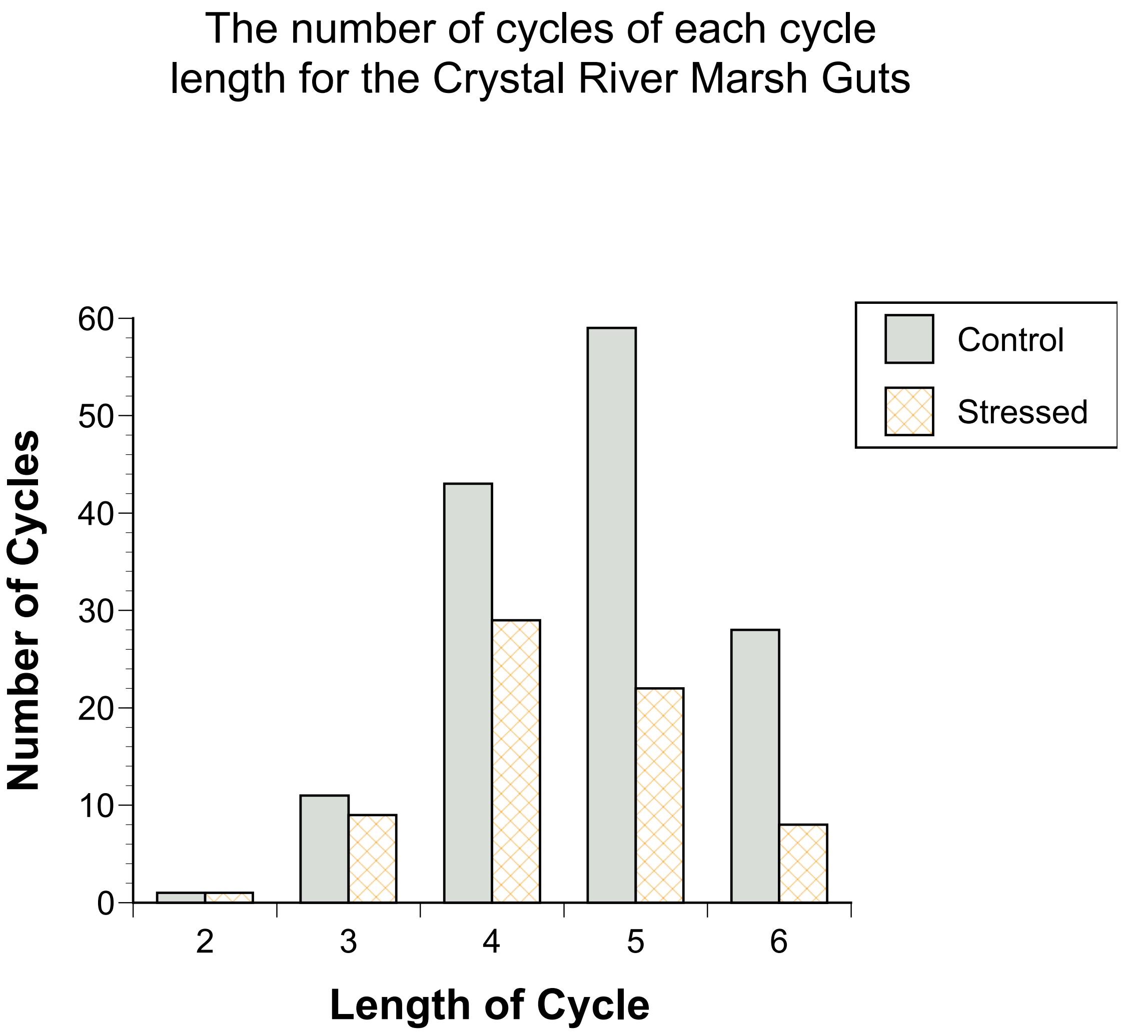
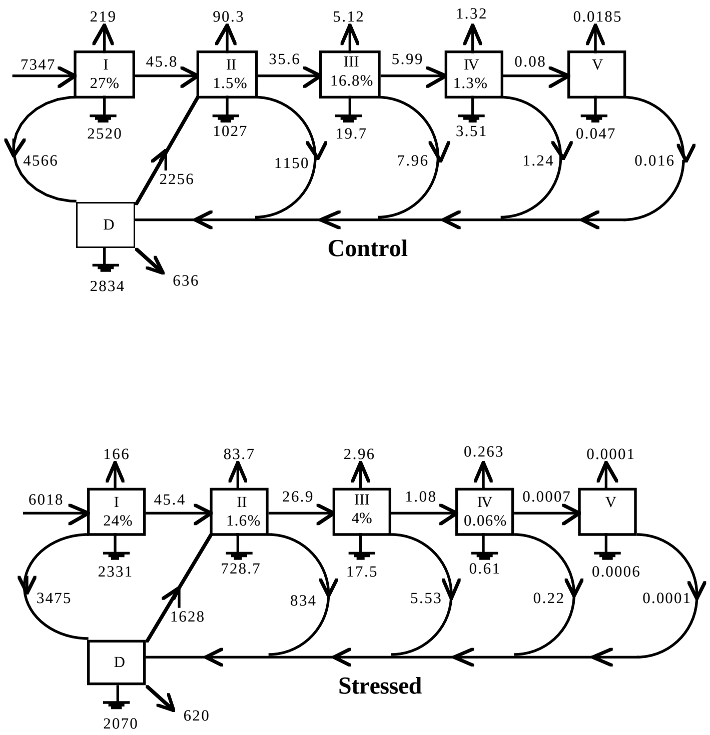
[1] A stressed individual will increase respiration and decrease excrement.

