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Trophic Flow Networks as Indicators of Ecosystem Stress

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Introduction

For many ecologists the notion of an ecosystem under stress is metaphorical at best. It is commonly accepted that an organism can respond to stress, but what about ecosystems? Do entire ecosystems respond to perturbations in any way that can be quantified either in the field or in the laboratory? Are there analogs to an organism's heartbeat rate, body temperature, or liver metabolism that legitimately can be applied to whole ecosystems?

One attribute of ecosystems that might serve in this capacity is their predilection to develop in a particular direction—a trend that has been labeled ecological succession (Odum and Odum, 1959). Prominent among the many attempts to single out those changes in attributes that characterize a developing ecosystem is the summary by Odum (1969) entitled, "The Strategy of Ecosystem Development." Although many have criticized Odum's use of the word strategy as unnecessarily teleological, some, if not most, of those same critics seem willing to accept that ecosystems undergo succession along definable lines. Odum summarizes the indicators of ecosystem development as involving, among other things, (1) Increasing species richness; (2) progressively greater trophic efficiency; (3) a richer structure for recycling materials; (4) more intense overall system activity; and (5) greater specialization in trophic interactions. (Those wishing a critique of the Odum scenario might wish to start with the comparison of Oksanen (1991)).

If, indeed, developing ecosystems follow

these pathways, then it should be possible to mark their progress in quantitative fashion. In the absence of major perturbation, we hypothesize that an ecosystem will advance in all or most of these indexes. Should one observe, however, significant retrogression in most of the indexes, the inclination is to search for some perturbing factor(s) that is (are) of sufficient magnitude or novelty as to constitute a stress upon the system. That is, on the scale of the ecosystem, we will assume that stress is that which gives rise to an inhibition or reversal of the natural progression that Odum has described as ecological succession.

It remains to become more precise about how to quantify the attributes pertaining to succession, or conversely to stress. In what follows, I will attempt to quantify stress in terms of the traces that it leaves upon the pattern and magnitudes of material or energetic transfers among the components making up an ecosystem. In particular, I wish to search for changes in the networks of trophic exchanges that occur once a definable stress has been placed upon the ecosystem. My search will be informed by the attributes listed above that presumably correlate with succession. They will guide where and how one may anticipate a response to stress. To be more precise, I posit three distinct hypotheses regarding the effects of stress on networks of trophic exchanges: (1) Ecosystem stresses decrement trophic efficiencies, (2) stresses degrade the structure of recycle pathways within the system, and (3) stresses negatively impact system size and organization. To date.

no unequivocal evidence exists to support any of these conjectures, precisely because the terms in which they are stated have yet to be fully quantified. I hope that exactly what is meant by the three hypotheses will become clearer during the course of the next three sections, each of which is devoted to a hypothesis in its turn.

Study Area and Methods

To estimate all the flows in an ecosystem of even moderate complexity is a laborious task, although one now made considerably less onerous by the recent appearance of software that assists the user in estimating networks of balanced (steady-state) flows (Vezina and Platt, 1988; Christensen and Pauly, 1992; Ulanowicz, 1989). Still, extremely few data exist that compare the network configuration of a disturbed system with that of its unimpacted counterpart. To date, most quantified networks of flows are simply single snapshots of community trophic transactions.

One of the few projects ever conceived to contrast the pattern and magnitudes of trophic exchanges between a stressed and an unperturbed ecosystem was executed by Homer, et al. (unpublished manuscript). They estimated the trophic interactions among approximately 20 functional groups in two tidal *Juncus* marsh creek ecosystems adjacent to the Crystal River along the Gulf coast of Florida. One of the creeks was continually subjected to heated water effluent (6°C maximum) from a nearby atomic power generating station. The other system served as the unimpacted control. Most unfortunately, the original rough manuscript of this work was never completed, due to disagreements among the primary authors. The rough draft has been widely circulated among investigators in network analysis, and what follows is a brief abstract of the methods described in that document.

