The Structure of Cycling in the Ythan Estuary

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Abstract

A method for identifying all the simple, directed cycles in a network of ecosystems flows is described. Furthermore, the cycles may be divided into distinct groups, or nexuses, distinguished by certain critical links. These groupings may also be used to analytically separate the network into two constituent graphs - one graph containing only cycled flow and the other consisting of only once-through pathways.

The analysis, when applied to the carbon flow in the Ythan estuary, graphically portrays both the importance and the vulnerability of the higher trophic level transfers.

Introduction

In his seminal article, "The Strategy of Ecosystem Development," E. P. Odum (1969) suggests the amount of material cycling as a prime indicator of mature, developed ecosystems. Later, he becomes even more specific by comparing the importance of detritus in slowly-varying benthic, marsh and terrestrial ecosystems with the predominantly once-through foodwebs of transitory pelagic food chains. Mathematical ecologists have been somewhat slow to give quantitative form to Odum's notions about cycling so that his hypothesis may be formally tested. It was not until seven years later that Finn (1976) was able to estimate the aggregate amount of material or energy which was being cycled in a given flow network. If Finn's index of cycled flow properply characterizes Odum's hypothesis, then presumably the index would possess a higher value in more developed ecosystem networks.

Finn's results were an outgrowth of economic input-output analysis. In the notation common to input-output analysis if one calls P_{ij} the flow of any given medium from i to j and T_i the total output from i, then $f_{ij} = P_{ij}/T_i$ represents the fraction of the total output of i which is contributed directly to j. If F is a matrix with components f_{ij}, then it is not too difficult to discern that the matrix

F^2 (F multiplied by itself) will consist of components representing the fraction of total output from i which flows to j over all pathways of length 2. Similarly, the components of F^3 will be the fractions of T_i which flow to j over all pathways of length 3, etc. By summing all powers of F, one obtains the output structure matrix, S, wherein S_{ij} represents the fraction of T_i which flows to j over all possible pathways:

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

Because F was conveniently normalized, this infinite series converges (Yan, 1969) to the value

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

where I is the identity matrix, and the minus one exponent represents matrix inversion.

Of particular interest to those concerned with cycling are the diagonal elements of S. In a closed system each S_{ii} has a minimum value of unity, and any excess over one represents the fraction of T_i which returns to i over all cycles of all lengths. Because this fraction of flow is inherent in all members having communication with i, one may imagine a matrix with entries of $(1 - S_{ii})$ in each of the i^{th} rows for which S_{ij} is not zero. If this cycling matrix is multiplied by the vectors of total outputs (that is the T_i), and the elements of the consequent vector are then summed, the total amount of cycled flow will result. The ratio of this amount of cycled flow to the total amount of flow in the system has come to be known as Finn's cycling index. One infers from Odum's remarks that the cycling index might be greater in more mature communities, or conversely less in networks subject to perturbations.

As intriguing as this analysis might be, the results when applied to real networks gave ambiguous results (Richey et al., 1978). Perturbed and eutrophic systems sometimes possess larger cycling indices. Clearly, events are occurring which are not readily discernible in terms of the aggregate index. It appears that a more detailed knowledge about the structure of the flow cycles might be helpful.

Cycle Analysis

Given a flow network or graph, it is a rather easy computational task to identify a set of fundamental cycles from which all possible cycles may be generated by linear combinations (Knuth, 1973). Unfortunately, there are in general many possible combinations of fundamental cycles, and it is by no means clear which of the combinations would be (biologically speaking) most pertinent. The next step up in detail from this rudimentary description would be to enumerate all the simple cycles in the network. A simple cycle is one in which no compartment appears more than once (see Fig. 1).

