Identifying the Structure of Cycling in Ecosystems

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ABSTRACT

Given a steady-state network of flows within an ecosystem, it becomes possible to systematically and automatically enumerate all distinct simple cycles of flows. Cycles may be grouped according to shared smallest arcs. The original network may then be decomposed into a web of purely cycled flow and a residual acyclic graph consisting of once-through pathways. The aggregation of elementary cycles according to shared vulnerable arcs seems particularly effective in locating those transfers which stress is most likely to disturb.

INTRODUCTION

A large fraction of the elements composing living matter reside at any instant of time in the world's biota. Because the earthly pool of these elements is limited and the rates of exchange among the various components of the biota are extremely fast with respect to geological time, it is quite evident that much of the same material is being incorporated again and again into different biological forms. This observation gives rise to the notion that, on the average, matter (and some amounts of energy) are involved in cycles.

Although an overwhelming amount of ecological research has been directed towards cycling as a mechanism of renewal and towards establishing the rates of individual transfer steps in cycles, relatively little effort has been expended in formally describing the aggregate structure of the loops. However, there are several theoretical and operational reasons why one might want to separate the nexus of cycled flow from its supporting single-pass network.

Perhaps the foremost reason for studying cycle structure is the notion that the positive feedback associated with these cycles is the critical phenomenon determining overall system structure. Positive feedback is self-stimulatory,
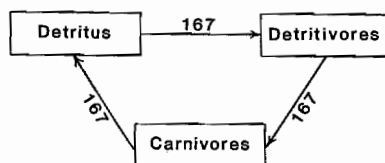
FIG. 1. Hypothetical perfect cycle of material or energy (see text).

that is, an increase in the output of any element in a cycle when traced around the loop will engender a further increase in the starting flow. For example, in the simple loop depicted in Figure 1, an increase in detritus is likely to enhance detritivory, thereby stimulating carnivory and eventually adding detritus to the starting compartment. In purely linear systems such feedback leads to global instability of the system. Positive feedback in real systems is limited, however, by the finite amount of matter or energy available and especially by the necessary losses incurred at each step in the feedback loop (the second law of thermodynamics); see also [1]. In the face of these limitations, those compartments engaged in positive cycling might possess a strong competitive advantage over nonparticipating compartments during any phase of total system growth. Furthermore, in systems with time lags positive feedback can actually be a stabilizing factor.[1]

A second reason for wanting to study the structure of cycling lies in the contribution of cycles to any autonomous behavior the system might exhibit. Autonomous behavior cannot be traced to exogenous causes. Most logical analysis concerns cause-effect, deterministic relationships; e.g., an increase in detritivory (cause) stimulates carnivory (effect). Each (nonautonomous) process is considered to be traceable to influences exterior to the system. Supposing, however, that the cycle in Figure 1 could exist in isolation, one is then confronted with a perfect causal loop. Detritivory (cause) becomes detritivory (effect). The behavior of the feedback loop cannot be attributed to external causes, nor will it suffice to consider only a segment of the cycle (nonautonomous by definition). Loop behavior is only properly perceived as an autonomous attribute of the entire cycle ensemble.

The fact that a perfect causal loop cannot exist in isolation does not make autonomous behavior irrelevant to real systems. As an example of the semiautonomous nature of most ecosystem networks, consider the energy-flow diagram of Cone Springs as depicted by Williams and Crouthamel[2] in Figure 2(a). By inspection one can identify five simple, directed cycles in the graph, as in Figure 2(b). (A simple cycle is one in which no node appears more than

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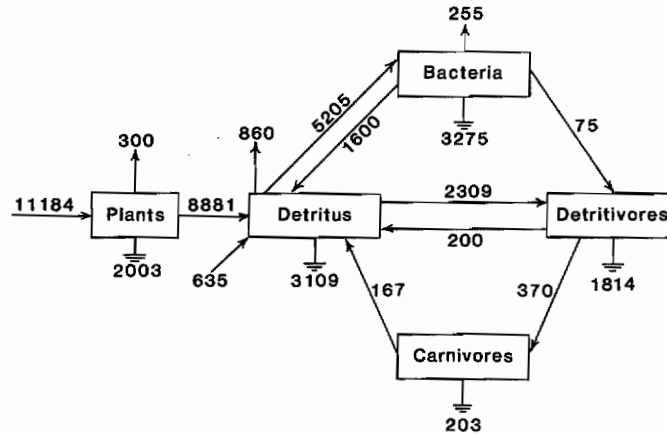
[1]R. Nisbet, personal communication.
[2]Unpublished manuscript.