Figure 7: The number of cycles of each cycle length for the Crystal River Ecosystems. The cycles in the stressed system are shorter and fewer in number, an indicator of structural disorganization.





The effective grazing chain and detritial recycling
for marsh guts near Crystal River Florida.
(The percentages in boxes are the overall trophic efficiencies.)

Figure 8: The effective grazing chain and detrital recycling for marsh gut ecosystems near Crystal River Florida. This shows that there is less energy moving up the grazing chain in the stressed ecosystem. The percentage in boxes are the overall trophic efficiencies. The numbers on the arcs are flows in mg/sq. m./day. For more detail see Figure 5.

Overall the impact of the effluent from the power station has been to decrease the size of the ecosystem and its consumption of resources while decreasing its ability to retain and utilize the resources it has captured. In short the impacted ecosystem is smaller, recycles less, and leaks. All of these are signs of disorganization and a step backward in development in a thermodynamic sense. In terms of the framework presented in Section 4 the change in the ecosystem corresponds to Case 2 (Figure 3). The ecosystem initially retrogresses, but 5 species leave the system and 5 new ones are observed. Thus the ecosystem is on a different developmental pathway. Its state of organization represents a different tradeoff (optimum operating point) between the thermodynamic and survival imperatives. However, all of the indicators examined indicate that the ecosystem's organization is negatively impacted.

6.3 COMPARISON OF TWO ESTUARINE ECOSYSTEMS

Wulff and Ulanowicz (1989) undertook a comparison of the Baltic Sea and the Chesapeake Bay using flow analysis techniques. The Baltic has a lower species diversity, its primary production is 1/3 that of Chesapeake, its total system throughput is 20% of Chesapeake's, and it is 33 times bigger (in spatial area) than Chesapeake Bay. These traditional measures normally would indicate that of the two ecosystems, the Baltic is in poorer shape than the Chesapeake. However Wulff and Ulanowicz found "...that the Baltic was trophically more efficient and possesses a more highly structured array of recycling loops than does the Chesapeake. ...these characteristics suggest that the Chesapeake is subject to a more intense set of stresses than the Baltic."

In particular Wulff and Ulanowicz found that overall the effective trophic level of each species was higher in the Baltic. (see figure 9) Species tend to be as highly trophically situated as possible, as this will result in the highest energy density in the food they catch. Lower effective trophic levels are therefore associated with stress. Overall, the Baltic has more trophic levels, 7 versus 6, than the Chesapeake. (See figure 10.) These results indicate that in some respects the Chesapeake is more stressed than the Baltic.

Effective trophic level of each species
in the Baltic Sea and Chesapeake Bay.