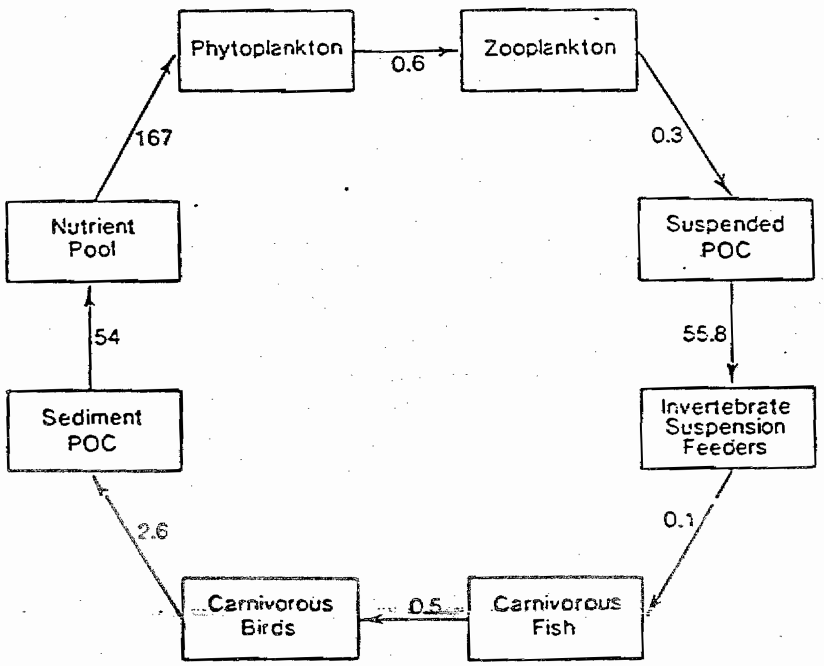

Figure 1 - A simple cycle. No repeated elements. Extracted from Baird and Milne (1981). See legend to Figure 2.

While it might appear that the systematic enumeration of the simple cycles in a graph should be a rather straightforward programming task, the time required for even a modern calculator to identify all cycles can easily get out of bounds. Those familiar with combinatorics will recognize that the number of possible cycles in a graph increases as the factorial of the number of nodes. Such an exponential increase in search time means that relatively small networks have the potential for exceeding the capabilities of even the faster machines available (n.b., 20! = 2.4 x 10^{18}).

Fortunately, ecosystem networks do not appear to be highly connected (May, 1973). Typically only 15-25% of the possible connections are realized, depending upon the strength of the interactions. Even with such simplification, it nonetheless behooves an investigator to choose algorithms which are as efficient as possible. Mateti and Deo (1976) in evaluating various methods for identifying cycles have concluded that backtracking search algorithms with suitable pruning methods (to eliminate many spurious search pathways) are the most efficient programs under the greatest number of circumstances.

In the backtracking algorithm one works with either a matrix of flows or a vector list of arcs. One orders the nodes in some convenient way (see below) and imagines the same order of n nodes to be repeated at n levels (see Figure 2). One begins with the first node and searches the node in the next level until an existing flow connection is found. One progresses to that node in the next level and searches the succeeding level for yet a subsequent connection. Only those nodes in the next level are considered which have not already appeared in the current pathway. One proceeds to increasing levels until one of two things happen. If an arc to the next level brings one back to the starting node, then a simple cycle has been identified and is reported and/or stored. If the search for a link from the th j^{th} node at the m^{th} level for a connection to the $(m+1)^{th}$ level has been exhausted, one "backtracks" to the ancestor node at the $(m-1)^{th}$ level and continues searching the m^{th} level beginning at the $(j+1)^{th}$ position. When further backtracking is impossible, one has identified all simple cycles containing the starting node. The starting node may be dropped from all future consideration and the dimension of the subsequent search may be decreased by one.

Read and Tarjan (1975) and Johnson (1975) give examples of constraints on the backtracking procedure which result in efficient searching. Ulanowicz (in press, Math. Biosciences) has found that for most ecological applications it suffices simply to order the nodes judiciously. In particular, one wishes to first search those nodes for which the probability of completing a cycle at any step is the greatest. This probability varies directly with the number of cycle arcs terminating in the node under consideration. (A cycle arc is a connection from a given arc to one of its ancestors.) As all the descendents of a given arc may readily be determined (Knuth, 1973), one may total the number of cycle arcs back into each node and order the nodes accordingly. Those nodes with no incoming cycle arcs need not be considered in the backtracking subroutine.