FIG. 2. (a) Energy flow in Cone Springs ecosystem, measured in kC/m^2 yr (Williams and Crouthamel, unpublished). Ground symbols represent losses to respiration.

once.) Furthermore, as will be seen, it is possible to assign flow values to each of the perfect cycles, so that when the cycles are subtracted from the original graph, the resultant network is acyclic, as shown in Figure 2(c). Although such decomposition is an analytical artifact, it nonetheless demonstrates that most real flow systems (and the behavior they exhibit) are interdependent combinations of autonomous and nonautonomous graph components. Certainly, the pure cycles cannot exist alone—their circulations are supported by the once-through flow system. Reciprocally, the magnitudes of the acyclic network are presumably abetted by the feedback cycles. I wish to associate the acyclic structure with the identification of trophic dynamics, whereas the cycles are to serve as the basis for autonomous behavior in ecosystems.

There has been much controversy about the existence of what has been termed either emergent or holistic behavior of ecosystems [2–7]. It appears likely that emergent behavior derives from the autonomous nature of ecosystem cycles. It should be remarked in passing that autonomous phenomena lie at the very foundations of ecology as a *systems* science. Otherwise, strict reductionists might be justified in their attempts to portray all ecological events as ultimately derived from biomolecular structures. By contrast, the ecosystems viewpoint recognizes behavior particular to each level of biological hierarchy, and events at any one level are involved cybernetically with (i.e., affect and are affected by) circumstances at levels above *and below* the level of observation.

In keeping with the notion that autonomous behavior is an earmark of more developed systems, E. P. Odum identified the degree of cycling as an
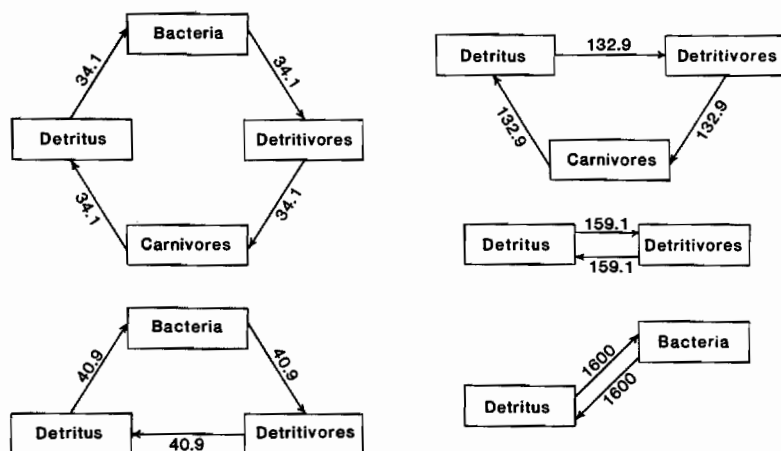
FIG. 2.   (b) Five simple cycles existing in the network in (a).

indicator of more mature communities [8]. Finn has defined an index of cycling to test this idea quantitatively, but his calculations concern only the quantity of cycled medium and do not touch upon the identification of cycle structure [9].

Odum cited twenty-three additional attributes of mature systems, and other theorists have since advanced other system attributes which they
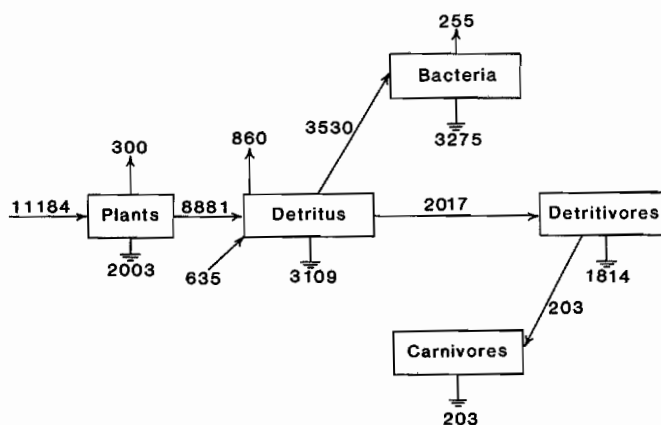

FIG. 2.   (c) Residual acyclic network after cycles in (b) have been subtracted from network in (a).

believe are optimized by more developed ecosystems [10–13]. Doubtless a better understanding of each of these ecosystem properties would result from a systematic description of the underlying network of cycled flow.

Finally, there are purely operational reasons why knowing the structure of cycled flow would be necessary to accomplish other analytical objectives. For instance, many algorithms available to optimize global properties of flow networks require at least a qualitative knowledge of cycle structure [14]. In ecology the effort to map an arbitrary flow network into concatenated discrete trophic levels has been complicated by the presence of cycles [15]. If, in general, one were able to decompose a network as in Figure 2, a trophic analysis of the residual acyclic network would yield a simplified picture of the trophic-dynamic status of the system. Trophic levels would thereby appear less as pure abstractions and more as objects which can be quantified.[3]

METHODS OF CYCLE ANALYSIS

The problem of completely specifying the cycle network has both qualitative and quantitative dimensions. Qualitatively, one usually needs to identify and enumerate every cycle in an arbitrary network. Quantitatively, one must assign a flow value to each cycle so that the set of cycles can be subtracted from the original network, leaving a realistic graph of unidirectional (acyclic) pathways. Finally, one should ask whether a scheme exists for aggregating the single cycles into subsets which are useful in the analysis of the effects of perturbations on ecosystems.