The standing stocks and rates of decomposition of the two dominant marsh grasses were measured by Young (1974) using conventional clipping, drying, and weighing techniques. Seasonal changes in stocks allowed Young to estimate net grass production rates; and CO₂ evolution, as measured in the field, helped establish the macrophyte respiration rates. Gibson (unpublished manu-

script) measured phytoplankton standing stocks, to which Homer (unpublished manuscript) applied data on O₂ evolution in light and dark bottles to calculate both production and respiration rates. Periphyton biomass was assessed by Homer in the field, and accompanying production and respiration rates were estimated using the data of Day et al. (1973) taken in Louisiana.

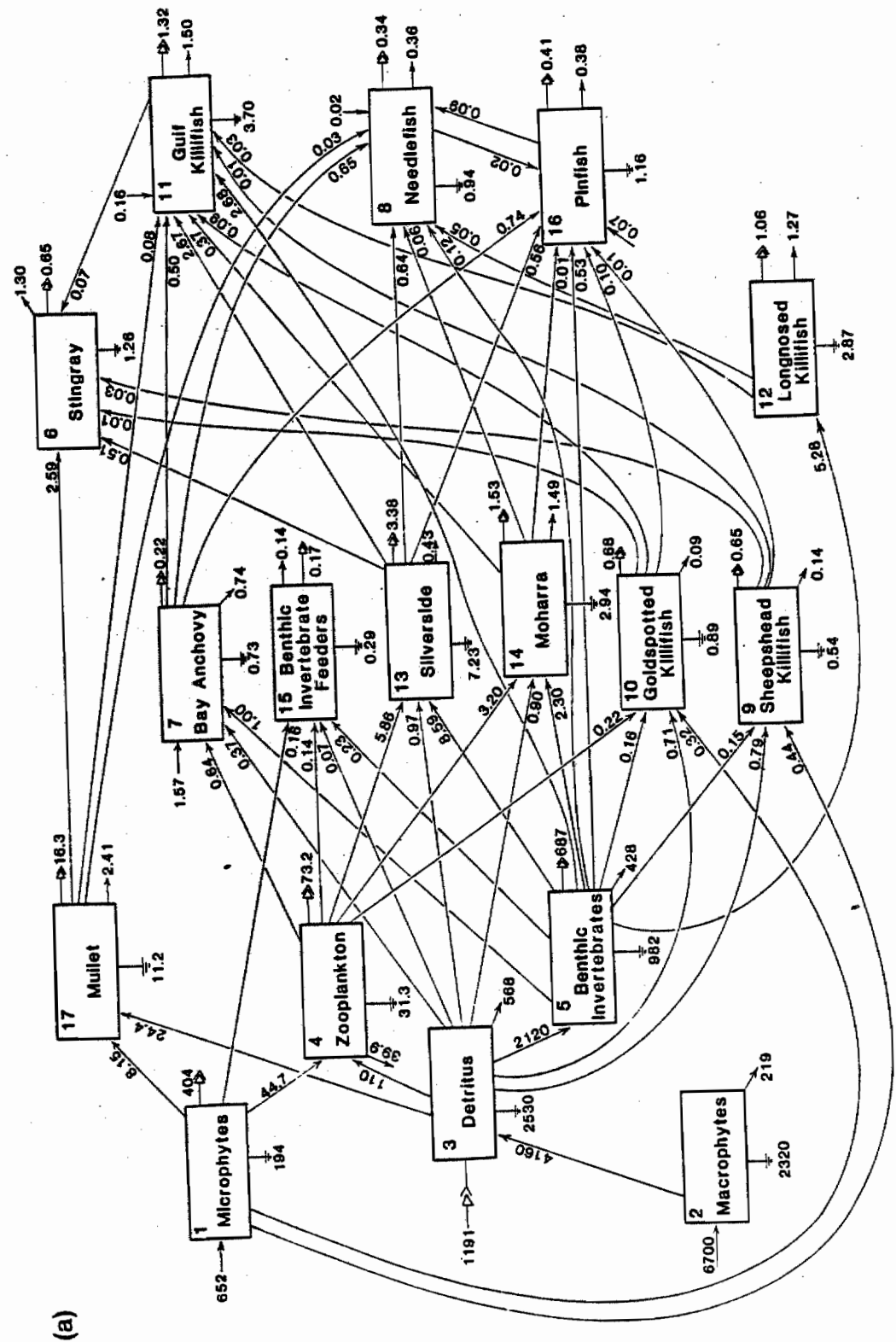
As regards heterotrophs, Maturo (1974) measured zooplankton standing stocks and production, whereas McKellar (1974) assessed their respiration rates. The standing stocks of some 60+ species of fish and macroinvertebrates were estimated by Homer (1974), who also conducted inspections of the stomach contents of a number of the specimens. Nekton production was calculated using Ricker's (1975) equation. Respiration and assimilation coefficients from a variety of sources (e.g., Winberg (1956), Odum (1971), and Day et al. (1973)) were applied to the measured biomasses. Consumption rates were estimated by dividing the sum of the production and respiration rates by the respective assimilation efficiency.