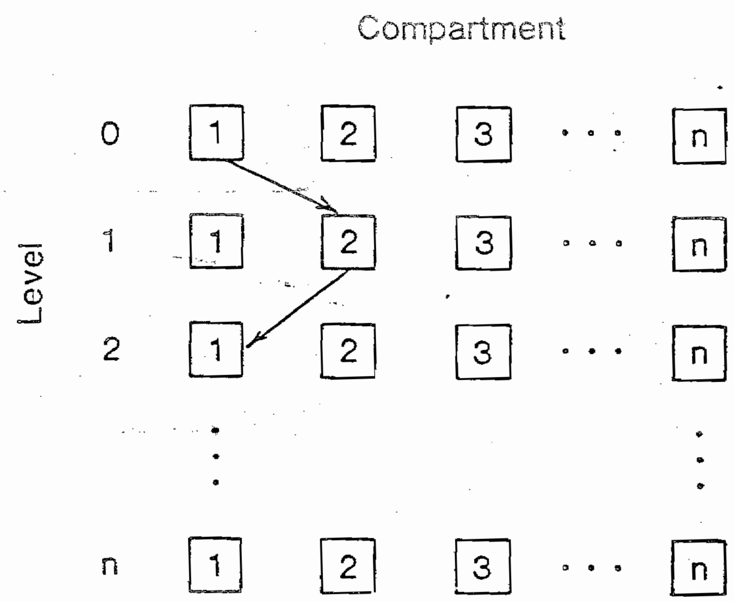

Figure 2 - Mnemonic diagram useful in description of the backtracking algorithm. Here the first cycle to be identified is 1-2-1.

Qualitatively knowing what the cycles in a network are can be very useful information in assessing autonomous behavior in an ecosystem. As cause and effect often follow material or energetic pathways in a system, a loop of flow back upon itself is a likely indicator of a cybernetic effect at operation in the system. Such causal loops (Hutchinson, 1948) frequently behave in ways which appear autonomous of the exchanges with the external world. The constellation of cycles in which a given compartment participates then defines the domain of self-regulation of the compartment in question. If one is interested in the fate of a particular species, it is certainly helpful to know its constellation of cycles. Similarly, if one is studying a given flow pathway, say of the predation of a particular species on another, it is useful qualitative information to know the constellation of cycles in which that particular transformation appears.

While a description of the various constellations is likely to be quite helpful, quantitative information about the relative strengths of the flows still needs to be exploited. It is said that a chain is only as strong as its weakest link, and this notion may apply to cycles as well. Tracing around the arcs of a cycle, one should in principle be able to identify a most vulnerable link according to some criterion. If no information is available other than the weighted network, one may make the assumption that the smallest (or slowest) link in the cycle dominates the behavior of that loop. (Control by the smallest link is analogous to the idea of the rate limiting step in chemical kinetics.) This assumption is only a pedagogical expedient, and if other information about the arcs of a cycle is available, those clues should be investigated to see if another criterion for the most vulnerable arc might be more appropriate.

All of the cycles in a graph may be individually examined to identify a set of most vulnerable arcs. Because some cycles share the same vulnerable arc, the number of most vulnerable arcs is smaller than the number of simple cycles. This homomorphic mapping of cycles into vulnerable arcs serves to define subsets of cycles called nexuses. A nexus is a collection of cycles all sharing the same most vulnerable arc. The magnitude of the most vulnerable arc quantifies the nexus.

In identifying the nexuses one has simplified the description of the structure of cycling and thereby made it more meaningful. The description is simplified because there are fewer nexuses than constellations (the set of most vulnerable arcs being a subset of all arcs), and the nexuses are somewhat smaller in the number of constituent cycles (the cycles for which an arc is most vulnerable being a subset of all the cycles in which it participates). If no two of the most vulnerable arcs are exactly equal in magnitude, the nexuses are disjoint. The nexuses are more meaningful than the constellations in that they focus attention upon a subset of critical interactions and better delimit their domains of influence.

Another advantage of the concept of a nexus is a convenient tool for separating the cycled flow from that flow which only passes straight through the system. If the vulnerable arc is defined as the smallest arc in a cycle, then the following algorithm will effect such a separation:

1. Zero the elements of the matrix of cycled flow.
2. Find the smallest non-zero vulnerable arc and call its magnitude V.
3. If no vulnerable arcs remain, go to 7.
4. For each of the m cycles in the nexus defined by the smallest vulnerable arc calculate the probability P_i ($i = 1,2, \ldots, m$) that a bit of medium starting at any node in the cycle will exactly follow the cycle to return to its starting point. This probability is simply the composite product of the f_{ij}'s associated with each arc in the cycle.
5. Go around each of the m cycles of the nexus defined by the smallest vulnerable arc, subtracting $V P_i / \sum_{j=1}^{m} P_j$ from each link of the starting graph and adding the same quantity to the corresponding entry of the cycles matrix.
6. Go to 2.
7. STOP.