Enumerating by inspection all five cycles in Figure 2(b) was an easy task. In general, however, the number of possible cycles in a network with even a moderate number of components can become quite large. Those familiar with combinatorics will recognize that the number of potential cycles increases at least as $n!$, where n is the number of components (nodes) in the network. As this number rises faster than exponentially, it does not take long to exceed the limits of even the largest and fastest computers available today.

Fortunately, the problem of identifying cycles in ecosystems is mitigated by the observation that most ecological networks realize only a small fraction of the number of possible direct connections ($\propto n^2$) [16], and most path lengths rarely exceed five transfers. Still, if one wishes to treat ecosystem networks with 25 or more components, it behooves one to choose algorithms which are as efficient as possible. Mateti and Deo have reviewed the general methods of enumerating cycles in graphs and have concluded that backtracking search algorithms with suitable pruning methods (to eliminate many futile search pathways) are the most efficient programs in the greatest number of circumstances [17].

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[3]B. C. Patten, personal communication.

Backtracking search algorithms are very compact programs, but require rather lengthy description. One begins by choosing an order in which to consider the various nodes, or compartments. Taking as an example the Cone Springs network, it is convenient (see below) to choose the order (1) detritus, (2) bacteria, (3) detritivores, (4) carnivores, and (5) plants. Next, as an aid to description it is useful to visualize the order of compartments repeated at six successive levels, beginning with level 0 as shown here:

	Compartment				
0	1	2	3	4	5
1	1	2	3	4	5
2	1	2	3	4	5
3	1	2	3	4	5
4	1	2	3	4	5
5	1	2	3	4	5

Level is labeled to the left of levels 0–5.

One always searches for connections in the array working from left to right. Starting at the first element in level 0, one checks the list of connections for the first entry in level 1 to which an arc exists (node 2 in this case). Attention then shifts up to level 1, and a search is begun for a further connection from node 2 in level 1 to a node in level 2. One proceeds in this manner to as high a level as possible, always keeping track of the positions last visited in each previous level. This list of the last node visited in each previous level defines the current pathway and is the only storage required beyond the list of actual links. To keep the search confined to simple cycles it is necessary to prohibit a move to the next level ending in a node which is already in the current pathway.

Such a "depth-first" search continues to ever higher levels, until one of two events takes place. If an arc exists to the starting node in the next level, then a cycle has been identified, and the current pathway is reported or stored. If all the possible nodes in the next level have been exhausted (one runs beyond the right-hand limits), then one "backtracks" to the node in the current pathway at the preceding level and starts searching the next higher level at the node to the right of the one from which backtracking took place. For example, if one is searching from node m in level q and runs out of possibilities in level $q + 1$, then one backtracks to node p (the $q - 1$ entry in the current pathway) in level $q - 1$ and resumes searching at level q with node $m + 1$. When no further backtracking is possible, all the cycles containing the present starting node have been identified. The present starting node may be eliminated from all further searching, and the dimension of the search originating from the next starting node is thereby reduced by one.

For the reader wishing to practice this method on the Cone Springs network, the following lists of key operations and current pathways for the

search beginning with the detritus compartment (1) should prove helpful:

Key operation	Current pathway
Begin with node 1 in level 0	1
Advance to level 1	1-2
Store cycle #1	1-2-1
Advance to level 2	1-2-3
Store cycle #2	1-2-3-1
Advance to level 3	1-2-3-4
Store cycle #3	1-2-3-4-1
Backtrack to level 2	1-2-3
Backtrack to level 1	1-2
Backtrack to level 0	1
Advance to level 1	1-3
Store cycle #4	1-3-1
Advance to level 2	1-3-4
Store cycle #5	1-3-4-1
Backtrack to level 1	1-3
Backtrack to level 0	1
Further backtracking impossible	—
Begin with node 2 in level 0	2
⋮	⋮

It accidentally happens that all cycles are found starting at the detritus node and searches beginning with the other nodes detect no further cycles.

Read and Tarjan [18] and Johnson [19] give examples of constraints on the backtracking procedure, which result in more efficient searching. For the purposes of this work it has proven sufficient to preordain in a judicious manner the sequence in which the candidate nodes are to be considered. One wishes to test first those nodes for which the probability of completing a cycle at any step is the greatest. This probability is proportional to the number of cycle arcs terminating in the given node. (A *cycle arc* with respect to a given node is any connection from a descendant node to one of that decendent's ancestors.) Since all the descendants of a given node may be quickly determined [20], it becomes an easy matter to count the cycle arcs back into each node and establish the proper sequence for testing nodes. Of course, nodes with no incoming cycle arcs may be eliminated from the backtracking procedure at the very outset. (It was never necessary to consider the plants in the Cone Spring example.)