Ulanowicz (1980) consolidated certain of the species particular to each system so as to create two networks, each parsed into 17 identical, common compartments. The quantified food web of the control system is depicted in Figure 34.1a, that of the stressed ecosystem in Figure 34.1b. The currency is carbon and flows are depicted in mg carbon m⁻²day⁻¹. These two networks make up the observations against which the three aforementioned hypotheses will be probed.

Bottom-Top Trophic Efficiencies

By bottom-top trophic efficiencies we mean that fraction of the carbon fixed by the autotrophs that eventually reaches the higher trophic levels. We might guess that under stress, proportionately less material will make its way to the top carnivores. To test whether or not this is so, it is necessary to trace the carbon fixed by the autotrophs through the manifold pathways it takes to reach the top trophic levels.

One could attempt to use brute force to enumerate all the pathways from a given initial donor to a designated final receptor and then to quantify the amount of medium that



survives passage over each route. It would seem that such a task could readily be handled by a computer (and such is the case in this particular instance). In general, however, the number of potential pathways can increase exponentially as the number of compartments rises (the combinatoric problem), so that dealing with 20 or more compartments potentially could bog down even the largest and fastest computers available today.

Fortunately, it is not necessary to employ brute force. The exchanges can be arrayed in matrix form (Leontief, 1951), the rows of the matrix suitably normalized (Augustinovic, 1970), and the ensuing matrix inverted and renormalized in such a way that the i - j entry of the result represents the fraction of flow through i that eventually reaches j over all possible pathways (Szyrmer and Ulanowicz, 1987). The results show, for example, that 0.034% of the microphyte production in the control ecosystem makes it to the needlefish, whereas only 0.014% gets there in the heated creek—a drop in efficiency of some 59%.

The method of Szyrmer and Ulanowicz (1987) employed to calculate these results is but one example from a field of computation called input-output (I-O) analysis that is popular in economics and ecology. Similar matrix manipulations can be used to achieve other ends related to trophic efficiency. For example, Levine (1980) demonstrates how one may employ I-O operations to compute the average trophic position at which each species feeds. For example, if a given compartment receives 45% of its sustenance at the herbivore level, 40% at that of a primary carnivore, and the remaining 15% as a secondary carnivore, then its average trophic position will be $0.45 \times 2 + 0.40 \times 3 + 0.15 \times 4 = 2.7$. The percentages are calculated for the general case from I-O analysis. One might guess that the effect of disturbance should be to decrease the trophic level at which most species feed. When applied to the two Crystal River networks, however, the changes for most species appeared inconsequential. Only the stingray experiences a drop from 3.83 to 3.69. Several species actually rise in trophic status (mullet, bay anchovy, and needlefish). It appears that the two top predators in the control network have either disappeared from the stressed system (Gulf flounder) or fallen in trophic position (stingray). This diminu-

tion of predation pressure from the very top may have allowed the three species cited above to feed higher in the web, but the results are hardly unambiguous.