As a result of step 5 the smallest vulnerable arc will be eliminated (set=0), thereby breaking all the cycles of the accompanying nexus. All of the other arcs associated with the nexus will remain positive.

In steps 4 and 5 the magnitude of the vulnerable arc is divided among the constituent cycles of the associated nexus in proportion to the probability that a particle in the vulnerable flow would actually complete a given cycle (suggested to the author by W. Silvert, personal communication). While this scheme is a very plausible one; it is, nonetheless, somewhat arbitrary. The reader wishing to implement a cycle analysis might wish to apportion the vulnerable flow according to some other scheme, such as the principle of maximum entropy (Jaynes, 1958) or the hypothesis of maximum ascendency (Ulanowicz, 1980).

An Example: Carbon Flow in the Ythan Estuary

An appropriate network with which to demonstrate the analysis is the graph of carbon flows among the compartments of the Ythan estuary ecosystem (Baird and Milne, 1981). The schematic diagram which Baird presented did not unambiguously define all the individual intercompartmental flows. Fortunately, Dr. Baird graciously assisted the author in estimating how the lumped flows might be separated into strictly pairwise transfers, and the resulting network is presented in Figure 3.

Three abiotic and ten living compartments of the Ythan ecosystem are identified. There are 2 exogenous inputs of carbon, ten exports of useable carbon and 39 internal exchanges (23% connectance). The degree of aggregation is about uniform over all trophic levels. All flows were reported in g carbon $m^{-2}y^{-1}$. The nutrient pool was originally measured in terms of nitrogen, phosphorous and silicon, but has been converted into equivalent dissolved organic carbon for the purposes of this analysis.

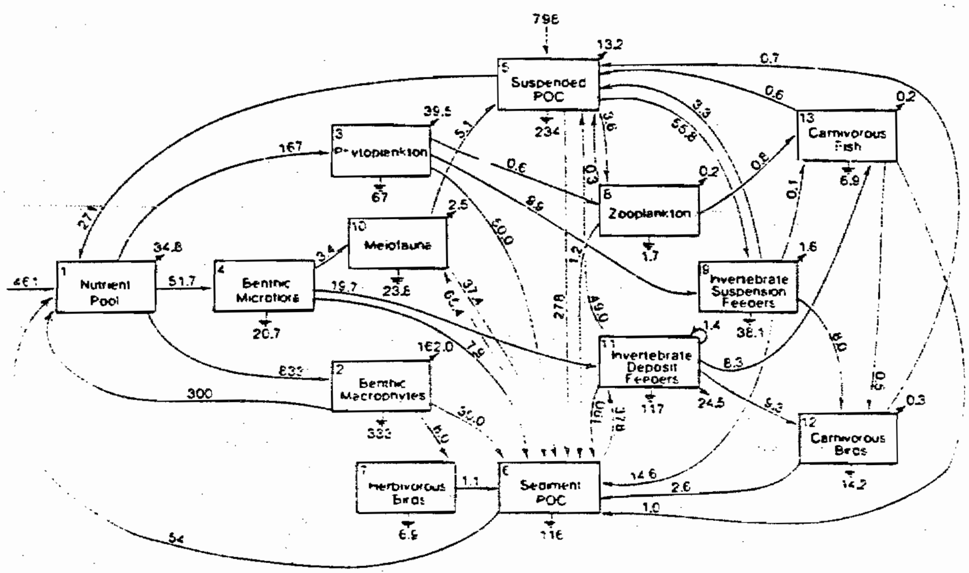

Figure 3 - Schematic diagram of carbon flow in the Ythan estuary, Scotland. Flows measured in $gCm^{-2}y^{-1}$. Ground symbols represent respiration; arrows with no origin, exogenous inputs; arrows not terminating in a box, exports a from the system. After Baird and Milne (1981).

A total of 170 simple cycles may be identified in the graph. These cycles may be grouped into 25 separate nexuses as seen in Appendix 1. The order in which the nexuses appear is interesting. Not unexpectedly, the smallest vulnerable arcs are associated with the higher trophic level compartments. These critical arcs define nexuses with many cycles, and the individual cycles tend to be long. Conversely, the vulnerable arcs of greater magnitude are associated with lower trophic components and have fewer (often only one) cycles. Also, those cycles are very short.