Having exhaustively enumerated the cycles, one now wishes to attach a quantity of flow to each loop, so that when all the cycle flows are subtracted from the original graph, no residual flow will become negative and no cycles

will remain. Obviously, the quantity assigned to a cycle must bear some relationship to the quantities of flow in the constituent arcs. But the various arcs in the cycle differ in magnitude. Is there some reason for placing more emphasis on one particular arc? The assumption made here is similar to the concept of the rate limiting step in chemical kinetics, i.e., the critical arc in a cycle is taken to be the one in which the smallest flow (or, equivalently, the slowest rate of transfer) takes place.

If the cycles in networks were never to overlap, the method for separating cycles from the underlying flow would be straightforward. One would identify the critical arc in each cycle and subtract the magnitude of that critical arc from each link in the cycle. The critical arc would disappear from the cycle network (thus breaking the cycle), and the residual flows would remain positive. Of course, cycles in networks do overlap. In fact, it often happens that several cycles share the same critical arc. This circumstance is actually more of a benefit than a bane. In networks with large numbers of constituent cycles the shared critical arcs suggest that the totality of many simple cycles may be viewed as consisting of a more tractable number of subgroups, or "nexuses." That is, a nexus is defined as a collection of simple cycles all sharing a common critical arc.

The remaining question becomes how to distribute the magnitude of the shared critical arc among the member cycles of its nexus. Perhaps the division with the most intuitive appeal is to assign a fraction of the critical flow to each constituent cycle in proportion to its circuit probability.[4] The circuit probability of a cycle is the probability that a quantum of medium starting at any point in the given cycle will follow the simple pathway prescribed by the cycle and return to its starting point.

Circuit probabilities are readily calculated from a quantitative network graph. In passing through a node the probability that a quantum will exit along a given pathway is estimated by that fraction of the total output from the node which contains the link in question. For example, the total output from the detritus compartment in Figure 2(a) is 11,483 kcal/m^2 yr. The probability that a quantum which enters the detritus from any source will subsequently exit to the detritivores is thus 2309/11,483, or 0.20108. In a similar manner the subsequent probabilities of flowing along the detritivore-carnivore and carnivore-detritus links are 0.1552 and 0.4514, respectively. The probability of completing the given cycle of length three is the product of these three quantities, or 0.0141. The circuit probability is independent of where the hypothetical quantum begins its journey.

To summarize the process of separating cycled from once-through flow, one first identifies all simple cycles in the network and seeks out the critical arc in each cycle. The smallest critical arc of all is then identified, and its

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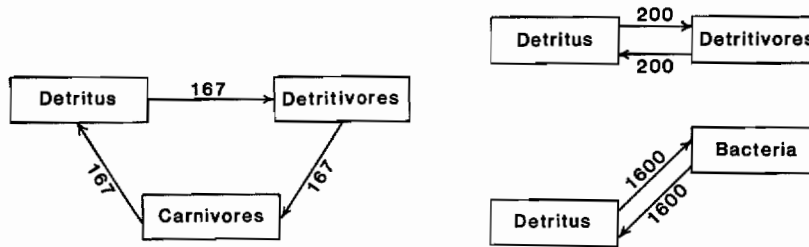[4] W. Silvert, personal communication.

FIG. 3. Three alternate cycles to those in Figure 2(b) which can be subtracted from the network in Figure 2(a) to yield an acyclic web of flows.

value is divided among all those cycles in which it appears in proportion to their respective circuit probabilities. The cycles of this nexus are then subtracted from the network link by link. The set of critical arcs in the remainder network is reevaluated, and the subtraction process is iterated until all nexuses have been removed. The separation of cycled flow in Cone Springs depicted in Figure 2 follows this scheme.

It should be mentioned that other means of designating the critical arc in a cycle and other schemes for distribution of flow among the member cycles of a nexus are theoretically possible. In the latter instance, if the upper limit on the amount of a given transfer were known (the channel capacity), then the arc with the flow nearest its maximum could be designated as the critical arc. Perhaps some other information about physiology or nutritional needs would point to a critical arc. R. Nisbet and W. Silvert[5] have suggested that the velocities (ratios of flows to standing crops) might point to a critical *node* in the cycle, and aggregation might be effected according to shared critical nodes.

Concerning the distribution of flow within a nexus, one could alternatively have chosen to divide the critical flow equally among the cycles, or to maximize the entropy of all the cycle magnitudes subject to the constraints that no residual arc becomes negative [21]. In contrast to this latter option, one could as well order the cycles according to their contributions to the network ascendency (a measure of organization in the network [13]) and remove their flows in sequence until all cycles have been eliminated. Simpler still, one could identify a set of fundamental cycles [20] in the network, as depicted in Figure 3, and subtract them sequentially from the network to yield an acyclic dendrogram. Although the assignments within a given nexus may vary radically according to the apportionment scheme chosen, it is reassuring to report that the residual networks left after removing all the nexuses change little as one switches algorithms. This is especially evident when there are many overlapping nexuses in the starting network.

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[5] Personal communication.