A clearer difference between the systems emerges when one regards the trophic structure which underlays the webs depicted in Figures 34.1a and 34.1b. The matrix algebra I-O analysis can be amended so as to map omnivorous species into several discrete trophic levels (Ulanowicz and Kemp, 1979; Ulanowicz, 1995). For example, the activity of the hypothetical species in the last paragraph could be apportioned 45% to the second trophic level, 40% to the third, and 15% to the fourth. This parsing can be accomplished in such a way that a balance of medium is maintained in the resulting trophic chain.

The aggregated trophic chain of the control network is depicted in Figure 34.2a; that of the stressed ecosystem in Figure 34.2b. One notices that the greatest impact has been at the highest trophic levels. Level V, present in the control, is entirely absent from the heated ecosystem, and proportionately far less carbon in the stressed system makes it to level IV. (This does not contradict the earlier observation that the average trophic levels of three near-top predators are higher in the heated system. Trophic position is an intensive [rate-independent] attribute, and can rise even though the overall throughputs of these species drop disproportionately, as they did in this comparison.) Some compensation may be discernible in the response of the disturbed community, however, as proportionately more primary production is reaching level III, presumably because of the reduced predation pressure from the highest levels.

The evidence in favor of the hypothesis that stress acts on ecosystems to degrade trophic efficiencies consists of (a) lower bottom-up transfer efficiencies; (b) a shorter aggregated trophic chain; and (c) diminished efficiencies along the trophic chain, especially at higher levels. The anticipated result that most species would feed at lower levels in the stressed system was not evident in this example. Although the species at the very top did fall off, more components at the middle levels advanced, presumably as a compensatory response.

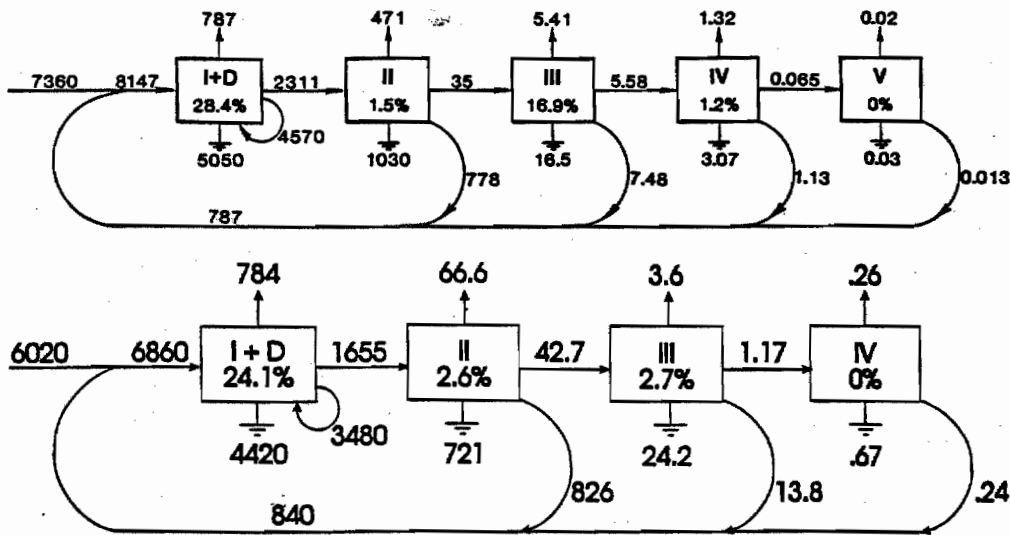


Figure 34.2. Straight chain trophic flows ($\text{mg carbon m}^{-2}\text{day}^{-1}$) equivalent to the webs depicted in Figures 34.1a and 34.1b, respectively.

Recycle Pathways

Odum (1969) lay particular emphasis upon recycling, saying that the role of detritus in system regeneration becomes more important as a system develops. Some took this to mean that cycling should increase as a proportion of total activity during the course of development. Finn (1976) used I-O methodology to calculate the fraction of whole system activity that comprises recycle. Early attempts to test whether the Finn index was a good indicator of developmental stage yielded ambiguous results at best (Richey et al., 1978). In fact, when the Finn index is calculated for the two Crystal River networks, it is seen that a larger fraction of total activity in the stressed system consists of recycle (9.4%) than is the case in the control (7.1%).

