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COMMUNITY MEASURES OF MARINE FOOD NETWORKS AND THEIR POSSIBLE APPLICATIONS

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INTRODUCTION

Ecology is the study of the relationships of organisms with one another and with their non-living environment. The keyword to notice in this definition is "relationships". Rather than fixing attention upon the organism or population itself, we as ecologists should be primarily concerned with what transpires between populations. As we also pretend to being scientists, we aim to quantify our observations on these relationships, and this is most readily done when those interactions involve a palpable transfer of either material or energy. When we describe the species composition and densities of phytoplankton and zooplankton in an open ocean gyre, we are behaving as good quantitative biologists. Not until we attempt to balance grazing rates with rates of respiration, nutrient uptake and sinking, are we acting as quantitative ecologists.

There are those who would point out that to measure the fluxes between populations, we first need to quantify the abundances of the participants. I do not wish to deny what is a methodological necessity in most (though not all) cases. What I am proposing here, however, is the perspective that the description of the network of flow exchanges is the key to approaching the ecological problem.

The prevailing attitude among most ecosystem modellers is that one seeks to describe a flow as the result of a putative force, which may be quantified by the states of the interacting populations. For example, zooplankton grazing is usually assumed to be some multivariate function of phytoplankton density, zooplankton density, ambient temperature, relative sizes of predator and prey, etc. In writing this multivariate function, one is implicitly describing a force which causes a resultant flow - the grazing rate. This approach often works well when only one, or a very few, processes are being studied. The problem arises when we attempt to predict the course of a linked network of many flows as being the aggregate result of the simple forces. The predictions of such coupled models are usually unreliable. Furthermore, with the fixed structure inherent in this procedure one cannot treat the various "emergent surprises" which enter the development of any real ecosystem. Even if one should try to vary the structure of the model in some fashion, one is still left in need of a criterion against which to evaluate the proposed changes.

A way out of this dilemma is afforded by adopting an alternative perspective in which the community flow network is not secondary to the attributes of the constituent populations. Whence, the density, size and age structures, respiration efficiency, ethology and other properties of any member population are affected by, and in the long run are formed by, how well the state properties of the individual species contribute to some as-yet-unspecified attribute of the <u>entire</u> community network of flows. Different modes of individual behavior, physiologies, genotypes, feeding links, even species themselves, may enter and leave the community. How long they remain depends upon their contribution to some property of the whole network of exchanges.

If it sounds as though cause and effect are being confused by this emphasis upon flows, then such observation is correct. Consider, for example, the perfect causal loop (see also Hutchinson, 1948) in Figure 1. Medium flows from A to B causing further flow from B to C, which in turn engenders flow from C back to A; and the original cause (flow from A to B) becomes its own effect. Of course, if one tries to identify this loop with any real cycle (e.g. A is nitrogen in the water column, B is nitrogen in the phytoplankton and C is nitrogen in the zooplankton as in Figure 2) the picture is complicated by obligatory losses, and imports. But the causal loop remains imbedded in the real network as an element to be reckoned with.

Causal loops usually give rise to positive feedback phenomena. Any change in the status of one of the components giving rise to an

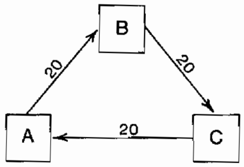

Fig. 1. An ideal flow loop (causal cycle).

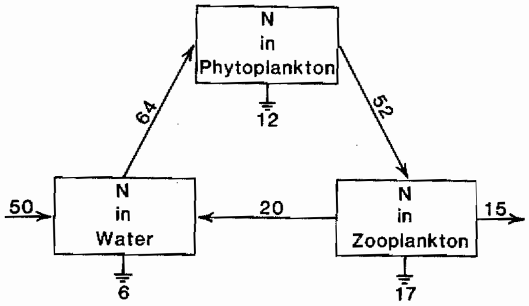

Fig. 2. A hypothetical cycle of nitrogen in a planktonic system ($gN/m^2/y$). The ground symbols represent respiratory losses.

increase in one of the flows will result in self-reward. Conversely, changes which diminish any flow in the cycle will be self-mitigated. The fluxes and the forces thereby became inextricably entwined. Now this is a bad turn of events only if one's goal is the explanation (at the subsystem level) of phenomena in a classical cause-effect fashion. If, however, one seeks (as in thermodynamics) only to quantitatively describe the eventual course of the whole system; one's task is actually made easier, because now one need measure only the perceptible flow network and ignore, for the time being, the obscure and elusive forces.

I suggest that the measurement of ecosystem flow networks is precisely the task of highest priority in ecology today. But questions remain: What constitutes an adequate description of a flow network? How can one use the flow network as a diagnostic tool in ecological research and management? And, perhaps most importantly, can one be more specific about the criterion which best describes the time evolution of an ecosystem flow network? Below I will briefly attempt to outline my opinions on these three issues with occasional examples drawn from the analysis of the carbon flow network of an estuarine marsh gut (i.e. embayment) ecosystem.

FLOW DATA REQUIRED

How much data need be collected depends largely upon decisions made at the very outset of any investigation as to what the essential components of the community will be. How the chosen aggregation affects the outcome of an analysis has always been a crucial question in ecosystems modeling (see Halfon, 1979; Cale et al., 1982; Schaffer, 1981). I will not dwell on this controversy, except to remark that my experience with the few networks I have been able to analyze leads me to believe that the conclusions drawn from global