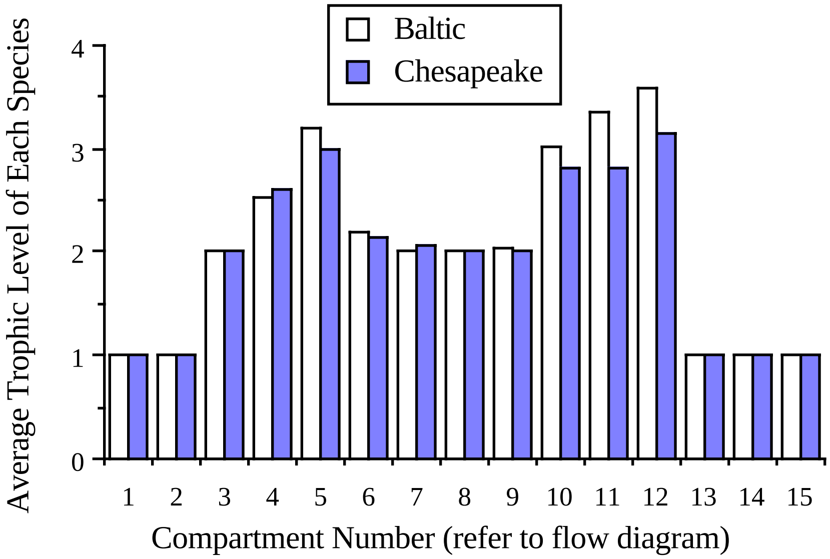
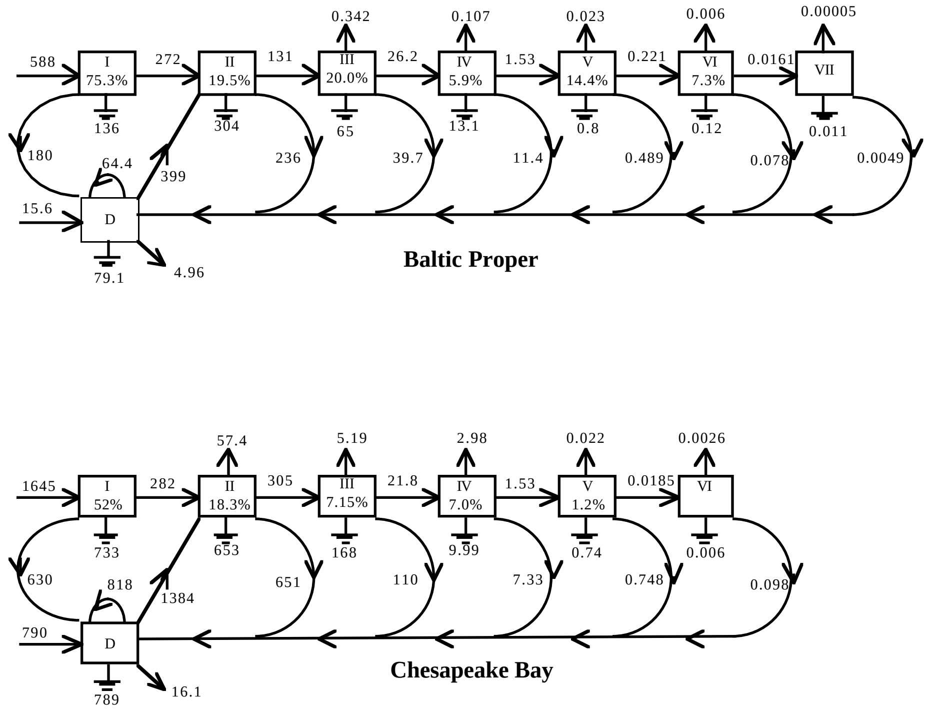


Figure 9: The effective trophic level of each species in the Baltic Sea and Chesapeake Bay. Overall species in the Baltic are at higher trophic levels.



The effective grazing chain and detritial recycling
for the Baltic Sea and Chesapeake Bay.
(The percentages in boxes are the overall trophic efficiencies.)
(After Wulff and Ulanowicz, 1989)

Figure 10: The effective grazing chain and detrital recycling for the Baltic Sea and Chesapeake Bay. This shows that the Chesapeake Bay has a shorter grazing chain. The percentage in boxes are the overall trophic efficiencies. The numbers on the arcs are flows in mg/sq. m./day. For more detail see Figure 5.

Furthermore the trophic efficiencies in the Baltic are much higher, more of the captured energy is passed up the food chain. Also the ratio of energy input to the grazing chain from detritus, relative to input from herbivory is 4:1 for the Chesapeake as versus 1.5:1 in the Baltic. Finally the number of cycles is higher in the Baltic (20 vs 14), and the length of the cycles is longer in the Baltic (see figure 11). This last two observations indicate more complete usage of the available resources in the Baltic. Overall this set of observations indicates that the Baltic is making better use of its captured resources. Its foodweb (i.e the ecosystem structure) is more organized than the Chesapeake's.

The number of cycles of each cycle length
for the Baltic Sea and Chesapeake Bay.