Greater is not necessarily more important, however, so that it behooves us to study the situation more carefully before rendering judgment on the second hypothesis. We should also inquire if the recycle activity is being expressed differently in the two configurations. That is, we seek to identify all the various routes by which carbon is retained in the system. It was mentioned in the last section, however, how finding and counting all the pathways in a network can become an impossible task, due to the potential for an enormous number of pathway combinations

in networks of even moderate dimension and connectivity. Cycles are a particular subset of all pathways, so that before giving up trying to count them we should ask whether there is anything special about material loops in ecosystems that might facilitate their identification.

It appears that recycle loops involving only living compartments are very rare in ecosystems (Pimm (1982), but see Polis (1991)). Almost all pathways for the reuse of materials involve at least one detrital or nonliving compartment. This bottleneck for recirculation provides a very convenient place from which to launch the search for cycles. Furthermore, there are topological techniques that can be employed to prioritize the order of search through the living compartments and to eliminate a priori those units that do not engage in any recycle (Ulanowicz, 1983). The result is a reasonably efficient search algorithm that can handle most moderate-sized networks (20–50 compartments) with reasonable connectivity (<25%).

Once a cycle has been identified, it remains to assign a quantity to the flow that circulates within it. If there were no overlap of cycle pathways, one simply could locate the smallest link in the cycle and assign that amount to each link in the loop. Alas, there often are more cycle pathways in a network than there are individual transfers, which implies that

at least some cycles must share a common smallest arc. The question then becomes how should one apportion a flow among the several cycles in which it appears as the smallest link? (Such an association of cycles is called a "nexus.") The most equitable solution seems to be to divide the critical flow among the nexus members in proportion to the relative probabilities that a quantum of the critical flow will complete each separate cycle (Ulanowicz, 1983).

When this algorithm for counting and weighting cycles is applied to the Crystal River ecosystem networks, it becomes obvious that many richer opportunities for recycle exist within the undisturbed system. The number of simple cycles (no repeated elements) in the control web is almost triple that of the impacted system (135 vs. 48), and the number of nexuses is almost double (44 vs. 29). Furthermore, the way cycling activity is expressed in the two systems is different. A greater amount of recycle in the stressed system occurs along the shorter cycles of lengths 1, 2, and 3, whereas the amounts over the longer cycles (lengths 4 and 5) were higher in the control network (Figure 34.3).

How, then to explain the larger proportion of cycling in the stressed ecosystem? One scenario might be that as a system develops, more cycles are created involving higher trophic levels, wherein the storage of medium is longer. Disturbance usually affects the higher levels disproportionately (Menge and Sutherland, 1987), releasing much of the medium stored as biomass. The compensatory response by the system might be to retain this material in circulation among the less-impacted lower trophic level elements.

We are led to conclude that stress changes the structure of recycle pathways by diminishing the numbers of both cycles and nexuses. As well, the trophic lengths of the remaining cycles are shorter, due to diminished participation by higher taxa. As regards the relative magnitude of recycle activity, it could increase as a way to compensate for diminished storage in higher trophic compartments.

Indices of Size and Organization

In order to quantify system size and organization, it is necessary first to introduce a suitable notation for the types of flows discussed earlier. Accordingly, in our system of n identifiable components, we will designate the flow from any arbitrary component i to any other taxon j as T_{ij} . We will designate imports from outside the system as originating from a virtual compartment labeled 0 (zero). That is, an import to box j will be denoted as T_{0j} . When an export of useful currency transpires, the destination index j will take on the value $n+1$; and when losses occur, the destination is assumed to be $n+2$ (Hirata and Ulanowicz, 1984).