As an example of the complex nexuses, consider the third nexus in Appendix 1. The vulnerable arc represents the predation on carnivorous fish by carnivorous birds. The associated nexus, depicted in Figure 4, involves all of the compartments of the ecosystem in 29 simple cycles. The ecological significance of this nexus can be interpreted in either of two ways. First, a perturbation anywhere in the system is capable of propagating to affect the vulnerable arc, although it is obvious from Figure 4 that perturbations to certain pathways are likely to have more impact than some other disturbances. For example, grazing by herbivorous birds is practically inconsequential to the feeding of their carnivorous counterparts (niche separation). However, disturbances to the invertebrate deposit feeders could have serious consequences on predation by carnivorous birds.

Because these cycles represent causal loops, it is possible to interpret the latter statements in reverse. That is, predation by carnivorous birds is capable of affecting almost all the other internal transfers in the system to a greater or lesser degree. Again, carnivorous birds might exert perceptible control over deposit feeders and zooplankton, but control over benthic macrophytes and herbivorous birds is likely to be weak at best.

The vast majority of the cycled material circulates inside the last three loops listed in the Appendix -- nutrient turnover in the macrophytes, detrital turnover by deposit feeders and nutrient turnover by sinking phytoplankton. The large magnitudes of these cycles probably impart some resistance to perturbation (Ulanowicz, in press). Their relative isolation from other compartments helps to insulate them from disturbances elsewhere in the ecosystem.

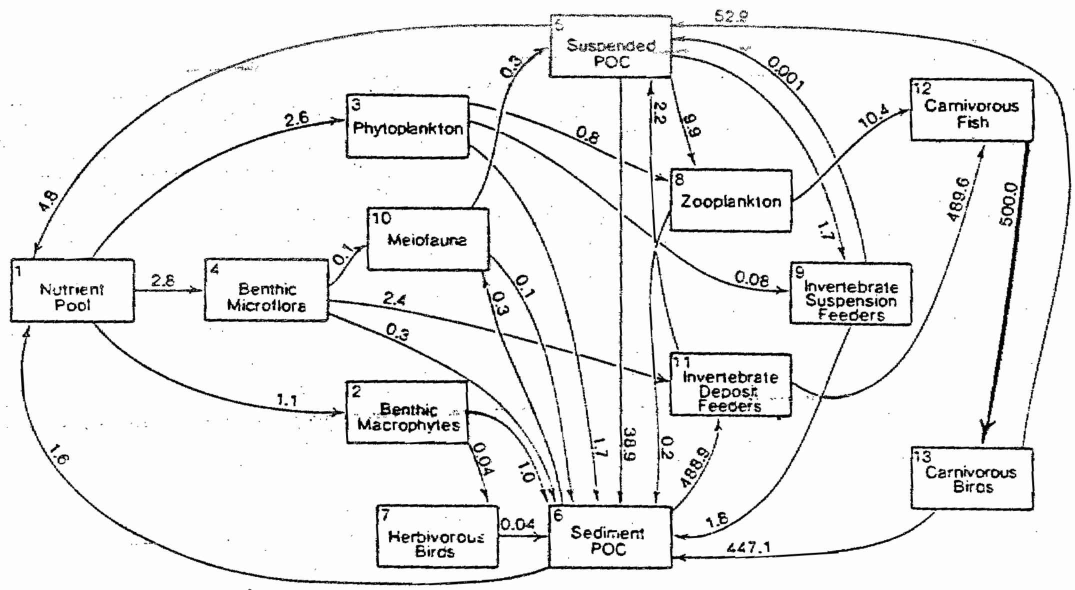

Figure 4 - The nexus of cycles associated with the predation on carnivorous fish by carnivorous birds (indicated by heavy black arrow). Extracted from graph in Figure 3. Flows are in mg Carbon m^{-2} y^{-1}.

It should be kept in mind that, like all other forms of flow analysis, this description of cycling is based upon a steady-state network. One may not infer that the dynamics of the system have thereby been accurately defined. In fact the system can play by very different rules after perturbation and conclusions drawn from the steady-state could be misleading.