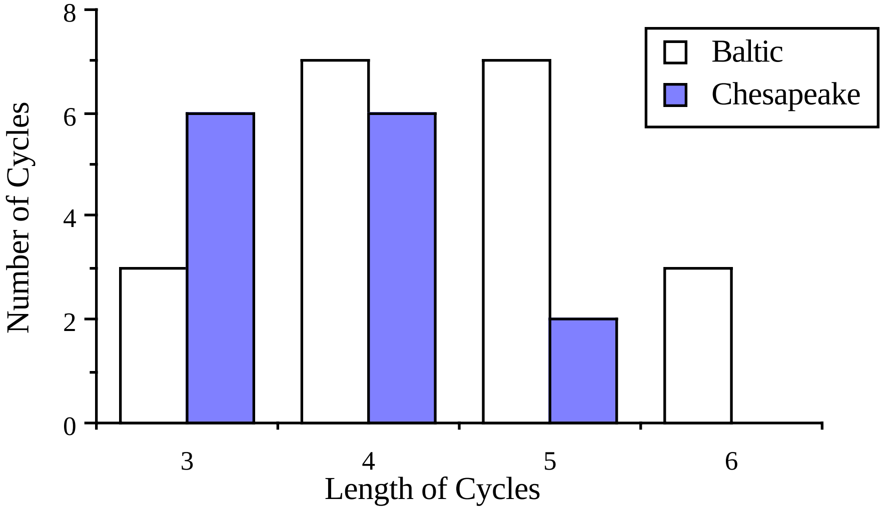
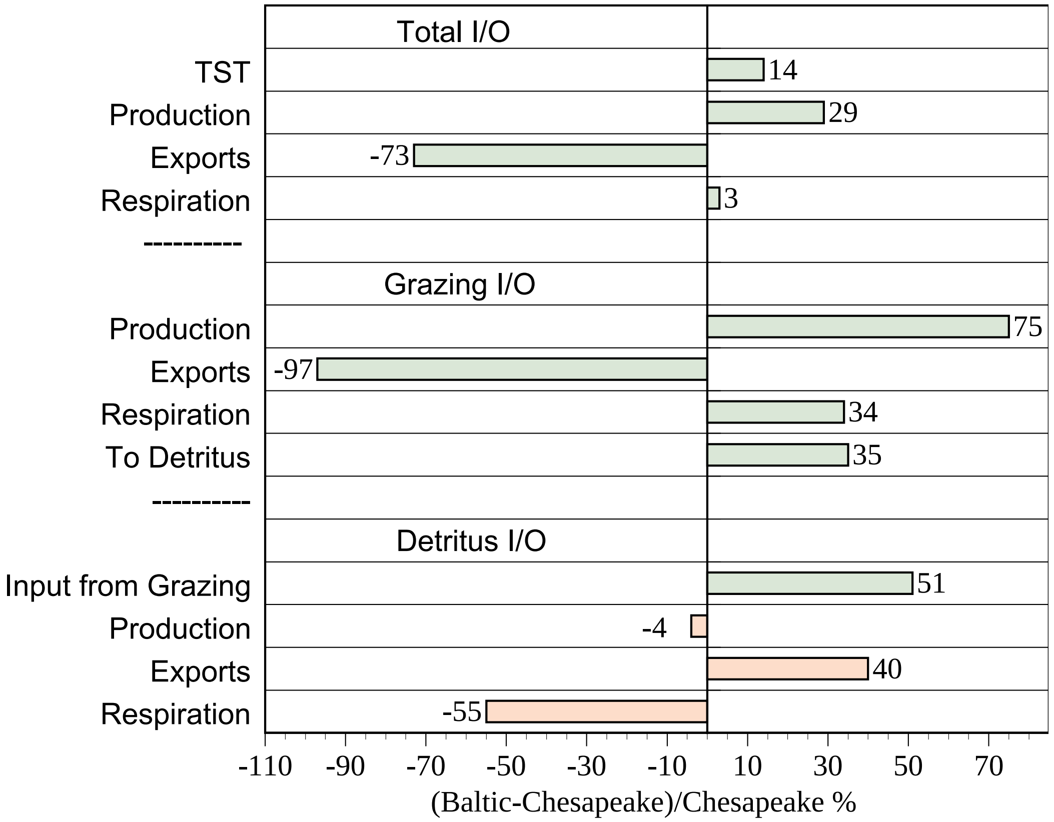


Figure 11: The number of cycles of each cycle length for the Baltic Sea and Chesapeake Bay Ecosystems. The cycles in the Chesapeake Bay are shorter and fewer in number, an indicator of less structural organization than in the Baltic..