Now, Odum dealt with 24 separate indicators of ecosystem development, which he aggregated into six categories. Elsewhere (Ulanowicz, 1980, 1986), I have attempted to coalesce these threads even further into a quantitative, unitary statement of ecosystem growth and development. This formulation begins with my adoption of the economists' measure of exchange activity as a way to reckon system size. That is, one adds together

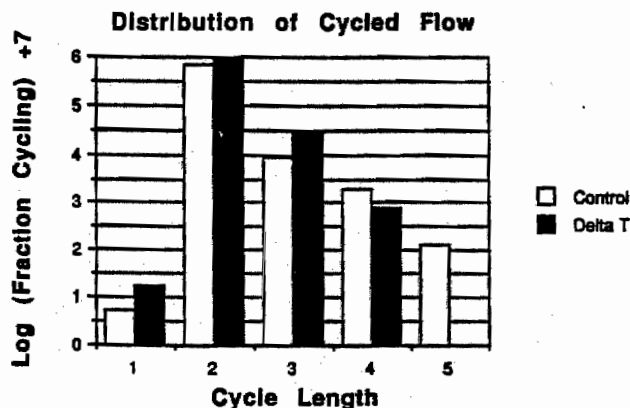


Figure 34.3. Logarithms of the fractions of overall activity devoted to recirculating carbon along cycles of different trophic lengths. Open bars represent the control system in Figure 34.1a, dark bars the stressed system in 34.1b.

all the flows occurring in an ecosystem into what is called total system throughput, T where

$$T = \sum_i \sum_j T_{ij}.$$

In case it should seem strange to measure size in terms of activity, one need only recall that we are bombarded daily with statistics on the gross national (or domestic) product as an index of how big the economy is and whether it is expanding or shrinking. On a more biological note, bacteria may be quite numerous, but inactive in aquatic systems with severe resource limitation. If food should suddenly appear, their throughput rates, but not their biomasses increase in response. (The new production is immediately harvested by microheterotrophs, such as flagellates.) Thus, growth will be defined as any increase in T , not as an increase in total biomass.

Development is not as easily quantified. We begin, however, by noting that development infers that a system is progressively departing from a state of randomness and stochasticity by accruing ever-greater definition and coherence among the workings of its parts. That is, in a developed system an event at any one node is not propagated randomly among all the other elements. Rather, its effects are manifested in one, or only a few, closely connected nodes. Another way of saying the same thing is that there is less ambiguity about exactly where the effects of an event at a particular node will appear.

Mention of the word ambiguity immediately prompts thoughts about probabilities and information, the latter of which Tribus and McIrvine (1971) define as anything that causes an adjustment to the former. Using the flows T_{ij} and the total system throughput T , one may readily estimate the probabilities of various events. For example, the quotient

$$f_{ij} = T_{ij} / \sum_k T_{kj}$$

approximates the conditional probability that a quantum of medium enters j , given that one has left i . Thus, in a highly developed system, for each donor i , at most a few of the f_{ij} will

remain significantly nonzero. This is another way of saying that the network of interactions becomes progressively better articulated.

In a system that is highly articulated, the origin of a quantum strongly constrains which compartment it will next enter. The measure from information theory that best expresses the amount of constraint inherent in the system as a whole is the average mutual information (Rutledge et al., 1976), which can be written in terms of the flow variables as

$$I = \sum_i \sum_j (T_{ij}/T) \log (T_{ij}T / \sum_k T_{kj} \sum_l T_{il}).$$

These definitions of size and organization at first sight appear unconnected. I have argued, however, that these two properties are respectively extensive (size-dependent) and intensive (size-independent) results of the unitary action of autocatalysis (Ulanowicz, 1989). I join the two, therefore, into a single index $A = T \times I$ that expresses the joint interaction of the two phenomena and is called the system ascendancy. Then, using the product rule for differentials, we would have

$$dA = IdT + TdI,$$

or in words, an increase in ascendancy equals growth plus development.