TABLE 1. Flows of Carbon among 17 Components in Two Tidal Marsh Creeks Near Crystal River, Florida[a]

(a) Undisturbed creek

	Mic.	Mac.	Det.	Zoo.	BI	Sti.	Bay	Nee.	She.	Gol.	Gul.	Lon.	Sil.	Moh.	BIF	Pin.	Mul.	
Microphytes	.	.	404.	44.70	.	.	.	.	.44	.32	.	.	.	.	.16	.	8.15	Mic.
Macrophytes	.	.	4163.	.	.	.	.37	.	.79	.71	.	.	.97	.90	.07	.	24.40	Mac.
Detritus	.	.	.	109.8	2117.9	.	.	.	.	.22	.	.	.	.	.	.	.	Det.
Zooplankton	.	.	73.20	.	.	.	.64	.	.	.	.	.	5.86	3.20	.	.	.	Zoo.
Benthic invertabrates	.	.	686.90	.	.	.	1.	.12	.15	.61	2.68	5.28	8.59	2.30	.23	.53	.	BI
Stingray	.	.	.65	.	.	.	.	.	.	.	.	.	.	.	.	.	.	Sti.
Bay anchovy	.	.	.22	.	.	.	.	.65	.	.	.50	.	.	.	.	.74	.	Bay.
Needlefish	.	.	.34	.	.	.	.	.	.	.	.	.	.	.	.	.	.	Nee.
Sheepshead killifish	.	.	.65	.	.	.03	.	.	.	.	.01	.	.	.	.	.01	.	She.
Goldspotted killifish	.	.	.68	.	.	.01	.	.	.	.	.09	.	.	.	.	.10	.	Gol.
Gulf killifish	.	.	1.32	.	.	.07	.	.05	.	.	.	.	.	.	.	.	.	Gul.
Longnosed killifish	.	.	1.06	.	.	.	.	.	.	.	.03	.	.	.	.	.	.	Lon.
Silverside	.	.	3.38	.	.	.51	.	.64	.	.	2.67	.	.	.	.	.56	.	Sil.
Moharra	.	.	1.53	.	.	.	.	.06	.	.	.37	.	.	.	.	.01	.	Moh.
Benthic inv. feeders	.	.	.17	.	.	.	.	.	.	.	.	.	.	.	.	.	.	BIF
Pinfish	.	.	.41	.	.	.	.	.09	.	.	.	.	.	.	.	.	.	Pin.
Mullet	.	.	16.29	.	.	2.59	.	.03	.	.	.08	.	.	.	.	.	.	Mul.
Inputs	651.77	6704.	.	.	.	.	1.57	.02	.	.	.16	.	.	.	.	.07	.	Inp.
Exports	.	219.	567.79	39.94	427.91	1.30	.74	.36	.14	.09	1.50	1.27	.43	1.49	.14	.38	2.41	Exp.
Respirations	194.	2322.	2530.10	31.30	981.60	1.26	.73	.94	.54	.89	3.70	2.87	7.23	2.94	.29	1.16	11.15	Res.

(b) *Similar nearby creek with elevated temperature (6°C average)*

	Mic.	Mac.	Det.	Zoo.	BI	Sti.	Bay	Nee.	She.	Gol.	Gul.	Lon.	Sil.	Moh.	BIF	Pin.	Mul.	
Microphytes			319.	39.05					.12	.10							6.08	Mic.
Macrophytes			3156.				7.74		.22	.22				.11			17.19	Mac.
Detritus				117.15	1485.1													Det.
Zooplankton			78.10				13.60			.07			.33	.40				Zoo.
Benthic invertebrates			742.60				2.10		.04	.19	1.71	3.48	.49	.28	2.38	.09		BI
Stingray			.01															Sti.
Bay anchovy			4.69			.04		.24			.37					.23		Bay
Needlefish			.06															Nee.
Sheepshead killifish			.18								.01							She.
Goldspotted killifish			.21								.01							Gol.
Gulf killifish			.54								.01							Gul.
Longnosed killifish			.70								.17							Lon.
Silverside			.18								.33							Sil.
Moharra			.16															Moh.
Benthic inv. feeders			.47															BIF
Pinfish			.07															Pin.
Mullet			11.64					.06			.06							Mul.
Inputs	530.	5488.														.02		Inp.
Exports	.65	166.	616.51	32.40	33.55	.04	.75	.01		.10	.73	.69	.05	.25	.52	.09	1.37	Exp.
Respirations	165.	2166.	2070.30	31.30	698.	.04	17.12	.23	.19	.26	1.39	.192	.32	.38	1.39	.18	10.13	Res.
	Mic.	Mac.	Det.	Zoo.	BI	Sti.	Bay	Nee.	She.	Gol.	Gul.	Lon.	Sil.	Moh.	BIF	Pin.	Mul.	

[a] Each entry represents a flow (g/m^2 yr) from the row to the column component.