Cycle analysis, however, does provide a graphic and semi-quantitative way of portraying what has long been known from experience -- namely, that transfers among higher trophic level components may be both more vulnerable and, obversely, exert more control over a wider domain of an ecosystem. One expects these critical transfers and their accompanying nexuses to be early victims of any disturbances. By contrast, the trophically lower, faster cycles appear less vulnerable to perturbations and might even benefit from the disappearance of higher structure. While these statements are not immediately obvious from the analysis of a single network presented here, comparative studies show that this appears to be precisely what happened in the ecosystems of tidal marsh creeks near the thermal effluent of the Crystal River power generating station (Ulanowicz, 1982) and what was predicted to happen if Gulf of Mexico benthic communities were exposed to brine releases from salt domes (B.C. Patten, personal communication).

Cycling index by itself, is thus seen to be an equivocal indicator of the response to ecosystem stress. It is only when the magnitudes of cycled flows are combined with a description of their structure that a coherent picture of ecological impact emerges.

Acknowledgements

This work, as well as the author's travel to the symposium, was supported by a grant from the U.S. National Science Foundation (ECS-8110035). The Computer Science Center of the University of Maryland also contributed some free computer time. The author extends special thanks to Professor Dan Baird, who spent an entire day with the author estimating how his measured flows might be partitioned so as to make the cycle analysis possible.

A Fortran subroutine for the identification and removal of cycles from a network is available from the author upon request.

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APPENDIX

*** CYCLE ANALYSES ***

27-CYCLE NEXUS WITH WEAK ARC (9,13) = .100

1. 6- 1- 3- 8- 5- 9-13- 6-
2. 6- 1- 3- 8- 5- 9-13-12- 6-
3. 6- 1- 3- 9-13- 6-
4. 6- 1- 3- 9-13- 5- 6-
5. 6- 1- 3- 9-13- 5- 8- 6-
6. 6- 1- 3- 9-13-12- 6-
7. 6- 1- 3- 9-13-12- 5- 6-
8. 6- 1- 3- 9-13-12- 5- 8- 6-
9. 6- 1- 4-11- 5- 9-13- 6-
10. 6- 1- 4-11- 5- 9-13-12- 6-
11. 6- 1- 4-11-12- 5- 9-13- 6-
12. 6- 1- 4-10- 5- 9-13- 6-
13. 6- 1- 4-10- 5- 9-13-12- 6-
14. 6-11- 5- 1- 3- 9-13- 6-
15. 6-11- 5- 1- 3- 9-13-12- 6-
16. 6-11- 5- 9-13- 6-
17. 6-11- 5- 9-13-12- 6-
18. 6-11-12- 5- 1- 3- 9-13- 6-
19. 6-11-12- 5- 9-13- 6-
20. 6-10- 5- 1- 3- 9-13- 6-
21. 6-10- 5- 1- 3- 9-13-12- 6-
22. 6-10- 5- 9-13- 6-
23. 6-10- 5- 9-13-12- 6-
24. 5- 1- 3- 9-13- 5-
25. 5- 1- 3- 9-13-12- 5-
26. 5- 9-13- 5-
27. 5- 9-13-12- 5-

5-CYCLE NEXUS WITH WEAK ARC (8, 5) = .300

28. 6- 1- 3- 8- 5- 6-
29. 6- 1- 3- 8- 5- 9- 6-
30. 6- 1- 3- 8- 5- 9-12- 6-
31. 5- 1- 3- 8- 5-
32. 5- 8- 5-

29-CYCLE NEXUS WITH WEAK ARC (13,12) = .500

33. 6- 1- 3- 8-13-12- 6-
34. 6- 1- 3- 8-13-12- 5- 6-
35. 6- 1- 3- 8-13-12- 5- 9- 6-
36. 6- 1- 3- 9- 5- 8-13-12- 6-
37. 6- 1- 4-11- 5- 8-13-12- 6-
38. 6- 1- 4-11-13-12- 6-
39. 6- 1- 4-11-13-12- 5- 6-
40. 6- 1- 4-11-13-12- 5- 8- 6-
41. 6- 1- 4-11-13-12- 5- 9- 6-
42. 6- 1- 4-10- 5- 8-13-12- 6-
43. 6-11- 5- 1- 3- 8-13-12- 6-
44. 6-11- 5- 8-13-12- 6-
45. 6-11-13-12- 6-
46. 6-11-13-12- 5- 6-
47. 6-11-13-12- 5- 1- 2- 6-
48. 6-11-13-12- 5- 1- 2- 7- 6-
49. 6-11-13-12- 5- 1- 3- 6-
50. 6-11-13-12- 5- 1- 3- 8- 6-
51. 6-11-13-12- 5- 1- 3- 9- 6-
52. 6-11-13-12- 5- 1- 4- 6-