Of course, no system can grow and develop without limits. From information theory we discover that one upper bound on I is given by the joint uncertainty, H , where

$$H = - \sum_i \sum_j (T_{ij}/T) \log (T_{ij}/T),$$

and $H \geq I \geq 0$. Scaling H by T in the same way that was used to give dimensions to I yields a quantity that I have called the system capacity $C = T \times H$, where $C \geq A \geq 0$. The non-negative difference $\Phi = C - A$, I have called the system overhead. It represents all the ambiguities of connection and incoherencies of flow, or what one might regard as disordered activities, in contrast to the ordered phenomena represented by A . It turns out, however, that a system can never divest itself of all overhead. From the hierarchical point of view

some overhead is necessary to maintain and create order at all levels.

Having thus defined the quantitative elements of growth and development, one should now ask how they are most likely to change in the face of disturbance? One could begin by guessing that the system's size would be reduced. Not only might it lose biomass, but the aggregate level of activities among the components might suffer. Because ascendancy was defined as a surrogate for growth and development, one anticipates that the ascendancy would fall in the face of stress (which we should recall was defined as a major perturbation). Experience tells us that the diversity inherent in the system capacity should also fall. With the decline of both C and A , it is unlikely that the absolute value of the overhead would rise. It is conceivable, however, and in fact to be expected, that the various components of the overhead would encumber larger fractions of the remaining total capacity.

How do these expectations square with the changes in indexes calculated from the Crystal River networks? The results are shown in Table 34.1. The total system throughput did indeed fall by almost 20%. (In fact, the total biomass also fell by a similar amount.) As the information indexes are all scaled by the total throughput, they were uniformly less in the impacted system.

These small adjustments notwithstanding, change in the Crystal River creeks may be characterized as predominantly extensive in nature. That is, a relatively constant structure is being modulated by the overall activity rate. Such was virtually the same response of the Chesapeake mesohaline ecosystem to changes in season, as noted by Baird and Ulanowicz (1989). Lacking more detailed

and precise data, one can only wonder whether the perceived constancy of ecosystem structure is real or only an inadvertent artifact. (In assembling such food webs from incomplete information, the investigator often is forced to estimate flows in different systems on the basis of changes in biomasses without being able to correct the metabolic constants used in the estimates for the attendant environmental differences. This could lend more apparent homeostasis to the network structure than actually exists.)

As regards the impact of this particular stress on the indices of size and organization, one could say that in this instance the disturbance did act to decrease the overall level of system activity; however, whether it served to decrement the indices of organization, remains equivocal.

Conclusions

To return to the question posed at the beginning of this essay, "Can we speak of the effects of stress on an ecosystem in more than a metaphorical sense?" I would answer in the positive. Such affirmation is predicated on the assumption that ecosystems are capable of coherent response to disturbance. Which is not to say that ecosystems are superorganisms in the sense of Clements. Rather, the postulate is milder—that ecosystems exhibit the dynamics of what is commonly (and to a point misleadingly) called self-organization. This capacity is shared with a spectrum of other systems—economic, political, sociological, and ontological. Regarding the last category, DePew and Weber (1994) have given cogent arguments why one should turn the Clementsian dictum on its head and refer to organisms as *superecosystems*!

Even if the reader happens to doubt the inherent developmental capacities of ecosystems, I hope it is clear from this exercise that there is at least instrumental and pragmatic value to treating ecosystems as entities whose response to stress can be quantified in concrete ways. Through repeated application of these methods of network analysis, it eventually should become clear whether or not a recognizable and reliable pattern of ecosystem response to stress emerges. Should one appear, we will enjoy a very significant in-

Table 34.1. Network Indexes of size and organization.

| Quantity | Control | ΔT |
|---------------------------------------|---------|------------|
| T (mgC/m ² /y) | 22,420 | 18,050 |
| Capacity (mgC-bits/m ² /y) | 70,712 | 56,315 |
| C/T (bits) | 3.15 | 3.12 |
| A/C | 0.401 | 0.398 |
| Φ_1/C | 0.045 | 0.046 |
| Φ_2/C | 0.088 | 0.069 |
| Φ_3/C | 0.260 | 0.267 |
| R/C | 0.206 | 0.220 |

sight into the essential nature of living systems.

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