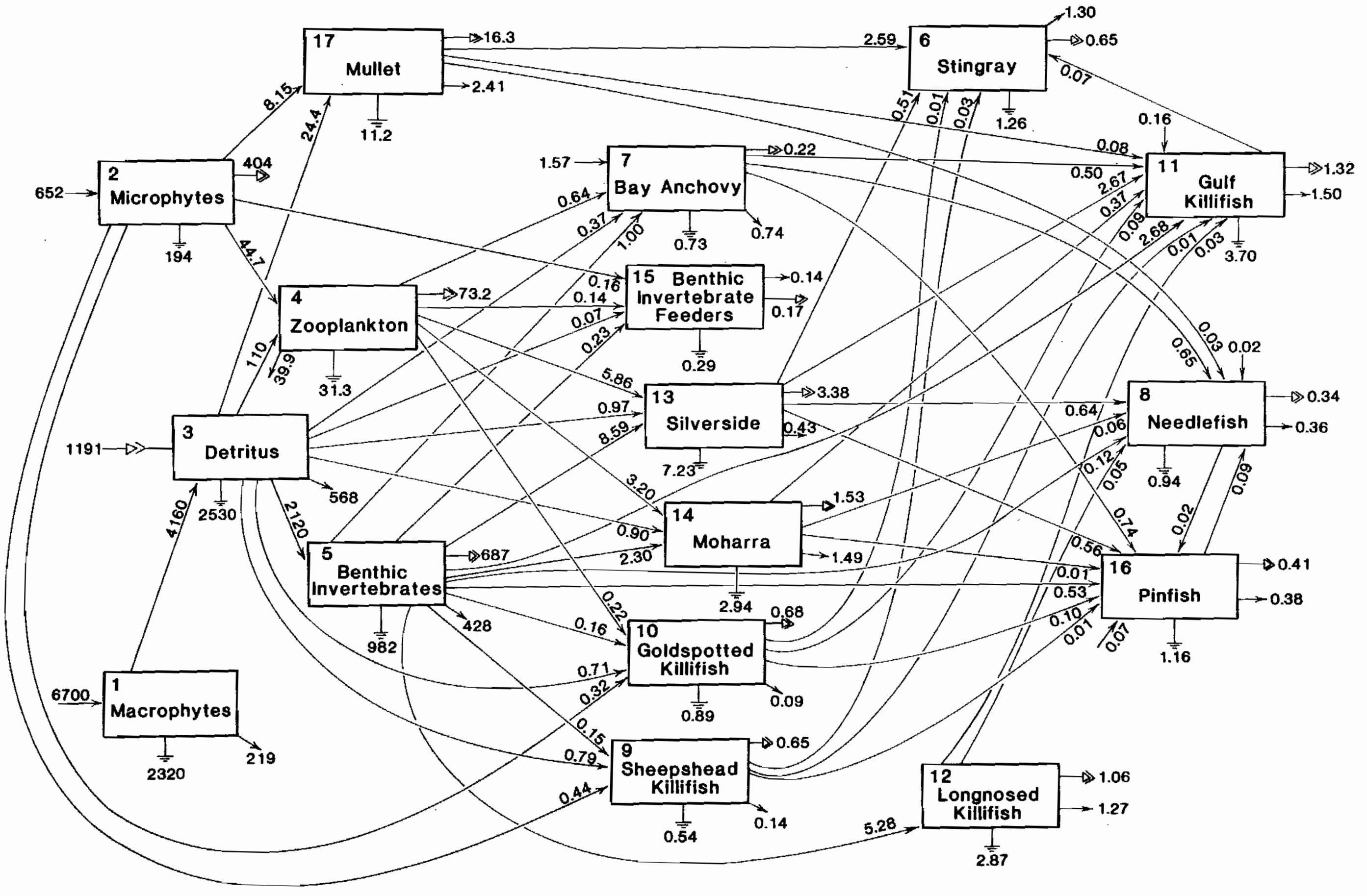

Fig. 3. A diagram of carbon flows among the taxa of a marsh gut ecosystem, Crystal River, Florida. All flows are in mgC/m^2/d. The ground symbols represent respiratory losses. The linked arrows (—▷▷—) represent returns to the detritus (M. Homer and W. M. Kemp, unpublished manuscript).

network variables seem more robust with respect to the degree of aggregation than do results issuing from deterministic modeling efforts. (Although the cycle analysis to be described later is very sensitive to the lumping of compartments).

The carbon flow network data to be used for illustration were collected by Homer and Kemp (unpublished manuscript) from a polyhaline marsh gut in the vicinity of the Crystal River estuary on the upper Gulf Coast of Florida. In the sample network 17 compartments are identified as in Figure 3. The compartments are mixed in degree of aggregation with the lower trophic level species being lumped into a few compartments, whereas the fish have been identified in several cases to the species level.

Generally speaking, the types of flows which need to be measured fall into four categories:

(1) exchanges among compartments within the system,
(2) inputs from sources outside the system,
(3) useable exports outside the system, and
(4) dissipation of medium into a form of no further use to any system.

Some investigators do not make a distinction between (3) and (4); but as will be seen later, there are compelling thermodynamic and hierarchical reasons for treating these flows separately. In our example network there are 69 internal exchanges, 6 inputs, 16 exports, and 17 respiratory flows. The flows balance around each compartment, i.e. the network is assumed to balance over the annual cycle. Steady-state is not, however, a requirement of most of the following analyses.

The given flows are in terms of carbon/area/time. Corresponding flow networks could have been measured in terms of energy, nitrogen, phosphorous, silicon, or other materials.

While the analysis of a solitary network can be performed, it is often not clear what significance to attach to the magnitudes of some of the resultant quantities. This problem can be circumvented, however, by seeking comparisons between two different systems or between the same system at different times or under different exogenous conditions. For example, we may wish to compare estuarine, coastal, gyral and abyssal marine networks. Or we may wish to contrast equitorial upwelling community networks under both light and heavy trade winds. A companion network to the example in Figure 3 has been quantified. It describes the exchanges in a nearby tidal gut under practically identical environmental conditions, save that the second community (which network is depicted in Figure 4) is continually subjected to a 6°C rise in temperature because of its proximity to thermal effluent from a nuclear power station.