53. 6-11-13-12- 5- 1- 4-10- 6-
54. 6-11-13-12- 5- 8- 6-
55. 6-11-13-12- 5- 9- 6-
56. 6-10- 5- 1- 3- 8-13-12- 6-
57. 6-10- 5- 1- 4-11-13-12- 6-
58. 6-10- 5- 8-13-12- 6-
59. 5- 1- 3- 8-13-12- 5-
60. 5- 1- 4-11-13-12- 5-
61. 5- 8-13-12- 5-

12-CYCLE NEXUS WITH WEAK ARC (3, 8) = .600

62. 6- 1- 3- 8- 6-
63. 6- 1- 3- 8-13- 6-
64. 6- 1- 3- 8-13- 5- 6-
65. 6- 1- 3- 8-13- 5- 9- 6-
66. 6- 1- 3- 8-13- 5- 9-12- 6-
67. 6-11- 5- 1- 3- 8- 6-
68. 6-11- 5- 1- 3- 8-13- 6-
69. 6-11-12- 5- 1- 3- 8- 6-
70. 6-11-12- 5- 1- 3- 8-13- 6-
71. 6-10- 5- 1- 3- 8- 6-
72. 6-10- 5- 1- 3- 8-13- 6-
73. 5- 1- 3- 8-13- 5-

18-CYCLE NEXUS WITH WEAK ARC (13, 5) = .600

74. 6- 1- 4-11-13- 5- 6-
75. 6- 1- 4-11-13- 5- 8- 6-
76. 6- 1- 4-11-13- 5- 9- 6-
77. 6- 1- 4-11-13- 5- 9-12- 6-
78. 6-11-13- 5- 6-
~~79. 6-11-13- 5- 1- 2- 6-~~
80. 6-11-13- 5- 1- 2- 7- 6-
81. 6-11-13- 5- 1- 3- 6-
82. 6-11-13- 5- 1- 3- 8- 6-
83. 6-11-13- 5- 1- 3- 9- 6-
84. 6-11-13- 5- 1- 3- 9-12- 6-
85. 6-11-13- 5- 1- 4- 6-
86. 6-11-13- 5- 1- 4-10- 6-
87. 6-11-13- 5- 8- 6-
88. 6-11-13- 5- 9- 6-
~~89. 6-11-13- 5- 9-12- 6-~~
90. 5- 1- 4-11-13- 5-
91. 5- 8-13- 5-

20-CYCLE NEXUS WITH WEAK ARC (12, 5) = .700

92. 6- 1- 3- 9-12- 5- 6-
93. 6- 1- 3- 9-12- 5- 8- 6-
94. 6- 1- 3- 9-12- 5- 8-13- 6-
95. 6- 1- 4-11-12- 5- 6-
96. 6- 1- 4-11-12- 5- 8- 6-
97. 6- 1- 4-11-12- 5- 8-13- 6-
98. 6- 1- 4-11-12- 5- 9- 6-
99. 6-11-12- 5- 6-
100. 6-11-12- 5- 1- 2- 6-
101. 6-11-12- 5- 1- 2- 7- 6-
102. 6-11-12- 5- 1- 3- 6-
103. 6-11-12- 5- 1- 3- 9- 6-
104. 6-11-12- 5- 1- 4- 6-
105. 6-11-12- 5- 1- 4-10- 6-
106. 6-11-12- 5- 8- 6-
107. 6-11-12- 5- 8-13- 6-
108. 6-11-12- 5- 9- 6-

109. 5- 1- 3- 9-12- 5-
110. 5- 1- 4-11-12- 5-
111. 5- 9-12- 5-

5-CYCLE NEXUS WITH WEAK ARC (8,13) = .800

112. 6- 1- 3- 9- 5- 8-13- 6-
113. 6- 1- 4-11- 5- 8-13- 6-
114. 6- 1- 4-10- 5- 8-13- 6-
115. 6-11- 5- 8-13- 6-
116. 6-10- 5- 8-13- 6-