Among all the options just discussed, the algorithm chosen for use in this paper appears plausible and is methodologically quite tractable. Whether it remains the method of choice in analyzing flow structure depends upon how effective it is in providing insights into ecological dynamics. To investigate what sort of insights the analysis may afford, it is necessary to consider data on an ecosystem network of more challenging complexity.

AN ILLUSTRATIVE ANALYSIS

Because of the high cost of gathering data on all the flows occurring in an ecosystem, extremely few networks with more than 10 nodes have been fully quantified. Still fewer pairs or sets of networks are available which allow comparison of the same or similar ecosystems under different environmental conditions. A notable exception to both restrictions is the carbon flow data among the populations of two tidal salt-marsh guts near Crystal River, Florida.[6] The lower trophic levels are highly aggregated, but the species of fish are considered in detail, so that carbon flows among 21 compartments are described in each tidal creek. One of the creeks is exposed to thermal effluent from a nuclear power station, raising its temperature 6°C (on the average) above ambient. Otherwise, the environments of the creeks do not significantly differ.

The carbon flow data are displayed as two 17-compartment networks in Table 1(a) and (b). The species lists of the two creeks were very similar; the few nonoverlapping species could easily be aggregated according to feeding patterns, so that both networks could be condensed into 17 common compartments. Such consolidation did not alter the qualitative nature of the results described below. The unperturbed flow network [corresponding to Table 1(a)] is depicted in Figure 4.

The composite cycled flows for the unperturbed creek computed using the methods described above are shown in Figure 5. The residual acyclic flows may be found by subtracting these cycled transfers from their original counterparts in Figure 4, and the results appear in Figure 6. When one aggregates these once-through flows into strict trophic transfers according to the method of Ulanowicz and Kemp [15], the resultant straight chain is certain to truncate in n steps or less (in an n-node network). In this particular instance no pathway exists with more than four internal transfers, resulting in a five-component trophic chain as depicted in Figure 7(a). The corresponding analysis performed on the perturbed creek yields the chain in Figure 7(b).

Most differences between the two chains are not overwhelming. One notices a decrease in the level of flow through the perturbed system,

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[6]M. Homer and W. Kemp, unpublished manuscript; see also [13].