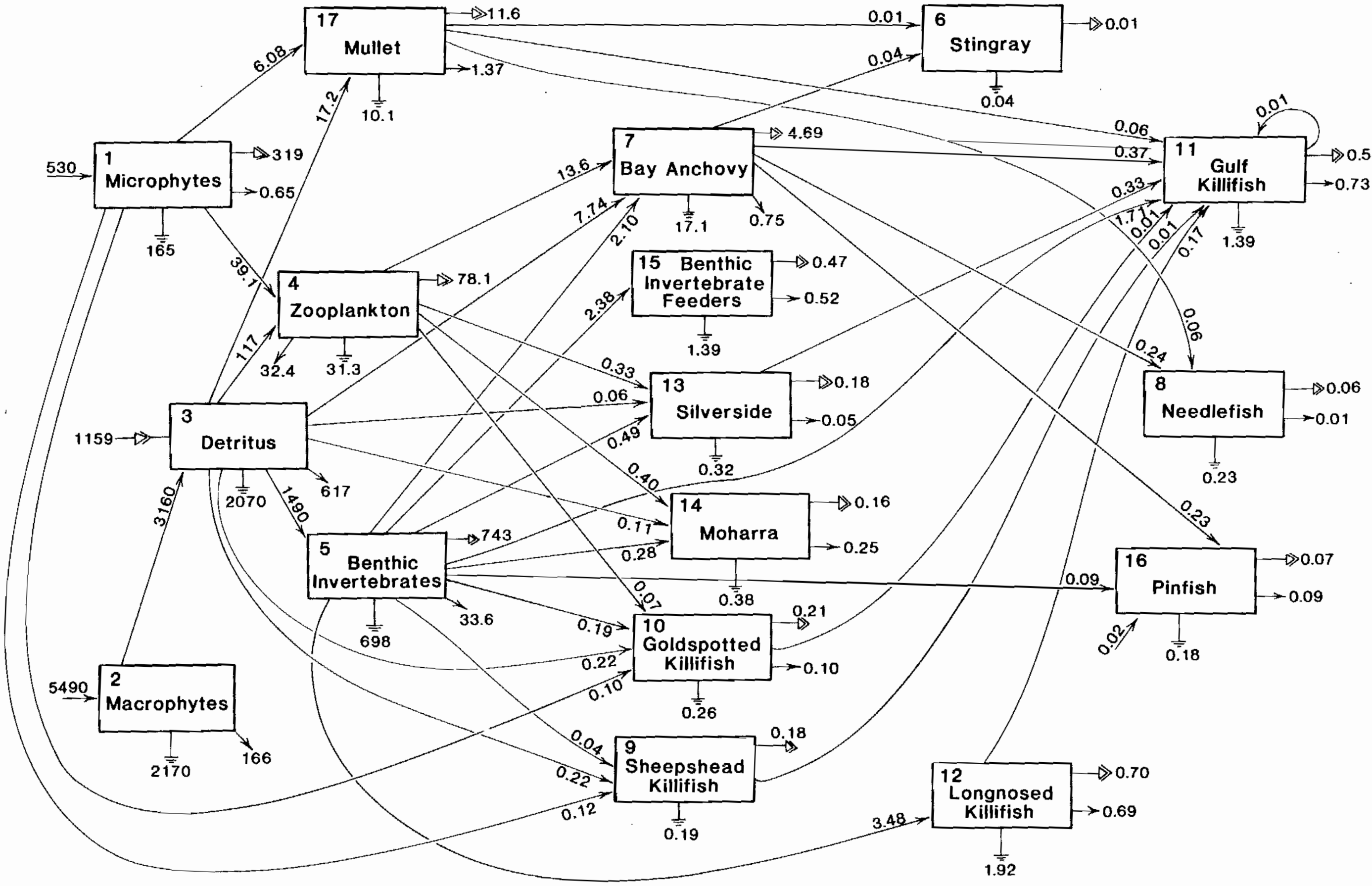

Fig. 4. Carbon flows among the taxa of a Crystal River, Florida marsh gut community that has been chronically exposed to a 6°C rise in ambient temperature. Units and symbols are the same as in Figure 3. Data from M. Homer and W. M. Kemp (unpublished manuscript).

INPUT-OUTPUT ANALYSIS

Given a flow network, one of the more detailed questions one can ask is how any one compartment is affecting (i.e. exchanging medium with) any other compartment over all pathways, direct and indirect. The direct interactions are manifest upon inspection of either the diagram of the network or of the two-dimensional matrix of internal exchanges. The indirect linkages are not always as easy to identify and enumerate. Fortunately, much information can be obtained about the indirect pathways through straightforward algebraic operations on the matrix of direct flows (see also Leontief, 1951; Hannon, 1973; Finn, 1976; Patten et al., 1976).

Calling P_{ij} the flow from i to j and T_i the total ouput from i, then $f_{ij} = P_{ij}/T_i$ will represent the fraction of output of i which is contributed directly to j. The F matrix for the control marsh gut appears in Table 1. If F is a matrix with components f_{ij}, it is easy to demonstrate that multiplying F by itself will yield a matrix F^2 wherein the i-j^th component represents the fraction of total output from i which flows to j over all pathways of exactly two steps. Similarly, F^3 will express the fractions transferred over all pathways of length three, and so forth ad infinitum. By summing all powers of F, we obtain the so-called output structure matrix, S, wherein the i-j^th component represents the fraction of output from i which flows to j over all possible pathways, i.e.

$$S = F^0 + F^1 + F^2 + F^3 + F^4 + \ldots$$

Because of the way in which F was normalized, this infinite sequence converges exactly to

$$S = (I-F)^{-1} ,$$

where I is the identity matrix (Yan, 1969), and the minus one exponent represents matrix inversion.

As an example of the use of the output structure matrix, the 1-7 component of the Crystal River marsh gut indicates that in the unperturbed web 5.46×10^{-4} of the microphyte throughput (652 $mgC/m^2/d$), or .356 $mg/m^2/d$, eventually reaches the Bay Anchovies (see Table 2). Curiously enough, about 15 times that amount is transferred between the same two compartments in the perturbed network.

One can also multiply S by vectors representing the inputs, exports and total throughputs of each compartment to obtain the answers to such questions as: What is the fate of each individual input to the network? Or, conversely, how much of each export can be attributed to the various inputs? For example, there are two major sources of carbon to the system, fixation of carbon by macrophytes and microphytes, with the macrophytes contribution 10.3 times greater than the planktonic production. Given that macrophytes are

Table 1. Output Fractions for the Unperturbed Crystal River Marsh Gut Ecosystem. Each Entry Represents the Fraction of the Row Throughput which Flows Directly to the Column Taxon

	Microphytes	Macrophytes	Detritus	Zooplankton	Benthic Invertebrates	Stingray	Bay Anchovy	Needlefish	Sheepshead Killifish	Gold spotted Killifish	Gulf Killifish	Longnosed Killifish	Silverside	Moharra	Benthic Invertebrate Feeders	Pinfish	Mullet
Microphytes	.0000	.0000	.6199	.0686	.0000	.0000	.0000	.0000	.0007	.0005	.0000	.0000	.0000	.0000	.0002	.0000	.0125
Macrophytes	.0000	.0000	.6210	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000
Detritus	.0000	.0000	.0000	.0205	.3956	.0000	.0001	.0000	.0001	.0001	.0000	.0000	.0002	.0002	.0000	.0000	.0046
Zooplankton	.0000	.0000	.4738	.0000	.0000	.0000	.0041	.0000	.0000	.0014	.0000	.0000	.0379	.0207	.0009	.0000	.0000
Benthic Inv.	.0000	.0000	.3243	.0000	.0000	.0000	.0005	.0001	.0001	.0003	.0013	.0025	.0041	.0011	.0001	.0003	.0000
Stingray	.0000	.0000	.2025	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000
Bay Anchovy	.0000	.0000	.0615	.0000	.0000	.0000	.0000	.1816	.0000	.0000	.1397	.0000	.0000	.0000	.0000	.2067	.0000
Needlefish	.0000	.0000	.2048	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0120	.0000
Sheepshd Killifish	.0000	.0000	.4710	.0000	.0000	.0217	.0000	.0000	.0000	.0000	.0072	.0000	.0000	.0000	.0000	.0072	.0000
Goldspotted Killifish	.0000	.0000	.3656	.0000	.0000	.0054	.0000	.0000	.0000	.0000	.0484	.0000	.0000	.0000	.0000	.0538	.0000
Gulf Killifish	.0000	.0000	.2003	.0000	.0000	.0106	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000
Longnosed Killifish	.0000	.0000	.2008	.0000	.0000	.0000	.0000	.0095	.0000	.0000	.0057	.0000	.0000	.0000	.0000	.0000	.0000
Silverside	.0000	.0000	.2192	.0000	.0000	.0331	.0000	.0415	.0000	.0000	.1732	.0000	.0000	.0000	.0000	.0363	.0000
Moharra	.0000	.0000	.2391	.0000	.0000	.0000	.0000	.0094	.0000	.0000	.0578	.0000	.0000	.0000	.0000	.0016	.0000
Benthic Inv. Feeders	.0000	.0000	.2833	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000
Pinfish	.0000	.0000	.2010	.0000	.0000	.0000	.0000	.0441	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000	.0000
Mullet	.0000	.0000	.5005	.0000	.0000	.0796	.0000	.0009	.0000	.0000	.0025	.0000	.0000	.0000	.0000	.0000	.0000