3-CYCLE NEXUS WITH WEAK ARC (13, 6) = 1.000

117. 6- 1- 4-11-13- 6-
118. 6-11-13- 6-
119. 6-10- 5- 1- 4-11-13- 6-

3-CYCLE NEXUS WITH WEAK ARC (7, 6) = 1.100

120. 6- 1- 2- 7- 6-
121. 6-11- 5- 1- 2- 7- 6-
122. 6-10- 5- 1- 2- 7- 6-

5-CYCLE NEXUS WITH WEAK ARC (8, 6) = 1.200

123. 6- 1- 3- 9- 5- 8- 6-
124. 6- 1- 4-11- 5- 8- 6-
125. 6- 1- 4-10- 5- 8- 6-
126. 6-11- 5- 8- 6-
127. 6-10- 5- 8- 6-

1-CYCLE NEXUS WITH WEAK ARC (11,11) = 1.400

128. 11-11-

10-CYCLE NEXUS WITH WEAK ARC (12, 6) = 2.600

129. 6- 1- 3- 9-12- 6-
130. 6- 1- 4-11- 5- 9-12- 6-
131. 6- 1- 4-11-12- 6-
132. 6- 1- 4-10- 5- 9-12- 6-
133. 6-11- 5- 1- 3- 9-12- 6-
134. 6-11- 5- 9-12- 6-
135. 6-11-12- 6-
136. 6-10- 5- 1- 3- 9-12- 6-
137. 6-10- 5- 1- 4-11-12- 6-
138. 6-10- 5- 9-12- 6-

3-CYCLE NEXUS WITH WEAK ARC (9, 5) = 3.300

139. 6- 1- 3- 9- 5- 6-
140. 5- 1- 3- 9- 5-
141. 5- 9- 5-

5-CYCLE NEXUS WITH WEAK ARC (4,10) = 3.400

142. 6- 1- 4-10- 6-
143. 6- 1- 4-10- 5- 6-
144. 6- 1- 4-10- 5- 9- 6-
145. 6-11- 5- 1- 4-10- 6-
146. 5- 1- 4-10- 5-

7-CYCLE NEXUS WITH WEAK ARC (10, 5) = 5.100

147. 6-10- 5- 6-
148. 6-10- 5- 1- 2- 6-
149. 6-10- 5- 1- 3- 6-
150. 6-10- 5- 1- 3- 9- 6-
151. 6-10- 5- 1- 4- 6-

152. 6-10- 5- 1- 4-11- 6-
153. 6-10- 5- 9- 6-

2-CYCLE NEXUS WITH WEAK ARC (4, 6) = 7.900
154. 6- 1- 4- 6-
155. 6-11- 5- 1- 4- 6-

2-CYCLE NEXUS WITH WEAK ARC (3, 9) = 9.900
156. 6- 1- 3- 9- 6-
157. 6-11- 5- 1- 3- 9- 6-

2-CYCLE NEXUS WITH WEAK ARC (9, 6) = 4.600
158. 6- 1- 4-11- 5- 9- 6-
159. 6-11- 5- 9- 6-

3-CYCLE NEXUS WITH WEAK ARC (4,11) = 19.700
160. 6- 1- 4-11- 6-
161. 6- 1- 4-11- 5- 6-
162. 5- 1- 4-11- 5-

2-CYCLE NEXUS WITH WEAK ARC (2, 6) = 30.000
163. 6- 1- 2- 6-
164. 6-11- 5- 1- 2- 6-

1-CYCLE NEXUS WITH WEAK ARC (10, 6) = 37.400
165. 6-10- 6-

2-CYCLE NEXUS WITH WEAK ARC (11, 5) = 49.000
166. 6-11- 5- 6-
167. 6-11- 5- 1- 3- 6-

1-CYCLE NEXUS WITH WEAK ARC (3, 6) = 50.000
168. 6- 1- 3- 6-

1-CYCLE NEXUS WITH WEAK ARC (11, 6) = 190.100
169. 6-11- 6-

1-CYCLE NEXUS WITH WEAK ARC (2, 1) = 300.000
170. 1- 2- 1-

Lecture Notes in
Biomathematics

Managing Editor: S. Levin

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Mathematical Ecology

Proceedings of the Autumn Course (Research Seminars),
held at the International Centre for Theoretical Physics,
Miramare-Trieste, Italy, 29 November – 10 December 1982

Edited by S. A. Levin and T. G. Hallam

Springer-Verlag
Berlin Heidelberg New York Tokyo 1984