FIG. 4. A schematic of carbon flows among the taxa of a marsh gut ecosystem, Crystal River, Florida. All flows are in (mg carbon)/m² day. The ground symbols represent respiratory losses. The linked arrows depict returns to the detritus (after M. Homer and W. M. Kemp, unpublished).
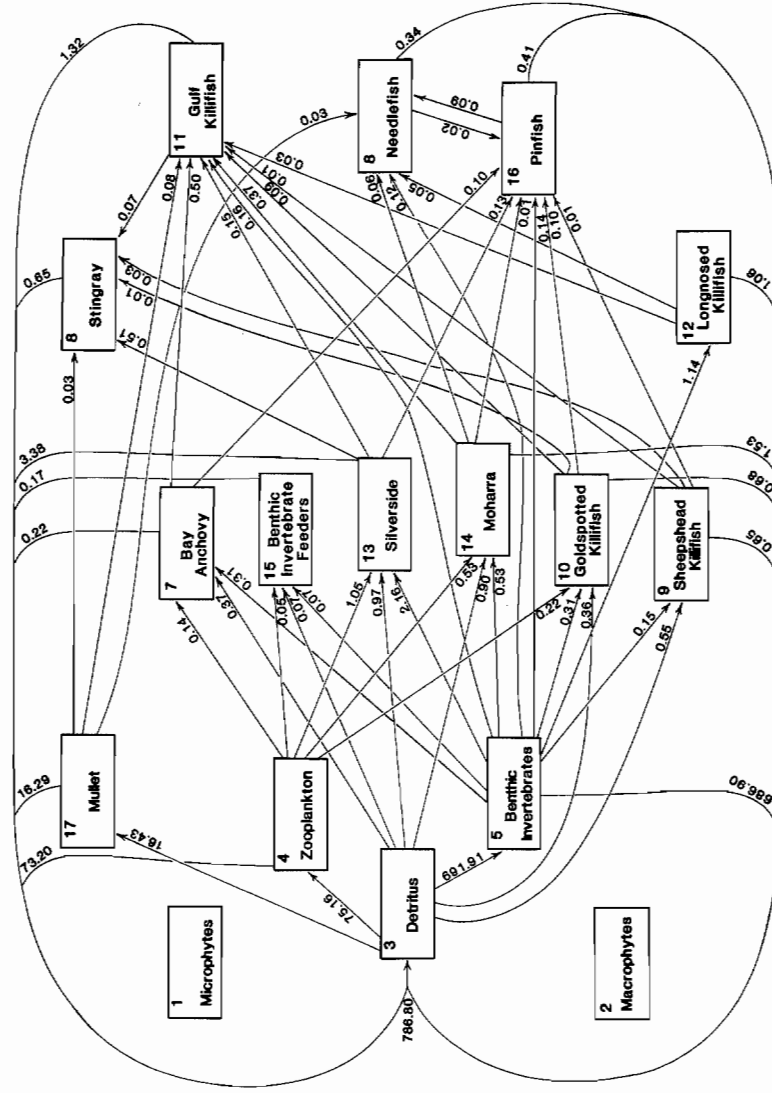
FIG. 5. The composite nexus of all cycled flow inherent in the network depicted in Figure 4. See legend of Figure 4 for further details.
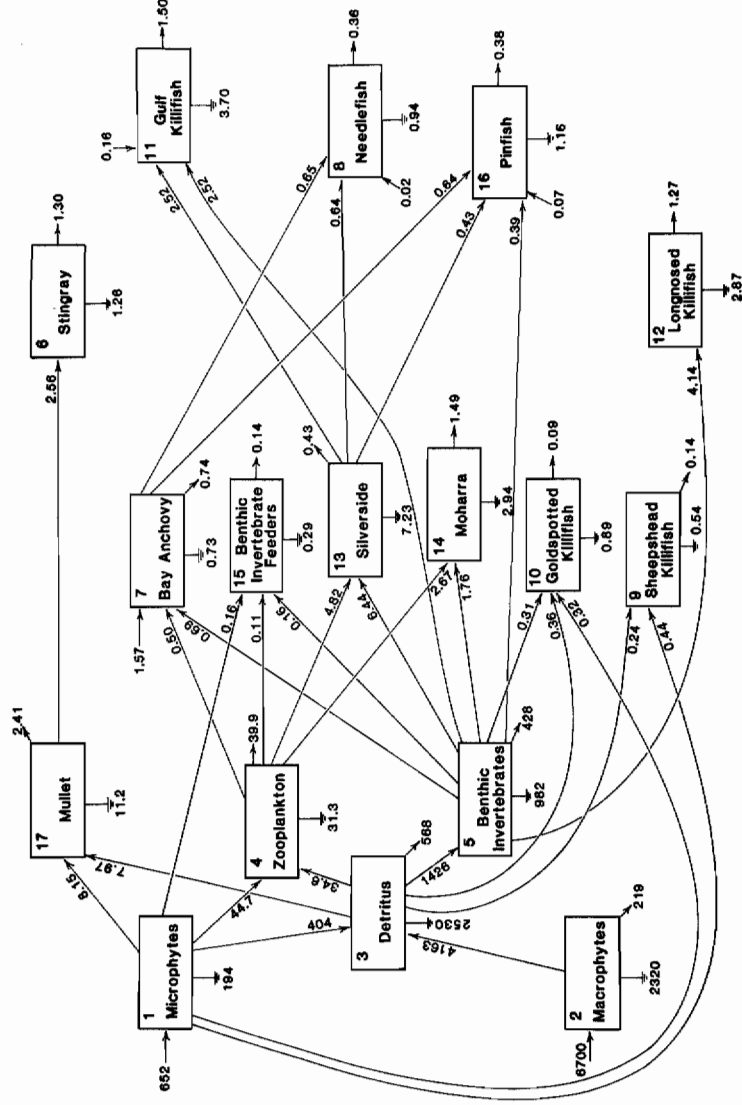
FIG. 6. The graph of acyclic flows remaining after the cycled flows (Figure 5) have been subtracted from the original flows (Figure 4). See legend of Figure 4 for further details.
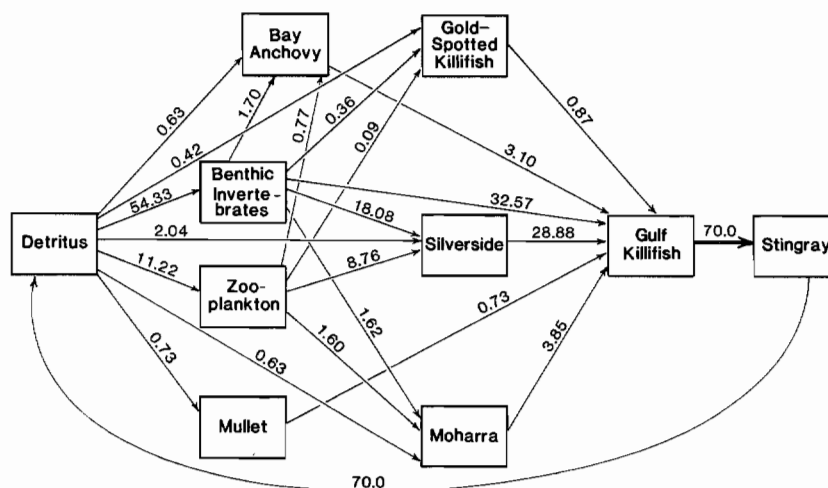
FIG. 8.   A 14-cycle nexus of circulated flows associated with the vulnerable arc (heavy arrow) depicting the grazing of Gulf killifish by stingray, measured in (mg carbon)/m² yr.

reflecting an 18% drop in primary productivity. The efficiency of the second trophic compartment has been somewhat impaired in the disturbed chain; however, these losses are compensated by a more efficient third trophic level. Possible system disturbances at higher trophic levels are suggested by a severalfold decrease in flow to the top trophic compartment.