Table 2. The Output Structure Matrix for the Unperturbed Crystal River Marsh Gut Ecosystem. Each Entry Designates the Fraction of the Row Throughput which Flows to the Column Taxon Over All Direct and Indirect Pathways

	Microphytes	Macrophytes	Detritus	Zooplankton	Benthic Invertebrates	Stingray	Bay Anchovy	Needlefish	Sheepshead Killifish	Gold spotted Killifish	Gulf Killifish	Longnosed Killifish	Silverside	Moharra	Benthic Invertebrate Feeders	Pinfish	Mullet
Microphytes	1.000	.0000	.7699	.0844	.3045	.0015	.0005	.0004	.0008	.0008	.0015	.0008	.0046	.0022	.0004	.0004	.0160
Macrophytes	.0000	1.000	.7237	.0148	.2863	.0003	.0002	.0002	.0001	.0002	.0008	.0007	.0019	.0007	.0001	.0002	.0033
Detritus	.0000	.0000	1.000	.0239	.4610	.0005	.0004	.0003	.0002	.0003	.0013	.0011	.0030	.0012	.0001	.0003	.0053
Zooplankton	.0000	.0000	.5723	1.000	.2264	.0016	.0043	.0028	.0001	.0016	.0090	.0006	.0394	.0213	.0009	.0025	.0026
Benthic Inv.	.0000	.0000	.3809	.0078	1.000	.0003	.0006	.0005	.0001	.0004	.0025	.0029	.0050	.0015	.0001	.0006	.0017
Stingray	.0000	.0000	.2360	.0048	.0934	1.000	.0001	.0001	.0000	.0001	.0003	.0002	.0006	.0002	.0000	.0001	.0011
Bay Anchovy	.0000	.0000	.1991	.0041	.0787	.0016	1.000	.1908	.0000	.0001	.1399	.0002	.0005	.0002	.0000	.2091	.0009
Needlefish	.0000	.0000	.2417	.0050	.0956	.0001	.0001	1.000	.0000	.0001	.0003	.0002	.0006	.0002	.0000	.0121	.0011
Sheepshd Killifish	.0000	.0000	.5575	.0114	.2206	.0221	.0002	.0004	1.000	.0002	.0078	.0005	.0014	.0006	.0000	.0074	.0025
Goldsptd. Killifish	.0000	.0000	.4519	.0093	.1788	.0061	.0002	.0025	.0001	1.000	.0489	.0004	.0012	.0005	.0000	.0539	.0021
Gulf Killifish	.0000	.0000	.2359	.0048	.0933	.0107	.0001	.0001	.0000	.0001	1.000	.0002	.0006	.0002	.0000	.0001	.0011
Longnosed Killifish	.0000	.0000	.2376	.0049	.0940	.0002	.0001	.0095	.0000	.0001	.0059	1.000	.0006	.0002	.0000	.0002	.0011
Silverside	.0000	.0000	.3230	.0066	.1278	.0351	.0001	.0432	.0001	.0001	.1735	.0003	1.000	.0003	.0000	.0369	.0015
Moharra	.0000	.0000	.2949	.0060	.1167	.0008	.0001	.0095	.0001	.0001	.0581	.0003	.0008	1.000	.0000	.0018	.0013
Benthic Inv. Feeders	.0000	.0000	.3302	.0068	.1306	.0002	.0001	.0001	.0001	.0001	.0004	.0003	.0008	.0003	1.000	.0001	.0015
Pinfish	.0000	.0000	.2449	.0050	.0969	.0001	.0001	.0442	.0000	.0001	.0003	.0002	.0006	.0003	.0000	1.000	.0011
Mullet	.0000	.0000	.6028	.0124	.2385	.0799	.0002	.0011	.0001	.0002	.0031	.0006	.0015	.0006	.0000	.0002	1.000

generally more refactory than microphytes, one might guess that the contributions to the exported detritus would be weighted more heavily in favor of the macrophytes. Such is not the case, however, as indirect pathways and cycling actually decrease the predominance of macrophytically-fixed carbon to microphytically-fixed carbon down to 9.7. By hindsight the reason for the decrease is apparent. Macrophytes contribute solely to the detrital pool; whereas microphytes are grazed by several species, most notably zooplankton and mullet; and are cycled in the foodweb, thereby lowering the effective respiration rate.

The matrix of specific exchanges, F, was derived from the exchange matrix, P, by normalizing according to outputs. One may also normalize according to inputs by defining $g_{ij} = P_{ij}/T_j$. The corresponding structure matrix,

$$S' = (I-G)^{-1} ,$$

contains information about the direct and indirect sources of input to each compartment. S'_{ij} describes the fraction of throughput j which is attributable to i as a source. (In the event of cycling this fraction can exceed unity).

S' possess another very useful property. It is not difficult to demonstrate that the sum of each column of S' represents the average trophic position of its respective compartment (Levine, 1980). For example, if a taxon obtains 50% of its throughput directly from outside the system, 30% along pathways one step removed from a primary input, and 20% along pathways two steps removed from original sources, then it functions 50% of a primary producer, 30% as a "herbivore" and 20% as a "carnivore". Its average trophic position is thereby 1.7 (=0.5x1 + 0.3x2 + 0.2x3). Here one assumes that all flux entering from outside the system is considered at the first trophic level; otherwise the trophic positions of the inputs would be added to the column sum.

The average trophic positions of the 17 taxa in both of the Crystal River marsh guts are displayed in Table 3. The changes in the relative trophic rankings among the taxa are rather unremarkable. Perhaps the biggest winner is the Bay Anchovy which jumped from fourth place to ninth in the trophic rankings, even though its dietary habits changed little. What is quite curious, however, is that the trophic values for practically all taxa have risen in the disturbed creek. These observations raise more questions than they answer, and to clarify the picture it is necessary to expand the scope of observation from pairwise interactions to whole cycles of medium.

CYCLE ANALYSIS

The central role which I assume cycles to play in the develop-

Table 3. Ranked Listing of the Average Trophic Levels at Which Each Taxon is Feeding. Listed on the left-hand side are the rankings of taxa in the unperturbed marsh gut. On the right side the same taxa feed at slightly different levels in an identical marsh gut which has been chronically exposed to a 6°C elevation in temperature.

	Control		ΔT Perturbed	
Rank	Taxon	Av. Trophic Value	Taxon	Av. Trophic Value
1	Microphytes	1.00	Microphytes	1.00
2	Macrophytes	1.00	Macrophytes	1.00
3	Detritus	2.34	Detritus	2.47
4	Bay Anchovy	2.70	Mullet	3.09
5	Zooplankton	2.95	Zooplankton	3.11
6	Mullet	3.00	Sheepshead Killifish	3.11
7	Sheepshead Killifish	3.02	Benthic Invertebrates	3.47
8	Benthic Invertebrates	3.34	Goldspotted Killifish	3.62
9	Goldspotted Killifish	3.51	Bay Anchovy	3.93
10	Benthic Inv. Feeders	3.51	Moharra	4.15
11	Moharra	4.00	Silverside	4.27
12	Silverside	4.13	Longnosed Killifish	4.47
13	Stingray	4.22	Benthic Inv. Feeders	4.47
14	Pinfish	4.23	Pinfish	4.58
15	Longnosed Killifish	4.34	Gulf Killifish	4.69
16	Needlefish	4.45	Stingray	4.76
17	Gulf Killifish	4.57	Needlefish	4.76

ment of an ecosystem has already been mentioned. It is desirable, therefore, to be able to identify all the cycles inherent in a network and to seek clues as to how these various cycles might interact.