However, an analysis similar to that in Table 2 (see Table 3 and Figure 12) does not clearly differentiate between the ecosystems. Functionally (as versus structurally) the ecosystems are different, not more or less organized. Looking at Figure 12 it can be seen that even though in absolute terms the Chesapeake has a higher production, the Baltic has a higher production relative to imports. Comparing the scaled indicators for the living and detritus reveals that the living subsystem of the Baltic is more productive, respires more and exports less than does the Chesapeake. However the detritus compartment does the reverse, it produces less, respires less and exports more. This indicates that the Chesapeake Bay ecosystem is more focused on the detrial aspects and the Baltic Sea more on the living. Their organizational emphases are different.

TABLE 3: Ecosystem Indicators for the Chesapeake Bay (Chesa) and Baltic Sea (Baltic) ecosystems. Definitions of all the measures can be found in Kay et al.(1989). The Δ% is the difference between the control value and the stressed value divided by the control value.

Estuarines	**Mg/Sq m/day**			**Scaled by by Import**		
	Chesa	**Baltic**	**Δ%**	**Chesa**	**Baltic**	**Δ%**
Total I/O						
Imports	2,435	603	-75%			
TST	9,081	2,567	-72%	3.73	4.25	14%
Production	4294.05	1,368	-68%	1.76	2.27	29%
Exports	82	5	-93%	0.034	0.009	-73%
Respiration	2,353	598	-75%	0.97	0.99	3%
Grazing I/O						
Production	2,076	899	-57%	0.85	1.49	75%
Exports	66	0	-99%	0.027	0.001	-97%
Respiration	1,564	519	-67%	0.64	0.86	34%
To Detritus	1,400	467	-67%	0.57	0.77	35%
Detritus I/O				**Scaled by Detritus Inputs**		
Import	790	16	-98%			
Input from Grazing	1,400	467	-67%	0.64	0.97	51%
Production	2,218	468	-79%	1.01	0.97	-4%
Exports	16	5	-69%	0.007	0.010	40%
Respiration	789	79	-90%	0.36	0.16	-55%
Food Web						
Cycles	14	20	43%			
Average Cycle Length	3.7	4.5	21%			
Nexuses	13	13	0%			
Finn Index	14%	23%	63%			
Trophic Levels	6	7	17%			
Average trophic level	1.97	2.06	5%			
Ascendency	15,650	4,449	-72%			
Other						
Biomass	345,375	892,869	159%	142	1480	943%
Production/Biomass	0.0124	0.0015	-88%	5.11E-06	2.54E-06	-50%



Difference in Ecosystem Indicators (scaled by Imports)
For the Baltic Sea Proper and the Chesapeake Bay

Figure 12: The differences between Ecosystem Integrity measures for the Baltic Sea and Chesapeake Bay. The measures are scaled by total imports. See Table 3 for details

This is a good example of two ecosystems which are on different developmental pathways with very different optimum operating point. To judge one of these ecosystems as being more developed overall or having more integrity overall is not meaningful. However this analysis does clearly indicate that there are overall organizational differences between the two ecosystems and that one is more structurally organized than the other.

7 CONCLUDING REMARKS

Ecology is a young discipline, particularly in the context of the study of ecosystems. We have shown that complex systems theory and thermodynamics can provide a basis for a theory of ecosystem organization and thus for the development of measures to evaluate ecosystem integrity. In many situations an unambiguous statement about the difference between two ecosystems is not possible from a purely scientific perspective. One ecosystem is not necessarily better than another. They are just different. Ecosystem managers must recognize this. In order to manage ecosystems it is necessary to make the management goals, including their anthropocentric component, explicit. We can make statements about the overall thermodynamic direction of ecosystem development and evolution, but this is always tempered by the imperatives of the need to survive in the specific environment. It is the interplay of these two which results in the rich diversity of life on this planet.

An important action to be undertaken by government is the formal support of both theoretical ecology at the ecosystem level and the collection of baseline data for ecosystems. The data sets analyzed in section 6 are the most detailed ones we are aware of. Unfortunately there are not other similar data sets to allow us to experiment with our ideas. Lack of baseline data severely constrains our ability to develop indicators of ecosystem integrity and health. Without such indicators and a good understanding of ecosystem dynamics, our ability to make good decisions about what constitutes sustainable development from an ecological perspective will continue to be impaired.

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