Other properties shared by the two networks do not appear to have changed drastically between the two configurations. The species lists were almost identical; structure among the lower trophic levels remains essentially unchanged; the percentage of the flow being cycled actually *rose* from 11 to 14% in the impacted creek; and, as predicted [13], the warmer creek had a lower network ascendency and a higher (proportion of) pathway redundancy than the control.

The only analysis showing a dramatic change between the two foodwebs is the vulnerable arc grouping of the simple cycles present in both ecosystems. One can identify 119 distinct simple cycles in the graph of the control creek, whereas only 46 cycles can be counted in that of the heated embayment. The aggregation of cycles by least arc shows that the number of nexuses has not decreased quite as drastically—from 41 nexuses in the control to 30 in the perturbed, with 25 vulnerable arcs common to both communities. The chief reason for the decrease in the number of identifiable cycles is the disappearance from the perturbed network of several many-cycle nexuses present in the control ecosystem. One 14-cycle, one 13-cycle, one 10-cycle and three 6-cycle nexuses are all absent from the disturbed network, which possessed a single 4-cycle nexus as its largest aggregation.
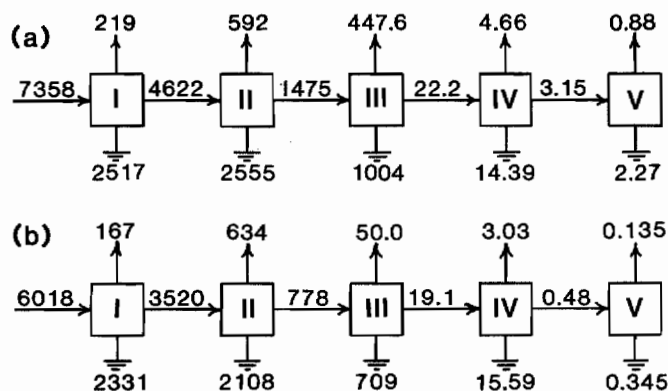
(a)

(b)

FIG. 7.   (a) Consolidation by trophic status of the residual flows [in (g carbon)/m^2 yr] which result from subtracting the cycled flows in an undisturbed tidal creek (Figure 5) from their counterparts in the original network in Figure 4. (b) Similar trophic aggregation for flows in the perturbed creek.

The 14-cycle nexus of the unperturbed network depicted in Figure 8 gives a clue to the differences between the two configurations. The vulnerable arc (indicated as a heavy arrow in the diagram) represents feeding by stingrays upon the Gulf killifish. Under normal conditions the various killifish are not a major portion of the diet of the stingray, which subsists mainly on mullet. In the presence of heated effluent, stingray feeding activity has fallen off considerably and is now focused upon anchovy and mullet. Apparently, under stress the (trophically more costly) feeding upon killifish has been abandoned in order to survive by concentrating on subsistence rations. Examination of the 13-, 10-, and 6-cycle nexuses in the control web indicates that similar changes in predation by the pinfish and needlefish are responsible for the demise of these cycle aggregations.

In a broader view of the changes in cycling structure between the two networks, one can say that the thermally stressed network exhibits symptoms akin to eutrophication. The higher-order (longer and presumably slower) cycles have disappeared under stress. The shorter, faster, trophically lower cycles now turn over more intensely. Faster cycling under stress has also been observed for a Gulf of Mexico shelf ecosystem subjected to high salinities.[7]

The advantages of cycle-structure analysis in describing the systems-level changes in ecosystems appear to be two-fold. First, subtle changes at higher

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[7]B. C. Patten, personal communication.

trophic levels are dramatically portrayed. The numbers of distinct cycles associated with any vulnerable flow is likely to increase geometrically with increasing trophic position of the critical transfer. In terms of the number of cycles identified, the analysis is therefore skewed towards being most sensitive to what would otherwise appear as insignificant changes. Furthermore, this particular analysis indicates that it may be possible to identify the most sensitive flows and species *prior to* the imposition of any stress. The designation of stingray, pinfish, and needlefish as "indicator species" in this ecosystem might have been possible on intuitive grounds; nonetheless, vulnerable-arc analysis of the unstressed system gives analytic support to such a choice.

DOCUMENTATION OF ALGORITHMS

All the above methods have been incorporated into a set of FORTRAN IV subroutines constituting a network analysis package, NETWRK, as documented by the author [22]. The package operates on an arbitrary steady-state flow network in four phases. Each phase addresses the flow network at increasingly higher levels of resolution. First, the traditional structure matrix [23] is constructed, allowing one to analyze the ancestors (causes) and descendants (effects) of any particular flow in the network (see also [24]). Next, the cycles are all identified and removed according to the least-arc aggregation scheme described above. Then the residual flows are transformed into a trophic-level concatenation, and finally the system-level attributes (ascendency, redundancy, tribute, and dissipation) are printed.

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