The enumeration of all the cycles in a graph is not always an easy task. In tracing through the various pathways of a network it soon becomes obvious that the number of possible paths and cycles can increase geometrically (or even factorially) as the number of components in the system rises. Hence, an arbitrary search for cycles in a network of, say, 20 components has the potential for quickly saturating the capabilities of even the larger modern computers ($20! = 24 \times 10^{18}$). Fortunately, however, algorithms are now available which efficiently enumerate cycles in networks of moderate size (Read and Tarjan, 1975; Johnson, 1975; Mateti and Deo, 1976; Ulanowicz, 1982a).

One might next ask whether the members of the list of cycles fall into any natural groupings. As ecologists we are often concerned with the vulnerability of any structure. To someone familiar with a given ecosystem, it may be possible for him to trace around the links of any chosen cycle and identify the most vulnerable transfer in the loop. Once a vulnerable link has been established in each cycle, the circuits can then be grouped in such a way that all the members of any group share the same most vulnerable arc. In a real sense each vulnerable arc is a weak spot in the network, and its domain of influence upon the feedback structure is defined by the collection of cycles in which it appears, hereinafter referred to as its nexus.

To be more specific, one counts 119 distinct cycles in the graph of the control creek, as listed in Appendix A. For the sake of discussion we shall choose the smallest link in each cycle to be that loop's most vulnerable arc. The 119 cycles segregate into 41 nexuses. Several of these aggregations are rather large, one consisting of 14 separate cycles, one of 13, one of 10, three of 6, etc. The largest nexus is depicted in Figure 5 (with the vulnerable link denoted by the heavy arrow). In contrast, the heated creek foodweb contains only 46 simple cycles belonging to 30 nexuses (Appendix B). None of the large nexuses cited in the control creek survives in the perturbed system. The largest nexus in the disturbed network is a single, 4-cycle grouping.

There are further differences between the two networks when one notes the magnitudes of the vulnerable arcs. The weak links in all

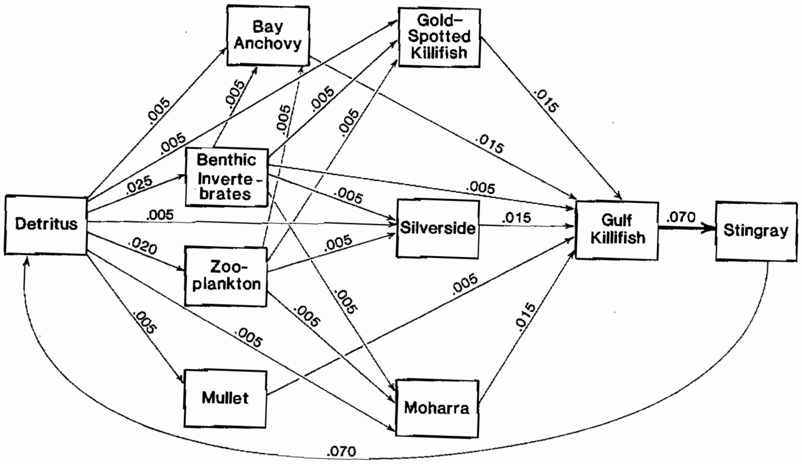

Fig. 5. The nexus of cycles associated with the cropping of Gulf Killifish (11) by Stingray (6). The flows shown (in mgC/m/d) are the amounts actually subtracted from the original flows in Figure 3 in the process of calculating the residual acyclic web.

of the many-cycled nexuses of the control system were small in magnitude, and the component cycles tended to consist of 4 or 5 links. In both systems the vulnerable arcs with the highest flows were associated with short, 2 step cycles. For example, the loop with largest flow in both webs was the immediate recycle of carbon between the detritus and the benthic invertebrates. This turnover actually increased from 687 in the control to 734 ($mgC/m^2/d$) in the perturbed system. Likewise, the turnover between zooplankton and detritus rose from 73 to 78 ($mgC/m^2/d$) in the disturbed creek. The fraction of total flow which was being cycled (see Finn, 1977) actually went up from 10.5% in the control to 14.0% in the heated system.

Some of these observations seem counterintuitive when viewed alone. For example, Finn echoed Odum's (1969) suggestion that a higher fraction of cycled flow was indicative of more mature, less disturbed networks. Nonetheless, cycle analysis reveals a coherent picture of what has happened to the heated system. It is a clear-cut instance of eutrophication. The higher-order (presumably slower) cycles have disappeared. The shorter, faster, trophically lower, turnovers now cycle more intensely. Whether the rise of the intense, short cycles caused the disappearance of the higher-order cycles (as is presumed to be the case in cultural eutrophication), or whether the increase in short cycling was occasioned by some dysfunctions in the longer loops is a moot point in the realm of cybernetics.

The trophic response of the Bay Anchovy to community stress is now clear. The diet of this species appears to consist entirely of detritus, zooplankton and benthic invertebrates - all of the players involved in the accelerated short cycles. It was in a perfect position to exploit the eutrophic changes. We also see that the general rise in trophic values after perturbation was somewhat misleading, as it was inflated by the rapid multiple passes through the shorter, but more intense, cycles.

A consistent picture of the underlying trophic dynamics in both networks can be obtained by first subtracting away all cycled flow and analyzing the residual acyclic webs. This decomposition of an arbitrary graph into cyclic and acyclic subgraphs is not a trivial problem. An approach based on the scheme of aggregation by smallest arc has been described by the author (Ulanowicz, 1982b). Suffice it to remark that in an acyclic network, any component which feeds at more than one trophic level can be unequivocally partitioned among the compartments of a finite, concatenated food chain in the sense of Lindemann (see also Ulanowicz and Kemp, 1979). In our previous example the species acting 50% as a primary producer, 30% as a herbivore and 20% as a carnivore would have its throughput, exports and respirations apportioned among the first three trophic compartments in the ratio 5:3:2. The acyclic subgraphs of the two creeks

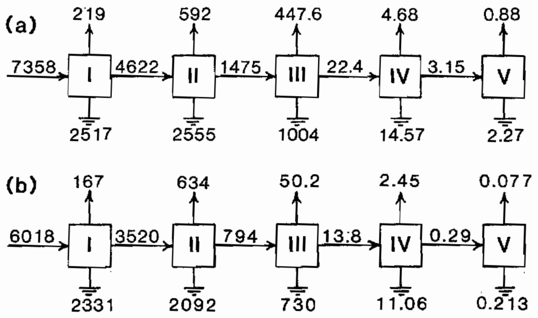

Fig. 6. Aggregated trophic flows of carbon (mgC/m^2/d) inherent in the web exchanges (Figures 3 and 4) after the cycled material has been removed from the network. (a) the control marsh gut; (b) the thermally stressed marsh gut.

can be mapped into straight trophic chains of length 5. The differences in the first two levels are small, but flows at the third level of the disturbed system are halved and fall off nearly tenfold at the fifth step (see Figure 6). Again, the effects of stress are more obvious at higher trophic levels.

GLOBAL COMMUNITY MEASURES

The story of network response to perturbation can be read in reverse to gain insights into the manner in which ecosystem networks develop in the relative absence of stress. Two attributes crucial to such a description are size and structure. One expects the winners in the evolutionary game to possess advantageous combinations of size and structure. (One need not think of systems competing with one another, rather one compares the actual state of the system with other putative nearby states).

A convenient measure of the size of a flow network is the total system throughput, the sum of all the individual throughputs, T_i. All other things being equal, one expects the total systems throughput to rise during the course of the development (living things grow); or, conversely, fall due to perturbation (as did the total throughput of the disturbed creek). It was also apparent how the diversity of the structure was adversely affected by perturbation and, conversely, would be expected to rise during unperturbed development. Hence, one is led to consider the diversity of the various throughputs as a measure of this complexity, i.e.

$$- \sum_i Q_i \log Q_i,$$

where Q_i ($=T_i/\sum_j T_j$) is the fraction of the total throughput particular to component i. The product of size and complexity is conveniently called the development capacity,

$$C = - T \sum_j Q_j \log Q_i,$$

where T has been taken to represent the total throughput ($\sum_j T_j$).

The inadequacy of using C as a measure of development is precisely what plagued the epochal diversity-stability arguments, namely how the compartments are related to one another does not appear in the formula. But the coefficients f_{ij} quantify how the output of one compartment is linked to the input of another. Accordingly, one may define

$$A = T \sum_i \sum_j f_{ij} Q_i \log (f_{ij} / \sum_k f_{kj} Q_k)$$

as a component of C which captures how coherently, or with what degree of definition, the elements are connected to one another (Rutledge et al., 1976; Ulanowicz, 1980).

One can show mathematically that C serves as an upper bound on A and that both quantities are inherently non-negative, i.e.,

$$C \geq A \geq 0$$

That portion of the capacity which does not appear as coherent structure (i.e., the difference, C-A) is termed the overhead, and may be further decomposed into three components. The first component results from the obligatory dissipative processes.

$$S = - T \sum_i r_i Q_i \log Q_i$$

where r_i is the fraction of T_i lost to dissipation, i.e. subsystem-scale processes. The second component allows for transfer to other systems.

$$E = - T \sum_i e_i Q_i \log Q_i$$

where e_i is the fraction of T_i flowing to another system. These exports make up the links in any assembled suprasystem and may be thought of as contributions to higher order structure. The residual overhead

$$R = - T \sum_i \sum_j f_{ij} Q_i \log(f_{ij} Q_i / \sum_k f_{kj} Q_k)$$

can also be shown to be non-negative and measures the average multiplicity of pathways among the components; or, alternatively, the degree of confusion as to where within the network an arbitrary output might flow. It is (like A) a property existing at the level of the system. Hence, the overhead has been partitioned along hierarchical lines.

Returning to A, the ascendency, it captures the tradeoff between system size and structure and could possibly serve as the criterion describing the time evolution of an ecosystem flow network. In fact the increases in A so paralleled the increases in other attributes of mature ecosystems (e.g. Odum, 1969) that I have elsewhere (Ulanowicz, 1980) hypothesized that self-organizing communities behave over an adequate interval of time so as to optimize their ascendencies subject to hierarchical and environmental constraints. Regardless of whether or not this hypothesis will subsequently be validated, the five quantities defined above provide a lexicon for describing community level change in flow networks.

Any data set on flows meeting the requirements specified earlier in this paper is sufficient to calculate the network ascendency and related variables. In the creek networks the ascendency has decreased from 7235 ($mgC/m^2/d$) in the control to 5349 in the disturbed creek, as one might expect from the converse of the ascendency hypothesis. The magnitude of the decrease is somewhat misleading, as it reflects mostly the decrease in systems throughput. The organizational factor in the ascendency has decreased by only 7%, indicating strong structural homeostatsis. The resistance of structure to change emphasizes the utility of the cycle analysis in dramatizing the otherwise subtle changes which have taken place in the network topology. The overall increase in the relative amount of overhead came from nearly equal increases in dissipation and redundancy. The fraction of C encumbered by tribute, E, actually fell in the disturbed network, reflecting the homeostatic response of the system in tightening the remaining cycles.

Concluding Remarks

I would like to end this brief synopsis of network flow analysis with the opinion that the approach is eminently ecological in nature. The focus is upon the interactions, rather than upon the taxa themselves. The field of vision encompasses the entire community of processes. The attitude is phenomenological, or empirical; one is concerned with a quantitative description of what actually happened, rather than with the supposition of causes, real or fictitious. This is not to denigrate the need for inference, but only to postpone suppositions until more familiarity with community level descriptions has been achieved. It is my belief that the sought-after inferences or laws will become most readily apparent at the level of the entire ecosystem.

This last probability is philosophically satisfying. Phenomena at a smaller scale may appear confusing, unexpected or contradictory. But the larger picture seems coherent and directions well-defined. Of course, this mirrors the results of the most phenomenological branch of physical science - thermodynamics. In fact ecological phenomenology, as typified by flow network analysis, may yet extend the frontiers of thermodynamics. Nevertheless, to formulate principles by searching at larger scales of observation violates the prevailing dogma of the biological sciences today — reductionism. In all likelihood the world, cybernetic as it appears, will reveal influences going in both holistic and reductionistic directions. Right now, however, such a small fraction of biological research effort is aimed at elucidating more global principles, that I believe a bottleneck impeding our deeper understanding of the natural work exists. It is to help overcome such an impediment that this conference has been called to promote the measurement of ensembles of flows occurring in marine ecosystems.

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APPENDIX A

Cycle Analyses (Control Creek)

3-Cycle Nexus with Weak Arc (10, 6) = .010

1. 3-10- 6- 3-
2. 3- 4-10- 6- 3-
3. 3. 5-10- 6- 3-

6-Cycle Nexus with Weak Arc (14,16) = .010

4. 3-14-16-3-
5. 3-14-16- 8- 3-
6. 3- 4-14-16- 3-
7. 3- 4-14-16- 8- 3-
8. 3- 5-14-16- 3-
9. 3- 5-14-16- 8- 3-

4-Cycle Nexus with Weak Arc (9,11) = .010

10. 3- 9-11- 3-
11. 3- 9-11- 6- 3-
12. 3- 5- 9-11- 3-
13. 3- 5- 9-11- 6- 3-

4-Cycle Nexus with Weak Arc (9,16) = .010

14. 3- 9-16- 3-
15. 3- 9-16- 8- 3-
16. 3- 5- 9-16- 3-
17. 3- 5- 9-16- 8- 3-

13-Cycle Nexus with Weak Arc (8,16) = .020

18. 3- 7- 8-16- 3-
19. 3-13- 8-16- 3-
20. 3-14- 8-16- 3-
21. 3- 4- 7- 8-16- 3-
22. 3- 4-13- 8-16- 3-
23. 3- 4-14- 8-16- 3-
24. 3- 5- 8-16- 3-
25. 3- 5- 7- 8-16- 3-
26. 3- 5-13- 8-16- 3-
27. 3- 5-14- 8-16- 3-
28. 3- 5-12- 8-16- 3-
29. 3-17- 8-16- 3-
30. 8-16- 8-

2-Cycle Nexus with Weak Arc (9, 6) = .030

31. 3- 9- 6- 3-
32. 3- 5- 9- 6- 3-

2-Cycle Nexus with Weak Arc (12,11) = .030

33. 3- 5-12-11- 3-
34. 3- 5-12-11- 6- 3-

1-Cycle Nexus with Weak Arc (17, 8) = .030

35. 3-17- 8- 3-

1-Cycle Nexus with Weak Arc (12, 8) = .050

36. 3- 5-12- 8- 3-

3-Cycle Nexus with Weak Arc (14, 8) = .060

37. 3- 14- 8- 3-
38. 3- 4-14- 8- 3-
39. 3- 5-14- 8- 3-

14-Cycle Nexus with Weak Arc (11, 6) = .070

40. 3- 7-11- 6- 3-
41. 3-10-11- 6- 3-
42. 3-13-11- 6- 3-
43. 3-14-11- 6- 3-
44. 3- 4- 7-11- 6- 3-

45. 3- 4-10-11- 6- 3-
46. 3- 4-13-11- 6- 3-
47. 3- 4-14-11- 6- 3-
48. 3- 5-11- 6- 3-
49. 3- 5- 7-11- 6- 3-
50. 3- 5-10-11- 6- 3-
51. 3- 5-13-11- 6- 3-
52. 3- 5-14-11- 6- 3-
53. 3-17-11- 6- 3-

1-Cycle Nexus with Weak Arc (3,15) = .070

54. 3-15- 3-

1-Cycle Nexus with Weak Arc (17,11) = .080

55. 3-17-11- 3-

10-Cycle Nexus with Weak Arc (16, 8) = .090

56. 3- 7-16- 8- 3-
57. 3-10-16- 8- 3-
58. 3-13-16- 8- 3-
59. 3- 4- 7-16- 8- 3-
60. 3- 4-10-16- 8- 3-
61. 3- 4-13-16- 8- 3-
62. 3- 5-16- 8- 3-
63. 3- 5- 7-16- 8- 3-
64. 3- 5-10-16- 8- 3-
65. 3- 5-13-16- 8- 3-

3-Cycle Nexus with Weak Arc (10,11) = .090

66. 3-10-11- 3-
67. 3- 4-10-11- 3-
68. 3- 5-10-11- 3-

3-Cycle Nexus with Weak Arc (10,16) = .100

69. 3-10-16- 3-
70. 3- 4-10-16- 3-
71. 3- 5-10-16- 3-

1-Cycle Nexus with Weak Arc (5, 8) = .120

72. 3- 5- 8- 3-

1-Cycle Nexus with Weak Arc (4,15) = .140

73. 3- 4-15- 3-

1-Cycle Nexus with Weak Arc (5, 9) = .150

74. 3- 5- 9- 3-

1-Cycle Nexus with Weak Arc (15, 3) = .170

75. 3- 5-15- 3-

3-Cycle Nexus with Weak Arc (7, 3) = .220

76. 3- 7- 3-
77. 3- 4- 7- 3-
78. 3- 5- 7- 3-

1-Cycle Nexus with Weak Arc (4,10) = .220

79. 3-4-10- 3-

6-Cycle Nexus with Weak Arc (8, 3) = .340

80. 3- 7- 8- 3-
81. 3-13- 8- 3-
82. 3- 4- 7- 8- 3-
83. 3- 4-13- 8- 3-
84. 3- 5- 7- 8- 3-
85. 3- 5-13- 8- 3-

2-Cycle Nexus with Weak Arc (3, 7) = .370

86. 3- 7-11- 3-
87. 3- 7-16- 3-

3-Cycle Nexus with Weak Arc (14,11) = .370

88. 3-14-11- 3-
89. 3- 4-14-11- 3-
90. 3- 5-14-11- 3-

6-Cycle Nexus with Weak Arc (16, 3) = .410

91. 3-13-16- 3-
92. 3- 4- 7-16- 3-
93. 3- 4-13-16- 3-
94. 3- 5-16- 3-
95. 3- 5- 7-16- 3-
96. 3- 5-13-16- 3-

2-Cycle Nexus with Weak Arc (7,11) = .500

97. 3- 4- 7-11- 3-
98. 3- 5- 7-11- 3-

3-Cycle Nexus with Weak Arc (13, 6) = .510

99. 3-13- 6- 3-
100. 3- 4-13- 6- 3-
101. 3- 5-13- 6- 3-

1-Cycle Nexus with Weak Arc (5,10) = .610

102. 3- 5-10- 3-

1-Cycle Nexus with Weak Arc (9, 3) = .650

103. 3- 9- 3-

1-Cycle Nexus with Weak Arc (6, 3) = .650

104. 3-17- 6- 3-

1-Cycle Nexus with Weak Arc (10, 3) = .680

105. 3-10- 3-

1-Cycle Nexus with Weak Arc (3,14) = .900

106. 3-14- 3-

2-Cycle Nexus with Weak Arc (3,13) = .970

107. 3-13- 3-
108. 3-13-11- 3-

1-Cycle Nexus with Weak Arc (12, 3) 1.060

109. 3- 5-12- 3-

3-Cycle Nexus with Weak Arc (11, 3) = 1.320

110. 3- 4-13-11- 3-
111. 3- 5-11- 3-
112. 3- 5-13-11- 3-

2-Cycle Nexus with Weak Arc (14, 3) 1.530

113. 3- 4-14- 3-
114. 3- 5-14- 3-

2-Cycle Nexus with Weak Arc (13, 3) 3.380

115. 3- 4-13- 3-
116. 3- 5-13- 3-

1-Cycle Nexus with Weak Arc (17, 3) = 16.290

117. 3-17- 3-

1-Cycle Nexus with Weak Arc (4, 3) = 73.200

118. 3- 4- 3-

1-Cycle Nexus with Weak Arc (5, 3) = 686.900

119. 3- 5- 3-

APPENDIX B

Cycle Analyses (Perturbed Creek)

3-Cycle Nexus with Weak Arc (6, 3) = .010

1. 3- 7- 6- 3-
2. 3- 4- 7- 6- 3-
3. 3- 5- 7- 6- 3-

3-Cycle Nexus with Weak Arc (10,11) = .010

4. 3-10-11- 3-
5. 3- 4-10-11- 3-
6. 3- 5-10-11- 3-

2-Cycle Nexus with Weak Arc (9,11) = .010

7. 3- 9-11- 3-
8. 3- 5- 9-11- 3-

1-Cycle Nexus with Weak Arc (17, 6) = .010

9. 3-17- 6- 3-

1-Cycle Nexus with Weak Arc (11,11) = .010

10. 11-11-

1-Cycle Nexus with Weak Arc (5, 9) = .040

11. 3- 5- 9- 3-

3-Cycle Nexus with Weak Arc (8, 3) = .060

12. 3- 7- 8- 3-
13. 3- 4- 7- 8- 3-
14. 3- 5- 7- 8- 3-

2-Cycle Nexus with Weak Arc (3, 13) = .060

15. 3-13- 3-
16. 3-13-11- 3-

1-Cycle Nexus with Weak Arc (17,11) = .060

17. 3-17-11- 3-

1-Cycle Nexus with Weak Arc (17, 8) = .060

18. 3- 17- 8- 3-

4-Cycle Nexus with Weak Arc (16, 3) = .070

19. 3- 7-16- 3-
20. 3- 4- 7-16- 3-
21. 3- 5- 7-16- 3-
22. 3- 5-16- 3-

1-Cycle Nexus with Weak Arc (4,10) = .070

23. 3- 4-10- 3-

1-Cycle Nexus with Weak Arc (3,14) = .110

24. 3-14- 3-

2-Cycle Nexus with Weak Arc (14, 3) = .160

25. 3- 4-14- 3-
26. 3- 5-14- 3-

1-Cycle Nexus with Weak Arc (12,11) = .170

27. 3- 5-12-11- 3-

1-Cycle Nexus with Weak Arc (9, 3) = .180

28. 3- 9- 3-

2-Cycle Nexus with Weak Arc (13, 3) = .180

29. 3- 4-13- 3-
30. 3- 5-13- 3-

1-Cycle Nexus with Weak Arc (5,10) = .190

31. 3- 5-10- 3-

1-Cycle Nexus with Weak Arc (10, 3) = .210

32. 3-10- 3-

1-Cycle Nexus with Weak Arc (4,13) = .330

33. 3- 4-13-11- 3-

1-Cycle Nexus with Weak Arc (13,11) = .330

34. 3- 5-13-11- 3-

3-Cycle Nexus with Weak Arc (7,11) = .370

35. 3- 7-11- 3-
36. 3- 4- 7-11- 3-
37. 3- 5- 7-11- 3-

1-Cycle Nexus with Weak Arc (15, 3) = .470

38. 3- 5-15- 3-

1-Cycle Nexus with Weak Arc (11, 3) = .540

39. 3- 5-11- 3-

1-Cycle Nexus with Weak Arc (12, 3) = .700

40. 3- 5-12- 3-

1-Cycle Nexus with Weak Arc (5, 7) = 2.100

41. 3- 5- 7- 3-

2-Cycle Nexus with Weak Arc (7, 3) = 4.690

42. 3- 7- 3-
43. 3- 4- 7- 3-

1-Cycle Nexus with Weak Arc (17, 3) = 11.640

44. 3- 17- 3-

1-Cycle Nexus with Weak Arc (4, 3) = 78.100

45. 3- 4- 3-

1-Cycle Nexus with Weak Arc (5, 3) = 742.600

46. 3- 5- 3-

BOOK REVIEW

Michael Conrad, *ADAPTABILITY: The Significance of Variability from Molecule to Ecosystem*, Plenum Press, 1983, 383 pp., $42.50

The author acknowledges in the preface that the writing of this book spanned 19 years, in more than 17 institutions, located in at least seven countries. The potential reader, in thumbing through the volume, might wonder whether a proportional commitment of time and energy is required to digest the work. Such fears are hardly exaggerated—this book is not for the casual reader. The crucial question, however, is whether perseverance on the part of the reader will be rewarded.

The central thesis is rather simple, but nonetheless profound. Biological dynamics are usually described using mathematical tools developed in the physical sciences, where variations on an underlying principle are considered noise to be discarded. Many biologists are convinced that it is wrong to neglect such variability, and theoreticians such as Ashby, Atlan, and Prigogine have highlighted the importance of variability in developing systems. Conrad goes further to contend that variability is *the fundamental object* from which dynamics (or more primitively, state transitions) are inferred.

If Conrad is correct in his assertion, then society needs to reconsider the ways in which it plans for the future. The designs of man are predominantly concerned with predictability and efficiency at the necessary expense of variability. But designs that are successful in achieving high efficiency are ultimately doomed to fail because they lack the requisite variability to deal with inevitable stochastic events.

If this seems rather self-evident to anyone with a tolerant frame of mind, one need not look far to find evidence of those who are blissfully unaware of such a paradox. For example, one reads accounts of efforts to simulate intelligence algorithmically on machines of high reliability and precision. Conrad points out the crucial role that stochasticity, unreliability, and imprecision play in the workings of the brain and in the development of true intelligence. He shows how the "gradual transformability" necessary for intelligence is impossible with the "nondecomposable" systems in use today, thus implying that the present attempts are akin to earlier efforts to realize perpetual motion. Of course, the number of persons concerned with artificial intelligence pales in comparison to the legion of political and economic ideologues who would impress their precise visions of an efficient society upon the world!

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Familiar tools, such as probabilities, entropies, and conditional entropies are used to give concrete mathematical expression to the different forms of variability. The algebra expressing the relationships among these forms is not tedious.

If the book bears upon such weighty and exciting matters using only intermediate level mathematics, what, then, makes it so excruciatingly difficult to digest? In my opinion the author tries to cover too much in one volume. He is understandably enamored of the generality of his thesis and is anxious to demonstrate its applicability to a wide range of systems extending "from molecule to ecosystem." To do this, he finds it necessary to create a seemingly endless array of verbal concepts and mathematical symbols.

To further complicate matters, there is simply no room to present enough background material on thermodynamics, information theory, genetics, evolution, physiology, ecology, molecular biology, and cybernetics, so the author presupposes that the reader is fluent in these fields. Therefore, anyone lacking depth in *all* these disciplines (and that includes virtually everyone) is apt to lose patience with the author at some point along the way.

"Needless to say, any formalism which is capable of coping with the full complexity of adaptability processes in nature must itself be complex," the author warns in the preface. But I strongly suspect that the significance of adaptability could be more effectively impressed upon the reader without having to consider "the full complexity." One can only wish that the author had rounded out a score of years and taken the time to ruthlessly prune the manuscript into a more efficient text. (But in all fairness the present form is at least self-consistent with the author's caution against overemphasis on design.)

Lest anyone get the wrong impression, I regard Michael Conrad as a strong contributor to the inchoate domain of ~~the~~ theoretical biology. Anyone in the field who is unwilling to tease out the author's insights from among the welter of definitions is likely to be at a disadvantage in the exciting debates that loom in the near future. If only someone could convince Professor Conrad to be a little less self-consistent!

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